



International Oaks

The Journal of the International Oak Society

Proceedings
7th International Oak Society Conference
9-29-12 / 10-2-12

Issue No. 24 / 2013 / ISSN 1941-2061



International Oaks

The Journal of the International Oak Society

Proceedings
7th International Oak Society Conference
9-29-12 / 10-2-12

Issue No. 24 / 2013 / ISSN 1941-2061





International Oak Society Officers and Board of Directors 2012-2015

Officers

President Béatrice Chassé (France)
Vice-President Charles Snyers d'Attenhoven (Belgium)
Secretary Gert Fortgens (The Netherlands)
Treasurer James E. Hitz (USA)

Board of Directors

Membership Director
Emily Griswold (USA)
Tour Director
Shaun Haddock (France)
International Oaks
Editor Béatrice Chassé
Co-Editor Allen Coombes (Mexico)
Oak News & Notes
Editor Ryan Russell (USA)
International Editor Roderick Cameron (Uruguay)
Website Administrator
Charles Snyers d'Attenhoven

Editorial Committee

Chairman
Béatrice Chassé
Members
Roderick Cameron
Allen Coombes
Shaun Haddock
Eike Jablonski (Luxemburg)
Ryan Russell
Charles Snyers d'Attenhoven
Reviewers
Andrew Hipp (USA)
Antoine Kremer (France)

For contributions to *International Oaks*

contact

Béatrice Chassé
pouyouleix.arboretum@gmail.com
0033553621353
Les Pouyouleix
24800 St.-Jory-de-Chalais
France

Author's guidelines for submissions can be found at
<http://www.internationaloaksociety.org/content/author-guidelines-journal-ios>

© 2013 International Oak Society.

Text, figures, and photographs © of individual authors and photographers.

Cover: Dominique Mansion (*Quercus robur* pollards in Brittany).

Photos: p. 7: James MacEwen (barriques bordelaises); p. 9: Lloyd Kenyon (*Quercus ithaburensis* subsp. *macrolepis* Hedge & Yalt.); p. 10: Guy Sternberg (Conference participants).

www.internationaloaksociety.org
Join the International Oak Society today!

Table of Contents

—/ 07 /—

Foreword
Of Oak and Vine
Charles Snyers d'Attenhoven

—/ 09 /—

From the Editor
Welcome to Your New *International Oaks!*
Béatrice Chassé

—/ 11 /—

Evolutionary Responses of European Oaks to Climate Change
Antoine Kremer

—/ 21 /—

Romania's Oak Forests: Past and Future
Stelian Radu and Corina Coandă

—/ 27 /—

Oaks of Cyprus
Eike Jablonski

—/ 35 /—

Madame Aimée Antoinette Camus: One of the Last Great Amateurs
Béatrice Chassé

—/ 48 /—

Taxonomy and Systematics of *Quercus* subgenus *Cyclobalanopsis*
Min Deng

—/ 61 /—

Using Phylogenomics to Infer the Evolutionary History of Oaks
Andrew Hipp, Paul S. Manos, Jeannine Cavender-Bares, and Deren A. Eaton

—/ 72 /—

Meeting With Oaks
Philippe de Spoelberch

—/ 77 /—

Black Truffles and Oak Trees in France and in Europe
Pierre Sourzat

—/ 88 /—

The Mark of the Oak Tree in Gascony: From Dugout Canoe to Brandy
Chantal Armagnac

—/ 99 /—

Bringing Scientific Oak Collections to Life for Garden Visitors
Emily Griswold

—/ 109 /—

Endangered Oak Resources in Europe and Around the Mediterranean Basin:
Marginal Populations and Minor Species
Alexis Ducouso

—/ 116 /—

Resources and Pollination Affect Oak Masting Behavior
Ian Pearse and Walt Koenig

—/ 122 /—

Micromorphological and Anatomical Characters Used to Differentiate Mediterranean Oaks
Francisco M. Vázquez Pardo

—/ 130 /—

Trognes, Tétards, Emondes, Plesses: the Multiple Aspects and Uses of the Farmer's Oak
Dominique Mansion

—/ 137 /—

The Bio-Geo-Chemical Process of Plant Nutrition and Soil Formation:
Can This Help Us Grow Healthier Oaks?
Michael Martin Meléndrez

—/ 145 /—

Botanic Collections: A Tool for Selecting Species Adapted to Climate Change
Hervé Le Boulter

—/ 151 /—

Pruning Oaks: Training the Young to Achieve Grandeur
Guy Sternberg

—/ 161 /—

New and Recently Described Oak Cultivars
Eike Jablonski

—/ 174 /—

Highest Altitude Population of *Quercus ilex* L. in France
Thierry Lamant and Vincent Parmain

—/ 178 /—

Pre-Conference Tour, September 26-29
Peter Laharraqe

—/ 185 /—

Post-Conference Tour, October 3-7
Allan Taylor

—/ 206 /—

Mission & Goals of the International Oak Society



FOREWORD

Of Oak and Vine

Six months have already passed since the 7th International Oak Society Conference that drew together over 90 IOS members, recent and long-standing, to gather in the majestic city of Bordeaux and share their interest in oaks.

The city and its region are better known for *Vitis vinifera* L. and its estimated 10,000 cultivars (only a few are cultivated in the area, the noble ‘Cabernet Sauvignon’ and ‘Merlot’ being the most famous) than for the genus *Quercus*. Quite appropriately, the Conference Gala Dinner was held in a charming wine estate, the Château Carbonnieux in Léognan.

Oak and wine, however, have long been associated and one of the novelties of this conference, namely the field trips, illustrated this association. Our first field trip to the Tonnellerie Nadalié, a local cooperage, taught us all about making the *barrisques bordelaises*, the casks made of French or American oak that, we learned, differ in the way the wood is sawed.

The second field trip was organized by Dr. Antoine Kremer, a fascinating half-day visit to the Institut national de la recherche agronomique (INRA) at Pierroton. The International Oak Society is indebted to Antoine Kremer for this as well as for agreeing to host the 7th International Oak Society Conference in the name of INRA and for his keynote presentation on the evolution of European oaks. It is also to him that we owe the original idea for the conference venue at the University of Bordeaux’s Espace Agora du Haut Carré.

I also record here the Society’s sincere thanks to Thierry Lamant, Conference Chair, Béatrice Chassé, the Society’s President and Shaun Haddock, our new Tour Director, for all the work they did to get the conference and tours off the ground, assemble a diverse group of speakers who delivered presentations ranging from botany and horticulture to culture and history, and make the conference a real success. I extend our thanks to the numerous contributors — members and speakers alike — who collected acorns in different parts of the world for the legendary IOS seed exchange. And finally we are

indebted to our generous donors. Donations indeed covered about 60% of the cost of this event. Without them, the IOS would not be able to organize the triennial conference.

Memorable and enjoyable Pre- and Post-Conference Tours were also on the program. I can personally report on the Post-Conference Tour. Among other stopovers, it took us to four remarkable oak collections of the greater Southwest of France. The first two of these gardens were the Arboretum de Chocha in Ustaritz, created by Michel Duhart, and the Jardín Botánico de Iturraran, actually located in Spain, very close to the French border and Saint-Jean-de-Luz (which is why I write the “greater Southwest”) with its magnificent woody plant collections assembled by Francisco Garin. These two gardens and their wonderful oak collections make you feel like moving to this region, with its mild climate and good rainfall to create a garden. From the Basque country, we moved north to Saint-Sardos to visit the Arboretum de la Bergerette, the oak collection established over the past twenty years by Shaun Haddock. Shaun has written about la Bergerette in *International Oaks*, Issue No. 23, 2012. Despite what he wrote about the difficulties encountered over the years, I can testify that, notwithstanding voles, rabbits, leaf-miners, hurricanes and drought, the collection at la Bergerette is a great oak collection and the garden is well laid out, allowing space for the trees to grow. Shaun and partner, Anke Mattern also treated us to a lunch that we will long remember. The fourth garden was the young and excellent collection of Béatrice Chassé and her husband, Gérard Lionet in the north of Dordogne, the Arboretum des Pouyouleix. Planted on 25 ha, the arboretum contains almost exclusively wild-collected accessions and is already a French National Collection for oaks.

I was told that the Pre-Conference Tour organized and led by Thierry Lamant was equally successful. Its starting point was the Jardin des Plantes and the Muséum national d’Histoire naturelle in Paris, where Aimée Camus spent so much time. Béatrice Chassé paid a warm homage to Aimée Camus during the conference in a passionate and vivid presentation. The tour reports in these *Proceedings* detail these tours.

Finally, our next triennial conference, in 2015, will take place at The Morton Arboretum, in Illinois. Andrew Hipp and Kunso Kim volunteered to organize the conference. I sincerely hope that this return to the origins of the Society will attract even more members than the 2012 conference.

I would like to say one last word about Bordeaux. Some IOS members know that I have a passion for the early history of the American Republic. Pauillac is one of the most famous *appellations* of Bordeaux, home to Château Lafite-Rothschild, Château Latour and Château Mouton-Rotschild. It is also a pleasant small town with a harbor. And it is from here that, on the 25th of March 1777, the Marquis de Lafayette sailed to North America on a ship named Victoire.



Charles Snyers d’Attenhoven
Vice-President



FROM THE EDITOR

Welcome to Your New *International Oaks!*

I would like to thank all of the speakers of the 7th International Oak Society for making these *Proceedings* possible. There is a fabulous array of subjects from contributors from many sectors of the oak world. Truffles, *armagnac* and the recolonization of Europe by oaks after the last Ice Age are at home in these pages together with pruning techniques, climate change, the importance of oak collections and innovative ways of increasing their interest for the general public, new cultivars, different *exposés* of oaks from around the world – and, of course, with accounts of the oak adventures afforded by the two conference tours.

If one looks at the complete collection of *International Oaks*, from Issue No. 1 published in 1992, a picture of an evolving and growing Society emerges. Style, content and number of pages; choices of paper, typography; the birth of the logo in the year 2000... This dynamic is the result of the resources provided by a growing membership and most importantly, the different skills and aspirations of the volunteers who, over the years, have devoted so much time to producing the journal of the International Oak Society. I would like to express my gratitude to the Editorial Committee and the Board of Directors of the IOS for their invaluable assistance in creating this new version of *International Oaks*. Your new, full-color, slightly larger format *International Oaks* is produced on roughly the same budget as previously. And there is room to grow as we effectively decrease costs in other areas, thanks mainly to our new website for which we are indebted to Charles Snyers d'Attenhoven, Vice-President of the IOS since 2009.

Technical and esthetic considerations are important for all of our media but the interest, and ultimately therefore the success, of all of them depends on the quality and diversity of the contributions we receive to fill them. Sharing your oak passions and experiences is also a way of keeping in touch. I will therefore take this opportunity to encourage all of you to contribute to *International Oaks*.


Béatrice Chassé



7th International Oak Society Conference participants in front of l'Agora du Haut Carré, Université de Bordeaux.



Evolutionary Responses of European Oaks to Climate Change

Antoine Kremer

INRA-University of Bordeaux 1

UMR BIOGECO

Cestas F-33610

France

Phone: 33 5 57 12 28 32

Fax: 33 5 57 12 28 81

antoine.kremer@pierroton.inra.fr

ABSTRACT

There are widespread concerns that trees, as long-lived species, may not be able to cope with future climate change. Trees experienced large climatic changes over much longer time periods during many previous interglacial periods. The evolutionary trajectories of trees during these periods were reconstructed in this study, in an attempt to predict how trees might respond to future environmental changes caused by climate change. Taking the European oaks as a study case, this review shows that rapid migration and adaptation, extensive gene flow and hybridization were the main processes that permitted oaks to track climatic warming in the past. Future evolutionary trends of oak populations in response to climate change are then considered. The potential for species to migrate via seed dispersal to more favorable locations (e.g., northwards) will be limited. On the other hand, it is likely that natural selection will act on a diverse gene pool (in part due to large population sizes), perhaps allowing local adaptation even if this ultimately reduces diversity. Substantial evolutionary shifts can be expected in a limited number of generations. The high levels of genetic diversity and gene flow from other populations will favor rapid adaptation. However, many tree populations may be tested to the limits of their adaptive potential, so some intervention may be needed. To enhance the adaptive potential of populations, it is recommended that genetic diversity be increased by “mixing” local stock with nonlocal material (seeds or seedlings). Guidelines, providing information on permitted directions and distances for the transfer of reproductive material (seed or seedling), should be developed based on current scientific information, especially on data from existing provenance tests.

Keywords: climate change, environmental response, gene flow, provenance research, hybridization, pollen dispersal

Introduction

There are widespread concerns that trees, as long-lived species, may not be able to cope with future climate change. Trees have experienced large climatic changes over much longer time periods during many previous interglacial periods. Although the rates of environmental change were lower than what is now occurring in response to climate change, the evolutionary mechanisms may be similar. It is therefore of the utmost importance to learn about past evolutionary trajectories to predict future responses.

The genetic and ecological mechanisms that have facilitated adaptation of trees during historical “natural” warming periods, taking European oaks as example species, are reviewed in this paper. Oaks are ideal species for this purpose. The postglacial history of temperate oaks in Europe has been reconstructed in detail by combining genetic and historical approaches (Kremer, 2002). Assembling information and results about the postglacial history and genetics (mainly provenance research) of oaks, this paper shows how oaks have responded rapidly to environmental change in the past, despite their low evolutionary rate at the gene level. Learning from the past, this paper also provides some clues about ongoing and future adaptive responses to climate change.

What have we learned about the evolutionary responses during natural warming?

During the Quaternary period, the earth’s climate was dominated by the succession of more than 15 glacial and interglacial periods. Glacial periods lasted between 70 and 100,000 years, while interglacial periods were much shorter (from 10 to 20,000 years) (Hays et al., 1976). These repeated drastic environmental changes were followed by important alternating retractions and expansions of tree species distribution, placing them in different habitats over time and space. These changes also represented very severe selection filters. Indeed, extinctions of European forest trees occurred between 2.4 and 1.7 million years ago, during the early and severe glacial cycles of the Quaternary.

Fossil evidence shows that many species in the *Fagaceae* family that existed in Europe at the end of the Tertiary have since disappeared and are now only present in North America and/or Asia (e.g., species belonging to *Fagaceae* genera *Lithocarpus*, *Castanopsis* and *Trigonobalanus*). There has been no tree species extinction during the most recent periods, suggesting that extant tree species in Europe have demonstrated an efficient ability to migrate and adapt to environmental change. Quaternary evolutionary history suggests therefore that in the face of drastic environmental changes these species developed mechanisms to help reduce the likelihood of extinction. Recent investigation in evolutionary and population genetics has identified at least four of those mechanisms: rapid migration, extensive gene flow through pollen dispersal, interspecific hybridization, and rapid adaptation.

Rapid migration

The distribution of temperate white oaks in Europe has shifted repeatedly from the Mediterranean to the boreal regions during interglacial and glacial periods. At the end of the last glacial maximum, oak forests were restricted to the Iberian Peninsula, Italy, and the Balkan Peninsula (Greece and the western coast of the Black Sea). A pan-European survey of fossil pollen remains (Brewer et al., 2002) showed that all refugial sites were



1/ *Quercus robur*, Bialowieza Forest, Belarus/Poland.

located in mountainous areas (e.g., Sierra Nevada in Spain, the Southern Apennine chain in Italy, and the Pindos mountains in Greece).

During the postglacial period, between 13,000 and 10,000 BP, oaks increased in abundance in mountainous areas (in the Pyrenees, the southeastern Alps, and the Carpathian mountains). The cooling of temperatures during 11,000 BP to 10,000 BP stopped this expansion and eventually resulted in a decrease in the size of the species' geographical range. After 10,000 BP, oaks spread throughout Europe and reached their current distribution at about 6,000 BP. The expansion was more rapid in the west and was reduced in the center and east due to the Alps and the Carpathian mountains. The velocity of oak migration during the postglacial recolonization period (between 15,000 to 6,000 BP) averaged 500 m/year (Brewer et al., 2002), reaching in some cases up to 1,000 m/year. These figures are much larger than those predicted by migration models based on dispersal agents. However, if rare long-distance dispersal events are included in the models, then the overall expansion rate generated by the aggregation of the many populations that were founded by the long-distance dispersal events may account for these rapid migration rates (Le Corre et al., 1997; Bialozyt et al., 2006).

Extensive gene flow through pollen dispersal

As migration proceeded northwards from the different source populations, the colonization routes merged in Central Europe resulting in genetic homogenization as these different populations interbred. The resulting genetic diversity was so great that the genetic imprint of the original refugia from which they were derived was virtually erased. Pollen-flow dynamics in *Quercus petraea* (Matt.) Liebl. and *Q. robur* L. stands have been studied (Valbuena-Carabana et al., 2005; Streiff et al., 1999). These studies revealed that more than half of the pollen contributing to the next generation came from outside the study stands, with pollen dispersion curves characterized by long "tails". The results of recent large-scale genetic surveys indicate that the level of genetic diversity at the northern edges of the natural distribution range reach the same levels as in the

refugial glacial areas (Zanetto and Kremer, 1995). This was also most likely the case as migration progressed. The end result of extensive gene flow is the maintenance of genetic diversity even at the migration front, allowing rapid adaptation of the newly colonizing populations.

Interspecific hybridization as a colonization process

Hybridization is common in oaks, but its evolutionary role during recolonization has only recently been investigated. One intriguing result was that hybridization can allow species to migrate via pollen instead of seed (Petit et al., 2003). There is now much evidence that hybridization permitted *Q. petraea* to colonize new sites by hybridizing with *Q. robur*.

The colonization scenario can be described as follows: because *Q. robur* tends to be a more pioneering species than *Q. petraea*, it was present at the northern edge of the oak migration front with *Q. petraea* somewhat behind, but still capable of hybridizing with *Q. robur* through pollen flow. If the first generation hybridization is followed by later backcrosses (e.g., between hybrids and parents) with *Q. petraea* as male parent, then successive introgression would lead to the restoration of *Q. petraea* trees within the *Q. robur* stand. The end result is that *Q. petraea* becomes established within the *Q. robur* stand, consequently enhancing species succession. The peculiar role of hybridization shows that colonization of newly available territories by oaks (for instance following successive ice ages) is facilitated by interspecific gene exchange, allowing some species to bypass colonization by seed to rapidly invade new sites.

Rapid adaptation

After colonizing a new site, the newly established populations begin to differentiate genetically from the source populations from which they were derived. There is now evidence that the genetic divergence among extant populations that can be observed in provenance tests is the result of adaptive evolution due to local selection from the time of establishment of populations on new sites (Kremer et al., 2010). Indeed most phenotypic traits show clinal variation, with different clinal patterns of variation for different traits (Ducouso et al., 2005). There is little evidence in current populations of any phenotypic or adaptive trait differentiation relating to refugial origin, even in neighbouring Central European populations that are known to have originated (through migration) from different refugia. This is interpreted as the result of extensive gene flow during admixture followed by local adaptation (Kremer et al., 2010). One may conclude from these analyses that most variation in provenance tests is the result of recent adaptive evolution.

How will evolutionary processes stimulate adaptive responses under climate change?

The response of natural tree populations to climate changes has been sketched out in three different scenarios: “persistence through migration to track ecological niches spatially, persistence through adaptation to new conditions in current locations, and extirpation.” (Aitken et al., 2008). The actual outcome for oak populations will depend on the interplay between the different evolutionary processes just described. It is important to evaluate how these natural mechanisms are activated in order to determine if human intervention is needed. In the following sections, predictions on the potential impact

of climate change on oak populations based on historical as well as on contemporary records are made.

Seed migration constrained by natural seed dispersion

Predicted future bioclimatic envelopes provide some rough indications on the distance that populations would need to shift to remain under the “same” bioclimatic conditions. In the case of *Q. petraea*, a shift of 200 to 500 km north and northeast by the end of the current century is predicted, depending on the level of greenhouse-gas emission (Thuiller et al., 2005). Under the most severe scenario (gas emission model A1F1; climate model HadCM3) the bioclimatic envelope excludes France, but would cover the southern half of Finland.

Information on seed velocity is available from the postglacial recolonization period and these data can be used to assess the likelihood that oaks will be able to migrate quickly enough in response to the displacement of the envelope. Palynological records indicate migration velocities ranging from 500 to 1,000 m/year, amounting to a displacement of 50 to 100 km in one century. At the most, oaks would be able to shift their range 100 km during the next hundred years, not taking into account the likely negative impact on migration caused by land fragmentation due to agricultural and other land uses. Future migration velocities, in response to climate change, inferred from past migration patterns may not be accurate (where it is assumed that dispersion capacities are the same under different environmental conditions). There is a large gap between the velocity estimates and the actual velocity needed to cope with the shift of the bioclimatic envelope.

Hybridization facilitating migration and succession

While there are only two temperate oak species (*Q. petraea* and *Q. robur*) in Europe, there are more than 20 species and subspecies located in central and Mediterranean areas (*Flora Europaea*, Schwarz, 1964). They belong to two main oak sections (*Cerris* and *Quercus* sensu Nixon) and hybridization within sections is quite common (Curtu et al., 2007; Lepais et al., 2009). Climatic change is expected to cause species migration, with more range overlaps and competition for new niches in the newly invaded sites. This might be expected to increase the opportunities for hybridization and introgression among species. There are two ways in which hybridization may enhance adaptation of oak populations to climate change.

Hybridization will accelerate species migration by repeated unidirectional interspecific crosses with *Q. robur*, just as hybridization permitted *Q. petraea* to migrate northwards during the postglacial period. Similar hybridization events may occur with other species combinations involving Mediterranean oaks, facilitating the establishment of Mediterranean species at more northerly latitudes. Hence hybridization may help overcome the limitations of species migration via seed that was limited to less than 100 km because pollen is dispersed over longer distances than seed.

Hybridization will facilitate establishment and species succession on new sites. Oak species are characterized by strong differences in site preferences. Just as *Q. robur* and *Q. petraea* differ in their water requirements, the Mediterranean oak species have different soil-type preferences. As hybridization will accelerate the migration of species, it will subsequently facilitate their establishment on the most suitable sites of those already occupied by temperate species. In the long run, this process will result in the replacement of one species by another, which in turn may accelerate ecological succession.

Gene flow enhancing adaptation

Local adaptation can be increased by “incoming genes” via pollen from populations



2/ *Quercus petraea*, Kosienice Forest, Poland.

exhibiting higher fitness than the receiving population. In the case of directional environmental changes towards higher temperature, it is likely that populations from more southerly latitudes may be an important source of this pollen (Kremer et al., 2012). The question raised here is whether pollen dispersal distances will be of sufficient magnitude to shift species' bioclimatic envelopes.

Gene flow may contribute to increasing the fitness of a given population that is under severe selective pressures. Migration of alien genes through gene flow will change the genetic composition of the receiving population. If the migrating gene has a positive effect on fitness, it will rapidly increase its frequency in the receiving population. The dynamics of migrating genes (migration rates, subsequent frequency, variation, and change in population fitness) have never been monitored in forest tree populations, but deserve more attention in light of the increasing focus on the impact of climate change. Clearly, a species that has a continuous distribution across contrasting ecological sites might be able to "import" genes contributing to higher fitness in areas exposed to severe stress. Most of these theoretical and experimental studies have shown that gene dispersion has both local and large-distance components, as revealed by the existence of the "fat tails" of the dispersion curve.

The second component is, of course, more relevant in the context of climate change. Sites that are currently considered moist are likely to become drier in the future, so trees growing on these sites would potentially benefit from genes that convey some drought tolerance. However, such genes are likely to exist only in stands located long distances away. Pollen dispersal in the upper layer of the atmosphere is possible, where it can be transported long distances but is also exposed to potentially damaging high UV radiation levels. Modeling approaches at the landscape level, taking into account pollen release, viability and deposition characteristics, suggest that viable oak pollen can be dispersed up to 100 km (Schueler et al., 2005).

Adaptation facilitated by genetic diversity

Local adaptation through natural selection results in the development of a phenotype that optimizes response to environmental pressures, with this phenotype corresponding to the highest fitness in the population. Under a changing environment, the required optimum is continuously shifting, but there is a time lag before this optimum phenotype is developed (by which time the environment may have changed again) (Bürger and Krall, 2004). The lag causes a reduction of fitness, with the risk that fitness will drop to a critical level too low to allow the population to replace itself (Bürger and Lynch, 1997). The lag can be compensated for in two complementary ways:

- Maintaining a large, genetically variable population with high rates of fecundity (Bürger and Lynch, 1995, 1997);
- The immigration of new genes with higher fitness via gene flow.

When applied to oaks, these predictions suggest that the lag can be reduced substantially if natural or artificial regeneration is used to renew forest stands. Indeed, the very high fecundity of trees and the large size of populations within most species will allow a considerable shift in a population's optimum from one generation to the next, allowing it to "track" environmental change.

While these conclusions are based on theoretical analysis only, they predict rapid evolution of oaks under environmental change, but they have not been supported by the results of experiments conducted over contemporary time scales. Large population sizes will maintain important genetic variation and hence increase the probability that



3/ *Quercus robur*, Hoperski Forest, Romania.

beneficial alleles favoring adaptation exist within the population. There is some indirect evidence of significant adaptive change over contemporary time scales from studies of genetic divergence in introduced exotic species in Europe, which may be relevant for the European oaks.

Northern red oak (*Q. rubra* L.) is a well-documented case. This species was introduced into Europe shortly after the French revolution and is now planted throughout the continent (Timbal et al., 1990). A large-scale provenance test was established in southwestern France, with collection data including progenies from introduced European stands and from the source populations in North America. Interestingly, the introduced populations, as a whole, exhibited a clear shift in the phenology of bud break and autumn leaf senescence from the source populations of the natural range (Daubree and Kremer, 1993). Although the genetic causes of genetic divergence are not precisely known, this example illustrates the capacity for rapid evolutionary change in oak. If the

changes in climate predicted for Europe come to be, then European oaks may have to respond in a similar manner as that illustrated for red oak.

How can we enhance adaptation to climate change?

The comparison between past and future trends suggests that migration and local adaptation will be differently affected by evolutionary processes. On the one hand, migration via seed dispersion will be limited if the climatic changes occur as rapidly as predicted. On the other hand, adaptation at local level via natural selection may be buffered considerably by significant inherent genetic variability and large population sizes. Interestingly, these data also showed that gene flow via pollen will enhance species migration and local adaptation, and will play a central role in species response to climate change. One can therefore anticipate different responses between species, depending on the nature of each species' geographic distribution. Species that have a continuous distribution are likely to benefit more from positive interactions between natural selection and gene flow than species that have a scattered distribution. It is also predicted that the evolutionary responses between populations located at the leading edge may differ from those at the rear end of distribution. Populations at the northern and eastern limit will be at the leading front of range shifts and may benefit from immigrating genes via pollen flow from southern latitudes; in contrast, adaptation may be more constrained at the rear edge, where populations are deprived of gene flow from "pre-adapted" populations.

Artificial measures could be implemented to enhance natural adaptive processes, especially in southern populations at the edge of the range. Suggested actions should be mainly directed towards modifying the genetic composition of stands during the regeneration process. New, nonlocal seeds (or seedlings) can be introduced. This “enrichment” introduces new genes, which may provide additional adaptive buffering capacity. With continuous directional shifts in climate, genotypes other than those of the contemporary populations eventually will become better suited to the new climate. As the climate changes, planting programs that involve moving appropriate genotypes between climate zones can accomplish in a single generation what would require several generations in nature. A newly regenerated stand with a mixed genetic composition is likely to have a greater potential to successfully regenerate in the future (i.e., greater fitness). The suitability of the introduced material used in sowing or planting should be determined based either on results of provenance tests or on projected future bioclimatic envelopes (if no provenance test data are available).

Guidelines on the transfer range for the direction and distance of movement of reproductive material can be developed from the geographical patterns observed in multisite provenance tests. Oak provenance tests were established since the mid 1900s, and have shown congruent geographical variation among species (Kleinschmit, 1993). The continuous or clinal patterns of variation that follow environmental gradients were observed for most traits (Ducouso et al., 1996; Deans and Harvey, 1995,1996; Liepe, 1993). This should therefore ease the choice of source populations. However, the final decision on the type of material to introduce into an area should be based on the potential impact of the new material on the overall fitness of populations rather than on the suitability of individual trait characteristics. Hence an overall meta-analysis should be carried out across all existing provenance tests in Europe to delineate seed zones for operational use.

Conclusion

This review outlines the inherent adaptive capacities of oak species to environmental changes, as witnessed by their history during natural warming over the last postglacial period. It predicts that substantial evolutionary shifts can be expected in a limited number of generations due to the high level of genetic diversity in oaks, and that gene flow will be an important driver of adaptive evolution.

To enhance their adaptive potential, it is recommended that the genetic diversity of local populations be increased by mixing local stock with seeds (or seedlings) from external sources during regeneration. Guidelines on the direction and distance of seed (or seedlings) transfers should be based on the results of up-to-date scientific evidence from studies in ecology and genetics, and on information on the patterns of geographic variation observed in existing provenance tests.

Although historical patterns have not been reconstructed in as much detail for other forest species as for oaks, some extrapolation to other species is warranted. Information from other species on the level of genetic variation, the extent of pollen flow, the existence of other inter-fertile species, and the pattern of distribution of the species (scattered or widespread) are important indicators of the potential adaptive responses of trees to climate change.

Photographers. Title page: Alexis Ducousso (*Quercus robur*). Photos 1-3: Alexis Ducousso.

Bibliography

- Aitken, S.N., S. Yeaman, J.A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration, or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95–111.
- Bialozyt, R., B. Ziegenhagen, and R.J. Petit. 2006. Contrasting effects of long distance seed dispersal on genetic diversity during range expansion. *Journal of Evolutionary Biology* 19: 12–20.
- Brewer, S., R. Cheddadi, J.L. De Beaulieu and M. Reille. 2002. The spread of deciduous *Quercus* throughout Europe since the last Glacial period. *Forest Ecology and Management* 156: 27–48.
- Bürger, R. and C. Krall. 2004. Quantitative-genetic models and changing environments. In *Evolutionary Conservation Biology*. Ferrière, R., Dieckmann, U. and Couvet, D., eds., Cambridge University Press.
- Bürger, R. and M. Lynch. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution* 49: 151–163.
- Bürger, R. and M. Lynch. 1997. Evolution and extinction in changing environments. In *Environmental stress, Adaptation, and Evolution*. Bijlsma, R. and Loeschke, V., eds., Birkhäuser Verlag.
- Curtu, A.L., O. Gailing, and R. Finkeldey. 2007. Evidence for hybridization and introgression within a species-rich oak (*Quercus* spp.) community. *BMC Evolutionary Biology* 7: 218.
- Daubree, J.B. and A. Kremer. 1993. Genetic and phenological differentiation between introduced and natural populations of *Quercus rubra* L. *Annales des Sciences Forestières*, 50 (Suppl. 1): 271s–280s.
- Deans, J.D. and F.J. Harvey. 1995. Phenologies of sixteen European provenances of sessile oak growing in Scotland. *Forestry* 68: 265–273.
- Deans, J.D. and F.J. Harvey. 1996. Frost hardiness of 16 European provenances of sessile oak growing in Scotland. *Forestry* 69: 5–11.
- Ducousso, A., J.P. Guyon, and A. Kremer. 1996. Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt.) Liebl.). *Annales des Sciences Forestières* 53: 775–782.
- Ducousso, A., J.M. Louvet, P. Jarret, and A. Kremer. 2005. Geographic variations of sessile oaks in French provenance tests. In *Proceedings of the Joint Meeting of IUFRO Working Groups, Genetics of oaks, and Improvement and Silviculture of oaks*, edited by R. Rogers, A. Ducousso, and A. Kanazashi. FFPRI (Forestry and Forest Products Research Institute) Scientific Meeting Report 3, Tsukuba, Japan, pp. 128–138.
- Dynesius, M. and R. Jansson. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* 97: 9115–9120.
- Hays, J.D., J. Imbrie, and N.J. Shackleton. 1976. Variations in the Earth's orbit: pacemaker of the ice ages. *Science*, 194: 1121–1132.
- Kleinschmit, J. 1993. Intraspecific variation of growth and adaptive traits in European oak species. *Annales des Sciences Forestières* 50: 166s–186s.
- Kremer, A., ed. 2002. Range wide distribution of chloroplast DNA diversity and pollen deposits in European white oaks: inferences about colonisation routes and management of oak genetic resources. *Forest Ecology and Management* 156: 1–223.
- Kremer, A., V. Le Corre, R.J. Petit, and A. Ducousso. 2010. Historical and contemporary dynamics of adaptive differentiation in European oaks. In *Molecular approaches in natural resource Conservation* edited by A. DeWoody, J. Bickham, C. Michler, K. Nichols, G. Rhodes, and K. Woeste. Cambridge University Press (in press).
- Kremer, A., O. Ronce, J.J. Robledo-Arnuncio, F. Guillaume, G. Bohrer, R. Nathan, J.R. Bridle, R. Gomulkiewicz, E.K. Klein, K. Ritland, A. Kuparinen, G. Gerber, and S. Schueler. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters* 15: 378392.
- Le Corre, V., N. Machon, R.J. Petit, and A. Kremer. 1997. Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: a simulation study. *Genetical Research* 69: 117–125.
- Lepais, O., R.J. Petit, E. Guichoux, E. Lavabre, F. Alberto, A. Kremer, and S. Gerber. 2009. Species relative abundance and direction of introgression in oaks. *Molecular Ecology* 18: 22282242
- Liepe, K. 1993. Growth chamber trial on frost hardiness and field trial on bud burst of sessile oak (*Quercus petraea* Liebl and *Q. robur* L.). *Annales des Sciences Forestières* 50: 208–214.
- Petit, R.J., C. Bodénès, A. Ducousso, G. Roussel, and A. Kremer. 2003. Hybridization as a mechanism of invasion in oaks. *New Phytologist* 161: 151–164.
- Schueler, S., K.H. Schlünzen, and F. Scholz. 2005. Viability and sensitivity of oak pollen and its implications for pollen-mediated gene flow. *Trends in Ecology and Evolution* 19: 154–161.
- Schwarz, O. 1964. *Quercus* L. In *Flora Europaea*, vol. 1: *Lycopodiaceae to Platanaceae*, edited by T.G. Tutin, V.H. Heywood, N.A. Burges, D.H. Valentine, S.M. Walters, and D.A. Webb. Cambridge University Press, pp. 61–64.
- Streiff, R., A. Ducousso, C. Lexer, H. Steinkellner, J. Gloessl, and A. Kremer. 1999. Pollen dispersal inferred from paternity analysis in a mixed oak stand of *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. *Molecular Ecology* 8: 831–841.
- Thuiller, W., S. Lavorel, M.B. Araujo, M.T. Sykes, and J.C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102: 82458250.
- Timbal, J., A. Kremer, N. Le Goff, and G. Nepveu. 1984. *Le chêne rouge d'Amérique*. Paris, France: Editions de l'INRA, 1984.
- Valbuena-Carabana, M., S.C. Gonzalez-Martinez, V.L. Sork, C. Collada, A. Soto, P.G. Goicoechea, and L. Gil. 2005. Gene flow and hybridisation in a mixed oak forest (*Quercus pyrenaica* Willd. and *Quercus petraea* (Matts.) Liebl.) in central Spain. *Heredity* 95: 457–485.
- Zanetto, A. and A. Kremer. 1995. Geographical structure of gene diversity in *Quercus petraea* (Matt.) Liebl. I. Monolocus patterns of variation. *Heredity* 75: 506–517



Romania's Oak Forests: Past and Future

Stelian Radu¹ and Corina Coandă²

1. Director Emeritus
Forest Research Station & Arboretum Simeria
Str. Aurel Vlaicu, 11
330005 Deva,
Romania
radu.stelian@yahoo.com

2. Forest Research Station & Arboretum Simeria
Str. Biscaria, 1
335900 Simeria,
Romania
arboretum.simeria@icashd.ro

ABSTRACT

According to the recent *Flora illustrata a Romani* (Ciocarlan, 2009) nine *Quercus* species grow spontaneously in Romania: *Q. robur* L., *Q. petraea* (Matt.) Liebl., *Q. polycarpa* Schur, *Q. dalechampii* Ten., *Q. cerris* L., *Q. frainetto* Ten., *Q. pedunculiflora* K. Koch, *Q. pubescens* Willd., and *Q. virgiliana* (Ten.) Ten., but the new taxonomic position of these species is discussed. In ancient times, when forests covered more than 75% of the country's territory, oak forests had a greater range. Over the centuries, oak forests have endured strong anthropic pressure. Periodical extensive deforestation for agriculture, incorrect practice of coppice systems, abusive grazing, air pollution, coupled with prolonged drought and severe defoliation by insects, have led to a dangerous reduction and fragmentation of ancient, large, well-structured, and durable oak stands. With a view to saving these valuable forests it is necessary to launch an active and comprehensive program for the conservation and ecological reconstruction of oak ecosystems, in spite of prolonged forest decline and the strong economic pressure on forests.

Keywords: *Quercus* species, anthropic pressure, deforestation, coppice system, defoliation, conservation, ecological reconstruction

Introduction

Romania is integrated in Europe from a geographical, natural, historical, and cultural point of view. Although of small surface area, the topography, altitudinal variation (0 to 2543 m/8343 ft), climate, and soil conditions of this Carpathian-Danubian country have produced landscapes of both incomparable beauty and extreme scientific relevance

Romania is the only European country that hosts five biogeographical regions (only a maximum of four is found in other countries in Europe) and four altitudinal, climate, and vegetation/soil layers. The floral and faunistic diversity can also be explained by Romania's location at the crossroads of different climatic and floral areas.



1/ Stelian Radu (white coat) with Alexis Ducousso (on Stelian's left) (1992).

Oaks of Romania

According to the recent *Flora illustrata a Romaniiei* (Ciocarlan, 2009), the following nine *Quercus* species are indigenous to Romania: *Q. robur* L., *Q. petraea* (Matt.) Liebl., *Q. polycarpa* Schur, *Q. dalechampii* Ten., *Q. cerris* L., *Q. frainetto* Ten., *Q. pedunculiflora* K. Koch, *Q. pubescens* Willd., and *Q. virgiliana* (Ten.) Ten.; but the taxonomic position of these species is subject to debate. Using different Romanian and European monographs, three conclusions can be drawn based on an analysis of the taxonomic position and the name attributed to the above-named species.

1) Four taxa, namely *Q. robur*, *Q. frainetto*, *Q. pubescens* and *Q. cerris*, are accepted and systematically found with their initial/classic name in all monographs, including in

- the recent *Guide illustré des Chênes* (le Hardÿ de Beaulieu and Lamant, 2006).
- 2) Although more work is needed on this question, *Q. petraea* has been segregated into three subspecies: *Q. petraea* subsp. *petraea*, *Q. petraea* subsp. *polycarpa*, and *Q. petraea* subsp. *dalechampii*. For a long time they were studied and managed in our forestry practice as distinct species.
 - 3) The latest monographic and genetic studies suggest the integration of *Q. pedunculiflora* with *Q. robur* and of *Q. virgiliana* with *Q. pubescens*.

Forests past and present

During the last 3 millennia, the proportion and shape of oak forests have been deeply modified from their primary state. Forest surface area has decreased from 75-80% to a mere 27% (from 18 to 6.3 million ha/44 to 15 million ac); the presence of oak has decreased from 44.5% to only 19.3% (1,139 ha/2,814 ac). Other forest species occur today as follows: beech, 30.4%; coniferous (mainly spruce), 30.3%; and other broad-leaved species, 20.0%.

Considered from a species point of view, the decrease is: *Q. petraea* from 22% to 11.6%; *Q. robur* from 10% to 2.4%; *Q. cerris* and *Q. frainetto*: 5% to 4.9% (both relatively stable); and *Q. pubescens* and *Q. pedunculiflora* from 7.5% to 0.4% (both are endangered species at present).

Over the centuries the extensive natural oak forests have endured strong anthropic pressure. Deforestation for agricultural crops and pasture land, incorrect practice of coppice systems, abusive grazing, acid rains with prolonged droughts, climate change, and occasional severe defoliation by insects, have led to a dangerous reduction and fragmentation of ancient, large, and lasting stands. To this long list of oak enemies must be added, since 1989, the wrongful transfer of state forests to the former owners, incorrect management, economic difficulties, poverty, illicit tree felling, corruption, and absence of a “forestry conscience”.

Research efforts and conservation

Concerns for different aspects of oaks and oak forests (systematic, ecological, management, and conservation) started in the middle of the 19th century with the first true scientific studies appearing in 1886 in the first issue of the centennial *Revista pădurilor* (*The Journal of Forests*). The creation in 1933 of the National Forest Institute (the present Institutul de Cercetări și Amenajări Silvice or ICAS) marked Romania's firm commitment to forestry science and research.

Oak ecological requirements were determined (Stănescu et al., 1997). *Q. petraea*, *Q. robur*, *Q. frainetto*, *Q. cerris*, and *Q. pubescens* were studied using factorial tables, ecological formulae, and cards based on 16 ecological factors and their favorable or limiting values. Valuable groups of genetic resources for the listed species were sorted out and also delimited by ICAS.

The so-called “dieback” of oaks was deeply studied on a systemic base (Alexe, 1984, 1986). This complex phenomenon has increased due to drought and reduced capillary waters, particularly along rivers where hydrological works have been carried out.

In order to stop the oak decline and to preserve these valuable forests, numerous forestry measures have been undertaken over the last 60 years on the basis of scientific research

done by ICAS. These measures were aimed at reducing cutting volumes and establishing conservation areas (protected forests or reserves) for the preservation of oak stands.

To help ensure natural regeneration, more sophisticated forestry management systems and a return of coppiced stands to high forest were introduced into management practices. Reforestation and, recently, ecological reconstruction have also been promoted. A strategy has recently been established for oak forest reconstruction concerning 11 distinct regions based on their location, oak species diversity, and ecology (Roșu, Radu et al., 2012. More details concerning Romania's oak forests and their problems can be found in former issues of *International Oaks* (No. 3, 1993; No. 10, 1999; No. 11, 2000; No. 13, 2002).

Six case studies in conservation

The selection and establishment of protected areas (national and nature parks, forest reserves, and Natura 2000 sites) represent effective measures to protect and conserve valuable oak forests in situ.

Mociar Forest (48 ha/119 ac)

Created in 1932, this small reserve includes 371 very old (between 500-720 years old) *Q. robur* trees, growing on heavy, moist, soils that are susceptible to waterlogging. The trees have conical-shaped trunks (3-4 m/9.8-13 ft in diameter at breast height (dbh) and 18 m/59 ft tall) with dried tops. The original habitat was impossible to reproduce but the understory has been restocked by planting.

Letea Forest (2,825 ha/6,980 ac)

This is the oldest natural reserve in Romania, established in 1938 and located in the Danube Delta. The Letea Forest Reserve was the first step in the foundation of the Danube Delta Biosphere Reserve (UNESCO 1992). Fragments of primary oak forest (with *Q. robur* and *Q. pedunculiflora*) cover depressed zones among higher old-stand dunes. The abundance of climbing liana (*Periploca* Tourn. ex L., *Vitis* L., *Clematis* L., *Humulus* L.) gives the impression of a subtropical forest. Despite its status of protected area, there is strong pressure from humans and domestic animals (horses).

The Breite (Sighișoara) wood pasture (70 ha/173 ac)

Four hundred fifty-four ancient *Quercus robur* pollards (between 400 and 600 years old) grow on this pastured plateau and in the surrounding forest stands. One of the oldest has a circumference of 620 cm/244 in and still shows great vitality. All the life stages can be found: live and vigorous as well as dying and dead trees, snags, and fallen trees – all very important for biodiversity. This type of wood pasture landscape is ascribed to the Saxon colonists, transferred here in the 12th century. Akeroyd considers the Breite oaks to be *Q. pedunculiflora* (Akeroyd, 2003).

Seaca – Optășani Forest Reserve (137-434 ha/339-1072 ac)

This forest is what remains of an ancient and historically one of the largest Romanian forests (2000 ha/4942 ac) with a pure population of monumental *Q. frainetto* (no *Q. cerris*). During his consulting mission in Romania (1888-1889) Gustave Huffel (later Prof. and Dept. Director of the famous Nancy Forestry School) paid many visits to this forest, measuring trees, some of which he found to be more than 200 years old and 32 m/105 ft tall, with a dbh of 1.2 m/3.9 ft. He sent trunk samples to Paris in order to promote export throughout the world of this almost unknown but valuable timber (recommended for making staves and fine furniture).



2/ Stelian Radu and Antoine Kremer (right) (1992).

Bejan Forest (70 ha/173 ac)

Protected since 1936, this forest is known for the fact that in its relatively limited area can be found eight native oak species (all except *Q. pedunculiflora*) and it is thus a remarkable center of hybridization. It has been widely studied in the past (Simonkai, Borbás, Borza, Nyárády, Cretzoiu, Schwarz) and more recently by Stănescu, Șofletea, Stanciu and Curtu. Stanciu found 11 hybrids in Bejan. I had the opportunity to participate in the Schwarz visit (1955) and I also accompanied A. Kremer and A. Ducouso (1992) as well as Guy and Edie Sternberg of the International Oak Society in 1995 (see *International Oaks*, No. 11, 2000). Recently Curtu (2007, 2011) started the taxonomic revision of Bejan oaks and Curtu (2006) and Curtu et al., (2011), the revision of hybrids. This forest is an urban green area for the nearby city of Deva, and as such is subject to strong human pressure.

Runcu – Groși Natural Reserve (262 ha/647 ac)

A reserve since 1982, it is a well conserved, old-growth mixture of *Q. polycarpa* and *Fagus sylvatica* subsp. *moesiaca* (K. Malý) Szafer. The oaks are 130-210 years old and attain diameters at breast height of more than 76 cm/30 in and heights of more than 43 m/141 ft. The beech trees are between 60 and 180 years old. The trees of both species present a large amount of dead wood. I have had the pleasure of accompanying and/or organizing a continuing pilgrimage of French foresters to this reserve, starting with A. Kremer and A. Ducouso in 1992, followed by visits from the GEVFP, WWF, Réserves Naturelles and others.



3/ *Quercus petraea*.

Conclusion

In conclusion, and as witness to our ongoing battle for Romania's oak forests, we are proud to report that the publication of our article "Let us save the remarkable trees – true living treasures, threatened by extinction" (Radu et al., 2006; Radu et al., 2010) finally generated the opening of a necessary *National Register and Album of Exceptional Trees of Romania*, starting with oaks.

Acknowledgments

Many thanks to Cătălina Drăgoi from The Grădiștea Muncelului – Cioclovina Nature Park Administration and the collective *Ovid Densusianu* County Library for their assistance in preparing this article.

Photographers. Title page: Alexis Ducouso (*Quercus petraea*). Photo 1: Antoine Kremer. Photos 2-3: Alexis Ducouso.

Bibliography

- Akeroyd, John. 2003. A Transylvania wood-pasture. *Plant Talk* 34: 34–37.
- Alexe, A. 1984. Rezultatele unor cercetări de biometrie, anatomie, fiziologie și biochimie la arborii sănătoși și la cei în curs de uscare. *Revista Pădurilor* 3: 135–139
- Alexe, A. 1986. Analiza sistemică a fenomenului de uscare a cvercineelor și cauzele acestuia, *Revista pădurilor*, 1, 2, 3: 5–15.
- Bolea, V., C. Balabasciuc, I. Florescu, and C.D. Stoiculescu. 2011. Proiect de lege privind conservarea arborilor excepționali din România. *Revista de Silvicultură și Cinegetică* 16: 61–62.
- Ciocarlan, Vasile. 2009. *Flora ilustrată a României*. Editura Ceres.
- Curtu, Alexandru L., O. Gailing, and R. Finkeldey. 2007. Evidence for hybridization and introgression within a species-rich oak (*Quercus* spp.) community. *BMC Evolutionary Biology* 7: 218.
- Curtu Alexandru L., N. Sofletea, A.V. Toader, and M.C. Enescu. 2011. Leaf morphological and genetic differentiation between *Quercus robur* L. and its closest relative, the drought-tolerant *Quercus pedunculiflora* K. Koch. *Annals of Forest Science* 68: 1163–1172.
- Le Hardy de Beaulieu, Antoine, and Thierry Lamant. 2006. *Guide illustré des chênes*. Editions du 8^{me}.
- Radu S. and C. Coandă. 2006. Arborii remarcabili - adevărate comori vii, pe cale de dispariție. *Al. XXII-lea simpozion național de istorie și retrologie agrară a României, Deva*: 329–341.
- Radu, S. and C. Coandă. 2010. Să salvăm arborii remarcabili - adevărate comori vii, pe cale de dispariție. *Revista de Silvicultură și Cinegetică*: 32–36.
- Roșu, C., S. Radu, et al. 2012. Cu privire la reconstrucția ecologică a pădurilor de stejar din România. Symposium, București.
- Stanciu, A. 1997. Cercetări taxonomice, morfologice și ecologice privind hibridii genului *Quercus* din Rezervația științifică Bejan – Deva. Teza de doctorat, Universitatea Transilvania din Brașov.
- Stanescu V., N. Sofletea, and O. Popescu. 1997. *Flora forestiera lemnoasă a României*. Editura Ceres.



Oaks of Cyprus

Eike J. Jablonski

LTA, Dept. Horticole, Arboretum
72, Avenue Salentiny
L-9001 Ettelbruck, Luxembourg
Phone: +352 691 864079
eike.jablonski@education.lu

ABSTRACT

The dendroflora of the island of Cyprus shows some remarkable features. The oaks, with only three indigenous species, are a prominent part of the dendrological inventory, including the endemic *Quercus alnifolia* Poech. The three indigenous oak taxa, together with a recently described form of *Q. alnifolia* and a recently described hybrid between *Q. alnifolia* and *Q. coccifera* L. subsp. *calliprinos* (Webb.) Holmboe are described, and their taxonomic status discussed.

Keywords: Cyprus, oaks, Mediterranean oaks, *Quercus alnifolia*, *Quercus coccifera* subsp. *calliprinos*, *Quercus infectoria* subsp. *veneris*, *Quercus* ×*campitica*, *Quercus alnifolia* var. *argentea*

Introduction

Cyprus is the third largest island of the Mediterranean, situated in the eastern Mediterranean Sea, about 60 km (40 miles) south of the Turkish coast, and 100 km (65 miles) west of Syria, with an area of approximately 9,251 km² (3,572 mi²). From sea level at the coastal belt the land rises to steep, rocky, diabase and serpentine peaks at the Troodos range with the highest peak at Olympos (Chionistra) at 1,952 m (6,401 ft.). The climate is typical arid Mediterranean, with a short, cool, wet winter and a long, dry, hot summer. Winter temperatures in the Troodos range can drop down to -10 °C/14 °F, with an average of 10 weeks of snow above 1,400 m (4,000 ft.) Rainfall varies between only 300 mm/year (12 in) on the central plain and more than 1,100 mm (43 in) on the upper slopes of Olympos peak.

In ancient times Cyprus was largely covered with forests but today most of this woodland is long gone. Remnants of it survive on the Troodos and Kyrenia ranges, with 18% of the island's vegetation being classified as woodland (31% of the land above 1,000 m/3,280 ft), that in some places is replaced by tall, shrubby *maquis* (4-6 m/13-20 ft high: *Arbutus andrachne* L., *Pistacia terebinthus* L., *Olea europaea* L., *Styrax officinalis* L. and *Quercus coccifera* L.), or mostly by sub-shrubby garigue (less than 3 m/9.9 ft high: *Cistus* spp., *Lithodora hispidula* (Sibth. & Sm.) Griseb. *Genista sphacelata* Decne. etc.

The flora of Cyprus is remarkably diverse, due to the varied edaphic and topographic character of the island. There are 128 plant species endemic to Cyprus, including the well-known Cyprus cedar (*Cedrus brevifolia* (Hook. f.) A. Henry) and the golden oak of Cyprus (*Q. alnifolia*). The plant endemism rate of the eco-region is about 7% of the total flora of 1,750 species (WWF, 2007). Human impact has been disastrous for the woodlands over the last 1,000 years, and today only small forest habitats are left intact. Old-growth black pine forest (*Pinus brutia* Tenore) is found only in the high mountain rocky summits. The endemic *Cedrus brevifolia* forest is represented by only a few hundred hectares. These forests owe their existence to none other than Winston Churchill. In 1907, as Under Secretary of State (and Junior Minister) responsible for Cyprus, he initiated a reforestation program to replace the famous forests destroyed by centuries of felling that provided fuel for smelting but also caused extensive systematic erosion (Barton, 2002).

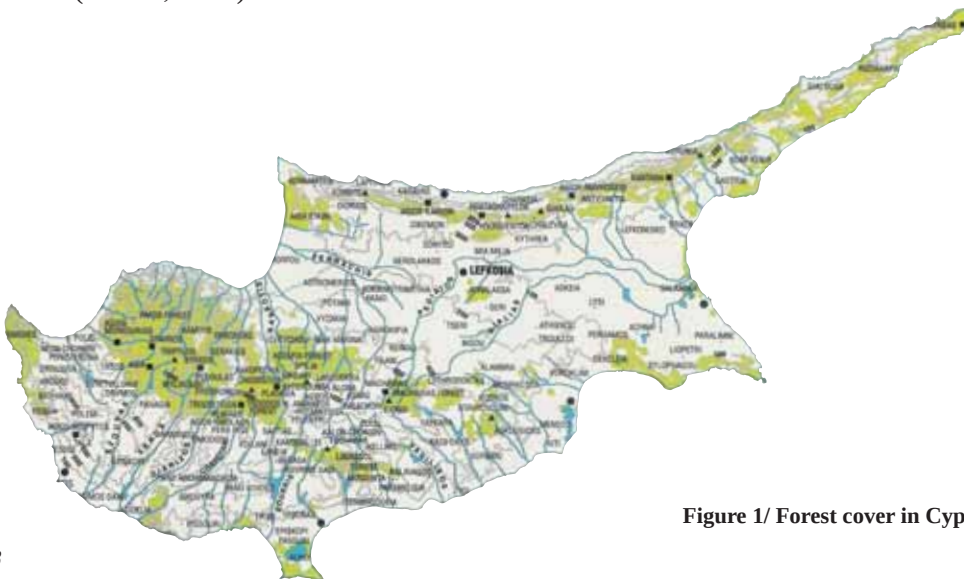


Figure 1/ Forest cover in Cyprus.



1/ Ripening acorns of *Q. infectoria* subsp. *veneris*.

Native oak species of Cyprus

Three species of oak are indigenous to Cyprus: the deciduous *Q. infectoria* Oliv. subsp. *veneris* (A. Kern) Meikle (Section *Quercus*) and two evergreen species, *Q. coccifera* L. subsp. *calliprinos* (Webb) Holmboe and *Q. alnifolia* Poech. (Section *Cerris*). Additionally, one possibly distinct variety of *Q. alnifolia* and one rare hybrid have been observed.

Quercus infectoria Oliv. subsp. *veneris* (A. Kern) Meikle (Section *Quercus*)

Cyprus oak, Aleppo oak: Deciduous to semi-deciduous tree, up to 18 × 25 m/59 × 82 ft (old specimens often wider than high with a spreading crown and a trunk that can easily reach a girth of more than 7 m/23 ft), bark dark grey, vertically fissured on the trunk; twigs hairy when young, leaves variously shaped, up to 15 × 7 cm (6 × 2.7 in), glabrous, shiny green abaxially, slightly tomentose beneath, margins sinuate to sinuate-serrate, petiole 5-30 mm (0.2-1.2 in); acorn shortly peduncled or sessile, 3-5 cm (1.2-1.6 in) long, cupule with adpressed scales, enclosing one-third of the acorn, ripening in the first year.

Nomenclatural note: Like other species of the genus, the taxonomy of *Q. infectoria* subsp. *veneris* is still controversial and several authors do not accept the subspecies epithet.

Basionym: *Q. veneris* A. Kern. (1904). Often incorrectly referred to as *Q. infectoria* subsp. *boissieri* (Reut.) O. Schwarz (1934), but with the inclusion of *Q. veneris* A. Kern. (1904) at subspecific rank within this taxon, the name has to be *Q. infectoria* subsp. *veneris* due to its priority at that rank being established by *Q. lusitanica* subsp. *veneris* (A. Kern.) Holmboe (1914); see ICBN Art 11.4 and its Ex. 15. Some authors refer to *Q. infectoria* subsp. *boissieri* (Reut.) Gürke, but Gürke in K. Richter, *Plantae Europaea* 2: 69 (1897) was unclear as to which rank he applied the epithet, so his combination cannot be taken into account for purposes of priority; see ICBN Art. 35.3. (Trehane, 2010).

Some authors place this taxon at species level because it is tree-like with larger, distinctly petiolate leaves, and large acorns, whereas *Q. infectoria* subsp. *infectoria* is shrub-like with small leaves, short petioles and smallish acorns.

This subspecies grows in Cyprus, Turkey and eastwards to Iran. In Cyprus, it is found in all districts in open woodland and cultivated fields from sea level up to 1,700 m (5,576 ft) altitude, but particularly in the western parts of Cyprus, in deep soils. A small forest of *Q. infectoria* subsp. *veneris* is found near the village of Agros, on the southwestern slopes of the Troodos Range, at 1,100 m (3,608 ft). Although the durable hard wood would make excellent fire wood or could be used in making tools, the tree is rarely cut down, possibly because the shade cast by their enormous crown was important for the people and husbandry (Chapman, 1945) or because of sacred connotations. In Cyprus many old, giant trees of this species are found, scattered on the island and often as single trees or in small stands, many of them now protected as natural monuments. The acorns have been an important fodder source for semi-wild pigs.



2/ One of the many impressive *Quercus infectoria* subsp. *veneris* that can be found in Cyprus. The age of this tree is estimated at 500 years.

Q. infectoria subsp. *veneris* is today overall a rare tree in the Mediterranean and only found in Cyprus within the European Union. The natural stands of this species were added in 2003 as an Annex I Habitat of Community Interest under the Habitats Directive (Anonymous, 2006). Natural factors contributing to the problems of *Q. infectoria* subsp. *veneris* include poor seed dispersal, probably due to the absence in the lowlands of the Eurasian jay (*Garrulus glandarius*) that normally feeds on acorns and thus spreads them accidentally. Survival of young oaks is also jeopardized by drought periods that have become more frequent in recent years (Anonymous, 2006).

Trees grown from wild-collected provenances have proven their hardiness in central Western Europe (Luxembourg, Germany). These mainly deciduous trees grow slowly but without major frost damage in these climates where winter temperatures drop below $-20\text{ }^{\circ}\text{C}$ ($-4\text{ }^{\circ}\text{F}$).

Quercus coccifera L. subsp. *calliprinos* (Webb) Holmboe (Section *Cerris*)

Kermes oak: Evergreen shrub to small tree, up to $10 \times 7\text{ m}$ ($33 \times 23\text{ ft}$), bark grey, smooth when young but vertically fissured with age; young twigs slightly pubescent; leaves variable in shape, up to $5 \times 2.5\text{ cm}$ ($2 \times 0.98\text{ in}$), leathery, shiny light dark green above, glabrous to slightly pubescent below; margins mostly spinose-dentate, often undulate; petiole up to 5 mm (0.2 in); acorn up to $3 \times 1.5\text{ cm}$ ($1.2 \times 0.6\text{ in}$), cupule up to 3 cm (1.2 in) in diameter, covered with loosely adpressed or distinctly recurved scales, enclosing one-third to three-fourths of the acorn; ripening the second year after flowering.

Native also in Turkey, Syria and Israel, the Kermes oak is found all over Cyprus from $100\text{--}1300\text{ m}$ ($328\text{--}4,264\text{ ft}$) in maquis and pine forests, forming small stands of shrubs. A few giant Kermes oaks are known. The wood was used for fuel, the acorns for pig fodder.

Q. coccifera subsp. *calliprinos* is host to the insect responsible for carmine scale, *Coccus ilicis* Planch. (Hemiptera: Coccoidae: Dactylopididae); the larvae appear as red

berries on twigs and leaves. A red dye was obtained from it in the past, and gave the species its name (*coccus coccineus*: red berry).

Like in other species of the genus, the taxonomy of *Q. coccifera* is still controversial and several authors do not accept the proposed subspecies. Until there is a modern revision of the species complex, it seems wise to accept the splitting and accept subsp. *calliprinos*, the eastern, more tree-like form of *Q. coccifera*.

Quercus alnifolia Poech (*Q. infectoria* Gaud., *Q. cypria* Jaub. & Spach, *Q. ilex* Sibth.) (Section *Cerris*)

golden oak of Cyprus: Evergreen shrub to small tree, up to 10 × 5 m (33 × 16.4 ft), bark grey, smooth when young and vertically fissured with age; young twigs at first densely grey tomentose; leaves thick and leathery, slightly convex, ovate, oblong, obovate or suborbicular, up to 6(-10) × 5(-8) cm/2.3(-3.9) × 2(-3.1) in, dark shiny green and glabrous above, below densely golden to brown or greenish tomentose (rarely silvery-grey) when young, turning dark brown or nearly black with age; margins dentate or lobulate; tomentose petiole 6-12 mm (0.23-0.47 in); acorn narrowly obovate or subcylindrical, up to 4 × 1.2 cm (1.6 × 0.47 in), cupule enclosing one-sixth to one-quarter of the acorn, covered with strongly recurved, linear scales; acorn ripening the first year.

Endemic to Cyprus, very common, but occurring only on the ultra-basic rock formations of the Troodos Massif from 300-1800 m/984-5,904 ft (rarely below 450 m/1,476 ft and scattered above 1,600 m/5,248 ft), *Q. alnifolia* is the dominant species of dry habitats in *Pinus brutia* forest or forms dense high maquis in mesic habitats. Very few giant trees of *Q. alnifolia* (10 m/33 ft) are known, and these are exceptional. The species has a high ecological value, since it thrives on stony and rocky mountainsides, preventing erosion. It coppices well from the base and thus reinstates itself after fires. The acorns form an important diet for the mountain fauna, the hard wood is suitable for the construction of tool handles and other small articles (Tsintides et al., 2002). The wood was also one of the principle fuel species used to make high-grade charcoal (Chapman, 1945).

The habitat type “Scrub and low forest vegetation of *Q. alnifolia* (9390)” is a priority habitat of Annex I, Directive 92/43/EEC. Therefore, large forest expanses have been proposed for inclusion in the *Natura 2000* network, to protect the endemic forests of golden oak. *Q. alnifolia* as a species is protected by Cyprus forest law. *The Red List of Oaks* (Oldfield & Eastwood, 2007) lists *Q. alnifolia* as a vulnerable species [Vu B1 ab(ii)] saying that “habitat degradation by fire, grazing, wood cutting and development” threatens the species. *Q. alnifolia* is the National Tree of Cyprus.

Drummond, who visited Cyprus in 1754, speaks of it as “...a kind of alder, the leaves of which shine like a green orange; the backs of them, when young, are yellow, but as they grow old, they turn brown.” (Chapman, 1945). The Austrian botanist



3/ *Quercus alnifolia* with the author.

Theodor Kotschy collected this oak at the end of October in 1840 “...with ripe acorns, on the eastern slopes of Olympos.” (Kotschy, 1862). He sent this material to his colleague Joseph Alois Poech in Vienna, who described *Q. alnifolia* in 1842 as well as a couple of the other plants of Cyprus collected by Kotschy. Already a couple of years earlier, in 1834, the French botanist Pierre Martin Rémi Aucher-Éloy collected “insufficient material from shrubby specimen, with undeveloped acorns” (Kotschy, 1862). One year after Poech’s description of *Q. alnifolia*, the French botanists Hippolyte François Comté



4/ The elegant acorns of *Quercus alnifolia*.

de Jaubert and Edouard Spach published in 1843 a description of the oak collected by Aucher-Éloy under the name *Q. cypria* Jaub. & Spach. The drawings of *Q. alnifolia* in Camus (1934) are made from the original material of Poech and also of Aucher-Eloy No. 2861, and the not fully developed acorn from the latter collection is clearly visible.

Kotschy (1862) states that the species may be hardy in southern Europe as it is covered more than a month with snow in its natural habitat. The species was introduced into Kew in 1885, where it proved to be “...perfectly hardy, but slow growing...the yellow indumentum of the leaves is only slightly developed with a more grayish undersurface.” (Bean, 1976). Semi-deciduous trees grown from wild-collected provenances have proven their hardiness in central Western Europe (Germany: Black Forest, 850 m/2,788 ft, Hardiness Zone 7a), growing slowly but without major frost damage in these climates where winter temperatures drop below -20 °C (-4 °F), under snow cover.

Quercus alnifolia Poech var. *argentea* Hadjik. & Hand (2005)

In 2005, Hadjikyriatou and Hand described a new variety of *Q. alnifolia*. They observed a number of populations of *Q. alnifolia* as small groups of plants with flattish leaves with slightly revolute margins and a silvery-tomentose lower surface. The authors consider this constant variation as remarkable enough to support the creation of a varietal level taxon (Hand, 2006), describing it as “*Quercus alnifolia* var. *alnifolia* foliis adultis

complanatis argenteis glanduloso-pilosis infra differt.” As the leaves of the golden oak are quite polymorphic, the above observed variation may not prove sufficient to maintain this varietal level taxon. *Etymology*: *argentea* = silvery

***Quercus* × *campitica* Hadjik. & Hand**

(*Quercus* × *campitica* nothosubsp. *hylatis* Hadjik. & Hand) [*Q. alnifolia* × *Q. coccifera* subsp. *calliprinos*]. Recently, hybridization between two species of Cyprus oaks has been described: The two evergreen Cyprian oak species, *Q. alnifolia* and *Q. coccifera* subsp. *calliprinos*, form mixed populations around the Troodos mountain range. It was known for quite a long time that the local inhabitants of the village of Kampos in the northwest part of the Troodos range had observed that some oaks within these mixed populations bear characteristics of both taxa. They adopted for them the vernacular name “*Lakopernia*” (from the Cyprian expressions for *Q. alnifolia* = *lakia*, and *Q. coccifera* subsp. *calliprinos* = *pernia* [*prinos*]). In 1999 several specimens were collected and the holotype was described in 2005 (Hand, 2006) as *Q. ×campitica* nothosubsp. *hylatis* Hadjik. & Hand, which was contrary to Art. 34.2 ICBN (2006). In 2007 Greuter & Raus published the name validly as: *Quercus* × *campitica* Hadjik. & Hand (*Q. alnifolia* × *Q. coccifera* subsp. *calliprinos*) (2005). (holotype: B, isotype: CYP. herb. Hadjikyriakou): Shrub to 5 m (16.4 ft), lamina up to 6.5 × 4 cm (2.5 × 1.6 in), ovate, ovate-oblong or oblong, leathery, dark shiny green above, rather densely silvery to pale golden yellow-tomentose below in young leaves and densely silvery-tomentose in mature leaves, except in the region of the rather prominent midrib; apex acute, spinose, base shallowly or distinctly cordate, margins spinose dentate with usually upwards directed pungent teeth; petiole 4-10 mm (0.16-0.39 in), stellate-tomentose. Cupule ca. 10 mm/0.4 in in diameter, with strongly recurved, hooked scales; acorns narrowly obovate or subcylindric, 2-3 cm/0.78-1.2 in long (Hand, 2006).

The hybrid is closer to *Q. alnifolia* with the leaves being a dark shiny green above with a rather dense indumentum below, and closer to *Q. coccifera* subsp. *calliprinos* in the acute, spinose apex, the distinctly or shallowly cordate base and the spinose dentate margins of the leaves.

It has been observed in the original location that *Q. coccifera* subsp. *calliprinos* flowered 10 days earlier than *Q. alnifolia*, and the hybrid of these two taxa about 10 days later than *Q. alnifolia*. Also, hybrid plants in all locations have been found growing near *Q. coccifera* subsp. *calliprinos*, with *Q. alnifolia* at some distance. This would indicate that *Q. alnifolia* pollinates the Kermes oak; equally acorns collected from Kermes oak produce hybrids (Hand, 2006). The hybrid was found in three widely separated localities. At the original locality near Kampos village only one specimen was found, in the other two sites respectively, 6 and 3 plants have been observed. In total not more than 10 specimens are known growing in the wild. *Etymology*: the epithet *campitica* is derived from the Latinized form of the word “*Kampitikoz*” meaning “coming from Kampos village”.

Q. coccifera subsp. *calliprinos* does show wide phenotypic variability, which may reflect a greater genetic variability than *Q. alnifolia*, which has a reduced morphological variability, possibly attributed to its narrower ecological range (Neophytou et al., 2006).

Recent studies on genetic differentiation and hybridization between *Q. coccifera* and *Q. alnifolia* in Cyprus (Neophytou, 2010) show that the two species are both morphologically and genetically distinct, with very limited chloroplast DNA introgression. Evidence for interspecific pollination was rare. Specifically, no interspecific pollination was detected

in *Q. alnifolia*, but rare pollination of *Q. coccifera* by *Q. alnifolia* could be inferred. This coincides with the observations made by Hand (2006). Reproductive barriers may be the reason for the limited genetic introgression between the two species.

An allozyme characterization of four Mediterranean evergreen oak species based on cladistic analysis (Toumi & Lumaret, 2001) has shown a cluster of four species (*Q. ilex* L., *Q. coccifera* and *Q. alnifolia*, with the Tibetan *Q. aquifolioides* Rehd. & Wils., whereas *Q. suber* L. and the Himalayan *Q. semecarpifolia* Sm. in A. Rees were both genetically very distinct). According to Toumi & Lumaret (2001) both *Q. alnifolia* and *Q. coccifera* should be classified in the same cluster of Mediterranean oaks that corresponds with Section *Cerris* sensu Nixon (subgenus *Sclerophyllodryis* sensu Schwartz).

Introduced oak species

In addition to the indigenous oaks, several species have been introduced, either for economical or ornamental reasons. These include *Q. ilex* L., *Q. ithaburensis* Decne. subsp. *macrolepis* Hedge & Yalt., and *Q. suber* L.

Conclusion

The flora of Cyprus shows a high diversity, with a total of 1,750 plant species known, due to the edaphically, climatic and topographic variation. The three indigenous oaks *Q. infectoria* subsp. *veneris*, *Q. coccifera* subsp. *calliprinos* and the endemic *Q. alnifolia* are described, as are the recently described hybrid *Q. ×campitica* and a purported variety *Q. alnifolia* var. *argentea*. Their taxonomic status and the possibility of occurrence is subject to discussion.

Photographers. Title page: Béatrice Chassé (*Quercus alnifolia*). Photos 1-4: Eike Jablonski.

Bibliography

- Anonymous. 2005. *Promoting Protection and Sustainable Management of the Oak Trees of Cyprus*. European Commission, Cypriot Civil Society in Action II Grant Program (Europeaid/127215/L/ACT/CY).
- Barton, G.A. 2002. *Empire Forestry and the Origins of Environmentalism*. New York: Cambridge University Press.
- Bean, W.J. 1976. *Trees & Shrubs Hardy in the British Isles*. 8th edition revised. Vol. III: 461-462. UK: J. Murray.
- Camus, A. 1934. *Les Chênes. Monographie du genre Quercus*. Atlas, Tome I, Pl. 40. Paris: Lechevalier & Fils.
- Chapman, E. S. 1945. *Cyprus Trees and Shrubs*. Nicosia: Public Information Office, Reprint (1965).
- Greuter, W. and T. Raus (ed.). 2007. Med-Checklist Notulae, 25. *Willdenowia* 37: 205-213.
- Hand, R. 2006. Supplementary notes to the Flora of Cyprus V. *Willdenowia* 36: 761-809.
- Meikle, R.D. 1977. *Flora of Cyprus*. Vol. I. UK: Royal Botanic Gardens, Kew.
- Neophytou, C. 2010. A study of genetic differentiation and hybridization among oak species with divergent ecological and evolutionary profiles. Thesis Faculty of Forest and Environmental Sciences, Albert-Ludwigs-Universität, Feiburg/Breisgau, Germany. 1-49.
- Neophytou, C., G. Palli, A. Dounavi and F.A. Aravanopoulos. 2007. Morphological Differentiation and Hybridization between *Quercus alnifolia* Poech and *Quercus coccifera* L. (*Fagaceae*) in Cyprus. *Silvae Genetica* 56: 271-277.
- Oldfield, S. and A. Eastwood. 2007. *The Red List of Oaks*. Cambridge: Fauna & Flora International.
- Toumi, L. and R. Lumaret. 2001. Allozyme characterization of four Mediterranean evergreen oak species. *Biochemical Systematics and Ecology* 29: 799-817.
- Trehane, P. (2010). Nomenclatural Note; see under *Q. infectoria* subsp. *veneris*, in: www.oaknames.org/search/fullname.asp?id=339 (visited 20 July 2012).
- Tsintides, T. C., G.N. Hadjikyriakou and C.S. Christodoulou. *Trees and Shrubs in Cyprus*. Lefkosia: Foundation A. G. Leventis & Cyprus Forest Association, 2002.
- WWF (World Wildlife Fund). 2007. *Cyprus Mediterranean Forests*. Rome: MedPO.



Madame Aimée Antoinette Camus: One of the Last Great Amateurs

Béatrice Chassé

Arboretum des Pouyouleix

Les Pouyouleix

F-24800 St.-Jory-de-Chalais, France

pouyouleix.arboretum@gmail.com

ABSTRACT

Aimée Antoinette Camus was born in Paris in 1879 and, after 86 years of what can only be described as an extraordinarily productive life, died there in 1965. She left Paris only a few times in her life, but through her work at the Muséum national d'Histoire naturelle, received countless hundreds of specimens from all over the world. Little is known of the personal life of this woman of whom history has left us but one portrait. In the forty-two years between the publication of *Les Chênes, Monographie du Genre Quercus* and her first botanical contribution in 1894 at the age of fifteen, Aimée Camus published hundreds of scientific articles and authored or coauthored several major monographs. *Les Chênes* remains to this day unique in its comprehensiveness. This presentation attempts to paint a clearer and more colorful portrait of Madame Camus while presenting *Les Chênes* in a historical perspective.

Keywords: *Quercus*, *Les Chênes*, *Monographie du Genre Quercus*, Muséum national d'Histoire naturelle, botany and French imperialism, Edmond Gustave Camus

Preface

The story that is about to follow is a mix of detective work and scholarship. For sure, scholarship always involves a bit of detective work – but this case literally started as the search for a missing person. The detective work has been very rewarding and for the value of the scholarship, it is for the reader to decide.

Three years ago, at the 6th International Oak Society Conference in Mexico, friend and fine oak artist Keiko Tokunaga and I were looking for *Q. eugeniifolia* Liebm. – today the Mexican plant that has been referred to under this name is called *Q. delgadoana* S. Valencia, Nixon & Kelly – somewhere near Real de Monte in the state of Hidalgo, when Keiko said to me “Béatrice, did you know that nobody knows who Madame Camus’ mother was?” I admitted that, no, I did not know this and continued looking for *Q. eugeniifolia*. I admit also not having given any thought at all to the question until the idea of presenting a paper on Madame Camus at the 7th International Oak Society Conference in France came up. Thus the detective story starts with the search for Madame Camus *mère* and led to Madame Mercedes Falgarona, the widow of the man who inherited a large part of the Camus estate when Blanche, Aimée’s younger sister, died in 1968. Madame Falgarona welcomed me to her home and shared with me the documents, photographs and paintings in her possession.

Introduction

Many of the readers of this journal will be surprised to learn that Madame Camus was not, in her time, especially known as Madame Oak. In the few primary sources of biographical information that can be found, more mention is made of her work with grasses and orchids – or at the very least, *Les Chênes*, for the monumental amount of work that it is, is never singled out by these authors as having been more important to her.¹ Her published work covers an incredible number of plant families and genera: *Salix*, *Cupressus*, *Carpinus*, *Castanopsis*, *Castanea*, *Lithocarpus*, *Quercus*, bamboos and other grasses, orchids, etc. In addition to her major work in systematics, Aimée Camus authored works of popular science, on the history of science (in particular, work on eighteenth and early nineteenth century French specialists on the grasses of North America)² and was heavily involved in many studies attempting to determine the economic value of indigenous plants arriving by the ton from the new French colonies (especially Madagascar and Indochina).

But who was she? Where was she born? Where did she study? What was her working relationship with the Muséum national d’Histoire naturelle? What did she think about taxonomy and natural history and the struggles of the Muséum to stay alive as a functioning scientific institution during the end of the 19th century and the first half of the 20th? Were these things discussed in what were in her time the very crowded hallways and overcrowded laboratories of number 10, rue de Buffon* where other workers were frenetically doing the same thing that she was, i.e., classifying the literally dozens of thousands of specimens arriving at the Muséum from the new French Empire?

So who was she? And, first of all, who was her mother?

* The Muséum national d’Histoire naturel is composed of different institutions, one of which is the Jardin des Plantes, in Paris. It forms a sort of lopsided rectangle bordered by rue de Buffon, rue Geoffroy St. Hilaire, rue Cuvier and quai St. Bernard. The herbarium and other botanical facilities are located in the building that can be accessed through 10, rue de Buffon.



1/ Aimée Antoinette Camus, painted by her sister Blanche.

The family

Her mother's name was Aimée Françoise Choinel, born on 19 May 1856 in the city of Paris in the 16th *arrondissement*.^{*3} The Choinel family were wealthy, upper-class citizens whose ancestry dated back to Louis-Denis Choinel, who in 1759 held the title of Advisor to Louis XV and to the City.

Monsieur Camus *père* was born in 1852 on the 15th of August in Paris to a wealthy and influential family⁴ (his father had been the Mayor of Champagne).⁵ Monsieur Camus and Mlle Aimée Françoise Choinel were married in 1878 in Paris.⁶

Aimée Antoinette Camus was born at 183, rue du Faubourg St. Antoine in the 11th *arrondissement* of the city of Paris on the 1st of May in the year 1879 (and not, as Wikipedia has it, in the place called l'Isle Adam, 50 miles north of Paris).⁷

In 1884 (Aimée would have been five years old) her sister Blanche is born, at a different address: 58, boulevard St. Marcel in the 5th *arrondissement* and exactly 660 meters from the Jardin des Plantes and number 10, rue de Buffon.⁸ From a note in the *Journal de Botanique*, we learn that the Camus were still living at 58, boulevard St. Marcel in 1888, when Aimée would have been 8 years old and in her fourth year of primary school.⁹ In 1897, when her paternal grandmother dies, the family's home is still at 58, boulevard St. Marcel and she is 18 years old.¹⁰ In 1915, when her father dies, the family had already moved to 48, rue de l'Abbé Groult.

* An *arrondissement* is an administrative term used to delimit a specific part of, for example, a city. In common parlance, the different neighborhoods in Paris are referred to as the 11th, 7th, 5th, etc... *arrondissement*.



2/ Aimée Antoinette Camus, Blanche Célestine Camus, Aimée Françoise (Choinel) Camus.

It is very difficult to say anything about the personal life and thought of Aimée Camus. For one, Madame Falgarona was the second wife of Monsieur José Falgarona and only arrived at 199, rue Lecourbe after Aimée had died. More importantly, the botanic library – and all the other botanic facilities of the Muséum at the Jardin des Plantes – have been closed since 2008 and, as the head librarian told me, Madame Camus’ correspondence, if it has been saved, has not been inventoried and so merely to find it would be quite the task.

One of the two primary sources of information that we have from a person that knew her is Jacques Léandri’s biographical notice. As all the secondary sources of information have repeated since, we learn there that Aimée Camus was devoted to her father and her sister. More intriguing though (but not repeated in any of the secondary sources), we learn specifically that Blanche was always ready to sacrifice her personal projects for the studies of her sister “a companion whose entire life had been

marked by emotional trials.”¹¹ What were these emotional trials? I do not have an answer to this question except to say that they were probably not due to a broken heart: according to Madame Falgarona, her husband, who knew both sisters well, assured her that neither Blanche nor Aimée ever had a boyfriend, lover or husband.¹²

The other primary source of information that exists is Henri Lecomte’s biographical notice on Aimée’s father, Edmond Gustave Camus. Henri Lecomte knew and worked with them both and he too assures us that Aimée was indeed devoted to collaborating with her father and shared his love for botany.¹³ “[S]hortly before his death he had undertaken, with Mlle A. Camus, a major study on grasses. His daughter – devoted and distinguished colleague – has not abandoned the task and she has presently undertaken its completion with her consummate experience and professional standards, that I should like to pay tribute to.”¹⁴

Education in 19th century France

It was only in 1880, the year after she was born, that a law was passed creating institutions of secondary education for girls (age 11 to 18). The curriculum for girls was markedly different in that it was not constructed around what is referred to as the *humanités classiques*, which formed students in Latin and Greek (indispensable at the time

* Citations from French texts have been translated by the author.

for going on to university), and, more importantly, only boys had access to the last year of secondary education, the *baccalauréat* and its exams, also indispensable for going on to higher education. Girls took different exams in the year before the *baccalauréat* and, if successful, would have a diploma that would allow them, at best, to pursue training with a view to becoming a primary or secondary school teacher. “Latin is not for young ladies, they should only be taught the rudiments, the same is true of mathematics. Encouraging young ladies to embrace the exact sciences would unfortunately develop their powers of abstraction. In addition, applied mathematics is not for them.”¹⁵ The goal really was to form good mothers and wives, not professionals in competition with men.¹⁶

If you had wealthy and indulgent parents, they could pay for private lessons to cover all of the material that the boys studied during that year, and then the *baccalauréat* examination could be passed. This situation changes only in 1924 when girls’ *lycées* are officially allowed to prepare their students for the *baccalauréat*.

Therefore, Aimée Antoinette Camus, at age 17 in 1897, would not have had official access to the year of study and examinations that she would have needed to continue her education at university level. She would have finished her secondary schooling with a year of botany taught by Madame Morot, wife of Louis Morot (1854-1915), Muséum botanist (*préparateur*) and founder of the *Journal de Botanique*.¹⁷

She would thus have had one year of botany classes with Madame Morot, at age 13 to 14. So what did she do? It is most probable that her family paid for private lessons, but fairly unlikely that she went on to formal higher education in pursuit of a degree. She was much too busy being a botanist...



3/ Blanche (left) and Aimée Camus.

Amateur and volunteer

I have not as yet been able to find any references to what Madame Morot taught in her botany classes; and, while this would certainly be interesting for historical reasons, it is in fact quite trivial in this story. Aimée Camus was fifteen – just one year after her year of botany with Madame Morot – when her first joint publication, with her father, appeared in the *Bulletin de la Société Botanique*.¹⁸ At this meeting were present 124 men, 15 women and one fifteen-year-old botanist.¹⁹

According to Jacques Léandri, after studying with Madame Morot, Aimée took classes with Gaston Bonnier (1853-1922), Professor at the Faculté des Sciences of the Sorbonne but Léandri does not say that she attended the Sorbonne.²⁰ Also according to Léandri, she later studied with Philippe Van Tieghem (1839-1914), who taught classes at the Muséum an institution that was never mandated to deliver diplomas. Likewise, there is no mention of her higher education or of any ensuing titles she may have acquired (which is always the way similar biographical notices start). Further, Madame Camus, who “worked” full time at the Muséum from roughly 1908 until 1963, was never paid: she was a volunteer.^{21;22} An amateur in, as we say, the noble sense of the word.

Jacques Léandri, in his homage to Aimée Camus, begins: “In our day, when both systematics and botany in the field, like so many other disciplines, are becoming the privilege of the staff of Scientific Institutions, where large cities push indigenous plant populations further and further away from city dwellers, we must not forget the “amateur” botanists, who throughout the century have served Science so well. They constituted the skeleton of the Société Botanique de France and many of them were indeed masters. Aimée Camus, one of the most remarkable of that group, has recently left us.”²³

Madame Camus may very well have obtained a diploma from an institution of higher learning but in actual fact, it didn’t matter: she lived at a time when her competence was (almost) all she needed to be taken seriously.

To name but a few of her honors and awards: in 1906, the Prix de Coincy awarded by the French Science Academy to honor significant contributions to taxonomy; in 1958, the title of Associé du Muséum, a prestigious honor given only rarely; in 1961, le Prix du Conseil de la Société Botanique de France, and she was appointed Chevalier de la Légion d’Honneur for outstanding civil service – in systematics – to her country.

From a document in Madame Falgarona’s possession (and dated somewhere between 1900 and 1903, we learn that Aimée, 21- to 23-years-old, receives a note from Monsieur Gaston Darboux, Permanent Secretary of the French Science Academy, Honorary Dean to the University of Paris Science Faculty, and President of the Friends of Science Assistance Society: “Please accept my warmest congratulations and hear my plea to not forget in this day those unhappy scholars and their families to whom the Friends of Science Assistance Society are devoted. Every day our needs are increasing without an equivalent rise in resources. Support from all of us is needed; yours would be particularly precious.”

What honor had she received, what achievement had she accomplished at such a young age to merit the “warmest congratulations” of such an important French figure of science as was Gaston Darboux? What was her “particularly precious” involvement in the Friends of Science Assistance Society? There are as yet no answers to these questions...

Nevertheless, not only was it a time when competence could take the place of titles but as history would have it, it was also a time when the Muséum was desperately in

need of competent taxonomists to classify the astounding amount of material that was arriving from throughout the French Empire. Between 1878 and 1907 the herbarium had tripled in size.²⁴ In 1908, Muséum Director Edmond Perrier bitterly criticizes the insufficient budget, buildings, work space and staff.²⁵ Henri Lecomte, Chair of Botany and Classification of New Families of Spermatophytes, in his critical *Deuxième rapport annuel* in 1910 reiterates these criticisms ending with a plea for improvements in the near future.²⁶

This same report tells us also that, of the volunteers “who classify and prepare the collections”, the most important for their invaluable work were “MM. Benoist, de Boisseau, Buchet, Mlle A. Camus, and Monsieur E. G. Camus” (p. iv).

Edmond Gustave Camus

It is without question that we owe to Aimée Camus’ father her passion for botany as well as her perspective on systematics. M. Camus was a pharmacist, who retired from this practice in 1908 to devote himself entirely to his passion for botany.²⁷

In the thirty years that E.G. Camus shared between being pharmacist and botanist, he published hundreds of articles and several major monographs (orchids, willows, bamboos). He was a major collaborator in several *Flore de France* and instrumental



4/ The corner of 148, rue de l'Abbé Groult and 199, rue Lecourbe, where the pharmacy that was Monsieur Camus’ still exists. After taking a few photographs, I went inside and before I could finish my introduction, “Hello, I’m doing some research on a very famous French lady botanist...” the pharmacist interrupted me with, “Madame Camus?” I nearly fell on the floor when she followed with, “If you want to learn about the Camus, perhaps you should meet Madame Falgarona, who is the widow of the man who inherited a large part of the Camus estate when Blanche died.” I followed her advice.



5/ Aimée Camus by Blanche Camus.

in bringing to life (as was Aimée) Henry Lecomte's, *Flore Générale de l'Indochine*. A fervent believer in the importance of knowing your own local flora and of spending a maximum amount of time in the field, Monsieur Camus traveled throughout France and in Switzerland (but never left the continent) botanizing, enriching his herbarium... and discovering hybrids. He stresses the importance of botanizing in the field as opposed to in gardens because, according to him, not only are plants in cultivation different from their wild counterparts, but the variation they show is not sufficient to grasp the degree of variation within a species.²⁸

Interested amateur and professional botanists of the time could read in the *Journal de Botanique* (1888), "A research committee has been formed, under the direction of Professor Chatin, to study problematical plants and to explore the different floristic stations near Paris, about

which as yet nothing has been published. Persons wishing to participate in the botanizing excursions that will be organized by this committee can obtain additional information from Monsieur Camus, 58, blvd. St. Marcel."²⁹

Of the hidden parts of plants

From very humble beginnings and with very little formal education as a young man, Gaspard Adolphe Chatin (1813-1901) went on to become medical doctor, pharmacist, and botanist. From 1874 onwards, E.G. Camus, who would have been 22, was a fervent disciple of Monsieur Chatin's approach to botany and his passion for botanizing in the field. But his most important influence on his students, and certainly on Monsieur Camus, was his belief that internal (hidden) characters were "linked" to external morphological characters and therefore that comparative anatomy was essential to systematics.³⁰ The title of his thesis, defended in 1840, is quite revealing: *Comparative anatomy of plants applied to classification. The translation of the internal organization or of the hidden parts of plants by those found at their surface*.³¹

This anatomical approach to classification (plus a penchant for hybrids, discussed below) is the Camus signature. Of their first major father and daughter publication, *La Classification des Saules d'Europe et Monographie des Saules d'Europe*, Henri Lecomte writes, "the authors have had the good idea ... of using both external morphological characters and those of organ structure; and one finds, for example, standard dichotomous keys followed by keys based on organ structure and a very original key designed to link the results from both. Not enough good can be said of introducing these anatomical characters into a domain that Botanists have for too long tried to restrict to external morphology."³²

In the joint publications with her father, Aimée Camus was responsible for all of the anatomical work and she continued with this method (morphology and anatomy) throughout her life (up until about half way through *Les Chênes*). Where did she learn these skills? For, with or without a diploma, everyone needs a teacher.

Anatomy and politics

Philippe Edouard Léon Van Tieghem (1839-1914) was a biologist, physicist, and lastly, botanist. In 1879, the year Aimée Camus is born, he is appointed to the Chair of Botany at the Muséum. Between 1853, when Adrian de Jussieu's Chair of Field Botany is transformed into the Chair of Paleontology, until 1874 when a new Chair is created (Classification and Natural Families) botany was nonexistent at the Muséum.³³ Between 1878 and 1907 the herbarium collections triple in size, but the Muséum is not prepared for this exponential explosion.

By 1890, after 11 years with Philippe Van Tieghem in charge of botany at the Muséum, things are put back on a naturalist track. By 1892, all of the Chairs without collections are abolished. The valorization of the only resource truly unique to the Muséum, the collections, was also a strategic choice for the Muséum, forced as it was to abandon little by little some of its historical prerogatives. This was then the golden age of the monograph, that provided a panoramic and at the same time (thanks to Philippe Van Tieghem's anatomical approach) a very detailed view of groups of living things based on an incredible number of microscopic manipulations and observations, minute measurements and comparisons. Anatomy was to give systematics its mathematical letters of nobility.

The hybrid question or, who wants to count pebbles anyway?

In *Les Orchidées Sauvages*, Sébastien Lesné, after recognizing the value of the work done by the Camus team on orchids, writes, "One is often confounded when faced with the plethora of varieties described by our two botanists. It is often difficult to distinguish between the names of these hybrids depending on which parent they more resemble. At the time of the triumph of splitting the Camus were indeed genial precursors."³⁴

Henri Lecomte, in his biographical notice on E.G. Camus, also points out his passion for hybrid plants.³⁵ And although I am sure that this was not his intention, Jacques Léandri, while describing the Camus' view on hybrids, points to the paradox of this position: "Identifying this multiplicity of hybrids allowed [them] to determine that species polymorphism is not as wide-spread as first appears."³⁶ Because of course the other way around: "Identifying the extent of species polymorphism allowed [them] to determine that hybridization is not as wide-spread as first appears", would be just as plausible.

Roughly at the same time, but not in France, the foundation for cladistics is being invented and it is interesting to note that it was in part the internal logical inconsistencies of the systematics of their day that led certain biologists to this new way of thinking. What did Madame Camus think about systematics from 1934 to 1954 as she progressed through the genus *Quercus*?

In a letter to Henry Fawcett in 1861, Charles Darwin criticizes the position that science is merely about collecting facts. "How profoundly ignorant B. must be of the very soul of observation! About thirty years ago there was much talk that geologists ought only to



6/ Aimée Antoinette Camus.

observe and not theorize; and I well remember someone saying that at this rate a man might as well go into a gravel-pit and count the pebbles and describe the colors. How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service!”³⁷

With what “view” was Madame Camus working? The answer to this question, lies in the French brand of resistance to Darwinism that remained strong in the first half of the 20th century.³⁸ The paradigm, during Madame Camus’ formative years and during much of her professional life at the Muséum, was greatly inspired by Isidore Geoffroy Saint Hilaire’s (1805-1861) version of transformism called the “limited-variability-of-type” theory. The name speaks for itself: if species (the type) show limited variation, then any marked difference or what is perceived as such requires the creation of new taxa.

The case for Quercus

Nevertheless, in this age of splitting, Madame Camus is critical of the extent to which her contemporaries indulged in this activity as concerns the genus *Quercus*. While stating her case for limited-variability-of-type: “In the genus *Quercus*, many species, especially those whose natural distribution is vast, are very polymorphic. After careful study, however, one will find that to the species type can be attached many varieties, subspecies and races.”³⁹, she also states, “This polymorphism ... has caused many authors to distinguish and to accept as species many varieties. [These] species have thus been

divided to dispersal and [this] has] resulted in a great number of synonyms.”⁴⁰

Of the 308 new names in *Les Chênes* by A. Camus (285) or Hickel & A. Camus (23), 52 are (still) accepted today. While this might not seem like a very good score, of her contemporary, Michel Gandoger’s (1850-1926), 224 published names of the genus, not one is accepted today.*

Following the method used in the Camus monograph on orchids and willows, Madame Camus often creates (or accepts) two names for hybrids, depending on which parent is more visible. Thus the hybrid between *Q. pyrenaica* Willd. and *Q. robur* L. should be identified as *Q. ×andegavensis* Hy if *Q. pyrenaica* is dominant, and *Q. ×rechini* (Rouy) Hy if *Q. robur* is dominant. Today, only the former is an accepted name for this hybrid.

Les Chênes, Monographie du Genre Quercus

The three volumes of text (2,839 pages) start with a 156-page introduction to the genus, 39 of which are devoted to morphology, 80 to anatomy, and 2 to chromosomes. The remaining 25 or so touch on different subjects: germination, cultivation, the uses and qualities of oak wood, natural distribution, and hybridity. The three atlases comprise 522 morphological plates and 97 anatomical plates. On each plate, the number of illustrations ranges from 5 to 40.

Les Chênes was published in a collection called the *Economic Encyclopedia of Forestry* along with Robert Hickel’s *Forestry Dendrology*, Arturo Bruttini’s *Forestry Dictionary*, and the Camus monographs on bamboo, *Cupressus*, *Castanea* and *Castanopsis* (these last two together in one monograph). *Les Chênes* was published in the great flurry of activity for the colonial effort that characterized French science from the end of the 19th century through the first half of the 20th.

The erroneous view that Madame Camus devoted a large part of her life to the genus *Quercus* comes, I think, from an editorial imprecision. The title of the book is always followed by the dates, 1934-1954. In fact it was not 20 uninterrupted “oak” years. Atlas I was published in 1934; atlas II plus tomes I and II were published between 1936 and 1939; atlas III was published in 1948 and finally, tome III (in two volumes) from 1952 to 1954, with the genus *Lithocarpus* taking up a large part of both of those. This is not to diminish the importance of *Les Chênes* – quite the contrary. Between 1934 and 1954, in other words in that same period of time, Jacques Léandri lists 150 different publications of only her major works, including many papers on the genus *Quercus*.^{41,42}

Regardless of its shortcomings, *Les Chênes* is to this day the most comprehensive classification that has ever been attempted of the genus, both from a geographic and from a specific point of view. If we compare all of the oak classification systems that have been proposed for oaks since 1871, we find that “although different groups of species within the genus were given different ranks by different authors, they roughly recognized the same major groups”.⁴³

Madame Camus’ Cyclobalanopsis

Madame Camus writes, “The subgenus *Cyclobalanopsis* comprises types of more closely related affinities than those in subgenus *Euquercus*. The divisions *Longiglans* and

* Many thanks to Jean-Louis Hélandot for having pointed out the significance of Mme Camus’ relatively “good score” on this issue.

Breviglans that I have accepted for *Cyclobalanopsis* are hardly more than subsectional groups and do not have the same value as the *Euquercus* sections. [The subgenus *Euquercus*] comprises markedly different types of multiple form.”⁴⁴

And yet, in this very complex *Euquercus* subgenus, anatomy is not wielded as the tool by which to know, by which to distinguish, the different species. Subgenus *Euquercus* is divided by Madame Camus into 6 sections, that are further subdivided into 105 subsections, 50 of which belong to the section *Erythrobalanus* (the red oaks).

Nowhere in *Les Chênes* is there this “original key”, such as the one in the Camus monograph on willows (a key to link the two other keys).

There are 44 new taxa (out of a total 93) described by Camus or Hickel & A. Camus in the *Cyclobalanopsis* section (tome I, pp. 178–373) plus 4 new species that appear in *Additions et Corrections* (pp. 1197–1215) at the end of tome III. Of these 48 names, 24 are accepted today, 10 are considered synonymous with other Camus taxa, and 14 are synonymous with taxa by other authors.

Of these 24, only 6 are represented by photographs (and/or herbarium specimens and Camus drawings) in *Le Guide des Chênes* by Antoine le Hardy de Beaulieu and Thierry Lamant.⁴⁵ Of the remaining 18, 8 are represented only by herbarium specimens and/or Camus plates and the remaining 10 are not included in *Le Guide*. Only 5 out of the 24 are reported in cultivation: *Q. argyrotricha*, *Q. gambleana*, *Q. macrocalyx*, *Q. saravanensis*, and *Q. stewardiana*.

Madame Camus writes at the end of her introduction to *Les Chênes*, “The oak forest that enabled our ancestors to fight against hunger, cold, darkness, that gave them shelter, weapons, construction materials, furniture, boats, means of transport, is today in part free from these obligations. Coal, iron, cement, concrete are all replacing wood; but the Oak with its qualities remains of great usefulness to man and its protection is of the utmost importance. Further, while industrial expansion has brought ugliness to so many places, is not the forest one of the last havens of beauty?”⁴⁶

Where are Madame Camus’ and Monsieur Hickel’s 24 *Cyclobalanopsis* today? Are some of them extinct? Are some of them endangered? Can some of them be saved? What do we know of them?

To date, none of them have been assessed by the IUCN, and in the *Red List of Oaks* by Oldfield and Eastwood, of the 6 that have been assessed, 2 are endangered and 4 are data deficient. So it would appear that to answer these questions we must get together a group of amateurs and go and find these oaks.

Acknowledgements

My deepest thanks go to Madame Mercedes Falgarona for sharing her memories, documents, paintings, and photographs with me. To Henri de Brem, who gave me his copy of *Les Chênes*, I do not know how to express my gratitude. To Lord Lloyd Kenyon and his dislike of feisty librarians that pushed him to undertake (and accomplish) the monstrous task of scanning all of the plates in *Les Chênes*, *mille mercis*.

Photographers. Title page: Béatrice Chassé (Aimée Antoinette Camus painted by Blanche Camus). Photos 1, 4, 5: Béatrice Chassé. Photos 2, 3, 6: unknown. All photos taken or reproduced with the kind permission of Mme Falgarona.

References

1. Jacques Léandri. Aimée Camus, 1er mai 1879-17 avril 1965, *Adansonia*, 1966. Vol. VI: 2–21. Mary R.S. Creese with Thomas M. Creese. *Ladies in the Laboratory II. West European Women in Science 1800-1900: A Survey of Their Contributions to Research* (Lanham Oxford: Scarecrow Press, 2004), 68–71, 91–94. Henri-Jean Humbert et André Aubréville. *Rapport pour l'attribution du Prix du Conseil de la Société botanique de France en 1961* (document from the private collection of Mme Falgarona).
2. Mary R.S. Creese with Thomas M. Creese. *Ladies in the Laboratory II*, 2004: p. 71.
3. Birth certificate Aimée Françoise Choinel. V3E/N487, p. 35. Archives reconstituées d'Etat Civil de la Ville de Paris (acts before 1860).
4. Sébastien Lesné, coordinateur. *Les Orchidées Sauvages de Paris* (Editions Quae, 2009).
5. Funeral announcement for Pierre Antoine Camus. Private collection Madame Falgarona.
6. Official wedding invitation. Private collection, Madame Falgarona.
7. Birth certificate Aimée Antoinette Camus. V4E3998: entry 2085, p.21. Archives d'Etat Civil de la Ville de Paris.
8. Birth certificate Blanche Augustine Camus, V4E5729: entry 2806, p. 3. Archives d'Etat Civil de la Ville de Paris.
9. René Louis Morot, ed. *Journal de Botanique*, Vol., II no. 9(1888): 96.
10. Funeral announcement for Julie-Célesteine Langlossé Camus. Private collection, Madame Falgarona.
11. Jacques Léandri, Aimée Camus, 3.
12. Private communication Mme Falgarona.
13. Henri Lecomte, Notice biographique sur Edmond-Gustave Camus, suivie de la « Liste des publications de Gustave Camus » in G. Camus et A. Camus, *Iconographie des Orchidées d'Europe et du Bassin méditerranéen* (Paris: Paul Lechevalier, 1927), 5.
14. Henri Lecomte, Notice biographique sur Edmond-Gustave Camus, 3.
15. Françoise Mayeur. *L'éducation des filles en France au XIXème siècle* (Perrin, 2008), 227.
16. http://fr.wikipedia.org/wiki/Lyc%C3%A9e_de_jeunes_filles. Accessed 10.05.2012. Excellent article on the subject of the education of young ladies in 19th and 20th century France.
17. Mary R.S. Creese with Thomas M. Creese, *Ladies in the Laboratory II*, 69.
18. G. Camus et A. Camus, Plantes récoltées à Morcles (canton de Vaud) et à la montagne de Fully (Valais). *Bulletin de la Société Botanique de France*, no. 41(1894): CCCXI.
19. Session Extraordinaire Tenue en Suisse au Mois d'Août 1894. *Bulletin de la Société Botanique de France*. No. 41(1894).
20. Jacques Léandri, Aimée Camus, 2–21.
21. Jacques Léandri, Aimée Camus, 1.
22. Henri Lecomte. *Deuxième rapport annuel sur le fonctionnement du Service de Botanique (Phanérogamie) 1910* (Paris: Librairie Paul Geuthner, 68 rue Mazarine, 1911), iv.
23. Jacques Léandri, Aimée Camus, 3.
24. Bonneuil, Christophe. *Mettre en ordre les tropiques : les sciences du végétal dans l'empire français*. (Thèse de doctorat, Université de Paris VII, 1997), 41–43.
25. Edmond Perrier, *Le Muséum National d'Histoire Naturelle* (Paris: Editions de la Revue Politique et Littéraire (Revue Bleu) et de la Revue Scientifique, 1908).
26. Henri Lecomte, *Deuxième rapport*, xvi.
27. Henri Lecomte, Notice biographique sur Edmond-Gustave Camus, 3–11
28. E.G. Camus, *Guide pratique de botanique rurale : à l'usage des botanistes, des étudiants en pharmacie, en médecine, des élèves des facultés des sciences et des gens du monde* (Paris: J. Lechevalier, 1884).
29. *Journal de Botanique*, Vol. II no. 7(1888): 160.
30. Adolphe Chatin. *Anatomie comparée végétale appliquée à la classification. Traduction de l'organisation intérieure ou des parties cachées des végétaux par celles placées à leur surface*. (Thèse présentée à l'Ecole de Pharmacie de Paris le 3 Novembre 1840).
31. Adolphe Chatin, *Anatomie comparée*, 16-18.
32. Henri Lecomte, Notice biographique sur Edmond-Gustave Camus, 7–8.
33. Paul Lemoine, *Troisième centenaire du Muséum national d'Histoire naturelle* (Paris: S.I. 196?).
34. Sébastien Lesné, *Les Orchidées*, 21-23.
35. Henri Lecomte, Notice biographique sur Edmond-Gustave Camus, 6.
36. Jacques Léandri, Aimée Camus, 5.
37. Charles Darwin. Letter 3257, to Henry Fawcett, 1861. The Darwin Correspondence Project. <http://www.darwinproject.ac.uk/entry-3257>. Accessed 17.05.2012.
38. Michael A. Osborne, *Nature, the Exotic and the Science of French Colonialism* (Bloomington Ind.: Indiana University Press, 1994), 64.
39. A. Camus, *Les Chênes. Monographie du genre Quercus (et Lithocarpus)* (Paris: Paul Lechevalier Editeur, 1934-1954), Vol. I: 146.
40. A. Camus, *Les Chênes*. Vol. I: v.
41. Aimée Camus, *Quercus ilex L.* et espèces asiatiques avec lesquelles il a été confondu. *C.R. Congrès Soc. Sav. Nice*, 1938.
42. Aimée Camus, Les chênes dans la production forestière indochinoise. *Rev. Bot. Appl. et Agric. Col.* 15(1935): 20–25.
43. Thomas Denk and Guido W. Grimm, The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers. *TAXON* 59(2)(1938): 351–366.
44. A. Camus, *Les Chênes*, Vol. I: 158.
45. Antoine le Hardy de Beaulieu et Thierry Lamant, *Guide illustré des Chênes* (Belgique: EDILENS, 2010).
46. A. Camus, *Les Chênes*, Vol. I: 4.

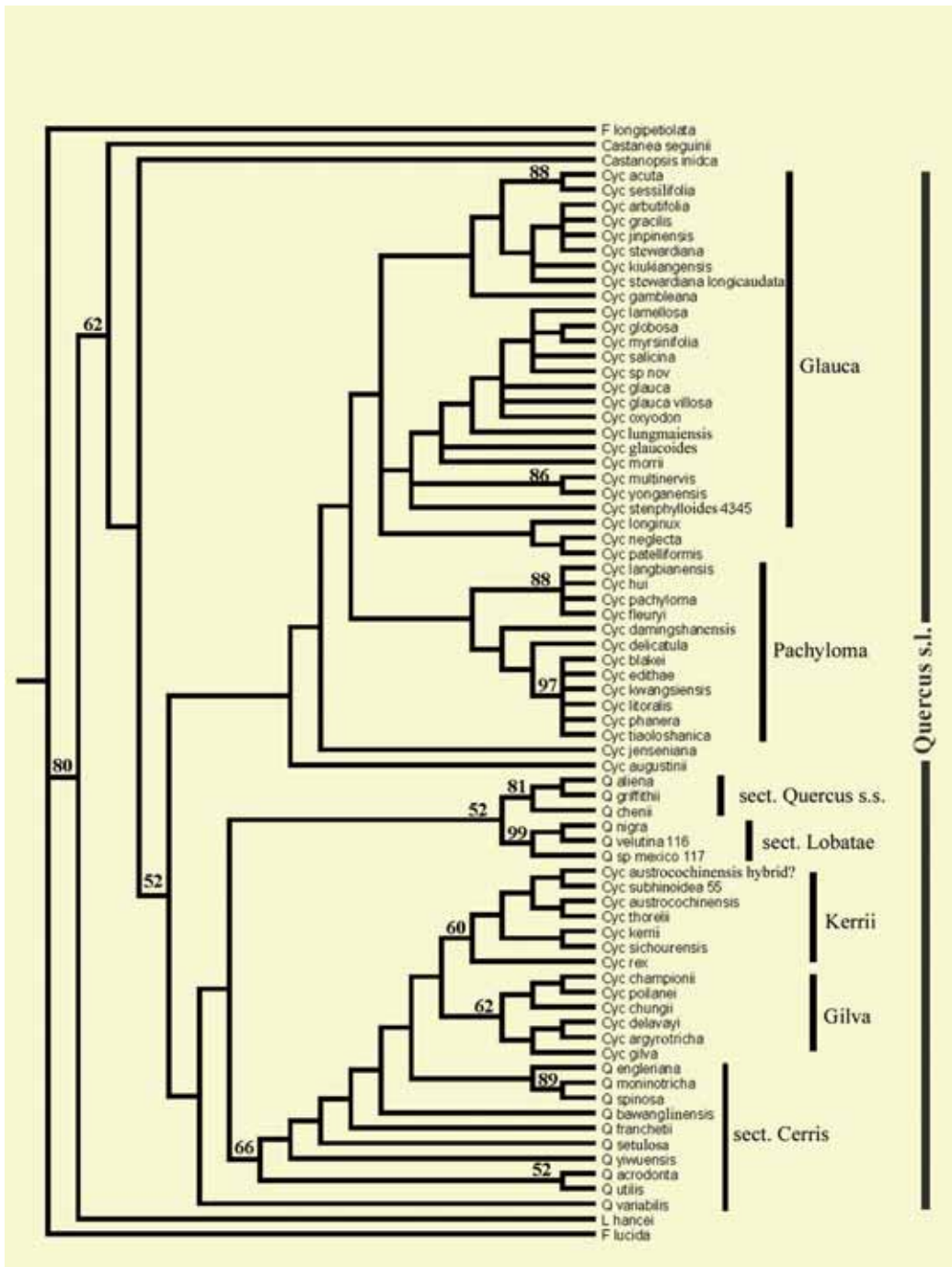


Figure 4/ Strict consensus tree of 600 MP cladograms from ITS (CI = 0.545; RI = 0.803). Bootstrap proportions using MP are indicated above branches (discussion, p. 55).



Taxonomy and Systematics of *Quercus* Subgenus *Cyclobalanopsis*

Min Deng¹, Zhekun Zhou^{2*}, Qiansheng Li³

2. Xishuangbanna Tropical Botanical Garden,
the Chinese Academy of Sciences,
Kunming, 650223, China.

3. School of Ecology,
Shanghai Institute of Technology,
100 Haiquan Rd.,
Shanghai, 201418, China

1. Chenshan Plant Sciences Research Center,
the Chinese Academy of Sciences,
Chenshan Botanical Garden,
3888 ChenHua Rd., Shanghai, 201602, China.
Phone: +86-21- 57 79 93 82;
Fax: + 86-21-67657811.
dengmin@sibs.ac.cn;

ABSTRACT

Quercus subgenus *Cyclobalanopsis* is one of the dominant woody plant groups in E and SE Asia, but comprehensive studies on its systematics and taxonomy are limited. In this study, we compared the leaf epidermal and acorn features of 52 species in subgenus *Cyclobalanopsis* and 15 species from *Quercus* subgenus *Quercus*. We also studied molecular phylogeny using DNA sequences from the nuclear ribosomal internal transcribed spacer (ITS) region and the chloroplast *psbA-trnH* and *trnT-trnL* regions. Both the leaf epidermal and acorn features indicated five morphologically distinct groups in *Cyclobalanopsis*: 1) *Gilva* group (fused stellate trichomes with compound trichome base); 2) *Kerrii* group (with fasciculate trichomes, and radicles emerging from the basal seed scar); 3) *Pachyloma* group (papillae on epidermal cells, but glabrous when mature and densely yellowish woolly on the cupule walls); 4) *Jenseniana* group (lamellae mostly fused to the cupule wall with only the rims free); 5) *Glauca* group (appressed-lateral-attached trichomes). Molecular phylogeny suggested 4 major clades in *Cyclobalanopsis* corresponding approximately to the morphological groups: *Kerrii* clade, *Gilva* clade, *Pachyloma* clade and *Glauca* clade; but the phylogenetic relationship of the 4 main clades is not resolved, nor is monophyly of *Cyclobalanopsis*. The stable morphological features that can be applied to delimit the species in *Cyclobalanopsis* are discussed.

Keywords: *Quercus* subgenus *Cyclobalanopsis*, oak phylogeny

Introduction

The genus *Quercus* s.l. is the biggest genus in *Fagaceae* with about 500 species worldwide (Frodin and Govaerts, 1998). The genus is widely distributed throughout the Northern Hemisphere (Nixon, 1993) and is one of the most economically important in temperate and subtropical areas (Camus, 1934-1954). The taxonomy and systematics of genus *Quercus*, especially for the species distributed in North and South America and Europe, have been well studied both at species level (Nixon, 1993; Nixon, 1997; Nixon, 1997; Manos et al., 1999; Manos and Stanford, 2001; Bellarosa et al., 2005; Oh and Manos, 2008; Denk and Grimm, 2010) and population level (Huang et al., 2002; Petit et al., 2002; Petit et al., 2002; Ainsworth et al., 2003; Lin et al., 2003; Shih et al., 2006; Neophytou et al., 2008). Based on cladistic analysis of morphological data, two subgenera are recognized: *Cyclobalanopsis* and *Quercus*. *Cyclobalanopsis* has also been recognized as an independent genus in some local floristic studies (Hsu and Sun, 1983; Hsu et al., 1985; Huang et al., 1999). Within subgenus *Quercus*, cladistic analysis of morphological data imply three sections: *Lobatae* (red oaks), *Protobalanus* (intermediate oaks), and *Quercus* (white oaks, including section *Cerris*) (Nixon, 1989; Nixon, 1993). This subdivision of *Quercus* s.l. was generally accepted in many taxonomical works (Nixon, 1997). However, molecular phylogenetic studies based on ITS have suggested that section *Cerris* forms a clade sister to all other oaks in subgenus *Quercus* (Manos et al., 1999; Manos and Stanford, 2001; Manos et al., 2001; Pearse and Hipp, 2009). Alternatively, phylogenetic reconstructions based on single-copy nuclear genes *CRABS* *CLAW* and ITS plus the nuclear ribosomal intergenic (IGS) spacer region suggested two major clades in *Quercus* s.l.: a New World clade that includes section *Protobalanus*, section *Lobatae* and section *Quercus* s.s.; and an Old World clade, comprising subgenus *Cyclobalanopsis* and section *Cerris* (Oh and Manos, 2008; Denk and Grimm, 2010). However, phylogenetic relationships within *Quercus* s.l. are still not well resolved since the bootstrap value of the node of the main sections and subgenus is generally missing or very low (54–66) (Oh and Manos, 2008; Denk and Grimm, 2010), and less is known about the tropical and subtropical oak lineages from E Asia and SE Asia.

Subgenus *Cyclobalanopsis* is restricted to subtropical and tropical regions in SE Asia, with 90–150 species (Luo and Zhou, 2000; Luo and Zhou, 2001; Deng, 2007). Based on cupule and vegetative features, subgenus *Cyclobalanopsis* was divided into 27 series (groups) (Camus 1934–1954). Later, Menitsky (1984) established 8 sections in subgenus *Cyclobalanopsis* based on features of the style and leaf architecture. However, neither taxonomic system for subgenus *Cyclobalanopsis* has been generally accepted, as they are based largely on variable characters rather than stable, discrete character states (Frodin and Govaerts, 1998). On the other hand, reproductive structures in *Fagaceae* exhibit high homoplasy (Manos et al., 2008; Oh and Manos, 2008) and thus offer few clues on the phylogeny of subgenus *Cyclobalanopsis*. Molecular data provide an independent test of morphological homologies to gain insight into the evolutionary history of this oak group. In the present study we investigated the phylogeny of subgenus *Cyclobalanopsis* and of other taxa in *Quercus* s.s. to: 1) explore the phylogeny of subgenus *Cyclobalanopsis* using two genomes (nuclear and plastid); and 2) evaluate the consistency between the molecular phylogenetic trees of cpDNA and ITS and the morphologically-based subdivisions of oak species in subgenus *Cyclobalanopsis*.

Materials and Methods

Materials

Leaf materials were collected from both wild populations and cultivated plants. 45 species from *Quercus* subgenus *Cyclobalanopsis* and 15 species from subgenus *Quercus* (with 9 from section *Cerris*, 3 from section *Quercus* s.s. and 3 from section *Lobatae*) were studied. One species each from *Lithocarpus*, *Castanopsis* and *Castanea* and two species from *Fagus* were included in phylogenetic construction. *Fagus* was used as an outgroup to root the tree on the basis of previous phylogenetic studies within *Fagaceae* (Manos et al., 1999, 2001, Oh and Manos, 2008).

Methods

1. Molecular phylogeny

DNA extraction and experiment setting. Leaf materials were dried in silica gel in the field. Genomic DNA was extracted following standard plant CTAB protocols (Doyle and Doyle, 1987) with slight modifications. Chloroplast *psbA-trnH* and *trnT-trnL* regions and the internal transcribed spacer (ITS) regions were selected as molecular markers. All PCR reactions were conducted using Takara rTaq DNA polymerase (Takara, China) in a Bio-Rad T100 thermal cycler (Bio-Rad, USA). The ITS region was amplified using primer sets ITS1 and ITS2 (Bellarosa et al., 2004) following Manos et al., (1999). ITS fragments for sequencing were obtained either directly from purified PCR products or by cloning. Purified PCR products of ITS regions that could not be sequenced directly were immediately cloned using the TA Cloning Kit (Takara, China). Plasmids were purified using a modified alkaline lysis method. Transformation efficiency was assessed by PCR using the ITS1 and ITS2 primers. Five positive clones for each sample were sequenced. Methods for sequencing *trnT-trnL* and *psbA-trnH* followed Huang et al., (2002) and Pei et al., (2011) respectively. Purified clones and PCR products were all sent to a professional laboratory (Sangon, Shanghai, China) for sequencing. Double-stranded sequences were assembled and edited using SEQUENCHER 4.01 (Gene Codes Corp., Ann Arbor, MI, U.S.A.).

2. Morphological features

Morphological data from leaf epidermal materials and acorn features were obtained from Deng (2007) and Luo and Zhou (2001). Taxonomically significant features were compared.

3. Data analysis

Data filtering. Several previous studies have reported the existence of nonfunctional, paralogous ITS sequences in *Fagaceae* (Coleman, 2003; Goertzen et al., 2003; Bellarosa et al., 2005; Ma and Zhou, 2006). Since our aim was to understand general differentiation patterns in *Quercus* s.l., all potentially pseudogeneous sequences were filtered prior to the analysis. Three criteria were applied to identify functional ITS copies: 1) minimal-length variation across the spacers and high levels of sequence conservation in the 5.8S gene; 2) modest amounts of sequence divergence with clades and among the entire sample, and 3) general “taxonomic sense” of preliminary results.

For multiple different ITS clones obtained from the same sample, we first ran the cladistic analysis. If those clones from the same sample were clustered in a clade with high bootstrap value then one clone would be chosen randomly to represent the ITS sequences of this sample. The clones from the same samples not clustered in a clade were excluded from phylogenetic tree construction.

Outgroups and rooting. *Fagus* species were chosen as outgroup taxa on the basis of previous phylogenetic studies within *Fagaceae* (Oh and Manos, 2008). *Castanea*, *Castanopsis* and *Lithocarpus* were included in the analysis (Manos et al., 2001; Oh and Manos, 2008)

Alignment and phylogenetic analysis. Optimal multiple alignment of ITS, *psbA-trnH* and *trnT-trnL* was obtained with CLUSTAL W in MEGA5 (Tamura et al., 2007), adjusted manually and checked by eye. Secondary structure models were helpful to resolve ambiguous alignments, as already reported in previous studies (Štorchová and Olson, 2007; Hao et al., 2010). To increase the homology of the matrix, we applied the phylogenetic information from the folding structure (the arms and loops) of ITS2 and *psbA-trnH* to improve the alignment. Ambiguous polystructures were excluded from further analysis.

Parsimony analyses were performed with PAUP*4.0b1 (Swofford, 2002). Heuristic searches were run with default options. All characters were weighted equally. The gaps were excluded for analysis. In regions where demonstrably different gaps showed partial overlap, the character was scored as missing in the appropriate cells of the supplemental binary matrix. Bootstrap (Felsenstein, 1985) resampling was performed (1000 replicates), using TBR branch-swapping on 100 random taxon-addition replicates per bootstrap replicate and MULTREES option in effect under parsimony criterion.

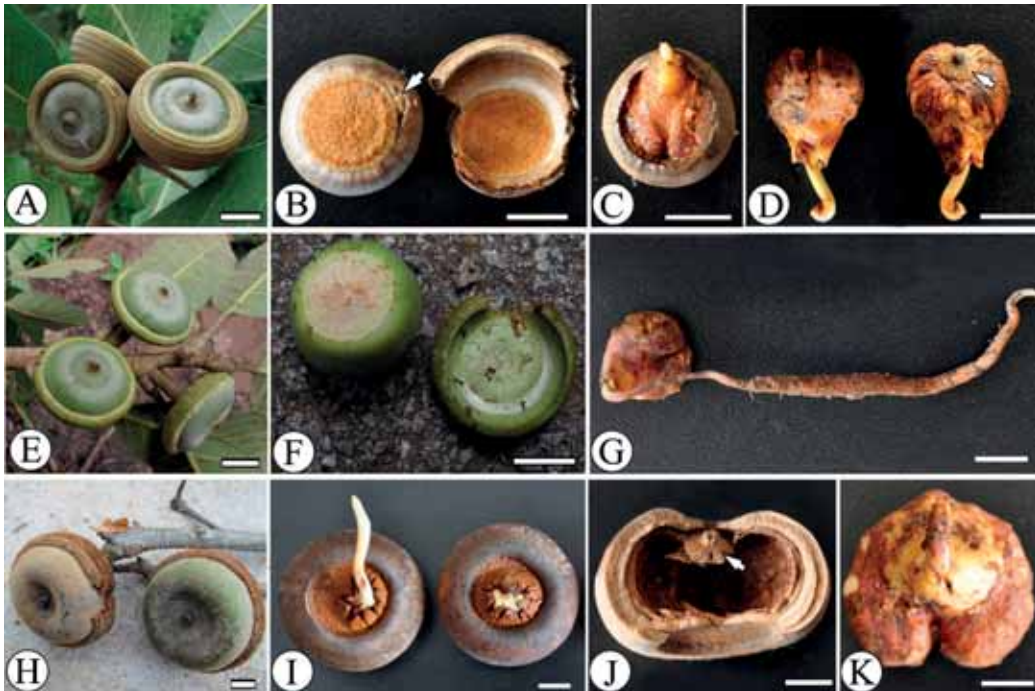


Figure 1/ Acorns of species in the Kerrii group.

(A-D) *Quercus austrocochinchinensis* bar=1 cm: (A) Fresh acorns; (B) Acorns and cupule; (C) Basal germination; (D) Elongated radicle / (E-G) *Quercus kerrii*, bar=1 cm: (E) Fresh acorns; (F) Acorn and cupule; (G) Germinated acorn showing the heart-shaped cotyledon and elongated radicle / (H-K) *Quercus rex*, bar=2 cm: (H) Fresh acorns; (I) Basal germination; (J) Transverse section of the acorn; the arrow shows the thick, fibrous, plug structure beneath the style base; (K) Germinated acorn showing the heart-shaped cotyledon.

Results

Morphological comparison

The acorn and cupule features offered limited information for grouping species in subgenus *Cyclobalanopsis*. In most species of the subgenus no discrete features from reproductive structures were found except for the heart shaped cotyledon, the radicle emerging from the basal seed-scar and the fibrous plug structure at the style base in species from tropical regions, e.g., *Q. austrocochinchinensis* Hick. & Camus (Figs. 1A-D), *Q. kerrii* Craib (Figs. 1E-G) and *Q. rex* Hemsl. (Figs. 1H-K).

A wide variation was found in leaf epidermal features. A total of ten trichome types were found in subgenus *Cyclobalanopsis*. Uniseriate solitary trichomes (Figs. 2A-B), fasciculate trichomes (Fig. 2C) generally present in *Quercus* subgenus *Quercus* and other genera of *Fagaceae*, indicating that it is a plesiomorphism. Fused stellate (Fig. 2D), multiradiate (Fig. 2E), stellate (Fig. 2F), and rosulate trichomes (Fig. 2G). Appressed-lateral-attached trichomes (ALA) (Figs. 2I-J) reported in *Quercus* subgenus *Quercus* were also found in subgenus *Cyclobalanopsis*. Jellyfish-like trichomes (Fig. 2H), and papillae on epidermal cells (Fig. 2L) were only detected in subgenus *Cyclobalanopsis* in the species used for comparison in this study. Simplified stellate trichomes (Fig. 2K) were only found in *Q. arbutifolia* Hick. & Camus. This trichome type is composed of

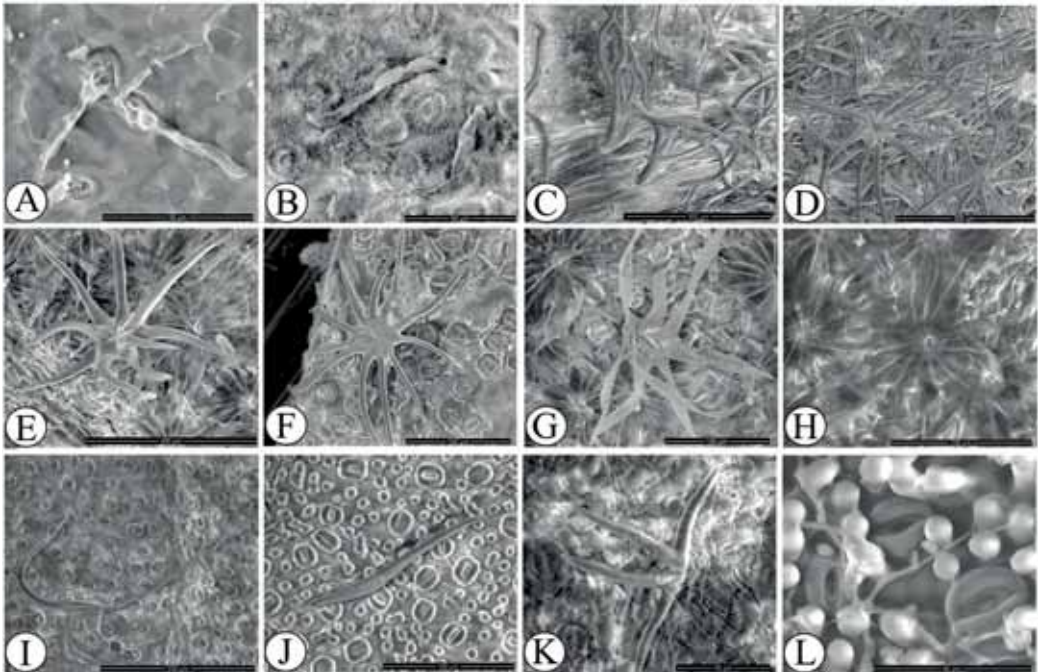


Figure 2/ Trichome types found in subgenus *Cyclobalanopsis*.

(A) Solitary trichome, *Quercus austrocochinchinensis*, bar=50 ηm ; (B) Solitary trichome, *Quercus glauca*, bar=50 ηm ; (C) Fasciculate trichome, *Quercus kerrii*, bar=300 ηm ; (D) Fused stellate trichome, *Quercus delavayi*, bar=200 ηm ; (E) Multiradiate trichome, *Quercus sichouensis*, bar=200 ηm ; (F) Stellate trichome, *Quercus patelliformis*, bar=100 ηm ; (G) Rosulate trichome, *Quercus sichouensis*, bar=100 ηm ; (H) Jellyfish-like trichome, *Quercus sichouensis*, bar=100 ηm ; (I) ALA trichome, *Quercus schottkyana*, bar=200 ηm ; (J) ALA trichome, *Quercus myrsinifolia* and papillae on epidermal cells, bar=100 ηm ; (K) Clustered ALA forming a stellate-like structure, *Quercus arbutifolia*, bar=50 ηm ; (L) Papillae, *Quercus langbianensis*, bar=40 ηm .

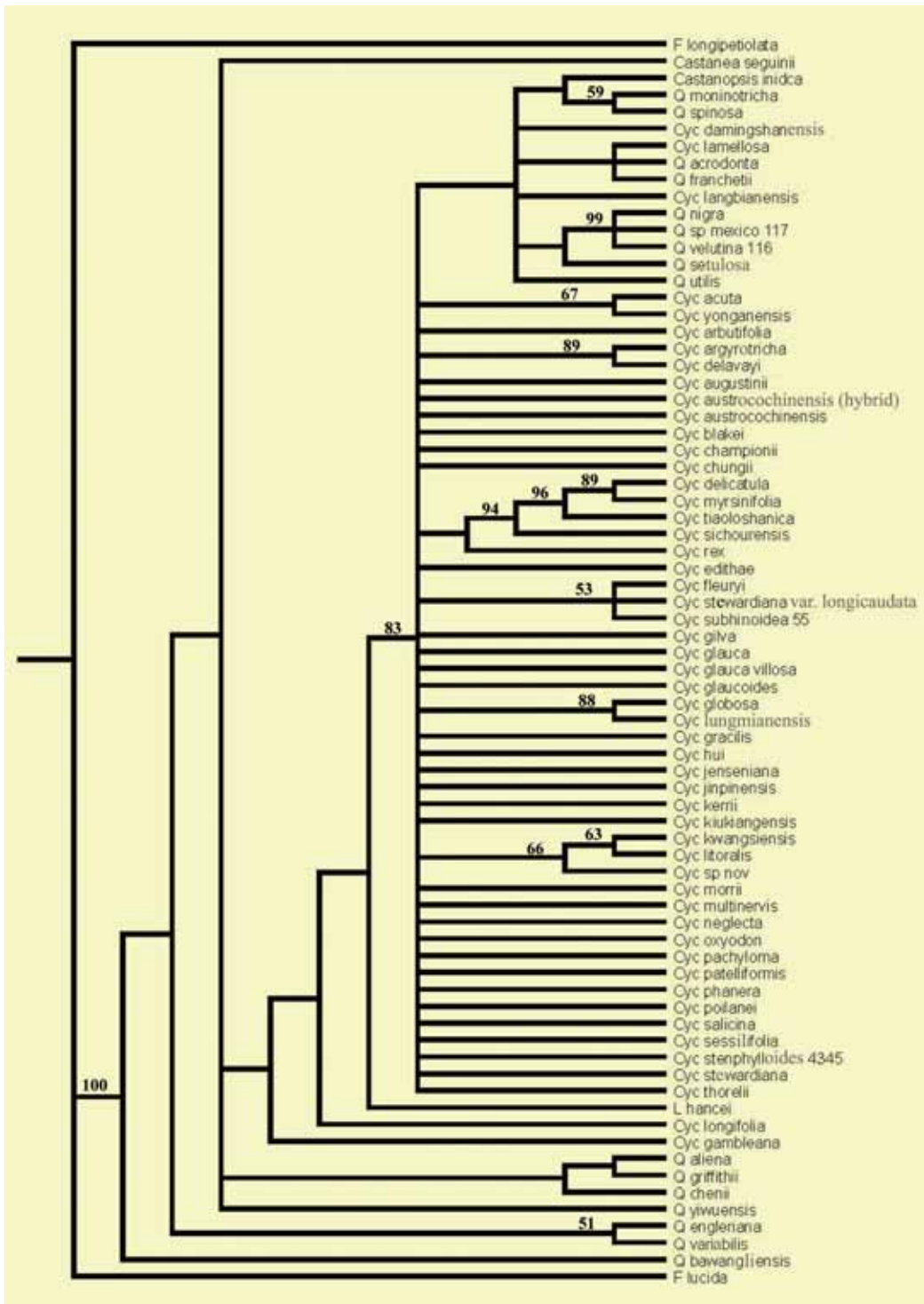


Figure 3/ Strict consensus tree of 2300 MP cladograms based on chloroplast psbA-trnH and trnT-trnL (CI = 0.729; RI = 0.446). Bootstrap proportions using MP are indicated above branches.

2-5 rays, however individual ray morphology was consistent with ALA that were also distributed in the species. Therefore, we still recognize this trichome type as a special form of ALA.

Based on epidermal and acorn features, five distinct groups in subgenus *Cyclobalanopsis* were detected:

- 1) Kerrii group: with fasciculate trichomes, radicle emerging from the basal seed scar, heart-shaped cotyledons with the placenta passing through to the style base, dense fiber plug at style base.
- 2) Gilva group: with stellate, fused stellate and multiradiate trichomes with compound trichome bases.
- 3) Pachyloma group: epidermal cells flat or with papillae; mature leaves glabrous except for scattered uniseriate trichomes, seed scar convex, acorn with 4-6 styles, cupule usually large with the wall densely covered by yellowish woolly or silky procumbent trichomes.
- 4) Jenseniana group: lamellae mostly fused to the cupule wall with only the rims free, no trichomes were detected on mature leaves, leaf epidermal cells with papillae.
- 5) Glauca group: with ALA trichomes or ALA clustered into a stellate-like structure with a simple trichome base.

Molecular phylogeny

In the matrix of final alignments, the length of the ITS, *psbA-trnH* and *trnT-trnL* regions for 52 taxa is 678 base pairs (bp), 563 bp and 889 bp long. The size of *psbA-trnH* ranged from 501 to 559, including a large number of poly-TA repeat regions in the middle. The phylogenetic information of the *psbA-trnH* folding structure was used to improve the alignment. However, it is still difficult to align the sequences of this region due to a few poly-A and poly-T structures and insertions/deletions. 116 ambiguous alignment sites were excluded from further analysis. The length of the *trnT-trnL* region of species from subgenus *Cyclobalanopsis* and section *Cerris* varies from 821 to 880 bp, with final alignment 889 bp long. 82 ambiguous sites were not counted in the analysis. Of the remaining 808 sites, 57 characters were parsimony-informative. 2300 MP trees were recovered in heuristic search. Strict consensus trees based on the combined dataset of *trnT-trnL* and *psbA-trnH* are shown in Fig. 3 with bootstrap annotated on the nodes. Retention index (RI) of the MP tree is equal to 0.803 and consistency index (CI) is 0.545. Combined analysis of *psbA-trnH* and *trnT-trnL* offered very little resolution within *Quercus* s.l., even at genus, section or subgenus level. Therefore, several major clades collapse in the strict consensus tree, the bootstrap only presented at the terminal and we even failed to discriminate *Lithocarpus* from *Quercus* using chloroplast DNA sequence.

ITS sequences were obtained either directly from purified PCR products or by cloning. Six samples from the subgenus *Cyclobalanopsis* each have a few distinct clones which distributed to different species clades supported by moderate bootstraps. These samples were excluded from phylogenetic analysis. The size of the ITS region ranges from 590 to 678 bp. The length variation between taxa is mainly derived from indels in intron areas. The poly-G- and poly-C-rich region has been detected in all ITS sequences from *Quercus* in this study and also previous molecular phylogenetic approaches (Manos et al., 1999, 2001), which could account for the difficulties in DNA sequencing and alignment. 108 ambiguous sites were excluded for analysis. Of the remaining (included) 572 sites, 332 are constant, 79 are variable but parsimony-uninformative, and 161 are parsimony-informative. Strict consensus trees from 600 MP trees are shown in Fig. 4 (p. 48) with bootstrap annotated above the nodes. MP tree scores were RI = 0.803

and CI = 0.545. Three major lineages in *Quercus* s.l. section *Cerris*, Gilva group and Kerrii group formed an independent clade with 66 bootstrap support; section *Quercus* and section *Lobatae* formed a clade with 55 bootstrap support, Glauca group and Pachyloma group clustered together but without bootstrap support ((section *Cerris* + Kerrii Group+Gilva Group (with bootstrap = 66) + (section *Quercus* + section *Lobatae*) (with bootstrap=52)]+(Glauca group+Pachyloma group). The four major clades formed by species from subgenus *Cyclobalanopsis* are weakly to moderately supported by ITS based on bootstrap resampling, and they correspond to the morphological groups: Glauca group, Pachyloma group, Kerrii group and Gilva group. Interestingly, the Kerrii and Gilva groups cluster with species from section *Cerris* with low bootstrap support, while the other species from *Cyclobalanopsis* form a clade but without strong bootstrap support (Fig. 4; p. 48). cpDNA data failed to reveal such a phylogenetic pattern.

Discussion of the systematics of subgenus Cyclobalanopsis and its affinities

The present study is a molecular phylogenetic study that includes representative oaks from subgenus *Cyclobalanopsis*. Previous phylogenetic studies using *ITS* and *CRABS CLAW* (Manos and Stanford, 2001; Oh and Manos, 2008; Denk and Grimm, 2010) revealed two major clades corresponding to geographic distribution: an Old World clade and a New World clade of *Quercus* s.l. However, in this study, the phylogeny based on ITS data revealed 3 major clades in *Quercus* s.l.: 1) an Old World clade comprising section *Cerris* and the Gilva and Kerrii groups of *Cyclobalanopsis*; 2) a New World clade comprising sections *Lobatae* and *Quercus* s.s.; and 3) a Cyclo oak clade, comprising the Pachyloma and Glauca groups, which falls sister to the Old World and New World clades. However, the bootstraps of the major clades are extremely low. Previous phylogeny studies of *Quercus* s.l. by Manos et al., (1999, 2001), Oh and Manos (2008) and Denk and Grimm (2010) as well as the present study could not provide high resolutions on the phylogeny of *Quercus* s.l. Although ITS strict consensus trees revealed some topology structures including the 4 major clades pattern in *Cyclobalanopsis*, these topologies need further assessment with other molecular markers, such as AFLP (Pearse and Hipp 2009) and DNA sequences (CRC gene, Oh & Manos, 2008) to provide a better solution for the phylogeny of these oaks. The phylogenetic relationships between these clades is still uncertain and section *Cerris* failed to cluster into a clade on a strict consensus tree. This indicates that ITS could not offer enough informative sites to resolve the phylogenetic relationships of *Quercus* s.l. Even the monophyletic status of subgenus *Cyclobalanopsis* and subgenus *Quercus* is questionable. Future in-depth studies need to include more species from subgenus *Cyclobalanopsis* for phylogenetic construction to obtain a better understanding of the evolutionary scenario in *Quercus* s.l.

The four main clades of *Cyclobalanopsis* were united by a series of synapomorphic morphological features, especially trichome types and epidermal cells which were useful to delimit the species in different groups: ALA trichomes in the Glauca group; uniseriate only with flat or papillose epidermal cells in the Pachyloma group; rosulate, jellyfish-like, fasciculate (including stipitate fasciculate) with compound trichome base in the Kerrii group and the dense stellate, fused stellate, multiradiate trichomes with a compound trichome base in the Gilva group can be applied as diagnostic features for each group. The heart-shaped cotyledon, basal germination and thick fiber plug structure at the style base were only found in the Kerrii group. The distribution of the Kerrii group is restricted

to tropical SE Asia. These unique features plus the narrow distribution of the Kerrii group indicates that it is a natural monophyletic clade, although this clade does not have very strong bootstrap support.

The trichome types can vary within a species depending on the growth stage and habitats. For example, dense hairs were present on young leaves of most species, but these hairs have a tendency to shed when the leaves mature in most species of *Cyclobalanopsis*. Generally, the trichomes on the mature leaves are far fewer or altogether lacking, but the more or less scattered trichome bases on both leaf surfaces are evidence of their existence. Luo and Zhou (2002) studied leaf architecture variation in subgenus *Cyclobalanopsis* and their results indicated that the marginal teeth type and secondary vein pattern also show stable and rich variation among the species. Although these features are mainly derived from convergent features, they are also very useful in identifying the species of *Cyclobalanopsis*. When comparing the leaf epidermal features of *Q. austrocochinchinensis*, *Q. kerrii* and their suspected hybrids, it can be seen that the anticlinal wall of the lower epidermal cells of the hybrids is a sinus, which is similar to that of *Q. austrocochinchinensis*. However, the leaf teeth are obtuse, which is close to those of *Q. kerrii* (our unpublished data). Therefore, the leaf epidermal features and leaf architecture features are informative to identify species from subgenus *Cyclobalanopsis* and even could assist with identifying hybridized individuals.

Remarkably, fasciculate, rosulate and multiradiate trichomes have also been reported in some species of section *Cerris* (Luo and Zhou, 2001; Tschan and Denk, 2012). Scanning electron microscope (SEM) of oak pollen also shows the tectum of the pollen grain in the Kerrii group (Deng 2007) and some species from section *Cerris* (“Ilex group”) (Denk and Grimm, 2009) with a plesiomorphic stage with rod-like ([micro] rugulate) to (micro) verrucate scattered elements. This morphological evidence indicates that the Kerrii group and some species from section *Cerris* may represent primitive stages in *Quercus* s.l.

Most interestingly in this study, ITS data recovered a clade with low bootstrap support (62%) formed by the closely related Kerrii group, Gilva group and section *Cerris*. Another clade comprising the remaining species from *Cyclobalanopsis* collapses in the strict consensus tree. Remarkably, both the Kerrii group and the Gilva group have the compound trichome base as in species from section *Cerris*. However, Kerrii group + Gilva group + section *Cerris* pattern were not detected in *psbA-trnH* and *trnT-trnL* combined analysis (Fig. 3). As in this study, previous work on phylogenetic and population genetics in *Quercus* s.l. revealed conserved nucleotide variations in chloroplast genomes (Huang et al., 2002; Lin et al., 2003), but great variations were found in nuclear rDNA (ITS, IGS, ETS) regions (Manos et al., 1999; Manos and Stanford 2001; Manos et al., 2008; Denk and Grimm, 2010) and nuclear low-copy sequences G3pdH (Shih et al., 2006) and 11S (original data downloaded from Pubmed and compared by ourselves). Furthermore, multiple different copies of rDNA sequence and G3pdH were found in many oak species. The different evolutionary pattern between the chloroplast and nuclear genomes indicated a scenario of recent species radiation events, followed by the dramatic genome re-assembling which may be caused by frequent hybridization of different genetic resources in *Quercus* s.l.

For many years, cupule ornamentation was regarded as an important characteristic to subdivide species in *Fagaceae* genera (Camus 1934-1954; Forman, 1966). However, this may be a trait derived from ecological adaptation rather than having a true phylogenetic basis (Kaul, 1985; Kaul, 1986; Kaul 1988). The new Kerrii group + section *Cerris* pattern

revealed by ITS data may offer us another view to examine the evolutionary pattern of cupule ornamentation in *Fagaceae*.

ITS is problematic for phylogenetic use because of multiple copies (Baldwin et al., 1995; Alvarez and Wendel, 2003; Coleman, 2003). Orthologous locus or DNA sequences are crucial to using gene trees to construct the phylogenetic relationship among the species. Based on the study of rDNA FISH patterns in *Fagaceae*, species from subgenus *Cyclobalanopsis* have different rDNA loci patterns (Chokchaichamnankit, et al., 2008; Alves et al., 2012). The 5S rDNA were conserved with only one pericentromeric locus in *Q. sessilifolia* Blume, *Q. glauca* Thunb. (Alves et al., 2012), *Q. brandisiana* Kurz and *Q. kerrii* (Chokchaichamnankit et al., 2008), but 18S-25S rDNA loci were variable both in chromosomal location and in the chromosomes bearing these genes, e.g., *Q. sessilifolia* (Glauc group), *Q. glauca* (Glauc group), *Q. brandisiana* (Kerrii group) and *Q. kerrii* (Kerrii group) with 5, 2, 2, 4 loci of 18s-25s rDNA gene, respectively (Chokchaichamnankit et al., 2008; Alves et al., 2012). Alves et al., (2012) suggested that unequal crossing over and transposition events contributed to diversified rDNA loci and multiple copies in oak species. As a result, it is difficult to distinguish orthologous from paralogous rDNA loci in oaks. Based on ITS and 5S-IGS data, Denk and Grimm (2010) concluded that subgenus *Cyclobalanopsis* shares a common ancestor with the *Cerris* and *Ilex* groups, and at the same time it is closer to other *Fagaceae* than to the rest of the species of *Quercus*. Oh and Manos (2008) constructed the phylogeny of *Quercus* based on the nuclear *CRABS CLAW* gene, but only limited samples of subgenus *Cyclobalanopsis* were analyzed. However, none of these studies offered a robust resolution in *Quercus* s.l. since bootstrap values of the nodes of section *Cerris* + and *Cyclobalanopsis* were also very low (54,70). No species from Kerrii group and Gilva group were ever sampled for analysis. In preliminary experiments, we tested 15 cpDNA universal primer sets (*psbA-trnH*, *trnT-trnL*, *atpB-trnH*, *trnC-trnG*, *ndhF*, *matK*, *rbcL*, *petG-trnH*, *atpF-atpH*, *trnS-trnM*, *rps16*, *ycf6-psbM*, *trnD-trnT*, *trnT-psbCr*, *rpoC1-trnCr*), but most of the nucleotide variations are too low to offer phylogenetic information. Therefore, more single (or low) copy genes from nuclear or DNA fingerprint-based molecular markers and more taxa should be added to future approaches and testing of *Quercus* s.l. phylogeny.

Numerous studies have reported hybridization between oak species, especially within *Quercus* subgenus *Quercus* (Hardin, 1975; Jensen et al., 1984; Bacilieri et al., 1996; Abrahamson et al., 1998; Graham, 2000; Marchelli and Gallo, 2001; Craft et al., 2002; Ishida et al., 2003; Schnitzler et al., 2004). In this study, we also detected distinct ITS sequences in predicted parental species; these ITS sequences are easily obtained from purified PCR products. In the predicted hybrids, two types of ITS clones were found, however, one of the parental haplotypes of *psbA-trnH* and *trnT-trnL* were found in the predicted hybrids, such as in *Q. kerrii*, *Q. austrocochinchinensis* and their suspected hybrid, *Q. glauca*, and in *Q. multinervis* (W.C. Cheng & T. Hong) Govaerts and suspected hybrids. Hybridization was proved to be occurring in those species. Considering the large number of plastic morphological features between the sympatric oak species from subgenus *Cyclobalanopsis* (Deng et al., 2007), the high conservation of karyotypes, the dramatic changes in the number of the 18s-25s rDNA loci and the locations on chromosomes (Ribeiro et al., 2011), and multiple ITS copies, hybridization-caused genome restructuring may be an important factor in the evolution of oak species from subgenus *Cyclobalanopsis*. Comprehensive further studies on introgression at population level can offer us better opportunities to understand the evolution of oak groups.

Acknowledgements

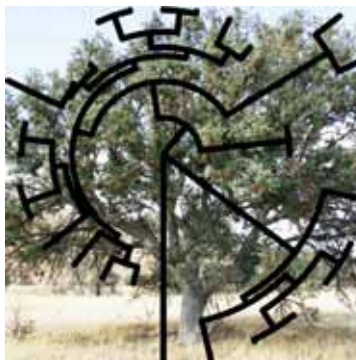
We thank the Sir Harold Hillier Gardens for providing the plant materials from Taiwan, Mr. Allen Coombes and Dr. Andrew Hipp for their kind help in revising the manuscript, Professor Paul Manos of Duke University and Dr. Yun Juan Zuo from CHS for substantial help on data analysis, Professor Hiroaki Setoguchi of Kyoto University for providing plant materials and help to sequence the *psbA-trnH* region. This work was supported by grants from the National Science Foundation of China (NSFC) (31270267 and 31100154), the Shanghai Municipal Administration of Forestation and City Appearances (F112419), the Shanghai Municipal Natural Science Foundation (11ZR1435500) and the Innovation Program of Shanghai Municipal Education Commission (12YZ157).

Photographers. Title page: Béatrice Chassé (*Quercus myrsinifolia* Blume). Photos in Figures 1-2: Min Deng.

Bibliography

- Abrahamson, W.G., G. Melika, R. Scrafford and G. Csoka. 1998. Gall-Inducing Insects Provide Insights into Plant Systematic Relationships. *American Journal of Botany* 85(8): 1159-1165.
- Ainsworth, E.A., P.J. Tranel, B.G. Drake and S.P. Long. 2003. The clonal structure of *Quercus geminata* revealed by conserved microsatellite loci. *Molecular Ecology* 12(2): 527-532.
- Alvarez, I. and J.F. Wendel. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29(3): 417-434.
- Alves, S., T. Ribeiro, V. Inácio, M. Rocheta and L. Morais-Cecilio. 2012. Genomic organization and dynamics of repetitive DNA sequences in representatives of three *Fagaceae* genera. *Genome* 55(5): 348-359.
- Bacilieri, R., A. Ducousso, R.J. Petit and A. Kremer. 1996. Mating System and Asymmetric Hybridization in a Mixed Stand of European Oaks. *Evolution* 50(2): 900-908.
- Baldwin, B.G., M.J. Sanderson, J.M. Porter, M.F. Wojciechowska, C.S. Campbell and M.J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247-277.
- Bellarosa, R., M.C. Simeone, A. Papini and B. Schirone. 2005. Utility of ITS sequence data for phylogenetic reconstruction of Italian *Quercus* spp. *Molecular Phylogenetics and Evolution* 34(2): 355-370.
- Camus, A. *Les Chênes. Monographie du genre Quercus and monographie du genre Lithocarpus*. Paris: Lechevalier, 1934-1954.
- Chokchachamankit, P., and K. Ananthawat-Jónsson. 2008. Chromosomal mapping of 18S-25S and 5S ribosomal genes on 15 species of *Fagaceae* from Northern Thailand. *Silvae Genetica* 57(1): 5-13.
- Coleman, A.W. 2003. ITS2 is a double-edged tool for eukaryote evolutionary comparisons. *Trends in Genetics* 19(7): 370-375.
- Craft, K.J., M.V. Ashley and W.D. Koenig. 2002. Limited hybridization between *Quercus lobata* and *Quercus douglasii* (*Fagaceae*) in a mixed stand in central coastal California. *American Journal of Botany* 89(11): 1792-1798.
- Deng, M. 2007. Anatomy, Taxonomy, Distribution & Phylogeny of *Quercus* subg. *Cyclobalanopsis*. Oersted. *Fagaceae*. Kunming Institute of Botany, Chinese Academy of Sciences. Beijing, Graduate School of Chinese Academy of Sciences. Ph.D. thesis
- Denk, T. and G.W. Grimm. 2009. Significance of pollen characteristics for infrageneric classification and phylogeny In *Quercus* (*Fagaceae*) *International Journal of Plant Sciences* 170(7): 926-940.
- Denk, T. and G.W. Grimm. 2010. The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers. *Taxon* 59(2): 351-366.
- Doyle, J.J. and J.L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemistry Bulletin* 19: 11-15.
- Felsenstein, J. 1985. Confidence Limits on Phylogenies: An Approach Using the Bootstrap. *Evolution* 39(4): 783-791.
- Forman, L.L. 1966. On the evolutionary of the cupules in the *Fagaceae*. *Kew Bulletin* 18: 385-419.
- Frodin, D.G. and R. Govaerts. *World Checklist and Bibliography of Fagales*. Betulaceae, Corylaceae, Fagaceae and Ticodendraceae. London: Kew Publishing, 1998.
- Goertzen, L.R., J.J. Cannone, R.R. Gutell and R.K. Jansen. 2003. ITS secondary structure derived from comparative analysis: implications for sequence alignment and phylogeny of the *Asteraceae*. *Molecular Phylogenetics and Evolution* 29(2): 216-234.
- Graham, M. 2000. rDNA and microsatellite evolution in two hybridizing oaks: *Quercus petraea*. Matt.) Liebl. and *Quercus robur* L. Belfast, Queen's University of Belfast. Thesis.
- Hao, D.C., S.L. Chen and P.G. Xiao. 2010. Sequence characteristics and divergent evolution of the chloroplast *psbA-trnH* noncoding region in gymnosperms. *Journal of Applied Genetics* 51(3): 259-273.
- Hardin, J.W. 1975. Hybridization and introgression in *Quercus alba*. *Journal of the Arnold Arboretum* 56: 336-363.
- Hsu, Y.C. and C.C. Hang. 1985. *Fagaceae*. *Sylva Sinica*. W.J. Cheng. Beijing, China Forestry Press. 2: 2311-2313.
- Hsu, Y.C. and B.S. Sun. 1983. Several new species of *Fagaceae* from Yunnan. *Acta Botanica Yunnanica* 5(4): 333-342.
- Huang, C.C., Y.T. Chang, et al., 1999. *Fagaceae*. *Flora of China*. C.Y. Wu and P.H. Raven. Beijing: Science Press and St. Louis: Missouri Botanical Garden Press. 4: 380-400.
- Huang, S.S.F., S.-Y. Hwang and T.-P. Lin. 2002. Spatial pattern of chloroplast DNA variation of *Cyclobalanopsis glauca* in Taiwan and East Asia. *Molecular Ecology* 11(11): 2349-2358.
- Ishida, T.A., K. Hattori, S. Hiroaki and M.T. Kimura. 2003. Differentiation and hybridization between *Quercus crispula* and *Q. dentata*

- (*Fagaceae*): insights from morphological traits, amplified fragment length polymorphism markers, and leaf miner composition. *American Journal of Botany* 90(5): 769–776.
- Jensen, R.J., R. DePiero and B.K. Smith. 1984. Vegetative Characters, Population Variation and the Hybrid Origin of *Quercus ellipsoidalis*. *American Midland Naturalist* 111(2): 364.
- Kaul, R.B. 1985. Reproductive Morphology of *Quercus*. *Fagaceae*. *American Journal of Botany* 72(12): 1962–1977.
- Kaul, R.B. 1986. Evolution and Reproductive Biology of Inflorescences in *Lithocarpus*, *Castanopsis*, *Castanea*, and *Quercus*. *Fagaceae*. *Annals of the Missouri Botanical Garden* 73(2): 284–296.
- Kaul, R.B. 1988. Cupular Structure in Paleotropical *Castanopsis* (*Fagaceae*). *Annals of the Missouri Botanical Garden* 75(4): 1480–1498.
- Lin, T.-P., W.-J. Chuang, S.S.F. Huang and S.-Y. Hwang. 2003. Evidence for the existence of some dissociation in an otherwise strong linkage disequilibrium between mitochondrial and chloroplastic genomes in *Cyclobalanopsis glauca*. *Molecular Ecology* 12(10): 266–2668.
- Luo, Y. and Z.-K. Zhou. 2000. Phytogeography of *Quercus* subgen. *Cyclobalanopsis*. *Acta Botanica Yunnanica* 23(1): 1–16.
- Luo, Y. and Z.-K. Zhou. 2001. Leaf epidermis of *Quercus* subgen. *Cyclobalanopsis*. (Oerst.) Schneid.. *Fagaceae*. *Acta Phytotaxonomica Sinica* 39(6): 489–501.
- Luo, Y. and Z.-K. Zhou. 2002. Leaf architecture in *Quercus* subgenus *Cyclobalanopsis* (*Fagaceae*) from China. *Botanical Journal of the Linnean Society* 140(3): 283–295.
- Ma, C.L. and Z.-K. Zhou. 2006. Effect of ITS Pseudogene on the Phylogenetic Study of *Quercus* (*Fagaceae*) and Its Revelation on the Plant Molecular Phylogenetics. *Acta Botanica Yunnanica* 28(2): 127–132.
- Manos, P.S., C.H. Cannon and S.-H. Oh. 2008. Phylogenetic relationships and taxonomic status of the paleoendemic *Fagaceae* of western North America: Recognition of a new genus, *Notholithocarpus*. *Madroño* 55(3): 18–190.
- Manos, P.S., J.J. Doyle and K.C. Nixon. 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus*. (*Fagaceae*). *Molecular Phylogenetics and Evolution* 12(3): 333–349.
- Manos, P.S. and A.M. Stanford. 2001. The historical biogeography of *Fagaceae*: Tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. *International Journal of Plant Science* 162: S77–S93.
- Manos, P.S., Z.-K. Zhou and C.H. Cannon. 2001. Systematics of *Fagaceae*: Phylogenetic Tests of Reproductive Tests of Reproductive Trait Evolution. *International Journal of Plant Science* 162(6): 136–1379.
- Marchelli, P. and L.A. Gallo. 2001. Genetic diversity and differentiation in a southern beech subjected to introgressive hybridization. *Heredity* 87(3): 284–293.
- Menitsky, L.L. 1984. Oaks of Asia. St. Petersburg, Leningosed Sciences.
- Neophytou, C., A. Dounavi and F.A. Aravanopoulos. 2008. Conservation of Nuclear SSR Loci Reveals High Affinity of *Quercus infectoria* ssp. *veneris* A. Kern. (*Fagaceae*) to Section *Robur*. *Plant Molecular Biology Reporter* 26(2): 133–141.
- Nixon, K.C. 1989. *Origins of Fagaceae. Evolution, systematics, and fossil history of the Hamamelidae*, Volume 2: 'Higher' Hamamelidae. P. R. Crane and S. Blackmore. Oxford, Clarendon Press Oxford. 40: 23–43.
- Nixon, K.C. 1993. Infrageneric classification of *Quercus* (*Fagaceae*) and typication of sectional names. *Annales des sciences forestières* 50(Suppl. 1): 25–34.
- Nixon, K.C. 1997. *Fagaceae*. In Flora of North America Editorial Committee, Flora of North America north of Mexico. New York, Oxford University Press.
- Nixon, K.C. 1997. *Quercus*. In Flora of North America, North of Mexico. Flora of North America Editorial Committee. eds. New York, Oxford Univ Press. 3: 436–437.
- Oh, S.H. and P.S. Manos. 2008. Molecular phylogenetics and cupule evolution in *Fagaceae* as inferred from nuclear CRABS CLAW sequences. *Taxon* 57(2): 434–451.
- Pearse, I.S., and A.L. Hipp. 2009. Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. *Proc Natl Acad Sci USA* 6: 18097–18102.
- Pei, N., J.-Y. Lian, D.L. Erickson, N.G. Swenson, W.J. Kress, W.-H. Ye and X.-J. Ge. 2011. Exploring Tree-Habitat Associations in a Chinese Subtropical Forest Plot Using a Molecular Phylogeny Generated from DNA Barcode Loci. *PLoS ONE* 6(6): e21273.
- Petit, R.J., S. Brewer, S. Bordács, K. Burg, R. Cheddadi, E. Coart, J. Cottrell, U.M. Csaikl, B. van Dam, J.D. Deans, S. Espinel, S. Fineschi, R. Finkeldey, I. Glaz, P.G. Goicoechea, J.S. Jensen, A.O. König, A.J. Lowe, S.F. Madsen, G. Mátyás, R.C. Munro, F. Popescu, D. Slade, H. Taberner, S.G.M. de Vries, B. Ziegenhagen, J.-L. de Beaulieu and A. Kremer. 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology and Management* 156(1-3): 49.
- Petit, R.J., U.M. Csaikl, S. Bordács, K. Burg, E. Coart, J. Cottrell, B. van Dam, J.D. Deans, S. Dumoulin-Lapègue, S. Fineschi, R. Finkeldey, A. Gillies, I. Glaz, P.G. Goicoechea, J.S. Jensen, A.O. König, A.J. Lowe, S.F. Madsen, G. Mátyás, R.C. Munro, M. Olalde, M.-H. Pemonge, F. Popescu, D. Slade, H. Taberner, D. Turchini, S.G.M. de Vries, B. Ziegenhagen and A. Kremer. 2002. Chloroplast DNA variation in European white oaks: Phylogeography and patterns of diversity based on data from over 2600 populations. *Forest Ecology and Management* 156(1-3): 5.
- Ribeiro, T., J. Loureiro, C. Santos, L. Morais-Cecilio. 2011. Evolution of rDNA FISH patterns in the *Fagaceae*. *Tree Genetics & Genomes* 7(6): 1113–1122.
- Schnitzler, J. P., R. Steinbrecher, I. Zimmer, D. Steigner and M. Fladung. 2004. Hybridization of European oaks. *Quercus ilex*, *Q. robur*) results in a mixed isoprenoid emitter type. *Plant Cell Environ* 27(5): 585–593.
- Shih, F. L., Y.-P. Cheng, S.-Y. Hwang and T.-P. Lin. 2006. Partial concordance between nuclear and organelle DNA in revealing the genetic divergence among *Quercus glauca*. (*Fagaceae*) populations in Taiwan. *International Journal of Plant Science* 167(4): 863–872.
- Štorchová, H. and M.S. Olson. 2007. The architecture of the chloroplast *psb A-trn H* non-coding region in angiosperms. *Plant Systematics and Evolution* 268(1): 235–256.
- Swofford, D.L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony. *and Other Methods. Version 4.0b10*. Massachusetts: Sinauer Associates, Sunderland.
- Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* 28: 2731–2739.
- Tschan, G.F. and T. Denk. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, *Quercus* subsection *Galliferae* (*Fagaceae*): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* 169(4): 611–644.



Using Phylogenomics to Infer the Evolutionary History of Oaks

Andrew L. Hipp^{1,2}, Deren A. Eaton^{2,3}, Jeannine Cavender-Bares⁴,
Rick Nipper⁵, Paul S. Manos⁶

1. The Morton Arboretum
4100 Illinois Route 53
Lisle, IL 60532-1293, USA
Phone: +1 630 725-2094
ahipp@mortonarb.org

2. The Field Museum
Department of Botany
1400 S. Lake Shore Drive
Chicago, IL 60605-2496, USA

3. University of Chicago
Committee on Evolutionary Biology
1025 E. 57th Street
Chicago, IL 60637, USA

4. University of Minnesota
College of Biological Sciences
123 Snyder Hall
1475 Gortner Ave
Saint Paul, MN 55108, USA

5. Floragenex, Inc.
44 West Broadway
Eugene, Oregon, 97401, USA

6. Duke University
Department of Biology
Box 90338
Durham, NC 27708, USA

ABSTRACT

One of the most basic questions about oaks has long vexed botanists, systematists, and oak enthusiasts of all stripes: **what is the shape and timing of the oak tree of life?** In this paper, we present new data from a genomic study of 19 oak individuals representing a broad swath of the oaks of the Americas. The paper explains how we are using next-generation sequencing methods to analyze millions of base pairs of DNA data for all individuals studied, and what we have learned to date from this work about the oak tree of life.

Keywords: phylogenetics, *Quercus*, restriction-site associated DNA (RAD) tags, systematics

Introduction

What do we need phylogenies for? Why is it important to understand the relationships among living creatures? From a classification standpoint, we study phylogeny to make meaningful classifications and to identify species boundaries. As Charles Darwin noted, our taxonomic system is hierarchical not just because humans think hierarchically, but because our taxonomic hierarchies reflect the branching structure of the tree of life. Characteristics of the groups that we have named evolve along the tree of life, and the branching structure of that tree of life forms nested groups of organisms. Many of these hierarchical levels have formally named ranks (e.g., domains, kingdoms, phyla, classes, orders, families, and genera). There are nonhierarchical components to the tree of life: we know, for example, that Eukaryotes enclose mitochondria that are descendants of proteobacteria, and plants enclose plastids whose ancestors are cyanobacteria. But a large component of the history of life has a hierarchical structure that we convey as the tree of life.

Beyond making meaningful classifications, why else should we study phylogeny? The relationships among populations within species provide us with information about what species there are in the world, a question of paramount importance to ecologists, restorationists, horticulturalists, naturalists, lawmakers and judges, and anyone else interested or at least concerned with cataloguing biodiversity. Phylogenies are also important for predicting ecological interactions and making management decisions. Just as the botanists in Darwin's day were using the ratio of species to genera to characterize endemism and biodiversity, today's botanists use phylogenetic diversity to prioritize areas for conservation^[1-3] and to track the biogeographic history and genetic connections among sensitive geographic areas or endemic taxa^[4-6] Phylogenies are used to study the formation and ongoing evolution of biotic communities.^[7-12] and to study species interactions integrated over time periods that are difficult to study experimentally. Phylogenies are used to study colonization history by invasive exotic species,^[13, 14] providing important perspectives on the biological determinants of invasiveness. Phylogenies aren't just for systematists.

Yet for organisms in which ecological and morphological differences persist even in the face of interspecific gene flow,^[15] phylogeny estimation can be problematic.^[16-18] This is a pronounced problem in many forest trees, in which interfertility, high rates of outcrossing, large effective population sizes, and long generation times^[19-21] make estimating phylogeny and patterns of trait evolution challenging. Oaks (*Quercus* L. : *Fagaceae* Dumort.) are notable for the difficulties they pose to systematists. Renowned as a "worst case scenario for the biological species concept"^[22] due to apparent local interspecific gene flow,^[15, 23-32] widespread oak species nonetheless exhibit genetic coherence across broad geographic ranges.^[33-35] We know relatively little about the phylogeny of this important genus. Traditional molecular approaches relying on chloroplast DNA^[30, 36] or a small number of nuclear genes^[37-39] often provide reliable information about broad-scale phylogenetic patterns ("what are the subgenera of oaks?"), but they typically fail to give answers for fine-scale phylogenetics ("what is the closest relative of *Quercus alba* L.?).

In this paper, we present preliminary results on the phylogeny of oaks using a new method of phylogenetic reconstruction, sequenced restriction associated DNA (RAD-Seq)^[40]. This method provides a much-needed tool for surveying the genome of organisms like oaks, in which we need to sample broadly across the genome without having a

sequenced reference genome as a roadmap. It also provides us with sequence data that we can use to relate our phylogeny to ongoing genomic work in oaks, potentially, in the near future, allowing us to figure out what genes move among oak species and lineages.^[41, 42] This level of detailed genomic inquiry was previously unavailable to us. Our study opens new doors to understanding how oaks have diversified and what constitutes an oak species or lineage. This paper focuses on explaining the methods we are using and their interpretation. Technical details of analysis will be left for a paper currently being submitted to a separate journal for publication.

Methods

Sampling

The target of this study is a clade of predominantly American oaks, comprising *Quercus* sections *Quercus*, *Lobatae* Loudon, and *Protobalanus* (Trelease) A. Camus^[37]. These sections are the white oaks, red or black oaks, and intermediate or golden oaks respectively. We selected 19 species from this clade and one member of section *Cerris* Dumort. to serve as an outgroup, the species we used to identify the root of the New World oak clade. The root is the oldest point on the phylogenetic tree, the putative ancestor of all species on the tree, and is typically identified using a more distantly related species, or outgroup. Samples were all drawn from previously collected material, many obtained from the seed exchange and field trip of the 2006 IOS Conference in Dallas, and reared in the greenhouse at the University of Minnesota.

DNA extraction

DNA was extracted from fresh material using the standard DNeasy plant extraction protocol (DNeasy, Qiagen, Valencia, CA), with modifications that we have used for previous studies in oaks.^[34, 43] In this method, fresh or frozen leaf tissue is ground thoroughly by hand in liquid nitrogen to a fine powder, using a mortar and pestle. The resulting leaf tissue powder is then incubated at 65°C in a solution of sodium dodecyl sulfate, a component of many detergents. The detergent digests cell walls and membranes without damaging the DNA inside the cells. RNase was included in this step to digest RNA, as our sequences of interest are all in the genomic DNA. Unwanted cell structures (proteins) and secondary compounds are all precipitated out of solution at near-freezing temperatures for 10 minutes, then centrifuged to separate these from the buffer that contains the DNA. This buffer is then sucked out using a pipette and applied to a filter that is centrifuged at high speed to separate the DNA (which passes through the filter) from cell debris. The cell debris remains on the filter, which is thrown away, and the DNA is precipitated in a salt and ethanol solution. The DNA precipitate is washed several times on a second filter before being suspended in a standard DNA buffer. This DNA extraction can then be frozen and used for years or decades of molecular study.

RAD sequencing

Restriction associated DNA sequencing (RAD-Seq) was conducted at Florigenex following the methods of Baird, Etter^[40]. RAD sequencing allows us to sample DNA sequence data from across the entire genome of an organism at fairly low cost, by subsampling just those regions of the genome that lie adjacent to a restriction cut site. Restriction cut sites are defined sequences, typically 4 to 8 base pairs long—i.e., 4–8 nucleotides in length, measuring just one strand of the double-stranded DNA molecule—

that a suite of bacterial/archaeobacterial restriction enzymes will cut. More than 3,000 restriction enzymes are known^[44], each of which cuts at a particular sequence, the restriction site. These enzymes act as a defensive mechanism for the bacteria against viruses, but they also serve well in the laboratory.

1. Restriction digestion

The first step in RAD sequencing is cutting the DNA using a restriction enzyme. In our oak work, we use *Pst*I, a restriction enzyme derived from the bacterium *Providencia stuartii* Ewing that cuts only at the 6-base-pair sequence



Like many other restriction enzymes, *Pst*I leaves a ragged end when it cuts, meaning that the cuts in each strand of the double-stranded DNA molecule (cuts indicated above by the ‘|’ symbol) do not exactly line up with each other. This is essential to the next step of the process, adapter ligation, for the ragged end serves as a sort of “sticky end” to which the adapter will fit like a puzzle piece. Assuming a GC content of 40%, a genome size of 500 million bases (both of which are typical of oaks), and a completely random draw of the four nucleotides that make up DNA (Adenine, Cytosine, Guanine, and Thymine), we expect about 72,000 *Pst*I cut sites in the oak genome.

2. Adapter ligation and shearing

The ragged ends left by *Pst*I serve as a platform to which we ligate a manufactured double-stranded DNA called an adapter. This first adapter (‘P1’) includes a nucleotide sequence needed for DNA amplification, a sequence required for DNA sequencing on the Illumina sequencer (see 3, Illumina sequencing, below) and a “barcode,” a unique combination of 5 nucleotides that identify the individual sequenced. Sequences are then randomly sheared to get fragments of varying lengths. After shearing, a second adapter (‘P2’) is ligated to the fragments, with a PCR amplification site embedded in it. We now have a pool of DNA fragments with a ‘P1’ site at one end and a ‘P2’ site at the other. Because the shearing process leaves some fragments without a restriction site, we also have a pool of fragments with a P2 at each end, which we don’t want to sequence. The P2 adapters are therefore built in such a way that only fragments with a restriction site at one end (and thus a P1 at one end and P2 at the other) will be duplicated in a subsequent round of DNA amplification. In this final stage of DNA preparation for sequencing, fragments with a restriction site are enriched by a factor of roughly 130,000. Thus, while a few sequences may show up that are not associated with a DNA restriction site, they should be very few indeed. At this point, our DNA is referred as a RAD library.

3. Illumina sequencing

There are several methods of massively parallel or “next-generation” sequencing. The method we are using generates, as of spring 2012, sequence reads of approximately 85 nucleotides in length on an Illumina/Solexa Genome Analyzer Iix. The data we present in this paper also includes sequencing runs from spring 2010 that returned 60 nucleotides of data per sequence from 19 individuals, of which we replicated seven individuals in 2012. In brief (see more complete introduction to next-generation sequencing technologies in^[45]) the RAD library is applied to a glass plate called a flow cell, in which individual DNA strands from the RAD library bind to separate sequencing sites on the plate. Each

DNA strand is then duplicated (amplified) on the flow cell surface to form a colony of thousands of identical DNA strands. In the final step, each DNA strand in each of these colonies is amplified in a stepwise process, during which a mix of fluorescently labeled is washed over the place, the next nucleotide in the sequence is added, a photo is snapped, then the plate is readied for addition of the next nucleotide. Because each nucleotide is labeled with a different color, the sequence of colors photographed for each colony spells out the DNA sequence for that colony. These sequences are stored by a computer hooked up to the sequencer, error-checked, and returned to us as a batch of sequences.

4. Preliminary data analysis

Processed data were returned from sequencing in the Illumina 1.3+ variant of the FASTQ format,^[46] with Phred quality scores for all bases.^[47] Quality, read lengths, and base composition of FASTQ data were assessed in R v. 2.15.2^[48] using the ShortRead package.^[49]

Creating a DNA data matrix

Data were analyzed following a custom pipeline that approximately follows the method of Catchen, Amores^[50]. In this method, sequences are clustered first by individual, and highly similar sequences are clustered into “stacks,” from which heterozygote base pair positions (i.e., positions of the genome in which the mother oak and father oak contributed different bases) are distinguished from sequencing errors. Each stack is referred to here as a locus, a term commonly used to reference a region of the genome not assumed to be a gene. For each individual, each sequence stack is summarized into a consensus sequence, and these consensus sequences are then clustered among individuals to generate a data matrix for each locus. Not every individual has a sequence in every locus. Nonetheless, loci are concatenated to make a data matrix with missing data (a hole-ly data matrix).

Several parameters must be specified in creating this data matrix, including the quality of sequencing reads, percent similarity required to cluster sequences, the depth of sequence stacks needed to make a locus, the minimum number of individuals per locus, and various properties of data variability. A range of parameter values was investigated for this study, and the basic topology recovered varied only in (1) the amount of statistical support of the placements recovered, and (2) the precise placement of *Quercus robur* L. Details of these analyses will be investigated in a future study. The analysis pipeline we utilize is coded in Python and utilizes UCLUST^[51] and MUSCLE^[52, 53] for clustering and multiple alignment respectively. Details of the pipeline and methods of assessing rates of error and heterozygosity are being published elsewhere (by DE). For this paper, we present analysis of clustering results in which a minimum of four individuals were required for each locus, and report on phylogenetic analyses conducted both with and without *Q. robur* L.

Phylogenetic analysis

To assess phylogenetic relationships, we used maximum likelihood as implemented in RAxML v7.2.6,^[54] which is optimized for large phylogenomic datasets. The maximum likelihood method as applied to phylogenetic inference is described in a thorough treatment by Felsenstein^[55]. In short, every phylogenetic tree is a hypothesis that confers a probability on our data matrix. In general, a dataset in which species A and B share lots of mutations that no other species share will tend to be most probable if species A and B are truly sister to each other. The maximum likelihood method in phylogenetics searches the space of phylogenetic hypotheses for trees that maximize the probability of the observed data under a quantitative model of nucleotide evolution. This is the standard

method of phylogenetic inference for DNA sequence data. Analyses were conducted using the ‘GTRGAMMA’ general time reversible model of nucleotide evolution. Under this model, all possible transitions among nucleotides (A, G, C, T) are allowed to differ in rate, but those rates are assumed to be symmetrical (e.g., the probability of an A to C mutation is assumed to be the same as the probability of a C to A mutation). These rates of mutation are not assumed to be constant along the entire length of the sequences we analyze, but to vary among site to site according to a gamma (Γ) distribution. Branch support was assessed using 200 nonparametric bootstrap replicates, which are simply reanalyses of the dataset, resampling nucleotides at random.

Results

RAD sequences

For the year 2010 (initial) run, individuals yielded 177,168 to 725,871 sequences (mean = 558,006, sd = 136,157) of 60 base pairs each (Figure 1, in red). For the 2012 (replicate) run, each individual yielded between 743,556 and 4,539,385 sequences (mean = 3,056,861, sd = 1,369,094) of 95 base pairs each (Figure 1, in black). This is a 5.5-fold increase in number of sequences yielded between 2010 and 2012. After removing the 5 base pairs left over from the *Pst*I cut and the 5-base-pair barcode from each sequence, and ignoring decreases in quality toward the ends of the reads, this is a 9.3-fold increase in total sequence data per individual between 2010 and 2012.

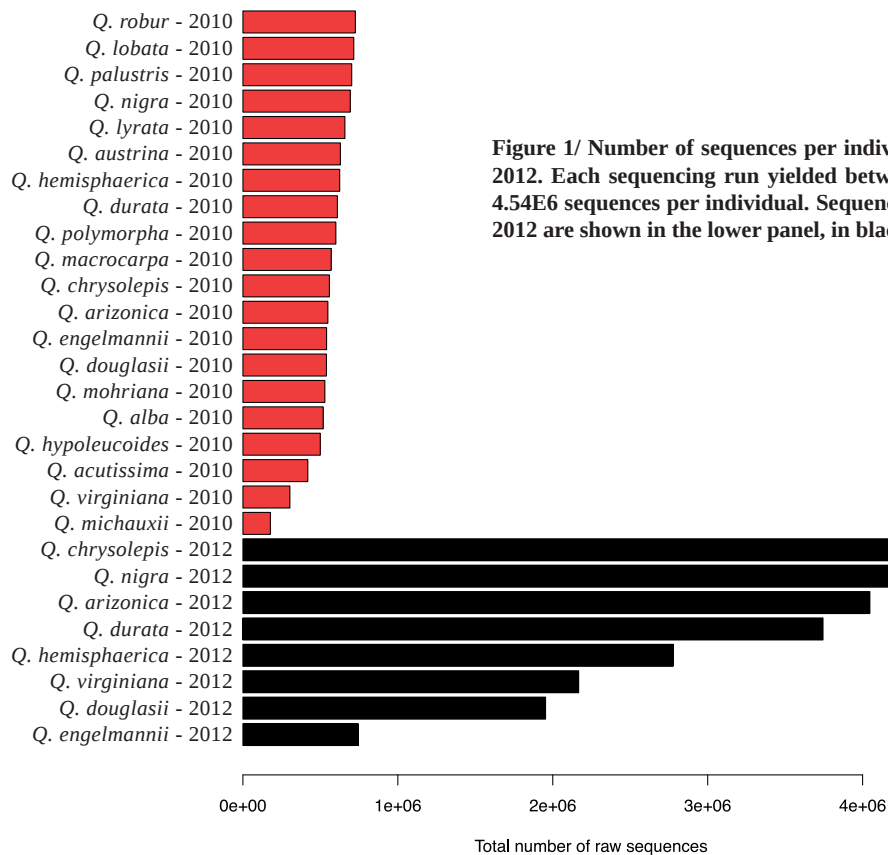


Figure 1/ Number of sequences per individual, 2010 and 2012. Each sequencing run yielded between 1.77E5 and 4.54E6 sequences per individual. Sequences replicated in 2012 are shown in the lower panel, in black.

DNA data matrix

Within individuals, the average number of sequences used to estimate the consensus sequence for each locus was 12.8 ± 0.8 (standard deviation) for 2010 data, 38.1 ± 13.2 for 2012 data. A total of 61,054 loci were inferred with a minimum of 4 individuals per locus, 24,778 with a minimum of 10 individuals per loci. By comparison, the longest previous DNA-based dataset utilized in oak phylogenetic inference^[43] utilized 2,932 AFLP bands, each of which reflects the evolution of 16 to 18 base pairs constituting the recognition sites flanking that band, a total of ca. 47,000 base pairs of data. All pairs of technical replicates share fewer than 52% of the loci found in the union set of loci for the pair. Locus coverage in the 2012 sequencing runs was 19% to 127% greater than the 2010 sequencing runs for the same individuals.

Phylogeny

Analysis of the aligned data matrix recovers section *Lobatae* as sister to sections *Quercus* and *Protobalanus*, and all three of these as monophyletic insofar as we have sampled them (Figure 2). It also places the live oaks of the *Virentes* group sister to the remainder of section *Quercus*. All of these relationships are recovered with 100% bootstrap support. This topology has also been recovered in previous phylogenetic studies on oaks based on DNA sequences^[37] and AFLP data,^[43] but with lower statistical support.

Phylogenetic analysis of the sequence data, treating missing loci as missing characters, places all 2012 technical replicates sister to their 2010 counterparts, with terminal branch lengths substantially shorter than the subtending internode (Figure 3; p. 68). This suggests that missing data have negligible effect on species placement on the tree, and that data are readily combined across sequencing runs. This is a substantial improvement over AFLP

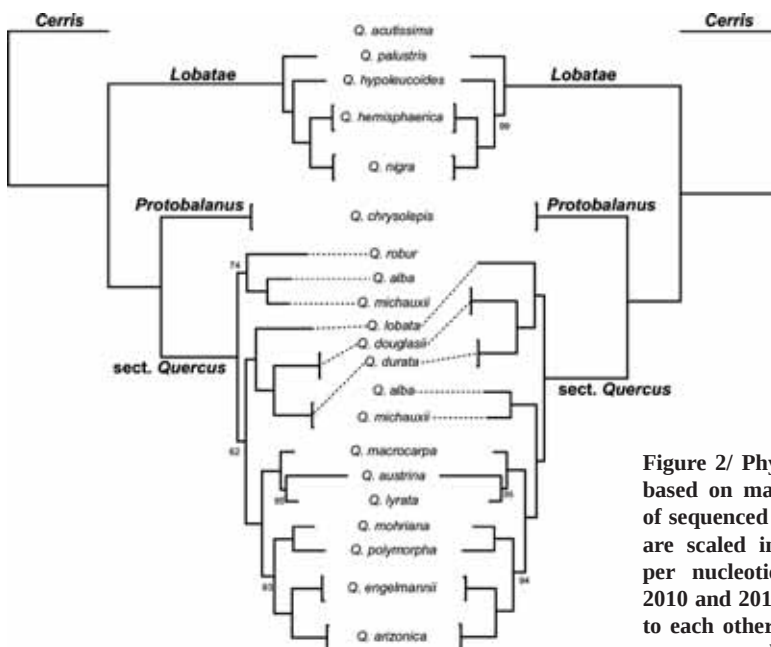


Figure 2/ Phylogenetic trees of *Quercus* based on maximum likelihood analysis of sequenced RAD data. Branch lengths are scaled in number of substitutions per nucleotide. Individuals from the 2010 and 2012 sequencing runs fall next to each other in all cases. Two analyses are presented: one in which all taxa are included (left panel), and one in which *Quercus robur* is excluded (right panel).

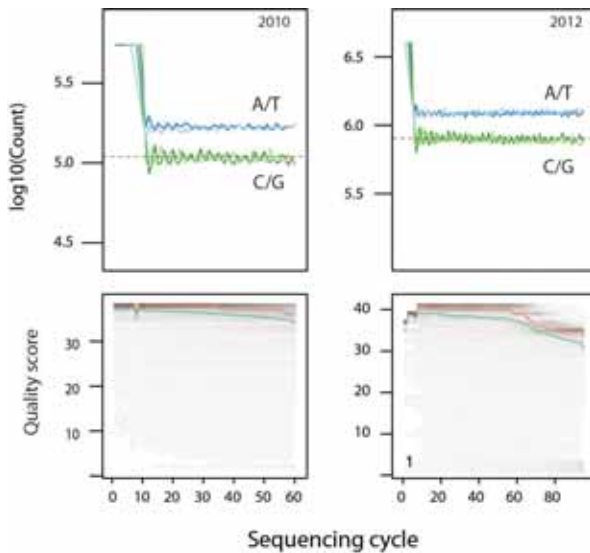


Figure 3/ Quality and base-pair composition of two representative sequencing runs. The same individual *Quercus alba* L. was sequenced in both 2010 (left panels) and 2012 (right panels), using the same extraction and RAD library preparation. DNA quality is reported using Phred quality scores, which have been in use for reporting DNA sequencing quality since 1998. Quality decreases toward the end of each read, and 2012 sequences exhibit lower quality commensurate with their longer sequencing reads. Percent C plus percent G also appears to decrease very slightly toward the ends of the reads in 2010 and 2012. Read quality and percent CG include the first 10 bases of each sequencing read, which comprise the individual-specific DNA barcode and five bases of the *Pst*I restriction cut site. These 10 bases are stripped off prior to all other analyses.

data, in which combining data across separate analyses is time-consuming, requiring rescoring of the entire data matrix, and often presents technical challenges.

Discussion

Despite our very sparse sampling (18 out of more than 250 in the New World oak clade), two phylogenetic results stand out in this study within section *Quercus* (the white oaks). First, this study supports previous findings^[37, 39, 43] that the Eurasian white oaks of section *Quercus* are embedded within the otherwise New World clade sampled here. The position we find, however, is novel: whereas we find *Quercus robur* to be embedded within or sister to one of the Eastern North American clades, previous study using AFLP data has suggested that the Eurasian white oaks are sister to the non-*Virentes* members of section *Quercus* from North America^[43], and a study utilizing nuclear ribosomal DNA sequences suggested a relationship between the Western North American *Q. sadleriana* R.Br.ter. and *Q. pontica* K. Koch of the Western Caucasus Mountains^[39]. Our placement of *Q. robur* is far from conclusive, however, as suggested by the fact that analysis with *Q. robur* appears to drag the Eastern North American *Q. alba* and *Q. michauxii* Nutt. to a position sister to the remainder of the white oaks, but with low statistical support for that placement (62%, nonparametric bootstrap). Moreover, the placement of *Q. robur* is highly sensitive to clustering parameters (alternative analyses not shown here), suggestive that different partitions of the RAD sequence dataset may encode different placements of *Q. robur*, due either to hybridization or to rapid diversification at the base of the section.^[56-59] Resolving the position of the Old World white oaks will certainly require additional sampling of both Eurasian and American species of section *Quercus* and thorough analysis of a large number of nuclear loci.

Second, our data separate the New World white oaks into small geographic clades, with the Eastern North American taxa non-monophyletic. Prior morphological studies of the genus (e.g.,^[60, 61]) have suggested some morphological groupings within subgenus

Quercus as a step toward an infrasectional classification of the genus. The results here, in which, for example, the Californian white oaks (*Q. lobata* Née, *Q. douglasii* Hook. & Arn., *Q. durata* Jeps.) form a clade distinct from the predominantly southwestern North American/Mexican oaks sampled (*Q. mohriana* Buckley ex Rydb., *Q. polymorpha* Schldtl. & Cham., *Q. engelmannii* Greene, *Q. arizonica* Sargent), suggest that such a classification may be within reach, and that that classification may rest strongly on biogeography.

Finally, our study demonstrates the utility of RAD data for reconstructing phylogenetic relationships in a problematic group, spanning roughly 40 million years of evolutionary history. As part of our currently funded work, we are sampling roughly 150 species of the New World oak clade (sections *Lobatae*, *Protobalanus*, and *Quercus*), using the same methods described in this paper. Our expectation is that within the coming few years, we will have a handle on the shape and timing of a large portion of the oak tree of life, which has for so long proved elusive.



1/ *Quercus alba*.

Acknowledgements

This work was supported by NSF Awards #1146488 to AH, #1146380 to JCB, and #1146102 to PM. Kari Koehler (UM, Minneapolis, Minnesota, U.S.A.) managed all plants in the greenhouse and performed all DNA extractions for this study. Tressa Atwood (Floragenex, Portland, Oregon, U.S.A.) executed all labwork and worked closely with participating labs (AH, JCB) to ensure quality of extractions and data. Antoine Kremer

(INRA, UMR BioGeCo, Cestas, France) reviewed this manuscript and hosted, with The International Oak Society, the meeting at which this work was presented. Béatrice Chassé graciously extended the invitation to AH to present this work, coordinated many of the aspects of the meeting and proceedings, and provided editorial feedback on the manuscript.

Author contributions

AH, PM, and JCB conceived the study and provided DNA extractions for sequencing. RN coordinated the RAD library preparation and sequencing. DE developed the analysis pipeline. DE and AH analyzed the data. All authors contributed to writing and editing of the paper.

Photographers. Title page: Andrew Hipp (trees of life). Photo 1: Philippe de Spoelberch.

References

1. D.P. Faith. 2008. Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conservation Biology* 22(6): 146–470.
2. D.P. Faith and A.M. Baker. 2006. Phylogenetic diversity (PD) and biodiversity conservation: some bioinformatics challenges. *Evolutionary Bioinformatics*, 2: p. 70–77.
3. S. Knapp, I. Kuhn, O. Schweiger, and S. Klotz. 2008. Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters* 11: 1054–1064.
4. M.H. Hoffmann and M. Röser. 2009. Taxon recruitment of the arctic flora: an analysis of phylogenies. *New Phytologist* 182(3): 774–780.
5. B.W. Van Ee, N. Jelinski, P.E. Berry, and A. Hipp. 2006. Phylogeny and biogeography of *Croton alabamensis* (Euphorbiaceae), a rare shrub from Texas and Alabama, using DNA sequence and AFLP data. *Molecular Ecology* 15(10): 2735–2751.
6. T.M. Harding, P.S. Soltis, and D.E. Soltis. 2000. Diversification of the North American shrub genus *Ceanothus* (Rhamnaceae): conflicting phylogenies from nuclear ribosomal DNA and chloroplast DNA. *Am. J. Bot.* 87(1): 108–123.
7. J. Cavender-Bares, K.H. Kozak, P.V.A. Fine, and S.W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12(7): 693–715.
8. C.O. Webb, D.D. Ackerly, M.A. McPeck, and M.J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505.
9. C.H. Graham and P.V.A. Fine. 2002. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters* 11(12): 1265–1277.
10. S.M. Vamasi, S.B. Heard, J.C. Vamasi, and C.C. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18(4): 572–592.
11. P.V.A. Fine, I. Mesones, and P.D. Coley. 2004. Herbivores Promote Habitat Specialization by Trees in Amazonian Forests. *Science* 305(5684): 663–665.
12. J. Cavender-Bares, D.D. Ackerly, D.A. Baum, and P.A. Bazaaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163(6): 823–843.
13. K. Saltonstall, Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. 2002. *Proceedings of the National Academy of Sciences of the United States of America* 99(4): 2445–2449.
14. C.E. Lee and G.W. Gelembiuk. 2008. Evolutionary origins of invasive populations. *Evolutionary Applications* 1(3): 427–448.
15. L. Van Valen. 1976. Ecological species, multispecies, and oaks. *Taxon* 25: 233–239.
16. L.S. Kubatko. 2009. Identifying Hybridization Events in the Presence of Coalescence via Model Selection. *Systematic Biology* 58(5): 478–488.
17. C. Meng and L.S. Kubatko. 2009. Detecting hybrid speciation in the presence of incomplete lineage sorting using gene tree incongruence: A model. *Theoretical Population Biology* 75(1): 35–45.
18. H. Huang, Q. He, L.S. Kubatko, and L.L. Knowles. 2010. Sources of Error Inherent in Species-Tree Estimation: Impact of Mutational and Coalescent Effects on Accuracy and Implications for Choosing among Different Methods. *Systematic Biology* 59(5): 573–583.
19. J.L. Hamrick. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management* 197(1-3): 323–335.
20. O. Savolainen, T. Pyhäjärvi, and T. Knurr. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology Evolution and Systematics*. 38: 595–619.
21. S.M. Hoban, T.S. McCleary, S.E. Schlarbaum, and J. Romero-Severson. 2009. Geographically extensive hybridization between the forest trees American butternut and Japanese walnut. *Biology Letters* 5(3): 324–327.
22. J.A. Coyne and H.A. Orr., *Speciation* (Sunderland, MA: Sinauer Associates, 2004).
23. R. Petit, C. Bodénès, A. Ducousso, G. Roussel, and A. Kremer. 2004. Hybridization as a mechanism of invasion in oaks. *New Phytologist* 161: 151–164.
24. C. Burgarella, Z. Lorenzo, R. Jabbour-Zahab, R. Lumaret, E. Guichoux, R.-J. Petit, Á. Soto, and L. Gil. 2009. Detection of hybrids in nature: application to oaks (*Quercus suber* and *Q. ilex*). *Heredity* 102(5): 442–452.
25. O. Lepais, R.-J. Petit, E. Guichoux, J.E. Lavabre, F. Alberto, A. Kremer, and S. Gerber. 2009. Species relative abundance and

- direction of introgression in oaks. *Molecular Ecology* 18: 2228–2242.
26. R.-J. Petit and L. Excoffier. 2009. Gene flow and species delimitation. *Trends in Ecology & Evolution* 24(7): 386–393.
 27. L. Lagache, E.K. Klein, E. Guichoux, and R.-J. Petit. Fine-scale environmental control of hybridization in oaks, *Molecular Ecology*, 2013. 22(2): 423–436.
 28. W.C. Burger. 1975. The species concept in *Quercus*. *Taxon* 24: 45–50.
 29. C. Lexer, A. Kremer, and R.J. Petit. 2006. Shared alleles in sympatric oaks: recurrent gene flow is a more parsimonious explanation than ancestral polymorphism. *Molecular Ecology* 15: 2007–2012.
 30. Whittemore, A.T. and B.A. Schaal. 1991. Interspecific gene flow in sympatric oaks. *Proceedings of the National Academy of Sciences USA* 88: p. 2540–2544.
 31. S. Dumolin-Lapegue, B. Demesure, S. Fineschi, V. Le Comte, and R.-J. Petit. 1997. Phylogeographic structure of white oaks throughout the European continent. *Genetics* 146: 1475–1487.
 32. J.W. Hardin. 1975. Hybridization and introgression in *Quercus alba*. *Journal of the Arnold Arboretum* 56: 336–363.
 33. A. González-Rodríguez, D.M. Arias, S. Valencia, and K. Oyama. 2004. Morphological and RAPD analysis of hybridization between *Quercus affinis* and *Q. laurina* (Fagaceae), two Mexican red oaks. *American Journal of Botany* 91(3): 40–409.
 34. A.L. Hipp and J.A. Weber. 2008. Taxonomy of Hill's Oak (*Quercus ellipsoidalis*: Fagaceae): Evidence from AFLP Dat. *Systematic Botany* 33: 148–158.
 35. G. Muir, C.C. Fleming, and C. Schlötterer. 2000. Species status of hybridizing oaks. *Nature* 405: 1016.
 36. R.-J. Petit, R., E. Pineau, B. Demesure, R. Bacilieri, A. Docouso, and A. Kremer. 1997. Chloroplast DNA footprints of postglacial recolonization by oaks. *Proceedings of the National Academy of Sciences USA* 94: 9996–10001.
 37. P.S. Manos, J.J. Doyle, and K.C. Nixon. 1999. Phylogeny, Biogeography, and Processes of Molecular Differentiation in *Quercus* Subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution* 12(3): 333–349.
 38. S.-H. Oh and P.S. Manos. 2008. Molecular phylogenetics and cupule evolution in Fagaceae as inferred from nuclear CRABS CLAW sequences. *Taxon* 57: 434–451.
 39. T. Denk and G.W. Grimm. 2010. The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers. *Taxon* 59: 351–366.
 40. N.A. Baird, P.D. Etter, T.S. Atwood, M.C. Currey, A.L. Shiver, Z.A. Lewis, E.U. Selker, and W.A. Cresko. 2008. *Rapid SNP Discovery and Genetic Mapping Using Sequenced RAD Markers*. *PLoS ONE*, 3(10): e3376.
 41. A. Kremer, A.G. Abbott, J.E. Carlson, P.S. Manos, C. Plomion, P. Sisco, M.E. Staton, S. Ueno, and G.G. Vendramin. 2012. Genomics of Fagaceae. *Tree Genetics & Genomes*, doi: 10.1007/s11295-012-0498-3.
 42. J. Durand, C. Bodénès, E. Chancerel, J.-M. Frigerio, G. Vendramin, F. Sebastiani, A. Buonamici, O. Gailing, H.-P. Koelwijn, F. Villani, C. Mttioni, M. Cherubini, P.G. Goicoechea, A. Herrán, Z. Ikarán, C.Cabané, S. Ueno, F. Alberto, P.-Y. Dumouline, E. Guichoux, A. de Daruvar, A. Kremer, and C. Plomion. 2010. A fast and cost-effective approach to develop and map EST-SSR markers: oak as a case study. *BMC Genomics* 11(1): 570.
 43. I.S. Pearse, and A.L. Hipp. 2009. Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks, *Proceedings of the National Academy of Sciences of the United States of America*. 106(43): 18097–18102.
 44. Wikipedia, *Restriction enzyme*. http://en.wikipedia.org/wiki/Restriction_enzyme 2013. Accessed 21 January 2013.
 45. E.R. Mardis. 2008. Next-Generation DNA Sequencing Methods. *Annual Review of Genomics and Human Genetics* 9(1): 387–402.
 46. P.J.A. Cock. 2010. The Sanger FASTQ file format for sequences with quality scores, and the Solexa/Illumina FASTQ variants. *Nucleic Acids Research* 38(6): 1767–1771.
 47. B. Ewing, L. Hillier, M.C. Wendl, and Phil Green. 1998. Base-Calling of Automated Sequencer Traces Using Phred.I. Accuracy Assessment. *Genome Research* 8(3): 175–185.
 48. Development-Core-Team, *R: A language and environment for statistical computing*, (Vienna: R.F.f.S. Computing, Editor, 2004).
 49. M. Morgan, S. Anders, M. Lawrence, P. Aboyoun, H. Pagès, and R. Gentleman. 2009. ShortRead: a bioconductor package for input, quality assessment and exploration of high-throughput sequence data. *Bioinformatics* 25(19): 2607–2608.
 50. J.M. Catchen, A. Amores, P. Hohenlohe, W. Cresko, and J.H. Postlethwait. 2011. Stacks: Building and Genotyping Loci De Novo From Short-Read Sequences. *G3: Genes, Genomes, Genetics* 1(3): 171–182.
 51. R.C. Edgar. 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26(19): 2460–2461.
 52. Edgar, R. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5(1): 113.
 53. R.C. Edgar. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797.
 54. A. Stamatakis and N. Alachiotis. 2010. Time and memory efficient likelihood-based tree searches on phylogenomic alignments with missing data. *Bioinformatics* 26(12): i132–9.
 55. J. Felsenstein, *Inferring Phylogenies* (Sunderland, Maryland: Sinauer Associates, Inc., 2004).
 56. L.L. Knowles and L. Kubatko, eds. *Estimating Species Trees: Practical and Theoretical Aspects* (Hoboken: Wiley-Blackwell & Sons, Inc. 2010).
 57. L.L. Knowles, *Estimating Species Trees: Methods of Phylogenetic Analysis When There Is Incongruence across Genes*, *Systematic Biology*, 2009. 58(5): 463–467.
 58. C. Ané, B. Larget, D.A. Baum, S.D. Smith, and A. Rokas. 2007. Bayesian Estimation of Concordance among Gene Trees. *Molecular Biology and Evolution* 24(2): 412–426.
 59. J.F. Wendel and J.J. Doyle, *Phylogenetic incongruence: window into genome history and molecular evolution*, ch. 10, in *Molecular systematics of plants II: DNA sequencing* D.E. Soltis, P.S. Soltis, and J.J. Doyle, Editors. (Norwell, Massachusetts: Kluwer Academic Publishers, 1998), 265–296.
 60. K.C. Nixon. 2002. The Oak (*Quercus*) Biodiversity of California and Adjacent Regions. *USDA Forest Service Gen. Tech. Rep., PSW-GTR-184*.
 61. W. Trelease, *The American Oaks. Memoirs of the National Academy of Sciences*, 1924. 20: 1–255.

Northeast Asia, Central and Southwest China, Himalayas





Meeting With Oaks

Philippe de Spoelberch

Arboretum Wespelaar

Herkenrode

Vijverbos 6

B-3150 Wespelaar, Belgium

ABSTRACT

Having traveled extensively through the temperate regions of the world, over the last 40 years, I have come to meet oaks from time to time. This has given me the occasion to exercise my hobby of plant photographer. But I must admit that my main interest has been for other genera such as *Acer*, *Rhododendron*, *Betula* and *Magnolia*. But oaks were always present. This portrait gallery of oaks as seen in the wild and botanic gardens is a grand tour of the world, going from Eastern North America all the way back to Western Europe. Not a particularly useful way to go about this visit, but one which might allow me to point out some of the diverse conditions in 7 different regions. Eastern and Central USA provide most of the portraits for that continent. Western North America adds a few important plants that might have been shown in the Mediterranean section. The red oaks are of course singled out. Landing on the Eastern coast of Asia provides another show of colors with deciduous members of the genus turning to bright autumn colors (another main interest of mine). Moving to Central and Southwest China toward the border with the Himalayas provides only a few portraits – this being the result of the limited number of plants in the temperate areas of these regions. Plants from the Caucasus and Balkans are among the favorites of West European gardens. Western Europe has but half a dozen indigenous oaks merging with Mediterranean oaks, themselves very linked to the previous group. All are reasonably hardy and happy in botanical gardens and in particular at Arboretum Wespelaar where about 100 species and cultivars can be found.

Keywords: oak images, *Quercus* images, Arboretum Wespelaar

United States of America



7



8



9



10



11

Europe





Northeast Asia, Central and Southwest China, Himalayas

- 1/ *Q. acutissima* Carruth. Arboretum Robert Lenoir, Rendeux, Belgium (2008).
- 2/ *Q. pannosa* Hand.-Mazz. Bamashan on the Sichuan-Yunnan border, China (2008).
- 3/ *Q. crispula* var. *horikawae* H. Ohba. Mount Zao, Honshu, Japan (2008).
- 4/ *Q. crispula* Blume. Norikura Mountain, Japan (2008).
- 5/ *Q. dentata* Thunb. 'Carl Ferris Miller' J. Hillier & Coombes. Arboretum Wespelaar, Haacht-Wespelaar, Belgium (2010).
- 6/ *Q. monimotricha* (Hand.-Mazz.) Hand.-Mazz. Yuhu, Lijiang, Yunnan, China (2008).

United States of America

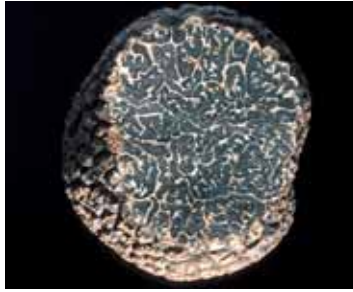
- 7/ *Q. bicolor* Willd. Scott Arboretum, Swarthmore College, Pennsylvania, USA (2011).
- 8/ *Q. palustris* L. Arboretum Wespelaar, Haacht-Wespelaar, Belgium (2011).
- 9/ *Q. ×brittonii* W.T. Davis (*Q. ilicifolia* × *Q. marilandica*). New Jersey Pine Barrens, USA.
- 10/ *Q. chrysolepis* Liebm. Yosemite National Park, California, USA (2010).
- 11/ *Q. vacciniifolia* Kellogg. Tenaya Lake, Yosemite National Park, California, USA (2010).

Europe

- 12/ *Q. 'Pondaim'* van Hoey Smith (*Q. dentata* Thunb. × *Q. pontica* K. Koch). Arboretum Wespelaar, Haacht-Wespelaar, Belgium (2007).
- 13/ *Q. frainetto* Ten. Arboretum Wespelaar, Haacht-Wespelaar, Belgium (2007).
- 14/ *Q. pubescens* Willd. La Sainte-Baume, France (2011).
- 15/ *Q. robur* L. Domaine Empain, Espeux, Belgium (1994).
- 16/ *Q. suber* L. La Garde-Freinet, France (2012).
- 17/ *Q. canariensis* Willd. Arboretum de Gratteloup, La Môle, France (2012).

To view the entire presentation of 241 photographs, see the IOS home page at <http://www.internationaloaksociety.org>

Photographers. Title page: Philippe de Spoelberch (*Q. rubra* 'Aurea', Arboretum Wespelaar). Photos 1-17: Philippe de Spoelberch.



Black Truffles and Oak Trees in France and in Europe

Pierre Sourzat

Station d'expérimentation sur la truffe
Lycée professionnel agricole de Cahors-Le-Montat
422, Lacoste, 46090 Le Montat, France
<http://perso.wanadoo.fr/station-truffe/>
station.truffe@wanadoo.fr

ABSTRACT

The black truffle *Tuber melanosporum* Vittad. is a xerophilous mycorrhizal fungus, suited to limestone soil. Since its common host tree is the oak, one often speaks of “truffle-oak cultivation” to produce truffles. Two species are well-known as very favorable for truffle cultivation: *Quercus pubescens* Willd. and *Q. ilex* L. Other species are used for truffle production with variable interest according to the region. In Southwest France, where *Q. pubescens* and *Q. ilex* are appreciated by truffle growers, the appearance of a fungal disease on the former has promoted its replacement with *Q. cerris* L. In the Southeast, *Q. robur* L., (the selection distributed as ‘Michelin’), is planted as well as *Q. pubescens* and *Q. ilex*. In Catalonia, *Q. coccifera* L. and *Q. suber* L. are mycorrhized and cultivated for truffle production. In the other regions of Spain, *Q. faginea* Lam. is commonly used with *Q. pubescens* and *Q. ilex* while in Italy, *Q. petraea* (Matt.) Liebl. can be added to this list. Other oak species are sometimes planted with more or less success.

Keywords: *Tuber melanosporum* Vittad., truffle cultivation, mycorrhizal fungus

Truffle oaks and truffles

Truffle oaks and truffles share a long history in southern France. We use the term “truffle oak” to describe a mycorrhizal symbiosis between trees and fungi that has developed either naturally or following human intervention.

One species of truffle that has acquired a reputation beyond France, a country known for its culinary traditions, is the black truffle *Tuber melanosporum* Vittad., also known as the Périgord truffle or *mélano*. The main areas where these truffles are harvested in France are in the Southwest: Lot, Dordogne, Aveyron, Tarn, Tarn et Garonne, and Corrèze, and parts of the Southeast: Drôme, Vaucluse, Var, Alpes de Haute-Provence, Gard, Hérault. Production has also developed in other regions, like the Languedoc-Roussillon, Poitou-Charentes, and Loire, which sometimes suffer drawbacks due to the climate. Black truffles (and other species) are also naturally present in Italy and Spain. Some other countries have also started growing truffles (New Zealand, Australia, Chile, Argentina, and the United States).

In France, the main botanical species of truffles harvested amongst the score that grow naturally are:

Périgord black truffle (*T. melanosporum* Vittad.); white summer truffle (*T. aestivum* Vittad.); Burgundy truffle (*T. uncinatum* Chatin) – this species is increasingly considered by the scientific community to be an ecotype of *T. aestivum*; winter or “musky” truffle (*T. brumale* Vittad.); Bagnoli truffle (*T. mesentericum* Vittad.); “dog-nose” or red truffle (*T. rufum* Pico); “hollow” truffle (*T. excavatum* Vittad.); white truffle (*T. maculatum* Vittad.) – found in Provence (Riousset et al., 2001; 2012).

Oaks are the quintessential host trees for the mycorrhizal association (a symbiotic association beneficial to both organisms) necessary for truffle production. The fungus absorbs minerals from the soil (particularly phosphorus and mineral nitrogen), thanks to its greater capacity to extract water and minerals than those of root hairs, and passes on these benefits to its host tree. The tree photosynthesizes, producing carbohydrates that provide nourishment for the fungus in its vegetative form (mycorrhizae, mycelium, and stromata), as well as for its fruiting body (ascocarp), according to recent research during the SYSTRUF program (a 4-year French research program on truffles). Thanks to this relationship, mycorrhizae develop on the tree roots and this triggers their fruiting mechanism that, in turn, results in the truffle harvest.

In their natural environment, truffle oaks can be identified by the presence of a vegetation-free area around or near their trunks, known as a “scorched” zone. Several hypotheses have been put forward to explain this “scorched” effect: the herbicidal action of the mycelium (production of phytotoxic substances), its monopolization of water resources in the soil, or a parasitic action of the mycelium on the plant’s root tissues. These three factors are probably at work within the scorched zone.

The two oak species preferred by French truffle growers are downy (*Q. pubescens* Willd.) and holm oak (*Q. ilex* L.) In addition to these two species, Austrian oak (*Q. cerris* L.), the *Q. robur* L. selection ‘Michelin’, kermes oak (*Q. coccifera* L.), and cork oak (*Q. suber* L.) are all worthy of mention. Portuguese oak (*Q. faginea* Lam.) is also used for truffle growing in Spain and sessile oak (*Q. petraea* (Matt.) Liebl.) in Italy. In China, *T. indicum* is harvested under *Q. incana* Roxb. (synonym of *Q. leucotrichophora* A. Camus) (Riousset et al., 2001; 2012).

The above-mentioned oaks (plus other trees) are “truffle trees” because they are



1/ *Quercus pubescens* and the “scorched zone” that indicates the presence of truffles.

ectomycorrhizal, i.e., they can be infected by fungi and produce ectomycorrhiza, in which (unlike endomycorrhiza) the mycelial threads (hyphae) do not penetrate inside the root tissue cells. In the case of ectomycorrhiza, the truffle hyphae and the root cortical cells form a Hartig net.

Truffle and truffle-oak ecology

Black truffles, *T. melanosporum*, are found in environmental conditions suited to their xero-thermo-calcicole ecological requirements. In fact, a good truffle-producing environment – and one enjoyed by oaks – is defined by several specific environmental features including soil type and climate.

Truffle-producing soils are limestone or calcareous, usually with a water pH between 7.8 and 8.3. They are well-aerated and well-drained, and have good biological activity. Truffle-producing soils are present in many parts of France, on limestone formations from various epochs, which determine some of their characteristics. Among these formations, secondary limestone is particularly significant, especially from the Jurassic and Cretaceous periods. Excellent truffle soils are also found on Tertiary formations (Oligocene, Eocene) and Quaternary alluvial deposits. These limestones contain variable amounts of calcium carbonate, the critical chemical compound in the carbonate content of truffle-producing soils. The hardest rocks (lithographic) have a calcium carbonate content above 90%, whereas calcareous sandstone has a high silica content and generally under 10% calcium carbonate.

The climate for *T. melanosporum* truffles is subMediterranean to Mediterranean with oceanic, montane, or even continental influences. The two key limiting factors are prolonged summer droughts and excessive winter cold, which freezes the truffles in the soil. Truffles grow on sites with good sun exposure. The traditional truffle-producing



2/ A *Quercus robur* truffle plantation in the foreground, and a *Q. ilex* truffle plantation, in the background (Drôme).

regions of Southwest (Lot, Dordogne, Tarn, Tarn-et-Garonne, etc.) and Southeast France (Vaucluse, Drome, Var, Alpes de Haute-Provence, Gard, etc.) have favorable climates for truffles. In Europe, black *T. melanosporum* truffles are produced between the 40th and 47th parallels. Latitude 40°N corresponds to the truffle fields in the Teruel area in southern Spain and those in the Loire Valley are around 47°N. Truffles may also be produced further north, in Burgundy, for example. There is a natural truffle field in the Verdun area (48°N) highly reputed for its black truffles. But northern producers are penalized in years when a cold snap freezes the truffles in the ground, while slightly warmer temperatures further south may save the harvest.

The climate required by truffles may be summarized in the following 4 points:

- relatively damp and warm in spring, with no late frosts, to promote the growth of mycelium and the fruiting of the truffles (starting in late spring);
- hot summers with thunderstorms, to bring the rain needed for the truffles to develop;
- no early frosts that destroy the truffles and no excessive rainfall in the autumn (as was the case in October/November 2012, particularly in the Périgord that had 300 mm of rain in some areas like in Sainte-Foy-de-Longas);
- winters with no hard frosts that freeze the ground solid for several days, as this is likely to destroy the truffles (five morning frosts with temperatures around -10 °C will freeze the truffles) and moderate rainfall to ensure that the truffles are harvested in good soil conditions.

Natural truffle fields and truffle fields planted around oak trees

T. melanosporum is considered to have the same organoleptic qualities, whether it is

harvested in its natural environment or from a plantation. There are no morphological or qualitative variations and certainly no difference in species between wild and farmed truffles.

Natural truffle fields

These usually form under moors, scrublands, or turf, around oaks naturally contaminated at random.

The first truffle-oak plantations

The first attempts at truffle cultivation involved planting truffles like potatoes. One such trial was carried out by Buffon, the famous naturalist, who attempted in vain to plant freshly collected truffles on his estate at Montbard, in Burgundy. In fact, truffle growing started approximately 200 years ago, by sowing acorns. Today, truffles are still cultivated indirectly, using the host tree to obtain the mushrooms.

The invention of truffle growing is attributed to Joseph Talon, a farmer and truffle hunter in Croagnes, a hamlet near Saint-Saturnin-les-Apt, in the Vaucluse. He created the first “artificial” truffle fields in year X of the French Revolution (Olivier et al., 1996; 2002; 2012). Henri Bonnet reports that, when Talon took ownership of a small farm, he purchased a few hectares of land to graze his flocks (Bonnet, 1869). In order to obtain a source of heating wood, he sowed sessile and holm oak acorns on the land. Eight or ten years later, he found superb truffles growing there. He then decided to coppice the trees *en rabassaiéré* (from the word *rabasso*, a common name for truffle in Provence) and the truffle harvest increased from year to year. Others followed his example, particularly another Joseph Talon, his cousin, who was apparently responsible for the “artificial” truffle fields created mainly in the vicinity of Apt, Buoux, and Les Agnells (Vaucluse). The Talon method, which can be summarized as, “If you want to harvest truffles, plant acorns!” was applied systematically by Mr. Rousseau, a truffle dealer in Carpentras, who created 7 hectares/17.29 acres of cultivated truffle fields on his Puits-du-Plan estate in 1847.

Truffle cultivation, based mainly on downy and holm oak trees, was then applied more widely in Provence and Southwest France, as described in detail by many authors, especially: Chatin, 1860; Bosredon, 1887; Ferry de La Bellone, 1888; and Pradel, 1914.

Growing truffles

The revolutionary marketing in 1974 of seedlings mycorrhized by truffles gave new hope to truffle growers following a huge decline in production after the First World War. Truffle growing consists of planting certified mycorrhized trees, mainly oaks, in limestone soils, in areas with a favorable climate. In France, the mycorrhization of the trees by *T. melanosporum* is certified by INRA (Institut national de la recherche agronomique) for two tree nurseries and by CTIFL (Centre Technique Interprofessionnel des Fruits et Légumes) for all of the others. Some local and regional authorities grant subsidies to truffle growers, on condition that they plant certified mycorrhized trees. Approximately 300,000 certified mycorrhized trees are produced and sold in France every year and two-thirds of them are oak trees. Holm and downy oaks represent 80-90% of the trees planted.

The truffle-bearing characteristics of various oak species

Downy oak, a typically sub-Mediterranean species, is certainly the tree with the greatest affinity for *T. melanosporum* truffles. This is due to its adaptation to the *causses* (dry limestone plateaus in Southwest France) and the fact that its roots grow at a rate



3/ *Quercus suber* truffle plantation (Pyrénées-Orientales).

compatible with mycorrhiza propagation. Truffle production used to begin when the trees were around 10- to 15-years-old. But today in intensive, irrigated plantations it has been brought forward to the age of 5 to 6. Downy oak is recommended for plantations in both Southwest and Southeast France, but sulphur treatments are required to prevent powdery mildew infection in the spring. The recent appearance of sensitivity to anthracnose among oak trees in the Périgord has led some growers to prefer Austrian oak (*Q. cerris*).

Holm oak is particularly well-suited to the Mediterranean climate and its rocky limestone soils. It is ideal for plantations in Southeast France, both on the Valensoles Plateau and in the Languedoc countryside, as well as in the deeper soils of the Tricastin area. It is increasingly popular among truffle growers in the Southwest. It is low-maintenance (minor pruning) and is recommended for non-irrigable plantations. Its disadvantage is its sensitivity to frost. Young, poorly lignified tissues are destroyed by any sudden drop in temperature below 0 °C/32 °F

The ‘Michelin’ selection of pedunculate oak is appreciated in the Southeast. It will produce truffles at an earlier age than holm oak in the Vaucluse and Drôme areas. Early bud-break makes it vulnerable to late frosts in the Southwest. In countries in the Southern Hemisphere, where truffles have been grown for the past two or three decades (New Zealand and Australia), pedunculate oak, sometimes known as English oak, produces truffles, but requires extensive pruning and trimming. It is also sensitive to early frosts, particularly in Tasmania (Australia).

Kermes oak is an excellent producer in the naturally calcareous environment of the Mediterranean scrublands in the Corbières and Hérault areas but it is relatively little used in truffle cultivation as it gives variable results, especially in Southwest France. Truffle hunters know that their truffle-hunting dogs do not like to get close too these prickly, shrubby trees looking for truffles!

Austrian oak is increasingly widely grown but only recently used for truffle growing. It is mainly planted in areas where the downy oaks are infected with anthracnose. Truffle production starts very early, when the trees are 5- to 6-years-old. As they are fast growing, they need to be strictly pruned to leave space for truffles to develop in the plantation.

Portuguese oak (*Q. faginea*) has replaced downy oak in many plantations in Spain, where it is easy to identify as it does not lose its leaves until late winter (marcescent foliage). Although it prefers cooler soils, the Spanish use it confidently for truffle production, together with holm oak. Its use is unknown in France.

Cork oaks very rarely produce truffles, as they prefer granite or shale soils with an acid pH. *T. melanosporum* may be produced naturally when the calcium content of the environment is temporarily raised (e.g., crushed limestone used on a roadbed further up the slope). They do not seem to suffer from the high-calcium environment when they are planted on deep limestone soils to produce *T. melanosporum*. However, their vigorous growth obliges truffle growers to prune the trees severely.

Sessile oak (*Q. petraea*) is not very well-known for *T. melanosporum* production in France. It is reported as a "...good producer of Burgundy truffles (*T. uncinatum*) on limestone plateaus in Burgundy and Lorraine, often mixed with hornbeam." (Chevalier, et al., 1997). It is known for the production of the famous white truffles of the Piedmont in Italy (*T. magnatum*) (Granetti, et al., 2005).

Q. incana Roxb. (= *Q. leucotrichophora* A. Camus) is reported as a *Tuber indicum* producer in China.

Some practical aspects of truffle growing

Once the plantation is in place, its maintenance consists of cultivating the oak trees together with the truffles. This requires maintaining the soil, controlling the water supply, pruning the trees, and treating diseases, mainly those affecting the trees.

The soil

The soil is traditionally maintained by tilling, as truffles grow larger in a well-aerated, living, environment with good water reserves. Traditionally the soil was tilled by hand, to a depth of 5-8 cm/2-3 in, using tools with one or more tines once the soil had settled. If the land is tilled with a tractor, the tined tools used are cultivators or tine harrows, while some growers prefer disc harrows that do not pull on the roots. Manual tillage using a hoe, known locally as a *bigos* (a tool with 3 or 4 tines), is preferable for trees that produce very good crops, taking care not to cut the roots.

In principle, this soil maintenance, necessary for the truffles, does no damage to the truffle oaks although some consider that harrowing the soil with mechanical tools may damage the root system. The use of tractor-driven tools has been cited as one cause of the decline in truffle production, due to deeper tillage of the soil and the resulting destruction of many fine, mycorrhized, truffle-bearing roots. Other producers take exactly the opposite view and trim the roots with tractor-driven tools to stimulate the growth of fine new roots likely to develop mycorrhizae.

Water control

During the first two years after planting, water control is to stimulate new growth on the trees. Then, when truffle production has started, it is not the trees that need watering but the truffles. Once the truffles are formed, in May or June, the aim of watering is to keep them alive. During the production phase, watering takes into account both the truffle cycle, with the most sensitive or critical period in August, and the fact that truffles are drought-resistant (up to 20-25 days on average, provided that temperatures are not excessively high). The truffles are usually formed in June. Microsprinkling, with low-flow sprinklers (40-80 litres/hour) operating at low pressure (1-2 bars), provides a

practical, economical solution. This system requires good filtration on the water intake. It is unnecessary to water unproductive scorched zones. Watering takes place every 15-20 days in July (20-25 mm/0.8-1 in); every 10-12 days in August (20-25 mm); and every 15-20 days in September (20-25 mm). Covering the soil with branches lengthens the time the truffles can resist drought and makes it possible to offset a lack or shortage of water.

Pruning and thinning

Different regions prefer different approaches to pruning truffle trees. A new approach has been defined by the Montat Truffle-Growing Research Unit (Sourzat, 2008). This consists of maintaining the mycorrhized tree in an equilibrium where the truffle fungus is stronger than the tree. This relationship is expressed in terms of the radius of the scorched zone (Rb) and the radius of the tree canopy (Rf). The assumption is that the scorched zone should always be larger, as expressed by: $R_b \geq 1.5 R_f$. The general rules are as follows:

- Start by pruning non-producing trees to give the truffle-producers more room.
- Prune productive trees later to maintain sustainable production.
- Truffle-producing trees should be pruned gradually. To reduce the risk of failure, it is advisable not to prune all the trees in a plantation at the same time, but only one-third each year.

- Pruning is carried out in early spring, generally in March. August pruning is most effective for reducing trees vigor.

- Thinning is based on the same principle as pruning. When the truffle mycorrhizae no longer have space to expand (e.g., in a clearing), they stop producing. A. De Bosredon had already observed this in 1887: “A truffle field that stops expanding, that is no longer moving in any direction, starts to waste away and soon dies.” The fact that a closed environment results in the end of truffle production can be explained by the loss of room for expansion in which case the truffle can no longer exercise the virulence necessary for it to bear fruit. It should also be added that, in addition to requiring an expansion area,



4/ Truffle plantation mainly with kermes oaks (*Quercus coccifera*) in the Pyrénées-Orientales.

truffles need host-trees (oak) with young, growing roots. Thinning consists of eliminating 60-80% of the trees in a plantation, which generally has 300-400 trees per ha (2.5 ac). Once thinning reaches a certain level, it is better to cut down the plantation and plant a new one.

The impact of pruning and trimming on the health of the oak trees is not really taken into consideration (it is done for the truffles!) other than by recommending that pruning take place in spring. However, certain practices, particularly in Italy (Sourzat, 2009), involve pruning and trimming almost all-year-round using a wide range of tools, from secateurs to chain saws, and hedge-trimmers. In France, the oaks are pollarded at a height of 2 to 3 m/6.7-9.9 ft. To a certain extent, truffle oaks are mistreated to promote *T. melanosporum* truffle production.

The main parasites of truffle oaks

The list of oak parasites treated by truffle growers is limited by comparison to the number of known diseases and pests.

1. Oak powdery mildew, which takes the form of a white, fuzzy coating on the oak leaves, mainly affects downy and pedunculate oaks. The damage is generally prevented by spraying the trees with micronized colloidal sulphur in late May to mid-June.

2. Oak anthracnose, a fungal disease that is especially widespread in the Périgord and northern Lot areas, causes premature leaf drop on durmast oaks. Successful treatment trials have been carried out using prochloraz and mancozeb, available commercially. Experimental treatment with 46 g prochloraz as the active ingredient in 100 litres water sprayed on the oak foliage once per month, from late May to late August, gave satisfactory results. Austrian oak is now being planted instead of durmast oak as a preventive measure.

3. Defoliating caterpillars caused considerable damage in the 20th century (1930-31), even destroying some truffle plantations by devouring all the foliage on the durmast oaks. The main culprits are *Lymantria dispar* L. caterpillars and the Plant Protection Service recommends biological pest control using *Bacillus thuringiensis* Berliner, also commercially available.

4. Oak roller moth (*Tortrix viridana* L.) caterpillars roll the young leaves into tubes to provide shelter for their cocoons. The damage is noticeable starting in April and the treatment is similar to that applied in the case of defoliating caterpillars.

5. Oak moths (*Lithocolletis joviella* Const.) live on holm oak leaves. The larvae remove the leaf cuticles to eat the inner tissue. The products used to treat defoliating caterpillars are also effective in this case.

6. Leopard moths are nocturnal members of the superfamily *Cossoidea*, whose larvae sometimes infest oak branches. It is curious to observe that the destruction of the top of an oak tree by leopard moth larvae is sometimes accompanied by the start of truffle production.

7. The oak burncow is a beetle that causes similar damage to leopard moths on holm and durmast oaks. It is advisable to burn any branches infested with this pest.

8. Oak canker or phomopsis causes swellings on the bark and crevasses of varying depths on the branches. This fungus is favored by imbalances and causes damage when the trees are suffering from drought or poor upkeep.

9. Lichens are not parasites. They colonize tree branches when the air is damp and unpolluted. However, truffle growers often have the impression that the proliferation of lichen on the branches is depriving the tree of nourishment.

10. Large and small animals may cause worrying damage to plantations. Wild boar

cause the most damage in young plantations, where they uproot the saplings, while in more mature plantations they dig up the soil looking for earthworms and often disturb immature truffles. The usual preventive measure is to install an electrified fence.

Future prospects

Climate warming is a limiting factor for truffle production. *T. melanosporum* is tending to spread northwards in France, in conjunction with holm oaks. Research at INRA has demonstrated how truffles accompanied oak trees in their recolonization of France after the last Ice Age, approximately 10,000 years ago. This work (highlighted by Francis Martin at INRA, Nancy) was based on phylogenetic analyses and considered the genetic and geographical distances between genotypes (Murat et al., 2004).

Initial results obtained by cloning mycorrhized oaks with different truffle strains is one avenue to be explored for improving truffle growing (Chevalier et al., 2008). Thanks to experiments carried out over more than 9 years by INRA in Clermont-Ferrand in Southeast France (Valensole), Gérard Chevalier demonstrated that the geographical origin of the truffles used to inoculate saplings of the same clone of downy oak had a major influence on production. This researcher has also collected around sixty strains of good truffle-producing downy oak from all over France. These strains were isolated by Jean-Philippe Lemaire (INRA) starting in 1998. These clone mothers are conserved by the State Tree Nursery at Guémené-Penfao (Loire-Atlantique). The Robin Tree Nursery (France) took cuttings from an excellent downy oak in the Hautes-Alpes and inoculated it with truffles from the production site. This clone is now commercially available. In Europe, certified mycorrhized truffle oaks are used to produce four truffle species: *T. melanosporum*, *T. uncinatum*, *T. aestivum*, *T. magnatum*.



5/ Nursery of mycorrhized oaks for *Tuber melanosporum* production.

The French Truffle Growers Federation is working on restoring truffle production to its earlier abundance, particularly through a scientific program (SYSTRUF) funded by ANR (Agence nationale de la recherche) and a series of experiments subsidized by FranceAgriMer and several local and regional authorities. While the quality of the plant material is no longer, apparently, a limiting factor, particularly with the mycorrhized seedlings certified by INRA and CTFIL, production seems to be subject to other constraints, particularly frequent summer droughts and fungal contamination from durmast oak woods around truffle plantations. Ultimately, this shows that, while oak trees are the best friends of truffles, they may also be their worst enemies.

Acknowledgements

Much of this information was collected thanks to theoretical and experimental research programs funded by FranceAgriMer (ONIFLHOR, VINIFLHOR), Région Midi-Pyrenees, Conseil Général du Lot, the French Ministry of Agriculture, Fisheries, and Food, and the European Union (FEOGA). Europe contributed to the dissemination of the findings via the FEADER program (measure 111B). Advice, comments, and encouragement from Jean Olivier, the coordinator of truffle experiments in France, have always been much appreciated in conducting the work presented here.

Photographers. Title page: Pierre Sourzat (*Tuber melanosporum*). Photos 1-5: Pierre Sourzat.

Bibliography

- Bonnet, Henri. 1869. *Etude sur les truffes comestibles*. Paris: Adrien Delahaye.
- Callot, G. 1999. *La truffe, la terre, la vie*. INRA Editions.
- Chatin A. *La Truffe*. 1869, 1892. Paris: J.B. Baillièrre et Fils.
- Chevalier, Gérard and Mario Palenzona. 2008. Les implications de 40 années de recherché sur les truffes: perspectives d'avenir. *Actes du 3e congrès international sur la truffe de Spoleto*.
- De Bosredon, A. 1887. *Manuel du Trufficulteur*. Périgueux: Laporte.
- Delmas, J. 1976. La truffe et sa culture. *S.E.I., Etude n° 60*.
- Ferry de la Bellone, F.M.C. de. *La Truffe*. 1888. Paris: J.B. Baillièrre et Fils.
- Murat, C., J. Diez, P. Luis, C. Delaruelle, and C. Dupré. 2004. Polymorphism at the ribosomal DNA ITS and its relation to postglacial recolonization routes of the Périgord truffle *Tuber melanosporum*. *New Phytologist*, 164: 401-41.
- Olivier, J.-M., J.-C. Savignac, and P. Sourzat. 1997, 2002. *Truffe et Trufficulture*. Périgueux: Editions FANLAC.
- Pradel, L. 1914. *Manuel de Trufficulture*. Paris: J.B. Baillièrre et Fils.
- Reyna, Santiago (coord.). 2007. *Truficultura: Fundamentos y técnicas*. Madrid: Mundi Prensa.
- Ricard, J.-M. 2003. *La truffe, guide technique*. Editions CTIFL.
- RiOUSSET, L., G. RiOUSSET, G. Chevalier, and M.C. Bardet. 2001. *Truffes d'Europe et de Chine*. Editions CTIFL et INRA.
- Sourzat, P., M. Kulifaj and C. Montant. 1993. *Résultats techniques sur la trufficulture à partir d'expérimentations conduites dans le Lot entre 1985 et 1992*. Le Montat: Station d'Expérimentation sur la Truffe / GIS Truffe.
- Sourzat, P. 2001. *Résultats techniques d'expérimentations à l'usage pratique des trufficulteurs*. Le Montat: Lycée professionnel agricole de Cahors.
- Sourzat, P. 1989, 1995, 2002. *Guide pratique de trufficulture*. Le Montat: Station d'Expérimentation sur la Truffe/Lycée professionnel agricole de Cahors.
- Sourzat, P. et al. 2008. *Les sols truffiers*. Paris: Fédération Française des Trufficulteurs.
- Sourzat, P. 2011. *Petit guide pratique de trufficulture*. Le Montat: Station d'Expérimentation sur la Truffe/Lycée professionnel agricole de Cahors.
- Sourzat, P. 2000, 2001, 2002, 2003, 2004, 2005, 2006. *Compte rendus des actions d'expérimentation sur la truffe (selon le programme validé par l'ONIFLHOR et la Région Midi-Pyrénées)*. Le Montat: Station d'Expérimentation sur la Truffe/Lycée professionnel agricole de Cahors.
- Sourzat, P. et al. 2004. *Questions d'écologie appliquées à la trufficulture*. Le Montat: Station d'Expérimentation sur la Truffe/Lycée professionnel agricole de Cahors.



1/ The Saint-Elix oak in the summer (Theux).



The Mark of the Oak Tree in Gascony: from Dugout Canoe to Brandy

Chantal Armagnac
La Rivière
F-81340 Trébas, France
chantal.armagnac@hotmail.fr

ABSTRACT

From Spain, the oak conquered Gascony with its different complementary forms (common oak, durmast oak, pubescent oak, Pyrenean oak, cork oak, evergreen oak) becoming established in different areas. A treasure trove for Gascony, these oaks became indispensable partners in successfully providing for essential needs such as protection, nourishment, building, conquest, embellishment, etc. Without the oak, establishing the grapevine would have been impossible. The author draws attention to remarkable and specific populations as well as to veteran, isolated trees that are powerful symbols of hope and imbued with mythology. The area considered by the author is delimited by the triangle formed between the Atlantic Ocean, Gascony and the Pyrenees and corresponds to what was known at the end of the first millennium as the Vasconie, the land of the Princes Vascons.

Keywords : oak usages, Gascon history, *armagnac*, winemaking, traditional medicine, artisan crafts

Introduction

My aim is to show that oaks have been providential trees for Gascons since ancient times. The Gascons have always had a privileged relationship with vines, but oaks have provided them with a very wide range of resources and services, and have affected their lives to a huge extent.

The geographic area and historical period selected for this research is Gascony around the year 1000, when the power of its founding princes, the Vascons, who originated from the Pyrenees mountains and gave Gascony its name, was at its peak. At the time, Gascony covered a triangular territory, bordered by the Pyrenees Mountains (which was the major water source for Gascony when the forest covered their slopes), the Atlantic Ocean, and the Garonne River.

I was born in the heart of this province of Gascony, in an area known as Armagnac Noir (Black Armagnac), which long deserved this somber title, reflected in the description published in 1902 by Paul Duffard, priest and keen ethnologist; "...vast woodlands populated with oaks that stood here in the time of the druids; heathland covered in heather and prickly broom; marshes clogged with reeds and undergrowth; and roads impassable for horses in winter..."

This study pays homage to all the ancient oaks (some of which, unfortunately, succumbed to the great storm in 2009) as well as to their more modest offspring, especially the one that, thanks to a forgetful or crafty jay, grows high up on the stone wall of the church where I was baptized, in Panjas, deep in Armagnac Noir.



2/ Oak forest in Monlezun.

Where did the Gascon oaks come from?

The migration of oak trees from southern Spain, where they were trapped during the last Ice Age, is an astonishing tale. As soon as the climate started to become warmer, oaks spread towards the north and crossed the colossal ramparts of the Pyrenees, preceded by the jays and crows. Pedunculate, sessile, pubescent, Pyrenean, cork, and holm oak all played the role of bridgeheads, helping each other to consolidate their colonization of Gascony. There is an oak capable of adapting to any situation: pedunculate oaks in deep, well-watered soils along the Adour River and Leyre rivers; sessile oaks on the dry hillsides of the Gers, in Auscitain country; Pyrenean oaks in Chalosse, as well as on the acid soils of *les landes**; pubescent oaks in the limestone soils of the Astarac and Lomagne areas; holm oaks on the south-facing slopes of the Pyrenees and the Atlantic dunes; cork oaks, known as *corsiers* in Marensin (a coastal area of *les landes*) and *sûriers* in the Pays d'Albret (around Mezin and Nérac).

There are even a few indomitable oaks at higher altitudes than expected: sessile oaks grow at 1,600 m (5,200 ft) in the Bareilles forest east of Arreau and at 1,700 m (5,576 ft) on the slopes of the Pic de Céciré, near Bagnères-de-Luchon. Pedunculate oaks continue to compete with beeches in the Irati forest at 1,300 m (4,264 ft).

The folks that followed the oaks

Some time after the oaks, men and animals ventured up into the mountains. Cromlechs and rock engravings mark the presence of these early inhabitants. The history of the Gascon people started among the oaks. The first huts were built in the oak's branches, its trunk provided our first tools, and it was easy to climb from branch to branch to pick acorns, then down to ground level to “go from honey to boletus mushrooms and truffles”! These ancestral oaks provided shelter and food, and mediated between the material world and the human imagination.

The history of humans and oaks in Gascony represents a superb love story between people and plants that starts in the most remote areas of the Basque Country, through the grazed forests of pollard oaks around the Rhune Mountain to the improbable holm oaks on the Soulac peninsula, and the ancient specimens at the *airial* farmstead in Sabres not to mention the cork oaks in Mézin, the oak avenue at Garaison near Lannemezan, and the oldest paper mill in Gascony at Cahuzac, with its skillfully woven branches, etc.

A source of food and healing

Oaks belong to the family *Fagaceae* (from the Greek word *phagô*, to nourish). And indeed, the acorns are as sought after as the blackberries that grow at the base of the tree or the honey made by the wild bees that live in it. In years when other crops failed, acorns were dried, ground into meal and mixed with cereal flours. The oak was king when wild berries and vegetables formed the base of the human diet and, afterwards, in times of need, acorns helped to offset shortages (for example, as a coffee substitute).

Acorns, are not only nourishing, they are also considered to be a fertility aid; this is

* Editor's note: *les landes* refers to a specific ecosystem composed of low-lying heaths and marshes, typical of certain areas in Southwest France and whence comes the administrative name of the department, Landes.

reflected linguistically since the same words in Latin, *glans*, *glandis*, mean both “acorn” and “penis tip”.

When the first animals were domesticated, they were brought to graze beneath oak trees – preferred to beech by the local shepherds. Local records confirm these customs, as well as the transhumance of sheep and pigs from Béarn. In the absence of transhumance, pedunculate oaks were planted at regular intervals to meet the needs of the villagers. These plantations, known locally as *plantades*, are still alive today: the best example is just on the outskirts of the village of Ibos, on the road to Pau. In years when crops failed, grazing animals in the *plantade* was prohibited and the acorns were reserved for human food.

The tradition (today successfully revived) of raising black Gascon pigs, one of the oldest breeds in France, is closely linked to oak trees. The production of Bayonne ham took root in the Adour valley thanks to the combination of three factors: extensive oak woods, the mild climate, and sources of salt water.

Pheasants, turtledoves and wood pigeons also grow fat on acorns. The wood pigeon migration routes lead to Gascony and its acorns which in turn has led to the tradition of pigeon hunting and the building of *palombières* (hides for pigeon shooting) – in oak trees.

Oaks are associated with other treasures such as boletus and chanterelle mushrooms, not to mention truffles! Indigenous durmast truffle oaks have been found in Montferran-Savès. The truffle market in Seissan, near Auch, becomes better known every year. Plantations of truffle oaks recently started operating successfully on the hillsides near Saint-Clar and Tournan in the Gers. Mycorrhized oaks have even been planted at Château Garreau in Labastide-d’Armagnac to promote the growth of boletus mushrooms.

If you are invited by locals to taste these specialties in their homes, you will surely notice the salt chest made of oak, displayed proudly in the corner by the fireplace, smoked to a lovely patina and polished by the rough fabric of all the trousers that have sat on it over



3/ Oak is king of the *airial landais*.

the years! Perhaps an ancestor, sitting on the chest, will tell you a story – one of the many that I have heard over the years. For example, about the many medicinal uses of the huge oak tree beside the house; how it provides shelter for carts and farm machinery, as well as perches for guinea fowl, chickens, and children. Or about how oak bark cures skin diseases and heals nasty wounds and throat infections. Note that only bark from young branches is used for medicinal purposes, while bark from adult limbs is reserved for tanning. At one of these farms, you may notice that a dog with new-born puppies in the yard is wearing a cork-oak-bark medallion, thought to hasten the end of the lactating period.

Perhaps your host will take you out to his vineyard, which traditionally has a few peach and walnut trees, as walnut wine and peaches preserved in wine are recommended for their fortifying properties. Or he may offer you a taste of *armagnac* (brandy). This grape spirit, aged in oak barrels, combines the health-giving qualities of both of its precursors. Oak toughens and wine cleanses.

Construction materials

Traditional, half-timbered houses, especially those in the Landes, have been dated on the basis of analyses carried out by Béatrice Szepertyski. Wood-core samples taken from the timber frames of these farm buildings indicated that they were built as long ago as the 18th or even the 12th century! These farms were built in the *airial* clearings, when the ancient deciduous forests of Gascony were felled, and not during the more recent colonization of the heathland. “An *airial*, both an architectural unit and an element in a subtle ecological balance, includes sots (pig pens), an oven, a well, a barn, off-ground chicken coops, water troughs, and houses. The kingpin in this balanced environment is certainly the oak tree: is it not the tree of the sun, protector of the earth and of houses?” (Daney, 1992).

Oaks also provided the roof timbers for our market halls and churches. It is said that a thousand oaks from the vast municipal woods were felled to provide the outstanding roof timbers of the Saint-Girons church in Monein in Béarn.

The Gascons also needed to defend themselves. Heavy oak palisades provided fortifications around the towns in Gascony during the Hundred Years’ War. Centuries later, on orders from Napoleon, oak timbers were taken from the hillsides in the Gers to strengthen the defenses of Bayonne, Saint-Jean-Pied-de-Port, Socoa, and Navarrenx.

Amazingly, some more unusual constructions have stood the test of time:

- lines of thick oak stakes, set deep into the clay, and used to support piled beams and planks, were discovered in the port of Bordeaux when archaeologists were exploring the ancient harbor that dates back to the first century of our era;

- a 300 m/984 ft dike, consisting of 3 rows of oak pillars and canal braces filled with compact masonry, and built to divert the Adour from Cap Breton and Port d’Albret towards Bayonne. This immense project was launched by Louis de Hay in 1572. Oak is rot-resistant provided it remains submerged in water. This is why oak from the Adour valley is still sought after today to make pilings for dikes in Holland and in the city of Venice.

Transportation

Very early on, people wanted to be able to move about freely and fords were



4/ Dugout canoe, Abbaye de Flaran (Gers).

inconvenient. Using oak beams they built roadways and constructed bridges over rivers. For centuries, it was easier to travel by water than overland, so it is no wonder that the Adour and Garonne rivers and their dense network of tributaries throughout Gascony are still revealing their secrets today. The oldest dugout canoes date from the Mesolithic era (8,000-9,000 years ago) and the most recent are barely a century old! The canoe found at the Lacaussade dike in 1995 (near Riscle-Gers), now kept at Flaran Abbey (Gers), is absolutely intact (6 m/19.7 ft long). Others may be seen in collections at Arthous Abbey (Landes) or the lake-site archaeological museum in Sanguinet (Landes).

Various types of craft were perfected over time: *galupes*, *bachets*, *chalands*, *couralins*, and *tilholes*. All are flat-bottomed, essential for travel on the shallow upper reaches of the Adour. The boat-builders' guild was active until 1930, sourcing oaks from the *barthes* (Adour flood plains). The boats would glide downstream to the port of Bayonne, loaded with wheat, honey, animal skins, and, from relatively early on, with wine and brandy. On the Garonne River, these flat-bottomed boats are known as *gabarres*. Although *galupes* and *gabarres* have almost disappeared (except for river tourism), the smallest of these boats, the *couralin* (a name derived from the Gascon word *couarou*, heartwood), is still used by fishermen.

For the needs of the French navy, Colbert sent Louis de Froidour to Gascony to prospect the woods and forests. Our finest oaks thus sailed the seas around the world. Furthermore, the woodsmen in the Pyrenees foothills knew how to train an oak – by planting it with beech – to obtain properly curved timbers needed in shipbuilding. Often naval orders insisted that the oak be sourced from the heart of Gascony (near Auch) but in 1760 the bullock drivers

from Labastide-d'Armagnac refused to obey orders to transport 1,680 ft³/47.6 m³ of oak from Auch to Bordeaux to build ships for the coastal defenses. The same reluctance to carry wood to the naval shipyards in Bayonne was reported in Baigt in Chalosse and later in Lannes. Was this an example of the typically Gascon rebellious spirit?

Everyday tools and gadgets

In Gascon farms in the 19th century daily life involved around twenty separate crafts. A farmer's skills included winemaking, cereal farming, animal breeding, forestry, mechanical repairs, woodcutting, carpentry, cabinet making, and maintenance. To carry out these tasks efficiently, a large range of tools, fitted with handles or attached to a base to multiply their strength, were made from oak wood. Oak wood was also used to make workbenches, vices, anvil blocks, turning benches, cog wheels, grape-crushing cylinders, and winepress screws. Wooden ploughs, harrows, and rollers were made to work the land. "To make the latter, the trunk of an *escos* (pollard oak) was chosen, leaving the branches to serve as fuel for heating and cooking. Because (these pollards) were cut back repeatedly, they grew much faster than normal trees. The trunk became extremely hard and dense. A roller made from this rock-like wood would easily break clumps of clay in the soil." (Roland Dumas, Panjas, Gers; personal communication.)

Gascony had a large number of mills: not only water and wind, but also tidal, mills at the mouth of the Adour. "Their functions (flour milling, fulling mills for wool and paper, sawmills, and oil presses) varied according to local resources and needs. In all cases, the floor of the mill race was lined with enormous oak trunks. This prolonged immersion was intended to harden and, at the same time color, the wood. Watermill gears, lock gates and farrier's shoeing stands required similar treatment. Similarly, oak statues in churches have withstood the test of time with the same treatment. The trees used to make the choir stalls in the Auch Cathedral (a jewel of Renaissance art) spent several years underwater in the Gers River." (Quereilhac, 1987)

We cannot do anything without oak wood: a hollowed trunk makes a good vat and cloth is dyed in it with oak ash, considered to be the best; heartwood planks are used to make washboards used at the spring; and cork is used to make beehives, floats for fishing nets, and stoppers for *cuyons*, flasks used by shepherds to carry beverages. When shepherds in Bigorre graze their sheep on land to be fertilized, they set up a mobile pen made of wooden barriers that they move every day. Every night, they sleep in a portable hut made of oak wood, called a *burguet*, which provides both bed and shelter.

"When we take the young heifers out to graze for the first time, they are bursting with energy. We prepare fetters using young shoots from the oaks that grow in the meadows. They must be thinner than a man's finger and we cut them in the spring when the sap is rising. It takes practice to twist them and make eyelets on both sides to attach them. When we take a pair of bullocks to market, we harness them with a *jouète*, a piece of oak about 10 cm/3.9 in in diameter and long enough to rest on the necks of the two animals. We then insert two *trabouns*, oak twigs as thick as a man's thumb and twisted in the fire, into the two holes at each end. The *trabouns* fit around the bullocks' horns and hold the harness in position." (Gilbert Lizé, Monclar-d'Armagnac; personal communication)

Oak is the champion for household purposes. It is used for winemaking containers (barrels and vats of various sizes); laundry vats; salting vats; barrels for storing gunpowder, salt, fish, oil, flour, etc. Children also use it to make tea sets for dolls with

acorns and cupules becoming miniature cups and glasses. My grandfather used dried oak galls to make toys: a forked oak stick, a gall pierced on three sides, a piece of thread 50 cm/19.5 in long, and a large piece of elder wood with the pith removed made a primitive noisemaker.

Oak wood sometimes found unexpected uses: on the hills around Lelin-Lapujolle in 1956, there was so much snow that some clever folks used oak staves from dismantled barrels as skis to move around when walking was impossible. Oak is also used in bullrings: the *talenquère*, a wooden fence 1.4 m/4.9 ft high behind which men could find protection from the cows and bulls, is, of course, made of oak. The bullrings in Estang and de Manciet, classified historical monuments, were built of oak donated by the villagers. In Vielle-Soubiran the ring was constructed between two ancient oaks which provide welcome shade for the audience during summer contests!

Traditionally, a Gascon girl's dowry consisted of an oak table and a carved chest where she stored her sheets, towels, and table-cloths, all made of linen. When money was needed for a wedding, to repair a roof, to buy a tractor, etc., the farmers drew on their savings by felling two or three oak trees. Occasional expenditures like these were made possible thanks to the trees. Our grandparents thought of oak trees as an investment that could be called on in case of need.

Perhaps, as our Gascon farmer was making the wedding chest for his daughter, he would set some planks aside for his own coffin. Some cabinet-makers and carpenters can identify the origin of a piece of oak immediately. The nicest specimens, from Mormès and Le Houga, are recognizable by their veining, color, aroma, and grain – as though the Armagnac soil nourished the trees better than any other!

Superstitious or simply fond of marvels?

A special oak log, larger than all the rest, was always set aside for Christmas. It took two people to set it on the firedogs and a large bundle of vine cuttings to set this huge block of wood alight. If the log took three days to burn, we were assured of good luck for the coming year. I remember that the charcoal produced from this oak log was carefully collected by my grandmother. She always used a piece of it to draw a cross on the door posts of the rabbit hutch and sheepfold, while the rest was ground to powder and dissolved in water for the poultry, to protect them. Our neighbor's wife used to protect her young poultry by collecting pollen from the vine flowers, waving it symbolically over the traditional Saint John's day fire, and mixing it with their food.

Intertwined destinies for vine and oak

Oaks are usually accompanied by a band of loyal helpers, which all contribute in different ways to the making of wine and brandy. Over the centuries, acacia has replaced oak for vine stakes, hazelnut and chestnut have been used as barrel hoops, and various varieties of alder trees have provided wood to heat brandy stills. Rushes, so plentiful in ponds around the Armagnac area, are used to seal the heads on the barrels. Oak has thus become devoted exclusively to the cask itself, with the added benefit that it enhances the content. By definition and according to the AOC (Appellation d'Origine Contrôlée) regulations, *armagnac* is a grape spirit aged in wood – and not just any wood – it must be Gascon oak! According to Joseph de Pesquidoux: "Our split-oak staves have their own



5/ *Armagnac*, matured in oak casks, changes color with time.

specific aroma. They smell of damp soil and marauding beasts, a sort of animal odor that gives the brandy a wild aroma even after five years in the barrel.” It is said that the best blends come from wood and vines that grow side-by-side.

Thus, some privileged producers, who own both forest and vines, invite their cooper to scour their land for a strongly rooted oak with solid branches and no frost damage or knots, to be felled preferably during a waning moon. The fast-growing trees of the forest fringe were never used for this as their wood makes leaky barrels. Comparative ageing tests using wood from different origins have demonstrated that the quality of the brandy varies in function of oak provenance. Factors such as the proximity to rivers and the type of soil where the tree grew have an impact on the types and diversity of the aromatic substances released from the oak into the spirit.

Oak trunks are cut into logs just over 1 m/3.3 ft long, then split into 2, 4, and, finally, eight sections. 5 m³/176 ft³ of stripped logs produce 1 m³/35 ft³ of finished wood, used to make seven traditional *pièces* (barrels) of roughly 400-420 l/88-111 gal. (Divine proportions considered the best size for *armagnac*-ageing barrels due to the ideal ratio between the surface area and volume.) The split logs are piled carefully in layers in alternating directions, so that water can drain off. The aromatic compounds present in each *pièce* also depend on two stages in the cooperage process: the natural seasoning of the staves and the degree of toasting of the barrel, during the bending operation to shape the staves into the finished barrel. Toasting leads to the development of compounds likely to enhance the aromas of the spirit and also produces tiny cracks that expose deeper layers of the wood, releasing different volatile substances. The wide range of aromatic substances produced (from toasted almonds to carnations, as well as smoky verbena) result in a finer *armagnac*. They add nuances to the supple oak tannins and rich aromas that gradually bring softness and complexity to offset the strength of the spirit. Note that oak chips (alternatives to barrel-ageing) are only permitted in winemaking. Their use is strictly prohibited in producing *armagnac*, which must be aged in the barrel.

The ageing cellars, with their masterpiece roof timbers, provide a superb setting for

time and oak to work their alchemy. The multiple uses of oak in the cellars reminds one of nested Russian dolls. The oak provides several protective layers for the grape spirit, from immediate contact to more distant uses. The barrels, made of oak, are supported by pieces of wood, known as *tins*, made of oak heartwood and they may be stacked on several levels, right up to the roof of the building, made of oak, supported on a careful assembly of beams and laths also made of oak!

Oak and art

While oak stimulates the sight and touch of cabinet-makers, and the taste of coopers and cellar masters, it also pleases the ear, as shown by the amazing work of José Le Piez, who taps on oak wood to detect the resonances specific to each oak log.

Another extraordinary piece of art was conceived by Ernest Pignon. Ernest, who was so impressed by the ancient oaks in the forest of *les landes* that he delved into botany and biology to create his famous Arbrorigènes: plant sculptures that embrace tree trunks and are nourished by water and light. Truly an artistic creation derived from a combination of biotechnology and ancient myths.

Conclusion

The most ancient brandy in France – *armagnac* – was born in Gascony (an ideal location with plenty of woods and vineyards) and nowhere else. During a fabulous period around the year one thousand, learned men from many cultures (Moslem, Jewish, and Christian) shared their knowledge and worked to spread it from East to West. Their fantastic translation work offered new perspectives to the whole world. *Armagnac*, the result of experiments in distillation, is thus also a lesson in tolerance.

But, without oaks, the vines would have come to nothing!

And what would people have done without oaks and vines?

Photographers. Title page: Chantal Armagnac (acorn flour). Photos 1-5: Chantal Armagnac.

Bibliography

- Armagnac, Chantal. 2008. *Le chêne, arbre roi de Gascogne*. Estang: Editions Le Vert en l'Air.
- Daney, Charles. 1992. *Dictionnaire de la lande française*. Portet-sur-Garonne: Editions Loubatières.
- Doussot Franck. Variabilité des teneurs en extractible des chênes sessile et pédonculé, influence sur l'élevage en barriques. Thèse de doctorat. Université de Bordeaux, 2010.
- Duffard, Paul. 1902. *L'Armagnac noir ou Bas-Armagnac*. Imprimerie centrale.
- Kerlorch, Gilles. 2012. *La batellerie de l'Adour en images*. Editions Cairn.
- Kremer, Antoine and R.-J. Petit. 2001. L'épopée des chênes européens. *La Recherche*, N° 342.
- Mussot-Goulard, Renée. 1996. *Histoire de la Gascogne*. Paris: Editions Presses Universitaires de France.
- Pesquidoux, Joseph de. 1984. *Chez nous en Gascogne, travaux et jeux rustiques*. Paris : Editions Plon.
- Quereilhac, Jean-Louis. 1987. *Meuniers et moulins au temps jadis*. Paris: Editions France Empire.
- Szepertyski, Béatrice et François Lalanne. 2002. *Airiaux des Landes de Gascogne*. Belin-Beliet: Editions Maison du Parc.



Bringing Scientific Oak Collections to Life for Garden Visitors

Emily Griswold

Director of GATEways Horticulture and Teaching Gardens
University of California Davis Arboretum
1 Shields Avenue
Davis, CA 95616, USA
Phone: +1 530 754 8038
ebgriswold@ucdavis.edu

ABSTRACT

Many scientific tree collections in public gardens hold great value for conservation and research but are not particularly appealing to visitors. These collections represent a missed opportunity for engaging visitors in science learning and instilling an appreciation for the value of plant biodiversity. Over the last three years, the UC Davis Arboretum has transformed Shields Oak Grove from a traditional, underappreciated scientific tree collection into a lively destination. First planted 50 years ago, the collection includes beautiful, mature specimens of over 90 taxa of oaks from around the world. A new interpretive trail, student-created art/science fusion installations, visitor-tested interpretive signs, musical performances, and a cell phone audio tour now engage visitors to the grove in new ways. These innovative programs, exhibits, and installations bring forward rich and compelling stories related to the natural and cultural history of the oaks that resonate with visitors of all ages.

Keywords: *Quercus*, UC Davis Arboretum, Shields Oak Grove, interpretation, education, art/science fusion

Introduction

In addition to their value for research, conservation, and university-level teaching, scientific plant collections in public gardens have the potential to play a significant role in public education and outreach. The challenge is figuring out how to engage garden visitors, who likely have no background in plant science, with a traditional taxonomic collection.

Today's public gardens tend to draw from two major historic traditions: the academy garden and the pleasure garden. In academy gardens, plants were grown in collections to support scholarly pursuits related to teaching and research. In pleasure gardens, plantings were developed to entertain, relieve stress and provide beauty and sensory delight for visitors. The most successful public gardens combine these two traditions to provide places of extraordinary beauty and scientific value. However, many still struggle to connect visitors with the meaning and value of their scientific collections; and scientific tree collections rarely compare with children's gardens, orchid exhibits, rose gardens or train gardens as popular visitor destinations.

In 2008, the UC Davis Arboretum received a grant from the US Institute of Museum and Library Services and took on the challenge of developing an interpretive trail, signage and educational programs to enhance the visitor-friendliness and educational value of the Peter J. Shields Oak Grove. Four years later, Shields Oak Grove serves as an interesting case study of how a scientific collection can be enhanced to also serve as an enlightening visitor destination.

About Shields Oak Grove

Started in 1962, Shields Oak Grove contains almost 300 trees representing over 90 taxa of oaks spread out over 10 acres/4 hectares in a park-like setting, making it one of the largest collections of oaks in the United States. In 2007, the collection was inducted into the North American Collections Consortium (NAPCC) Multisite *Quercus* Collection in recognition of its diversity and conservation value. Researchers had been using the collection for decades for studies on oak taxonomy, ecology and pathology; and oak enthusiasts made annual pilgrimages to collect acorns and examine the trees. To a limited extent, the collection was also used for university teaching and laboratory exercises.

From the perspective of most visitors, however, Shields Oak Grove was a pretty park – a place to throw a Frisbee or have a picnic. Despite the presence of plant labels, the tremendous diversity of the tree collection remained largely invisible to casual visitors. Without a trail system, there was not a clear way to explore the deeper reaches of the grove. Some of our more urban visitors expressed fears that if they went in too deep that they would get lost and wouldn't know how to get back out. The occasional guided tour would reveal some of the rich stories about the oaks, but otherwise the arboretum's most significant scientific collection was largely unacknowledged and unrecognized by all but a few arboretum staff, docents and oak specialists.

Despite this situation, the arboretum staff saw in Shields Oak Grove the raw potential for a popular and engaging visitor exhibit. The collection had:

- *Beauty*: The grove was full of majestic, mature trees – many over 40 years old.
- *Name recognition and charisma*: Oaks are widely recognized and valued as an iconic element of the California landscape.



1/ A new trail system and benches contribute to visitor comfort in the oak collection. Native grass understory plantings complement the natural beauty of the trees.

- *Great visual variety:* With a mix of tree and shrub species from temperate, subtropical, and Mediterranean climates, the collection had examples of the diverse forms of oaks.

- *Cultural connections:* We could tap rich stories about ethnobotany of oaks, human uses of oaks around the world, and oaks in religion, mythology, literature, and art.

- *Horticultural promise:* The collection could be used to aid in tree selection for gardens and to demonstrate techniques for gardening under oaks.

- *Wildlife connections:* Oaks provide food and shelter for an extraordinary diversity of wildlife and insects. For visitors with a strong natural affinity for animals, these creatures can be a “hook” to encourage learning about plants

In order to have the broadest impact, we selected the regional visitor as the primary audience for the oak grove improvements, rather than, for example, university faculty or students. As a university garden, we aim to use the arboretum as a stage to showcase the academic work of UC Davis to our regional visitors. Our first step in the process of transforming Shields Oak Grove was to conduct a visitor survey to assess our regional visitors’ basic knowledge about oaks and interest level in various topics about oaks. The results of the survey showed that visitors were most interested in: traditional uses of oaks, cultural connections, gardening under oaks, Sudden Oak Death, the habitat oaks provide and the history of Shields Oak Grove. By tapping into visitors’ natural areas of interest, we knew we could make more compelling interpretive materials and educational programs.

Our efforts to transform Shields Oak Grove into a more educational and visitor-friendly destination included physical improvements to the site and the creation of new educational programs. The physical

improvements were designed to improve visitor comfort and access, highlight the beauty of collection, provide basic interpretation, and create artistic attractions.

Improve visitor comfort and access

Creating a new trail system had one of the most transformational impacts on the visitor experience in Shields Oak Grove. The trail provided a welcoming invitation to explore the grove in a more structured way and a guarantee against getting lost. After the Oak Discovery Trail and Oak Diversity Trail were installed, many long-time arboretum enthusiasts, and even several staff members, mentioned to me that the trail introduced them to parts of the grove that they had never seen before. The random-seeming meanders of the trail were carefully designed with the goal of escorting visitors past key tree specimens with interesting features for interpretation.

Along with the trail system, we added seating – both traditional park benches and a pair of long curved benches at the entry to the grove. Benches invite visitors to relax and linger in the collection and are particularly important as rest stops for visitors with limited mobility. The curved benches at the entry to Shields Oak Grove are sited under the cathedral-like canopies of four 90-foot tall *Quercus castaneifolia* C.A. Mey. The benches can seat 40 or more people and they serve as a gathering area for tours, an outdoor classroom, a venue for special events and a peaceful, shady refuge for visitors.

Highlight collection beauty

Our goal is for beautiful, mature, healthy, and well-maintained trees to be the centerpiece of Shields Oak Grove. Before we started our renovation, the ground plane under the trees was either mulch or turf. The flatness of the understory gave the grove a rather sterile, two-dimensional character and made the grove feel more like an urban park than a natural space. By adding an understory of native grasses and wildflowers, we were able to infuse more natural character back into the grove, giving it the feeling of an oak savanna. The understory grasses catch the light, sway in the breeze, and add more visual interest and complexity to the Shields Oak Grove environment. They create the sense of immersion in a natural habitat and prime visitors for learning about the nature and biology of oaks.

Provide basic interpretation

Ideally, a knowledgeable expert would always be on hand to lead oak tours and answer visitor questions. Since this is not possible, we use interpretive signs and plant labels to convey basic, foundational-level information about the trees for visitors. The seven interpretive signs along the Oak Discovery Trail address some of the topics that rated most highly in the visitor survey. A successful sign will attract and hold visitor attention and effectively communicate a message. Although this may sound simple, designing effective interpretive signs is challenging, because informal visitors come with their own personal agenda and interests.

The UC Davis Arboretum uses an innovative interpretive sign development process that involves teams of people from different disciplines and different audience segments to generate sign content. For this project, we had six arboretum staff, including both

horticultural and educational experts, and 14 community volunteers working for an intensive week on rapidly creating sign mock-ups, testing them in the grove with actual visitors, and revising them based on visitor feedback. Exhibit teams observed visitors interacting with the sign mock-ups and, finally, interviewed them about what they understood the messages to be (Photo 2). Following revisions from this formative evaluation, we submitted the most successful sign mockups to our graphic designer, who created the final designs. This process greatly increases the signs' ability to attract and educate visitors.

Display plant labels in Shields Oak Grove have been designed to hold information that would be of interest to both experts and casual visitors. This information includes the common name, scientific name, family name, section and/or subgenus name, native distribution and museum accession number.



2/ Arboretum interns evaluated the sign mock-up in Shields Oak Grove. Interpretation volunteers also observed casual visitors interacting with the sign to determine its effectiveness at attracting and holding visitor attention.

Create artistic attractions

We have found that art installations can attract new audiences to our plant collections and broaden their appeal among visitors. In Shields Oak Grove, we have focused on working with UC Davis academic programs to create site-specific art that helps visitors connect with educational messages about oaks.

The arboretum has partnered with the UC Davis Art/Science Fusion program since 2006 to create innovative collection-themed installations. Five of these projects over the

years have been in Shields Oak Grove, and we now have:

- “Tree of Life” – A mural focused on the biodiversity supported by the valley oak (*Quercus lobata* Née).
- “Oak Family Tree” – A mural depicting an evolutionary tree of oaks growing in the Arboretum collection.
- A series of 35 mosaic tree label plaques (Photo 3).
- “Oak Food Chain” – A bench-top installation showing a food chain connected to the coast live oak (*Q. agrifolia* Née).
- “Oak Circle of Life” – A bench-top installation illustrating the 800 year lifespan of an English oak (*Q. robur* L.) (Photo 4).



3/ One of the 35 mosaic tree label plaques that are positioned in front of key tree specimens along the trails.

The UC Davis Art/Science Fusion program is an undergraduate curriculum that links scientific learning with artistic expression. The co-founders of the Art/Science Fusion program, a ceramic artist and a faculty entomologist, teach an undergraduate class every fall – Entomology 1: Art, Science, and the World of Insects – in which students learn basic entomology and participate in the creation of a public ceramic art installation that depicts insects in the environment.

In fall of 2009, the Art/Science Fusion program created a series of 35 mosaic plant label plaques for key tree specimens along the Oak Discovery Trail and Oak Diversity Trail. Each student in Entomology 1 was responsible for making a label plaque profiling one oak species and an associated insect from the tree’s place of origin (Photo 3). Volunteer community members and local high school students also participated in making tiles of leaves, acorns and oak-associated wildlife for these beautiful plaques. The plaques have been very effective at drawing visitor attention to the unique features of each tree and

emphasizing the diversity and vitality of the collection. The expressive visual and tactile qualities of the plaques also make them very appealing to children.

The arboretum also serves as a rotating gallery space for students in the art, design and landscape architecture departments to mount temporary art installations. Last year, a landscape architecture student brought new life to a dying 150-year old valley oak (*Q. lobata* Née) by using the branches to create an impressive arch-shaped art installation in Shields Oak Grove. The installation calls attention to the “afterlife” of the tree as the decomposing bark and wood provide habitat for wildlife and insects. Temporary installations like this keep the garden fresh for returning visitors.



4/ “Oak Circle of Life” is a ceramic art installation on the surface of a curved bench at the entry to Shields Oak Grove. The bench serves as an outdoor classroom and informal gathering area.

Develop educational programming

To accompany and expand on the physical improvements to Shields Oak Grove, we developed a series of educational programs for arboretum visitors, UC Davis students and the regional community.

Attending a docent-led tour is a great way for visitors to get more in-depth information about a plant collection than interpretive signs could ever offer. Before the visitor-friendly physical improvements were made to Shields Oak Grove, only two arboretum docents were comfortable leading tours in the oak collection. Docent training became a key foundation to our plans for increased educational programming, because we needed a stronger base of volunteers who would feel knowledgeable enough about oaks to lead visitor tours and programs. In 2010, I led the first oak-themed docent training in over 15 years. Docents,

volunteers and student interns were invited to participate, and 30 individuals registered for the 12-hour training spread over four weeks. Participants learned about the basics of oak biology and ecology, human uses of oaks, oaks in horticulture and the history and management of the tree collection in Shields Oak Grove. In addition to leading public tours, the recently trained docents have assisted with interpretive sign development and helped with outreach events in the collection.

In addition to docents, UC Davis undergraduate environmental leadership interns, the “Arboretum Ambassadors,” have been integrally involved in the development and implementation of oak-related educational programs (Photo 5). The ambassador interns have planned major public outreach events, developed public tours of the oak collection, created a “*Quercus Crew*” club for kids and organized a series of environmental stewardship field day programs for underserved children in the region. The ambassadors effectively expand the scope and reach of our educational programs while they gain valuable experience in event planning, informal education, marketing and leadership. It is truly inspiring to see these college students get sparked with an interest in oaks and pass it along to children and families in the community.



5/ The Arboretum Ambassador interns in 2010 selected Shields Oak Grove as the focus of their outreach activities.

Arboretum Ambassadors were integral to the planning of Oak Discovery Day, an oak-themed festival, which was held in 2010 among the trees on the Oak Discovery Trail. With 18 activities ranging from an Arbor Day ceremony and oak song-writing workshop to natural history exhibits and a Native American acorn-grinding demonstration, the afternoon was packed with oak-related attractions. The event was also advertised as an International Oak

Society Oak Open Day, and Doug McCreary represented the Society with an information table. Hundreds of visitors attended this free event which served as a “grand opening” for the new visitor attractions in Shields Oak Grove.

Much as visual arts expand the audience for a scientific collection, so can performing arts. In summer of 2011, the arboretum hosted a progressive concert through Shields Oak Grove performed by the Sacramento City College World Music Ensemble. Named “Around the World in 80 Oaks”, the concert celebrated and honored the diverse origins of the oak collection. Over 200 people came to stroll through the grove, stopping along the way to hear music from some of the countries that are home to the (slightly more than) 80 varieties of oak trees in the arboretum. The program also included a poetry reading by the city of Davis poet-laureate and commentary by arboretum docents relating to the oak trees. We were overwhelmed by the positive response to this event and hope to be able to host similar events in the future.

Results

Because the arboretum is unfenced and integrated into the fabric of the UC Davis

campus, it is difficult for us to accurately track visitation. Observationally, we have seen a significant increase in visitors to Shields Oak Grove. It is now common to see visitors exploring the trails, reading the signs, enjoying the art installations, and relaxing on the benches. New tours and events in the grove have been well-attended. With increased attention on the oak collection, we have also received more private donations to commemorate trees, ceramic art, and benches that support the ongoing maintenance and development of the collection.

Next steps

Although we have made great strides to improve the accessibility of Shields Oak Grove, we still have room for improvement. We look forward to expanding our programming to continue sharing the riches of the oak collection with more visitors. The following are some of the plans we have been developing to build on the success of previous efforts with additional interpretation and educational programming.

Oak Discovery Day was a successful event but it required a large investment of resources to coordinate all the activities. If we scale back the number of activities, refine them so they are more attractive and educationally effective and increase volunteer training and involvement, we have the potential to be able to hold “Oak Discovery Drop-in Days” more regularly.

Visitors are hungry for more information about all the insects and animals depicted on the art/science fusion ceramic installations. However, we haven’t wanted to distract from the beauty of these art features by putting an interpretive sign next to each one. One alternative would be to create a paper brochure with labeled photos of the ceramic tiles. The brochure could be distributed at the entrance to the grove and made available on the arboretum website for visitors to download and print before their visit. Another more modern approach would be to integrate this information into an interactive smart phone application. UC Davis computer science students have already been working on programming a smart phone application that would serve as a visitor guide to the arboretum. After the first phase of development is complete, we hope to have them work on integrating an interactive map of Shields Oak Grove.

Hearing a story is quite a different experience from reading one – it can free your eyes to explore the environment and make observations. Many museums and botanic gardens are now making audio tours available for visitors via cell phone. Signage in the exhibit will prompt visitors with a phone number to call and a tour stop number to select in order to hear the message. The arboretum staff has been working on a cell phone audio tour that will reflect the voices of a variety of UC Davis experts speaking about the great diversity and many values and uses of the trees in Shields Oak Grove.

Photographers. Title page: Nikhil Joshi (in Shields Oak Grove). Photos 1, 3: Emily Griswold. Photo 2: Carmia Feldman. Photo 4: Allan Jones. Photo 5: Rose Swift.

Resources

You can find more information about the UC Davis Arboretum’s oak collection and copies of our interpretive signs by visiting our website (<http://arboretum.ucdavis.edu/oak-collection.aspx>). For more information about connecting visitors with collections, look to the National Association for Interpretation (<http://www.interpnet.com/>), an organization dedicated to supporting the profession of natural and cultural heritage interpretation, for publications and training events.

SPECIES	DISTRIBUTION	THREATS
Globally threatened		
<i>Quercus alpestris</i> Boiss.	Sierra de las Nieves	Overgrazing, loss of habitat, erosion
<i>Quercus alnifolia</i> Poech	Troodos Mountains, Cyprus	Fire, overgrazing, felling, human development
<i>Quercus aucheri</i> Jaub. & Spach	Aegean region and Anatolia (Turkey)	Small isolated populations
<i>Quercus ilex</i> L. subsp. <i>ballota</i> (Desf.) Samp.	Portugal and Spain	Fire, over grazing, loss of habitat
<i>Quercus pontica</i> K. Koch	Georgia and Turkey	Overgrazing
<i>Quercus robur</i> L. subsp. <i>imeretina</i> (Steven ex Woronow) Menitsky	Georgia and Russia	Felling and loss of habitat
<i>Quercus vulcanica</i> Boiss. & Heldr. ex Kotschy	Isparta province (Turkey)	Few isolated populations
Least concern		
<i>Quercus brantii</i> Lindl.	Turkey	
<i>Quercus cerris</i> L.	Central, East and Southeast Europe, Turkey	
<i>Quercus coccifera</i> L.	Mediterranean region	
<i>Quercus dalechampii</i> Ten.	Central, East and Southeast Europe	
<i>Quercus frainetto</i> Ten.	Southern and Central Italy, Balkan Peninsula, Northwest Turkey	
<i>Quercus ilex</i> L.	Mediterranean region	
<i>Quercus infectoria</i> Oliv.	Greece	
<i>Quercus ithaburensis</i> Decne.	Southeastern Italy to Eastern Mediterranean	
<i>Quercus libani</i> Oliv.	Turkey	
<i>Quercus petraea</i> (Matt.) Liebl.	Europe	
<i>Quercus petraea</i> (Matt.) Liebl. subsp. <i>huguetiana</i> Franco & G. López	Southern France and North Spain	
<i>Quercus robur</i> L.	Europe	
<i>Quercus pubescens</i> Willd.	Eastern, Central and Southern Europe, Northern Turkey	
<i>Quercus suber</i> L.	Western Mediterranean Basin	

Table 1/ List of threatened species according to the IUCN (Oldfield and Eastwood, 2007).



Endangered Oak Resources in Europe and Around the Mediterranean Basin: Marginal Populations and Minor Species

Alexis Ducouso
UMR BIOGECO, INRA
69 route d'Arcachon
F-33610 Cestas, France
Phone: +33.(0)5.57.12.28.28
Fax: +33.(0)5.57.12.28.81
alexis.ducouso@pierroton.inra.fr

ABSTRACT

Oaks are common species in Europe and around the Mediterranean Basin where they are a major component of forest ecosystems and economy. According to Govaerts and Frodin (1998) this region hosts 29 species and 44 taxa. We will first try to establish a tentative list of species. “Try” because oaks form a complex of species that does not fit the classical definition of a species. We will then look at the different threats that exist at both population and species level, reviewing climate change, new emergent diseases, human impact (forestry practices, overgrazing, fire, housing, and so forth), endemism, etc. We will focus on climate change and the risk of introduction of *Ceratocystis fagacearum* (Bretz) Hunt. Oaks from warm and dry climates are key species for the future because they have a high adaptation potential due to high genetic diversity, high gene flow within and between species and large genetic diversity. Today, several marginal populations and rare species like *Quercus crenata* Lam. or *Q. sicula* Borzi are endangered. We will propose different strategies for adaptation and conservation of these valuable and noble trees.

Keywords: European oaks, *Quercus*, taxonomy, biodiversity, genetic resources, threat

Introduction

In Europe, oaks are a major forest component from the Mediterranean Basin to southern Scandinavia and from Ireland to the Ural Mountains. Even if Europe doesn't host the high diversity of oaks found in North America and Southeast Asia, there is nevertheless important diversity. Oaks are a major component of many different ecosystems: plain forest, riparian forest, Mediterranean scrublands, calcareous plateaus. Today, oaks in Europe are subject to different threats. The aim of this paper is to list European oak diversity and then to review the main threats facing it.

Oaks in Europe and around the Mediterranean Basin

How many species?

We have established the European oaks list from two sources: the *World Checklist and Bibliography of Fagales* (Govaerts and Frodin, 1998) that can be consulted on the Kew Garden website <http://apps.kew.org/wcsp/home.do> and Cristofolini and Crema, 2005. According to this source, Europe hosts 29 species divided into 44 taxa. 11 species belong to section *Cerris* and 18 species to section *Quercus*.



1/ *Quercus crenata*, France (1999).

This list is not satisfactory because the definition of a species that is used is based only on morphological criteria. Oaks form a complex of species with intense gene flow between species and therefore clear-cut divisions between species are difficult to establish. This remark can be illustrated with two examples

First, the natural ranges of *Quercus ilex* L. and *Q. rotundifolia* Lam. overlap widely. In this overlapping zone, we can observe a gradient from pure *Quercus ilex* L. to pure *Q. rotundifolia* Lam. Lumaret et al. (2002) observed a discrepancy between morphology and molecular variations. The authors

explain that morphological variation is an adaptive response to climate not a taxonomical differentiation between two species

The second example is *Q. crenata* Lam. This species is accepted as a species since 2005 (Cristofolini and Crema, 2005) but the status of this taxon is not clear. The hybrid origin of this taxon (*Q. cerris* L. × *Q. suber* L.) is well established (Conte et al., 2009) but the hybrid status is not clear because it may be a fixed hybrid or it may represent the offspring of current hybridization between the two parental species or both (Cristofolini and Crema, 2005). If it is a fixed hybrid, it must be considered a species and therefore maintained in this list, if not, it must be removed.

Distribution

For oaks we observe a classical gradient of biodiversity from the Mediterranean region to northern Europe. In the north we find only 2 species (*Q. robur* L. and *Q. petraea* (Matt.) Liebl.); in the intermediate zone 5 species (*Q. petraea*, *Q. robur*, *Q. pubescens* Willd., *Q. pyrenaica* Willd. and *Q. cerris* L.) and all of the 29 species and 44 taxa are found in the south of Europe which is a key region for oaks

Threat levels

Biodiversity has three levels: ecosystemic, specific and genetic. In this section we will look at examples of threat for oaks at each of these levels.

Ecosystemic

An ecosystem can disappear through destruction or degradation. In Europe, some forest ecosystems have dramatically regressed: temperate broad-leaved forest (75%), Mediterranean forest (78%), riparian forest (90%) (Halkka and Lappalainen, 2001). In these forests, oaks are frequently dominant

Specific

Several oak species are endangered. Oldfield and Eastwood (2007) have recorded 7 oak taxa threatened throughout Europe and 14 taxa of least concern (Table 1). However, this list is not satisfactory because: (i) the nomenclature needs to be updated; (ii) several endangered species are missing (*Q. aucheri* Jaub. & Spach., *Q. brantii* Lindl., *Q. canariensis* Willd., *Q. crenata* Lam. and *Q. sicula* Borzi ex Lojac.) and, (iii) there is no clear distinction between the different risk categories. IUCN has identified different threats: loss of habitat, overgrazing and felling, endemism, fire, etc. In this paper, we have retained only three examples of threat: climate change, pathological problems and endemism.

Genetic

The two main threats on the genetic level are 1) genetic drift and 2) genetic transfer.

1. Genetic drift

Is the change in the frequency of a gene variant or allele in a population due to random sampling between generations. Genetic drift may cause gene variants to disappear completely and thereby reduce genetic variation. Marginal populations are at high risk because many of them are disappearing, they have very often less than 2,000 breeding individuals and are isolated. Genetic drift could impoverish diversity because gene flow could not compensate for this loss due to this isolation. Marginal populations are concentrated on the outer edges of natural ranges. Southern margins host thermophilic and drought resistant populations that have high adaptation potential regarding current climatic change. The genetic resources of these populations could be very useful for boosting adaptation of populations in central Europe.

2. Genetic transfer

Foresters resort to planting because of lack of natural regeneration or in their eagerness to increase productivity. Most often though genetic resources used for this regeneration are not local. This exogenous source of genetic material is the main disturbance of genetic diversity (Lesur, 1999). Lesur has studied genetic resources in the 600 compartments of the national forest of Compiègne (France) with cpDNA markers. She found that since the 70s, the provenance of most plantations has a very distant geographical origin. About 20%

of the regeneration comes from eastern Europe. This study reveals that genetic transfer is a major disturbance for the distribution of genetic diversity. Nevertheless we must not consider these plantations only from a negative point of view. They could increase local genetic diversity and therefore enhance oak adaptability to current climate change. On the other hand, they raise a major problem for conserving the genetics resources of sessile and pedunculate oaks that would also represent a loss of adaptive capacity.

Origin of risk: global changes

Human impact: housing, fire, overgrazing, plantation

These threats are often cited as major concerns for oaks, although for the most part without clear studies to corroborate such claims. They are well documented only at forest level. There is a tendency in Europe to artificialize lands through, for example, urbanization. In France 1,380,000 ha were urbanized between 1982-2003 (Pointerau and Coulon, 2009). Forest fires concern mainly the Mediterranean region, with from 0.19% (France) to 1.23% (Portugal) of the forest surface burnt each year.

Diseases

Hosts and pathogens have evolved together through continuous and reciprocal coadaptation that promotes fitness (Van Valen, 1973). It is an armed peace: in the long term, hosts and pathogens are in equilibrium. With the rapidity of modern transportation in the global market the arrival rate of new pathogens is greatly increased. Coevolution and adaptation on the other hand, need time – without it, these new pathogens can inflict severe damage to host species especially when they arrive in industrial quantities. Below we review one example of a probable past introduction and one example of a possible future introduction along with its potential risk

1. Powdery oak mildew

Erysiphe alphitoides (Griffon & Maubl.) U. Braun & S. Takam, *E. hypophylla* (Nevod.) U. Braun & J.H. Cunnington, *E. quercicola* Schwein., and related species. Powdery mildew is a major fungal disease of European oaks. A recent study (Mougou-Hamdane et al., 2010) shows that several species are involved in this epidemic: *Erysiphe alphitoides*, *E. hypophylla*, *E. quercicola*, etc. Probably the result of an introduction (Marçais et Desprez-Loustau, 2007), the disease, appeared suddenly and spread to almost all of Europe in the early 20th century. It was particularly severe on *Q. robur* and foresters were afraid that powdery mildew would decimate indigenous oaks (Mougou et al., 2008). Pyrenean oak is very sensitive to this pathogen and, since the beginning of this epidemic, populations of Pyrenean oak have declined (Mougnou-Hadane et al., 2010).

2. Oak wilt (*Ceratocystis fagacearum* (T. W. Bretz) J. Hunt)

Oak wilt is due to this fungus whose natural range extends from Texas to Wisconsin and from Arkansas to Pennsylvania (Juzwik et al., 2011). Due to low dispersal, the disease attacks are limited to small patches. European white oaks are very sensitive to this pathogen (Pinon et al., 2003). Moreover, in Europe *Scolytus intricatus* (Ratzeburg, 1837) could be a very efficient dispersal agent. The introduction of this fungus through the wood trade, could lead to a very serious epidemic.

Climate change

Thuillez (2003) and Thuillez et al., (2005) have modeled the climatic envelop of *Q. petraea* today and in the future using different climatic models. A global shift northward

of several hundred kilometres (100 km = 63 mi) is predicted for the end of this century. It is probable that sessile oak will not be able to keep pace with this rate of change. Also predicted is the loss of all of the southern marginal populations that host very valuable genetic resources because they are very close to glacial refugia and have evolved in warm climates.

Origin of risk: population structure

Range (endemism)

Several European oaks have a narrow, natural range. These endemic species include, amongst others, *Q. alnifolia* Poech, *Q. crenata*, *Q. sicula*, *Q. vulcanica* Boiss. & Heldr. ex Kotschy. Due to endemism these species are very vulnerable for demographic and genetic reasons. *Q. vulcanica* forests cover 8,000 ha (Balaban & Yilgor, 1999) represented by 12 isolated populations in Turkey (Avci, 1996). These populations will not be able to expand because they are surrounded by hostile regions (urban zones, orchards, steppes, etc.) and if one population disappears, it could not be restored naturally. The population of *Q. crenata* is estimated at about 1,000 individuals in Italy, several dozen in France and just a few individuals in Slovenia and Croatia. (Conte et al., 2007)

Demography

Minimum viable population (MVP) is the critical limit of a species below which it can not reproduce in the wild (Schaffer, 1981). Current numbers of breeding individuals



2/ *Quercus vulcanica*, Turkey (2010).



3/ *Quercus faginea* (2008).

alnifolia in Cyprus, *Q. vulcanica* in Turkey. In France the CRGF (Commission Ressources Génétiques Forestières) manages 20 Conservation Units of sessile oak. This program will be extended to other oak species. It is very difficult to establish a list of programs at regional level, but two examples exist in France under the auspices of the Espaces Naturels Sensibles organization that purchases valuable ecosystems. In Italy, different regions also have programs to protect *Q. crenata*.

Several conservation strategies must be developed for European oaks based on geographic distribution, ecological requirements, genetic structure and demographic parameters. Examples include:

- *Q. vulcanica*: this species need to be assisted in its migration to the north; this can be accomplished through the creation of additional populations in the future potential natural range.

- *Q. crenata*: conservation strategy will depend on the taxonomical status of this species. If individuals are offspring of current hybridization between the two parental species the best strategy is to restore genetic contact between the two parental species. If it is a fixed hybrid, then seed orchards must be created with the resultant acorns used for planting new populations in order to promote intraspecific genetic diversity.

- *Q. petraea*: only marginal populations are threatened. These populations must be duplicated in safer zones (in consideration of future climate), in other words where there is no anthropomorphic risk such as urbanization, fire, etc.

- *Ceratocystis fagacearum*: there must be greater restrictions in the wood trade with

are very low for several oaks species (*Q. crenata*, *Q. sicula*, etc.). They could, under the MVP requirements, be considered as very vulnerable species.

Conservation efforts

Different conservation efforts that include oak populations and resources have been undertaken. The aim of NATURA 2000 is to assure the long-term survival of Europe's most valuable and most threatened species and habitats. This European policy concerns several ecosystems hosting oaks and different oak species. EUFORGEN is a European program to promote conservation of forest genetic resources, protecting the genetic resources eleven oak species in Conservation Units. Many initiatives for oak and oak ecosystem conservation have also been taken at national level (national parks, natural reserves, etc.). Several oaks species are protected in different countries, for example, *Q. crenata* in France, *Q.*

the USA; areas surrounding points of entry for wood imports must be monitored several times a year in order to reduce the possibility of introduction.

Conclusion

Oaks are common in Europe and are very important for economical, ecological and sociological reasons. One would think that they are very well known but, surprisingly, this paper reveals a lack of basic knowledge of these species. Taxonomical and genetic work are urgently needed in order to correctly determine the number of taxa in Europe and the Mediterranean Basin in order to establish conservation and management strategies. The importance of threat is dependent on distribution and population size. Even common species like *Q. petraea* are threatened at the genetic resource level. Obviously minor oak species like *Q. sicula* are at high risk of becoming extinct

A major problem exists only in the northern zone. Genetic resources are threatened in two regions, the center and the south. Most oak species in the southern region are subject to threat at all three risk levels.

Photographers. Title page: Alexis Ducouso (*Quercus frainetto*). Photos 1, 3: Alexis Ducouso. Photo 2: Béatrice Chassé.

Bibliography

- Avcı, M. 1996. A new distribution area of an endemic oak species, *Quercus vulcanica* Boiss. ex Kotschy. *Türk Coğrafya Dergisi* 31: 283–289.
- Balaban, M. and N. Yilgör. 1999. Chemical Characteristics of Endemic Oak-Wood *Quercus vulcanica* Boiss. & Heldr. ex Kotschy. *Holz als Roh- und Werkstoff* 57: 152–153.
- Conte, L.C. Cotti and G. Cristofolini. 2007. Molecular evidence for hybrid origin of *Quercus crenata* Lam. (*Fagaceae*) from *Q. cerris* L. and *Q. suber* L. *PLANT BIOSYSTEMS* 141(2): 181–193.
- Cristofolini G. and S. Crema. 2005. A morphometric study of the *Quercus crenata* Lam. species complex (*Fagaceae*). *Bot. Helv.* 115: 155–167.
- Govaerts, R. and D.G. Frodin. 1998. *World Checklist and Bibliography of Fagales*. UK: Royal Botanic Gardens, Kew.
- Halkka, A. and L. Lappalainen. 2001. *Rapport WWF. La protection des forêts en Europe*. Finland: WWF, Ed. Forssa.
- Juzwik J., D.N. Appel, W.L. MacDonald and S. Burks. 2011. Challenges and successes in managing oak wilt in the United States. *Plant Disease* 95(8): 888–900.
- Lesur I. *Repérage moléculaire et comparaisons de provenances exotiques et locales de chênes pédonculés en forêt domaniale de Compiègne*. D.E.A. INAPG-INRA, 1999.
- Lumaret M., C. Mir, H. Michaud and Raynal V. 2002. Phylogeographical variation of chloroplast DNA in holm oak (*Quercus ilex* L.). *Molecular Ecology* 11: 2327–2336.
- Marçais B. and M.L. Desprez-Loustau. 2007. Le réchauffement climatique a-t-il un impact sur les maladies forestières ? *RDV techniques ONF*, HS(3): 47–52.
- Mougou A., C. Dutech and M.-L. Desprez-Loustau. 2008. New insights into the identity and origin of the causal agent of oak powdery mildew in Europe. *For. Pathol.* 38: 275–287.
- Mougou-Hamdane A., X. Giresse, C. Dutech and M.L. Desprez-Loustau. 2010. Spatial distribution of lineages of oak powdery mildew fungi in France, using quick molecular detection methods. *Ann. For. Sci.* 67: 212.
- Oldfield S. and A. Eastwood. 2007. *Red List of Oaks*. Cambridge: Fauna & Flora International.
- Pinon J., M. MacDonald, M. Double and F. Tainter. 2003. Les risques pour la chênaie européenne d'introduction de *Ceratocystis fagacearum* en provenances de Etats-Unis. *Compte-rendu, Académie Agriculture de France, 19 November 2003*: 1–5.
- Pointereau P., and F. Coulon. 2009. Abandon et artificialisation des terres agricoles. *Courrier de l'environnement de l'INRA* 57: 109–114.
- Shaffer M.L. 1981. Minimum population sizes for species conservation. *BioScience* 31(2): 131–134.
- Thuiller W., 2003. BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* (2003) 9: 1353–1362.
- Thuiller W., Lavorel S., Araújo M.B., Sykes M.T., I. Prentice C. and Harold A., 2005. Climate Change Threats to Plant Diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102(23): 8245–8250.
- Van Valen L., 1973. A new evolutionary law. *Evolutionary Theory* 1: 1–30.



1/ Is pollination the key to understanding oak masting?



Acorns, Acorns Everywhere, But Not in Every Year

Ian Pearse and Walt Koenig
Cornell University Lab of Ornithology
159 Sapsucker Woods
Ithaca, NY 14850, USA
ianspearse@gmail.com

ABSTRACT

Populations of oaks have mast seed production, where the entire population of trees produces either a large or small acorn crop in a given year. The ecological consequences of mast or non-mast years are profound and affect the abundance of everything from deer to insects to Lyme disease pathogens, but the causes of oak mast are poorly understood. We analyzed 30-year dataset of acorn production in *Quercus lobata* Née throughout California. We found a high degree of synchrony of acorn crop among *Q. lobata* trees. Acorn production in a given year showed a strong negative correlation with acorn production in a previous year and a strong positive correlation with weather patterns. Populations with highly synchronized flowering produce more acorns. These factors combined predicted over 60% of the variation in the size of acorn crops in a given year suggesting that acorn crops may be forecast with knowledge of flowering, spring weather, and the production of acorns in the previous year.

Keywords: oak mast, acorn, seed set, Moran effect, pollination

Introduction

It was fall 2006 in Northern California. I had just moved across the country and reentered the university with a budding interest in oaks. On the hunt for valley oak acorns (*Quercus lobata* Née), I purchased an orchard ladder and searched several trees around my girlfriend's cabin near Lodi. None of them had any acorns. I drove 50 mi/80 km to Davis to find a few squirrel-damaged acorns, I continued to Oakland where I found only a handful of acorns within the reach of my ladder, and I decided that I would have to plant something else, as it was just too difficult to find these seemingly rare Californian acorns.

The mysteries of masting

People refer to the “boom or bust” patterns of seed set in populations of plants as “masting” or “masting behavior”. How and why plants mast remains an unsolved mystery for ecologists, but there is little doubt of the enormous ecological consequences of masting that reach far beyond the hapless acorn collector. A bad year for acorns results in high death rates and low birthrates of animals that eat acorns such as deer, mice, and many birds (McShea, 2000). In fact, the idea that granivores will not be able to eat all the acorns in a masting year is the main theory for why masting behavior is so important for oak reproduction, on an evolutionary time scale. In low-production years, the decrease in population of these consumers cascades throughout the entire ecosystem often with unexpected consequences for organisms that have little to do with acorns directly. For example, in the oak forests of eastern North America, the prevalence of Lyme disease is linked to oak masting. The ticks that carry Lyme disease feed on deer and mice that feed on acorns (Jones et al., 1998). Equally unexpected, low acorn crops seem to be related to outbreaks of gypsy moths, a common forest pest. In low-acorns years, mouse populations decrease, and fewer gypsy moth pupae get eaten by mice (Elkinton et al., 1996). The relationship between pulsed acorn production and granivory is a bit of a cat and mouse game but it is still unclear how oaks manage to pull it off.

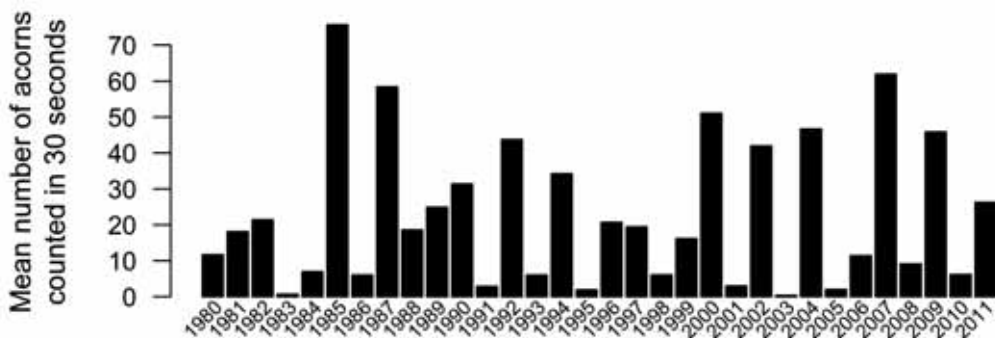


Figure 1/ Valley oak acorns counted at Hastings Reserve over the last 32 years. The crop of acorns varied dramatically between years, and this is indicative of masting.

What is known

From decade-long surveys of acorns (Figure 1), we know three main things about mastings in oaks. First, individual trees have extremely variable acorn crops from year to year. This is the boom or bust that characterizes mastings. Second, most of the trees within a population or even over a very broad geographic range tend to be synchronized in the size of their acorn crops. So, in 2006, even if I had driven 600 km/372 mi south to Los Angeles to find acorns, I would have likely been equally disappointed. Third, the pattern of acorn production in oaks is not cyclical or periodical. This is to say that oaks do not have a good acorn year every other year or every third year or at any other predictable time interval. So, knowing that 2006 was a bad acorn year and 2007 was a good acorn year, there would have been no way to predict that 2008 was going to be an intermediate acorn year for valley oaks.

The Moran Effect

And herein lies the mystery: there are relatively few ways to imagine entire populations of oaks across thousands of kilometers synchronizing their acorn crop. Research has focused on two main explanations for the synchrony of oak mastings. First, it is possible that the synchrony in events is simply driven by some external factor like weather. For example, on February 1, 2011 an above-average number of airline passengers slept in airports from Oklahoma City to Toronto. These individuals did not all independently choose uncomfortable sleeping arrangements at the same time, nor did they decide to do this as a group. They were all simply ticket holders on flights that happened to be delayed because of a large winter storm. This idea, known to ecologists as the Moran Effect, is an appealing explanation for large-scale population trends, as weather patterns tend to be similar over large distances. Because of this, the Moran Effect is the most common hypothesis for explaining oak mastings (Koenig et al., 1999). Curiously, though, the years with weather patterns that seem good for acorn production (like years with adequate rain or temperatures) are not necessarily years with high acorn production (Koenig et al., 1996). This suggests that if weather is the driving factor that synchronizes the production of acorns across regions, it is some more subtle side-effect of weather, not simply those years with weather that allows the trees to generally do better. In fact, the one component of weather that correlates very well with the size of the acorn crop in several species is early springtime temperature (Koenig et al., 1999; Perez-Ramos et al., 2010). Early springtime weather may then affect how many female flowers get pollinated.

Synchronization

The second hypothesis is that synchronized events may occur if there is coordination between individuals. For example, at one minute and sixteen seconds into the Russian 2012 Olympic synchronized swimming routine, all of the swimmers emerged feet-first from the swimming pool. Their perfect synchrony was not because each swimmer independently thought that would be a great time to surface, nor was it because of some external event affecting London. It was because those swimmers had coordinated between themselves beforehand. Here, the analogy to oaks is more difficult, as it is hard to imagine oak trees conferring among each other to decide when to set seed. However,

there is at least one major social event in the life of an oak where an individual interacts with others in a population: during sex. Specifically, the receipt of pollen on a female oak flower is dependent upon both the quantity and the timing of pollen production by its neighbors. The possibility that acorn masting may be caused by pollen interactions between trees is so intriguing that it has attracted several mathematicians, who have shown that the local effects of pollen interactions can synchronize acorn production over very broad geographic scales (Satake and Iwasa, 2000; 2002). This is also consistent with patterns of acorn production that we observe in forests.



2/ The phenology (timing) of oak flowering affects the acorn set of oak trees.

Is pollination the key to understanding masting?

Interestingly, both the Moran Effect (weather) hypothesis and the coordination hypothesis suggest that pollination might be the key to understanding oak masting. Historically, researchers have thought that pollination was simply never a problem for oaks, as they are wind pollinated and they tend to produce a lot of pollen. I mean, each spring millions of those little oak pollen grains even try to pollinate my nose!

Researchers have thus assumed that it is the sheer energy that it takes to mature a full crop of acorns that limits their production, not pollination. Recently, however, some workers have found substantial indirect evidence that pollen limitation, a reduction in acorn set based on a lack of pollen receipt by flowers, may actually be important for oaks. First, estimates of the distance that pollen travels vary substantially, and some suggest that most of the pollen from an individual tree may only travel a matter of meters (Sork

et al., 2002), though this is a matter of considerable current debate (Abraham et al.,). Moreover, isolated trees in at least some cases produce correspondingly fewer acorns than trees with many pollen-bearing neighbors (Knapp et al., 2001; Abraham et al., 2011).

Looking at isolation in a different way, it has been found that oak trees that flower at the extremes of the season (either very early or very late) are isolated in time from their neighbor, and they also produce fewer acorns than trees that flower in the middle of spring (Koenig et al., 2012). If trees that are isolated in either space or time depend on very specific conditions to get enough pollen to produce a full acorn crop, this may determine which years are good or bad for acorn crops.

Conclusion

Acorn mastings is a conspicuous and important feature of oak forests. The study of masting in oaks is quite a commitment in that it requires counting acorns over many years at many places. Many people are making that commitment, and our understanding of masting behavior is increasing dramatically. It appears that, in particular, large-scale weather events as well as population-level events like pollination are important in determining whether it is a mast year or not. Simultaneously, research is showing that individual trees might suffer from a lack of pollination in some years, further pointing to pollination as an important factor in acorn set. Putting all of this information together allows us to predict acorn production before it happens. So, next year we hope to be able to guess how many acorns will be on your oak trees before they are actually matured!

Photographers. Title page: Ian Pearse (a masting year for *Quercus lobata*). Photos 1-2: Ian Pearse.

Bibliography

- Abraham, S.T., D.N. Zaya, W.D. Koenig, and M.V. Ashley. 2011. Interspecific and intraspecific pollination patterns of valley oak, *Quercus lobata*, in a mixed stand in coastal central California. *International Journal of Plant Sciences* 172:691–699.
- Elkinton, J.S., W.M. Healy, J.P. Buonaccorsi, G.H. Boettner, A.M. Hazzard, H.R. Smith, and A.M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77: 2332–2342.
- Jones, C.G., R.S. Ostfeld, M.P. Richard, E.M. Schaubert, and J.O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279: 1023–1026.
- Knapp, E.E., M.A. Goedde, and K.J. Rice. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128: 48–55.
- Koenig, W.D., K. A. Funk, T.S. Kraft, W.J. Carmen, B.C. Barringer, and J.M.H. Knops. 2012. Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. *Journal of Ecology* 100: 758–763.
- Koenig, W.D., J.M. H.Knops, W.J. Carmen, and M.T. Stanback. 1999. Spatial dynamics in the absence of dispersal: acorn production by oaks in central coastal California. *Ecography* 22: 499–506.
- Koenig, W.D., J.M. H. Knops, W.J. Carmen, M.T. Stanback, and R.L. Mumme. 1996. Acorn production by oaks in central coastal California: Influence of weather at three levels. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 26: 1677–1683.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 81: 228–238.
- Perez-Ramos, I.M., J.M. Ourcival, J.M. Limousin, and S. Rambal. 2010. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology* 91: 3057–3068.
- Satake, A., and Y. Iwasa. 2000. Pollen coupling of forest trees: Forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology* 203:63-84.
- Satake, A., and Y. Iwasa. 2002. Spatially limited pollen exchange and a long-range synchronization of trees. *Ecology* 83: 993–1005.
- Sork, V.L., F.W. Davis, P.E. Smouse, V.J. Apsit, R.J. Dyer, J.F. Fernandez, and B. Kuhn. 2002. Pollen movement in declining populations of California Valley oak, *Quercus lobata*: where have all the fathers gone? *Molecular Ecology* 11: 1657–1668.



Figure 3/ *Quercus pyrenaica* has fasciculate, radiate, stipitate hairs (bar = 100 η m; discussion, p. 125).



Figure 4/ *Quercus estremadurens* shows uniseriate-branched, smooth hairs (bar = 30 η m; discussion, p. 126).

Species/Hairs	Simple 1	Simple 2	Simple 3	Bulb	Branched	Fascic. 1	Fascic. 2	Radiate	Stellate	Rosulate
<i>Q. faginea</i> subsp. <i>alpestris</i>	-/-	-/+	+/+	+/-	-/-	-/+	+/+	-/-	+/+	-/+
<i>Q. broteroi</i>	-/-	-/+	+/+	+/-	-/-	-/+	+/+	-/+	+/+	-/+
<i>Q. canariensis</i>	-/+	-/+	+/+	-/+	-/-	+/+	+/+	-/-	-/+	-/-
<i>Q. coccifera</i>	-/-	-/+	-/+	+/-	-/-	-/-	-/-	-/-	+/+	-/-
<i>Q. estremadurensis</i>	-/+	-/+	+/+	+/+	-/+	-/+	+/+	-/-	-/+	-/-
<i>Q. faginea</i>	-/-	-/+	+/+	+/-	-/-	-/+	+/+	-/-	+/+	-/-
<i>Q. lusitanica</i>	-/-	-/+	+/+	+/-	-/-	-/+	+/+	-/+	+/+	+/+
<i>Q. pyrenaica</i>	-/-	+/+	+/+	+/-	-/-	+/+	+/-	-/-	+/+	-/-
<i>Q. rotundifolia</i>	-/-	-/+	+/+	+/-	-/-	+/+	+/+	-/+	+/+	+/+
<i>Q. suber</i>	-/-	-/+	+/+	+/-	-/-	-/+	+/+	-/-	+/+	-/-

Table 1/ Hair types and distribution on adaxial/abaxial leaf blade surfaces of Mediterranean oaks from SW Iberian Peninsula. **Simple 1:** Simple, uniseriate, smooth base; **Simple 2:** Simple, uniseriate, scaly base; **Simple 3:** Long, simple not uniseriate; **Fascic. 1:** Fasciculate, stipitate; **Fascic. 2:** Fasciculate, not stipitate (discussion, p. 125).



Micromorphological and Anatomical Characters Used to Differentiate Mediterranean Oaks

Francisco M. Vázquez

Grupo de Investigación HABITAT. Departamento de Producción Forestal.
Centro de Investigación La Orden. Apartado 22. 06080 Badajoz. Spain.
frvazquez50@hotmail.com

ABSTRACT

This study discusses the foliage, floral and reproductive microcharacters used for the separation of species of the genus *Quercus* in the Mediterranean. Results for species of the SW Iberian Peninsula show the presence of some microcharacters such as foliar trichomes that allow the separation of taxa at a specific level. Other microcharacters such as the micromorphology of the stomata, the cells of the epidermis, the anthers, or pollen grains, make it possible to separate clearly the three subgenera represented in the territory: *Cerris* (Spach) Örsted, *Sclerophylloids* O. Schwarz and *Quercus*. Finally some typical microcharacters of *Quercus* species were found which had not been previously observed in oaks of the SW Iberian Peninsula, such as: verrucate stomata (*Q. faginea* subsp. *alpestris* (Boiss.) Maire), uniseriate-branched hairs (*Q. estremadurensis* O. Schwarz), and apiculate and pilose anthers (*Q. suber* L.)

Keywords: *Quercus*, stomata, trichome, anatomy, anther, pollen, micromorphology

Introduction

Taxonomic studies of the genus *Quercus* in the Western Mediterranean have relied mainly on visible morphological characters. Most authors of the 19th and 20th centuries used leaf blade and fruit characters, and to a lesser extent, those of flowers, to segregate and characterize different species of *Quercus* (Camus 1936-1954; Coutinho, 1888; De Candolle, 1868; Huguet de Villar, 1957; Schwarz, 1936, 1964).

In the mid-20th century, scientific advances in microscopic and ultra-microscopic equipment allowed for more detailed studies of pollen and leaf trichome morphology on which to base the segregation of *Quercus* species worldwide, especially in North America and Europe (Dyal, 1936; Hardin, 1976, 1979; Solomon, 1983a; 1983b; Stairs, 1964; Van de Campo and Elhai, 1956). The end of the past century marked the beginning of descriptive studies of the diversity of foliar trichomes of Western Mediterranean species of the genus *Quercus* (Bussotti and Grossoni, 1997; Llamas et al., 1995; Penas et al., 1994), and of pollen morphology (Colomo et al., 1983; Gomez-Casero et al., 2004; Ruiz del Castillo, 1988). The increase of descriptive studies of micromorphological characters of the pollen grain and of the leaf blade surface has provided a more accurate method of species segregation within the genus. However, some species of the Southwest Iberian Peninsula have not been studied and therefore the objective of this work is to increase knowledge of the micromorphology and anatomy of these species.

Methodology

Samples

Leaf samples were obtained from the HSS Herbarium (Holmgren et al., 2003), while the reproductive organ samples were collected April 10-26, 2012 in the *Quercus* collection of the Research Center La Orden.

Anatomical study

For leaf surface study, the samples underwent forced hydration for 4 hours in distilled water at 55 °C, and were subsequently prepared following the latest methodology described by Devesa (1992) for the study of the foliar epidermis in *Poaceae*.

Microscopic observation and photography were carried out with a LEICA DMBR model. The terminology used for the description of the samples is according to Jones (1986); Lou and Zhou, (2001); Liu et al., (2009).

SEM study

The pollen grains were investigated and documented by scanning electron microscopy (SEM, single grain technique by Hesse et al., 2009). SEM stubs with pollen are stored in the palynological collection of the Department of Forest Production, Research Center La Orden, (HSS-PAL) under the numbers 2554-2589. Terminology for pollen descriptions follows Punt et al., (2007); Hesse et al., (2009); Rowley & Gabarayeva (2004) and Denk and Grimm (2009); the trichome terminology used for classification is that suggested by Hardin (1976, 1979); Jones (1986); Llamas et al., (1995); Uzunova et al., (1997); and the terminology of Safou et al., (1988) is used for the stomata.

A ZEISS, EVO-10 model at 10-20 KeV was used for the SEM observations and photographs.

Presentation of results

The results are presented in a table and figures that allow the identification of the

characters mentioned in the text. Taxonomic treatment follows Amaral Franco (1990) and Nixon (1997).

Results and Discussion

Study of the leaf blade characters

1. Leaf anatomy

The study of the leaf epidermis shows two species groups: a) evergreen species with short, rounded cells and thick-walled cells, that includes species of the subgenera *Sclerophyllodrys* O. Schwarz and *Cerris* (Spach) Ørsted (Figure 1); and b) deciduous species, with large, elongated cells and thin-walled cells, that includes species of subgenus *Quercus* (Figure 2).

The cellular structure in the leaf blade epidermis is related to habitat. Taxa of arid zones, like the evergreen species from the SW Iberian Peninsula, have leaves with a thick cuticle and short, thick-walled cells. The taxa of humid habitats have thin cuticles and cells with long, thin walls, such as the deciduous species of our study (Clements, 1905; Hanson, 1917).

2. Trichomes

The study of foliar trichomes and their distribution in the leaf blade reveals the presence of species-characteristic trichomes. Rosulate-type trichomes appear in *Q. faginea* subsp. *alpestris* (Boiss.) Maire, *Q. broteroi* (Coutinho) Rivas-Martínez, *Q. lusitanica* Lam., and *Q. rotundifolia* Lam. All of these species belong to two of the subgenera studied: *Quercus* and *Sclerophyllodrys*.

In the deciduous species of cool areas the trichomes appear only on the abaxial surface of the blade, while those of the evergreen species of drier areas appear on both leaf surfaces (Table 1; p. 122).

Radiate type hairs are found only in two species (*Q. broteroi*, and *Q. rotundifolia*), belonging to two different subgenera: *Quercus* and *Sclerophyllodrys*. This type is common in *Quercus* species (Hardin, 1976, 1979; Jones, 1989, Llamas et al., 1995), however in our study they have not appeared frequently.

The most frequently found hairs are fasciculate types (radiated fasciculate; stipitate fasciculate; parallel fasciculate) with the simple, uniseriate and not uniseriate, appearing in all studied species (Figure 3 and Table 1; p. 122).

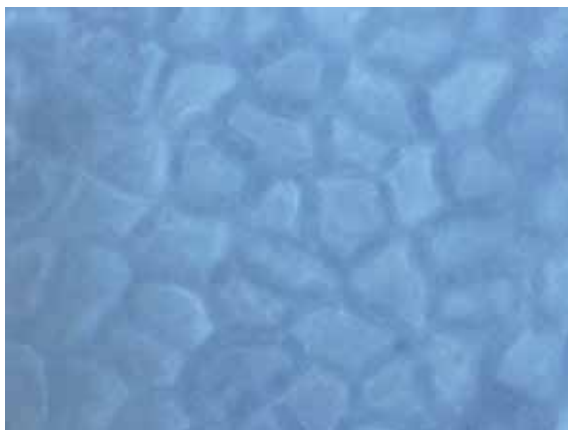


Figure 1/ Adaxial leaf blade epidermis of *Quercus suber* with rounded cells and thick-walled cells (bar = 450 μ m).



Figure 2/ Adaxial leaf blade epidermis of *Quercus broteroi* with elongated cells and thick-walled cells (bar = 450 μ m).

It is necessary to highlight the presence of uniseriate-branched smooth hairs in *Q. estremadurensis* O. Schwarz (Figure 4; p. 122). This type of hair had not been detected to date in species of the Mediterranean, although they have been recorded in some species from North America such as *Q. palmeri* Engelm. (Hardin, 1976; Jones, 1986). The uniseriate, simple and branched hairs are included in glandular hair types (Jones, 1986), or secretory hair types by Camus (1936-54).

The results analysis shows that trichome type allows the separation of some species as shown by previous authors (Llamas et al., 1995; Penas et al., 1994; Thomson and Mohlenbrock, 1979).



Figure 5/ *Quercus rotundifolia* with crested, rounded stomata and verrucate stomata (black open point) (bar = 10 η m).

3. Stomata

The stomata found can be divided into four types: a) smooth, elongated stomata; b) smooth, rounded stomata; c) crested, elongated stomata, and d) crested, rounded stomata. The rounded stomata appear mainly in evergreen species, subgenera *Sclerophyllodrys* and *Cerris*, while elongated stomata appear mainly in deciduous species of the subgenus *Quercus*. These results differ from those found

by previous authors (Bussotti and Grossoni, 1997; Safou et al., 1988). In our study the ornamentation of the surface of the cells is not systematically related to phylogeny, but more to environmental parameters. In species such as *Q. estremadurensis*, *Q. canariensis* Willd., and *Q. faginea* subsp. *alpestris*, stomata have been found interchangeably with smooth and ornate (crested) guard cells attached. However, in evergreen species the stomata have ornate guard cells. The ornamentation degree of guard cells changes from slightly ornamented (with the stomata pore visible) to heavily ornamented (with the stomata pore not visible). Finally *Q. faginea* subsp. *alpestris*, has stomata with verrucate guard cells, similar to stomata of *Q. infectoria* Oliv., from Iran (Panahi et al., 2012) (Figure 5).

Study of floral and reproductive characters

1. Anthers

Anther morphology of the oaks of the SW Iberian Peninsula species segregate between the three subgenera studied: a) subgenus *Quercus* with rounded and smooth anthers of medium to large size; b) subgenus *Cerris* with apiculate and pilose anthers of medium to small size; and subgenus *Sclerophyllodrys* with apiculate and smooth anthers of medium to large size.

For hybrid taxa, anther studies have revealed anthers intermediate between the parents. Anthers of *Q. ×pacensis* F.M. Vázquez (= *Q. broteroi* × *Q. suber*), are rounded, of medium size and pilose (Figure 6). These results confirm that anther morphology can be used as a discriminating character between subgenera and some taxa.

2. Pollen

The results allow us to differentiate with clarity different groups of the genus *Quercus* in the SW Iberian Peninsula. If we look at the size of the pollen grains there are at least two major groups: a) species with pollen grains of up to 25 μm , represented by species of the subgenus *Sclerophyllodrys* and b) taxa with pollen grains of more than 28 μm , of the subgenera *Cerris* and *Quercus*. In addition, we can distinguish in the first group

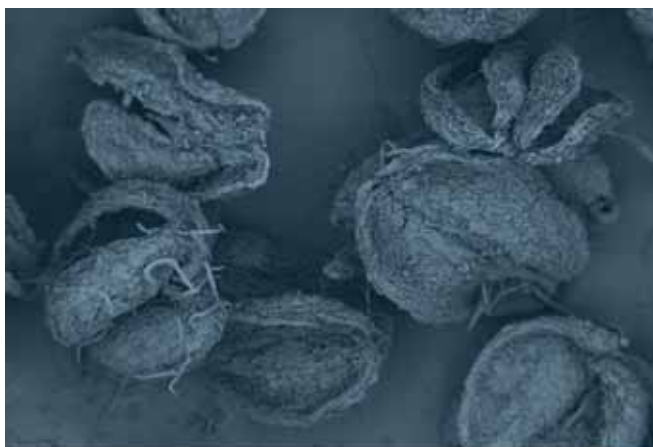


Figure 6/ *Quercus x pacensis* with pilose and rounded anther (bar = 200 μm).

the species *Q. rotundifolia* and *Q. coccifera* L. by the pollen surface ornamentation. In *Q. rotundifolia* there is a surface with jagged ridges, and in *Q. coccifera*, a finely verrucate-jagged surface. In the case of the second group (b) pollen of species of the subgenus *Quercus* has a strongly verrucate surface, and that of the representative of the subgenus *Cerris* has a weakly verrucate pollen grain surface. (Figures 7 and 8).

These results were partially shown by Suárez (1987), Ruiz del Castillo (1988) and Denk and Grimm (2009); however these authors did not show the same results for *Q. broteroi* and *Q. faginea* subsp. *alpestris*. Also, they did not show a relationship between the surface of the pollen grains and the phylogenetic origin: (a) grains of pollen from species of the *Sclerophyllodrys* group, that grow in dry places, have ridges, while those of the other groups (b), that grow in cooler, wetter places, are verrucate (Denk and Grimm, 2009). The surface of the pollen grains is shown as a phylogenetic character, which may be related in some areas to the species habitat.

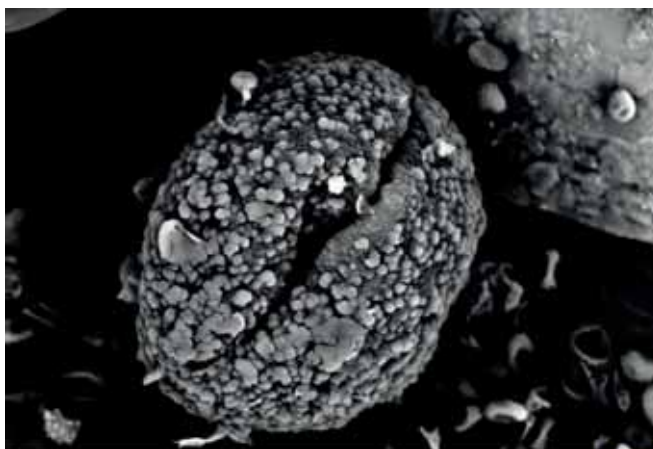


Figure 7/ Pollen grain surface of *Quercus faginea* subsp. *alpestris* (bar = 2 μm).

Conclusion

These results highlight the foliage, floral and reproductive microcharacters that enable the segregation of *Quercus* species of the SW Iberian Peninsula. The characters studied that show the greatest diversity and expression are those associated with leaf morphology. Almost all species of the genus that have been studied can be differentiated by the foliar

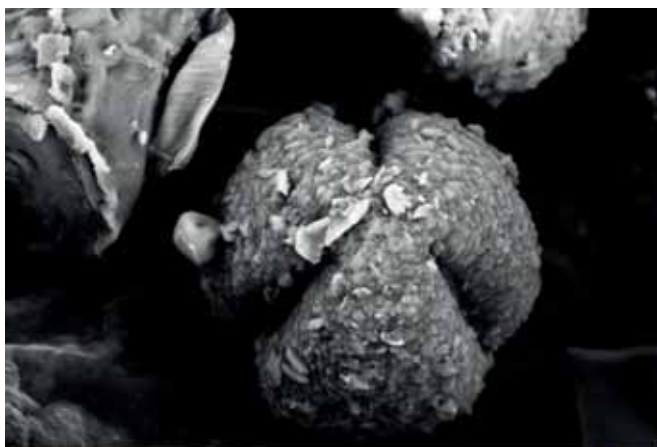


Figure 8/ Pollen grain surface of *Quercus rotundifolia* (bar = 3 μm).

trichomes. These results have previously been expressed by Llamas et al., 1995 and Penas et al., 1994 from the north of the Iberian Peninsula; Hardin, 1976, 1979 and Thomson and Mohlenbrock 1979, from North America; and Panahi et al., 2012 from Iran.

The micromorphology of the pollen grain, the stomata, the anthers as well as leaf anatomy, represent characters that allow for the segregation of the different groups studied

(subgenera) of the genus *Quercus*, as determined by previous authors: Panahi et al., 2012, stomata; Denk and Grimm, 2009, pollen grain; and Hanson, 1917, leaf anatomy.

This study noted that environmental conditions create significant variations in some microcharacters. The thick walls of the epidemical cells appear in arid areas, the stomata with crested guard cells occur in species from dry places and the presence of multi-stellate hairs is associated with such habitats.

Finally, we found some typical microcharacters of *Quercus* species, which had not been previously observed in oaks of the SW Iberian Peninsula, such as: verrucate stomata (*Q. faginea* subsp. *alpestris*) uniseriate-branched hairs (*Q. estremadurensis*) and apiculate and pilose anthers (*Q. suber*).

Acknowledgements

The author would like to express his gratitude to the herbarium HSS curator, and to Allen Coombes for his help and revision of the final manuscript version. This work was supported by the project GROUP HABITAT RN006 (20011-2014), financed by Consejería de Empleo, Empresa e Innovación of the Extremadura Government,

Photographers. Title page: Allan Taylor (*Quercus rotundifolia*). Photos in Figures 1-8: Francisco M. Vázquez

Bibliography

- Bussotti, F. and P. Grossoni. 1997. European and Mediterranean oaks (*Quercus* L.; Fagaceae): SEM characterization of the micromorphology of the abaxial leaf surface. *Bot. Jour. Linn. Soc.* 124: 183-199.
- Clements, S. 1905. The Relation of Leaf Structure to Physical Factors. *Transactions of the American Microscopical Society* 26: 19-98.
- Hanson, H. C. 1917. Leaf-Structure as Related to Environment. *Amer. Jour. Bot.* 4(9): 533-560.
- Panahi, P., Z. Jamzad, M.R. Pourmajidian, A. Fallah, and M. Pourhashemi. 2012. Foliar epidermis morphology in *Quercus* (subgenus *Quercus*, section *Quercus*) in Iran. *Act. Bot. Croat.* 71(1): 95-113.
- Camus A. 1936-1954. *Les chênes, Monographie du genre Quercus et Monographie du genre Lithocarpus*. Encyclopédie Economique de Sylviculture. Vol. VI, VII, VIII. Editions Lechevalier. Paris.
- Nixon, K.C. 1997. *Quercus*. in: *Flora of North America* Editorial Committee, eds, *Flora of North America North of Mexico*. Vol. 3: 445-447. Oxford University Press, New York.
- Colombo, P.M., F. Chiesura Lorenzoni, and F. Grigoletto. 1983. Pollen grain morphology supports the taxonomical discrimination of Mediterranean oaks (*Quercus*, Fagaceae). *Plat Syst. Evol.* 141(3): 273-284.
- Coutinho, A.X. 1888. *Os Quercus de Portugal*. Lisboa.
- De Candolle, A.P. 1868. *Prodromus systematics naturalis regni vegetabilis. Cupuliferae*, Part 16 (2). Victoris Masson & Filii,

Paris.

- Thomson, P.M. and R.H. Mohlenbrock. 1979. Foliar trichomes of *Quercus* subgenus *Quercus* in the Eastern United States. *Jour. Arnold Arboretum* 60: 350-366.
- Denk, T. and G.W. Grimm. 2009. Significance of pollen characteristics for infrageneric classification and phylogeny in *Quercus* (Fagaceae). *International Journal of Plant Sciences* 170 : 926-940.
- Amaral Franco, J. 1990. *Quercus* L. In G. López (ed) *Flora Ibérica*. Real Jardín Botánico de Madrid, Servicio de Publicaciones del CSIC, vol. II: 15-36.
- Devesa, J.A. 1992. *Anatomía foliar y palinología de las gramíneas extremeñas*. Servicio publicaciones UEX. Badajoz.
- Dyal, S.A. 1936. A key to the species of oaks of eastern North America based on foliage and twig characters. *Rhodora* 38: 53-63.
- Gómez-Casero, T., M. Hidalgo, H. García-Mozo, E. Domínguez, and C. Galán. 2004. Pollen biology in four Mediterranean *Quercus* species. *Grana* 43: 22-30.
- Hardin, J.W. 1976. Terminology and classification of *Quercus* trichomes. *Jour. Mitch. Soc.* 92: 151-161.
- Hardin, J.W., 1979. Patterns of variation in foliar trichomes of eastern North American *Quercus*. *American Journal Botany* 66(5): 576-585.
- Hesse, M., H. Halbritter, R. Zetter, M. Weber, R. Buchner, A. Frosch-Radivo, and S. Ulrich. 2009 . *Pollen terminology — An illustrated handbook*. Springer, New York, New York, USA.
- Holmgren P.K. and N.H. Holmgren N. H. 2003: Additions to Index Herbariorum (Herbaria), edition 8- Fourteenth Series. *Taxon* 52: 385-389.
- Huguet del Villar, E. 1957. Estudios sobre los *Quercus* del Oeste mediterráneo. *Anal. Inst. Bot. Cavanilles* 15(1): 3-114.
- Jones, J.H. 1986. Evolution of the Fagaceae: The Implications of Foliar Features. *Annals of the Missouri Botanical Garden* 73:228-275.
- Liu, M.Q. M. Deng, and Z.K. Zhou. 2009. Taxonomic and ecological implications of leaf cuticular morphology in *Castanopsis*, *Castanea*, and *Chrysolepis*. *Plant Syst. Evol.* 283: 111-123.
- Llamas, F., C. Pérez-Morales, C. Acedo, and A. Penas. 1995. Foliar trichomes of the evergreen and semideciduous species of the genus *Quercus* (Fagaceae) in the Iberian Peninsula. *Bot. Jour. Linn. Soc.* 117: 47-57.
- Diez, M.J. and M. Suárez. 1987. *Fagaceae* en: B. Vladés, MJ. Diez & I. Fernández. *Atlas polínico de Andalucía Occidental*. 94-96. Cádiz.
- Denk, T. and G.W. Grimm. 2009. Significance of pollen characteristics for infrageneric classification and phylogeny in *Quercus* (Fagaceae). *Int. J. Plant Sci.* 170(7): 926-940.
- Lou, Y. and Z.K. Zhou. 2001. Leaf epidermis of *Quercus* subgen. *Cyclobalanopsis* (Oerst.) Schneid. (Fagaceae). *Acta Phytotaxonomica Sinica* 39(6): 489-501.
- Penas, A., F. Llamas, C. Pérez-Morales, and C. Acedo. 1994. Aportaciones al conocimiento del género *Quercus* en la cordillera Cantábrica. I. Tricomas foliares de las especies caducifolias. *Lagascalia* 17(2): 311-324.
- Punt, W., P.P. Hoen., S. Blackmore , S. Nilsson and A. Le Thomas. 2007 . Glossary of pollen and spore terminology. *Review of Palaeobotany and Palynology* 143: 1-81.
- Rowley , J.R. and N.I. Gabarayeva. 2004. Microspore development in *Quercus robur* (Fagaceae). *Review of Palaeobotany and Palynology* 132 : 115 – 132 .
- Ruiz del Castillo, J. 1988. Estudio palinológico de trece *Quercus*. *Revista Instituto Pirenaico* (Jaca (homenaje a P. Montserrat)): 339-345.
- Schwarz O. 1936. Entwurf zu einen natürlichen System der Cupuliferen und der Gattung *Quercus* L. *Notizbl. Bot. Gart. Berlin-Dahlem* 8: 1-22.
- Schwarz O. 1964. *Quercus* L. In: Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds) *Flora Europaea*, vol. 1: *Lycopodiaceae* to *Platanaceae*, pp. 61-64. Cambridge University Press, Cambridge
- Solomon , A.M. 1983a. Pollen morphology and plant taxonomy of white oaks in eastern North America. *American Journal of Botany* 70 : 481 – 494.
- Solomon , A.M. 1983b . Pollen morphology and plant taxonomy of red oaks in eastern North America. *American Journal of Botany* 70 :495 – 507 .
- Stairs, G.R. 1964. Microsporogenesis and embryogenesis in *Quercus*. *Bot. Gaz.* (Chicago) 125: 115 – 121.
- Sufou, O., M. Saint-Martin and P. Rouane. 1988. Stomates et cires dans le genre *Quercus*. *Comptes Rendus Acad. Sciences Paris Serie 3.* 307: 701-707.
- Uzunova, K., E. Palamarev, and F. Ehrendorfer, F. 1997. Anatomical changes and evolutionary trends in the foliar epidermis of extant and fossil Euro-Mediterranean oaks (Fagaceae). *Plant Syst. Evol.* 204: 141-159.
- Van de Campo, M. and Elhai, H. 1956. Étude comparative des pollens de quelques chênes. Application a une turbière normade. *Bull. Soc. Bot. Fr.* 103: 254-260.



*Frightening shapes, in country lanes at nightfall,
bizarre dancers, or monsters with upraised arms,
brooding over lanes,
run! run!
from the dead limbs hanging on for dear life,
from these threatening gargoyles of toughened wood.*





Trognes, Tétards, Emondés, Plesses: the Multiple Aspects and Uses of the Farmer's Oak

Dominique Mansion

Maison Botanique, Centre Européen des Trognés de Boursay
La Guignière
F-41270 Boursay, France
Phone: +33 (0) 6 76 88 28 74
dominique.mansion@orange.fr

ABSTRACT

Ancestral techniques employed by farmers have created trees of greatly different morphology and stature than those managed by foresters. This presentation will show the multiple forms of the farmer's oak, destined to serve a vast array of situations and uses. Regularly pollarded, the life expectancy of these trees is surprisingly long which is why they are host to a rare and remarkable biological community. Long criticized by forestry and tree specialists, who value above all the quality of the timber, this empirical method for cultivating oaks deserves to be better studied and known. Used today for luxurious woodwork, the farmer's pollard has much to teach us, notably in agroforestry but also about biodiversity and sustainable development. And, if only for their extraordinary diversity of form, they merit our complete attention.

Keywords: oak, pollard, agroforestry

Introduction

Everyone in France knows the majestic, tall oaks in the Bercé National Forest in the Sarthe or the or the Tronçais forest in the Allier, superbly managed for timber production by the French National Forestry Commission. Here we will not be discussing the trees in these prestigious forests, but those of not so well known “forests”, currently under much greater threat: I am referring to those forest formations composed of pollards and coppiced trees (that have over 200 regional names in French).

Also known as a high coppice, hanging forest, forest on stilts, or tree meadow forests, they have marked our landscapes for thousands of years. This traditional technique for managing oak trees (other deciduous species are also managed in this way) consists of cutting all the young trees off at the same height and pruning them back regularly at the same level(s) to provide renewable production of wood, leaves, and fruit, out of reach of grazing herbivores.

History

The oldest pollards were no doubt grown in pasture woodlands. These practices continue to survive in many European countries as in certain pasture woodlands of pedunculate oak (*Quercus robur* L.) in Béarn. In the Basque Country the height of the pollards is often quite remarkable, with some trained in candelabra shape (Photo 5). Some of these forests of pollard *Q. robur* and, to a lesser extent, *Q. pyrenaica* (Matt.) Liebl., continued to be maintained by the French Forestry Commission until the 1930s. Today, in some areas, these woodlands are still managed in the traditional way, in Poitou-Charente, for example by the Nature Conservancy.



1/ A traditionally managed pollard woodland in Deux-Sèvres.

In the Iberian Peninsula *dehesas* represent a very ancient form of agroforestry. Still today, in Spain, *dehesas* cover nearly 2 million hectares. Holm oak, *Q. ilex* L., is the most widely used species. The central part of each oak is pruned regularly so that it spreads out in a parasol shape, providing shade for cattle or crops. In the southern part of Aragon, also in Spain, you can still see old pollard holm oaks that must have been cut back to ground level at one time. Cork oak, *Q. suber* L., is also used, especially in the Portuguese *montado*.

Traditionally in France, large numbers of pollard oaks grew in the hedges surrounding small fields in the *bocage*. Pedunculate oak pollards are still a common feature of the landscape in the Rennes area of Brittany. This technique, intended to promote the production of a maximum number of side shoots, is not specific to this region, even if today it is most visible there.

Traditionally, the trunk of a pollard belonged to the landowner whereas the coppiced wood to the tenant farmer. This often led to conflicts between the landowner and his tenant, as the former wanted to produce valuable timber by growing tall trees and the latter wanted to pollard them as much as possible!

The history of pollards sometimes intersects with major events: during the First World War observers on the front lines were posted in pollard hollows and, during the Second World War, there are trees that can still be seen today that are known to have served as hideouts for those trying to escape the German concentration camps.

From certain historical remains it is possible to have an idea of how old these pollarding and coppicing techniques are. To name but a few, a pollard found in the River Trent in England, has been dated at 3,400 years old, whilst a coppiced tree, discovered in the Meuse river in Belgium, was estimated at a mere 1,800 years!



2/ Pollards with bent branches at the bottom are often the remains of pleached hedges used to fence fields or woods.

What they were used for

In many countries, firewood was the main resource drawn from pollards. Hundreds of millions of bundles of firewood were burnt in fireplaces; bread and hemp ovens; brick, tile, lime, and plaster kilns, etc. Before coal became widely used, small logs, or *charbonnettes*, were turned into charcoal fuel for forges, iron and glass furnaces, etc. Some farmers still continue to coppice trees to produce logs for firewood. Small firewood and *charbonnettes* are often burnt in the fields.

Pollards were also used in many regions as boundary markers. The coppiced wood was shared between the neighbouring farmers. Oak leaves were not prized as animal feed, unlike those of ash (*Fraxinus excelsior* L.) and elm (*Ulmus minor* Mill.) trees. However, during the heat wave of 2003 in France, farmers in the Sarthe revived this practice by partially trimming their pedunculate oak pollards and feeding the leafy shoots and acorns to their cattle.

Certain pollard forests that can be seen today in the Basque Country and on the outskirts of London were created by the use of this technique for the production of large quantities of charcoal. Certain trees were specially trained to make curved timbers for shipbuilding whilst logs from long pollards were used to make roof timbers for houses and furniture. And, of course, acorns were used to feed the pigs.

Biological and ecological considerations

Pollards adapt remarkably to landscape constraints, spreading their branches and achieving harmony with both artificial and natural obstacles.

In pollarding, swellings develop where branches are cut and from these swellings new trunks often grow. Additionally, pollard shoots often produce roots high on their own trunk, in hollows filled with compost. These shoots are considered trees rather than branches! The compost that forms in these hollows used to be collected for flower pots, flower beds and vegetable gardens. In the Perche region, this compost is known as “pollard blood”. Many seeds borne by wind or animals germinate in this compost. Trees may even



3/ Chemin des Trognons (Boursay).



4/ “Dancing” pollards.

grow there and their roots work their way down to ground level. I have seen a weeping birch (*Betula pendula* Roth.) growing in compost on a pollarded pedunculate oak. Its roots reached the ground, the compost disappeared when the branch split, uncovering a birch root which has since become a trunk growing inside the trunk of the oak tree. Now there is a pollard willow inside a pollard oak that the farmer prunes back at the same time!

Conservation

In recent years, pollards have been pillaged to make luxury furniture without any concern for replacing them, or for the fate of any of the rare or more common protected species sheltered in them. The combined factors of the mechanization of agriculture in the latter half of the twentieth century and the substitution by fossil fuels and synthetic materials for many of the products that came traditionally from pollarding, has led to the disappearance of these noble trees.

In 1999, to raise awareness of this loss, I set up the Pollard Garden at the International Garden Festival in Chaumont-sur-Loire, featuring 27 pedunculate oak pollards that had been destroyed by farmers in my home village of Boursay. This installation was maintained until 2001 when it was dismantled and the pollards returned to Boursay, to be installed with 15 other specimens along a special path: the Chemin des Trognés. In 2003, the Maison Botanique (inaugurated in 2000) opened the Centre Européen des Trognés and, in 2006, the first European symposium on pollards, held in the Vendôme, brought together 24 speakers from 8 countries throughout Europe. An exhibition on pollards is currently on display in a small barn adjoining the Maison Botanique.



5/ Pollards in the Basque Country.

Creating new pollards and envisaging the future

The Maison Botanique encourages and monitors the creation of new pollards. The future of pollards will involve the woodchip industry, capable of processing all pollard wood with minimal handling, as well as agroforestry projects to put pollards back into the fields. These are intended to promote local production of wood chips for mulch or biomass, as well as enhance biodiversity and fix carbon.

Photographers. Title page: Dominique Mansion (sculptures by André Morvan). Photos 1-5 and p. 130: Dominique Mansion.

Further reading

Mansion, Dominique. 2010. *Les trognes: l'arbre paysan aux mille usages*. Editions Ouest-France.

Dumont, E., coord. 2007. *Les trognes en Europe. Actes du premier colloque européen sur les trognes, 2006*. Editions Maison Botanique de Boursay.

Read, H. 2000. *Veteran Tree: A Guide to Good Management*. Birmingham: English Nature.

Read, H. 1996. *Pollard and Veteran Tree Management, II*. Corporation of London.



The Bio-Geo-Chemical Process of Plant Nutrition and Soil Formation: Can This Help Us Grow Healthier Oaks?

Michael Martin Meléndrez

Soil Secrets Worldwide LLC & Trees That Please Tree Farm

Mail Only: 9 Gilcrease Road

Los Lunas, New Mexico 87031, USA

Michael@soilsecrets.com

ABSTRACT

For many decades, urban landscapers, horticulturists, farmers and agronomists have utilized the balanced fertilizer concept of N-P-K with a few minor plant nutrients thrown in from time to time. Fertilizers were formulated to stay in a soil solution for as long as possible, so that plants had a chance of utilizing them. For the objective of increasing the yield of an annual crop, fertilizers worked very well; however, they did so at a cost to the biological health of soils. Trees and specifically oak trees are obviously not an annual crop, but the same issue of soil decline can inflict maladies of poor nutrition if the soil's biological health is not managed properly! Nature's Bio-Geo-Chemical process is sabotaged by the use of the 'brute force' paradigm of modern agriculture and urban horticulture, causing chaos and death within the terrestrial biosphere, ultimately also causing the soil to lose the pipeline of Humic Acids. While the theme of this conference is oak trees, the problem of soils can be exemplified by what's happened to our food quality and nutrient density over the past few generations. There are many studies coming from all regions of the globe showing a decline in the density of vitamins and minerals found in our food. This presentation will cover the basics of soil chemistry and the mutualistic biology provided by bacteria and fungus, often called the Soil Food Web. I will show how and why Humic Acids are capable of changing a soil's chemistry and biology so that we can successfully grow a wider range of trees and plants in places they are not necessarily native to.

Keywords: anion, mycorrhizae, cation exchange, humic substances, RoundUp ready, soil food web, trophic levels

Introduction

Trees—specifically for this Conference, oak trees—are fascinating plants, because they live for many years and they grow tall, which challenges the conventional wisdom of how water and mineral nutrients are transported higher than a few feet. Water flows up into the organism, transporting soil minerals that are purified into elements, but many things must fall into place before this can happen. Nature finds a way to turn rock into soil and make the mineral elements of the rock into a nutrient that is valuable to a plant; this is called the **Bio-Geo-Chemical Process**. Many of these valuable elements are removed from the site because of the way we manage and maintain sites. When grass is mowed and leaves are raked and hauled away, or trees are harvested and removed from the site, soils are not being re-mineralized with the minerals cycled back in the form of decomposing organic debris. The problem is that neither agriculture nor urban horticulture is sustainable if we don't work with Nature's process of soil building. The situation is exemplified in agriculture where food is produced on modern farms, using modern chemicals, big tractors, soil fumigants (needed to fight soil disease), and GMO crops that are 'RoundUp Ready'—and the food being produced may not be very good for us. Many USDA affiliated officials, County Agricultural Agents and professors from agriculture colleges will argue that we cannot feed the world's bulging population without modernizing agriculture worldwide. However a scarier threat to the survival of mankind is the loss of healthy top soil, reducing our ability to produce quality food without poisoning our environment with chemicals.

For many decades, urban landscapers, horticulturists, farmers and agronomists have utilized the balanced fertilizer concept of N-P-K with a few minor plant nutrients thrown in from time to time. Fertilizers were formulated to dissolve into a soil water solution, so that plants have a chance of utilizing them. However, some of that fertilizer washes down into our ground water aquifers, into our streams, rivers and oceans—never a good situation. For the objective of increasing the yield of an annual crop, concentrated N-P-K fertilizers worked very well, but they did so at a cost to the biological health of soils. With better yields came more disease pressure on the crop, poor nutrition to the consumer, loss of soil structure, and a decline in top soil. Recalcitrant soil carbon is in decline globally; more specifically, Humic Acids and the precursor processes for making more Humic Acids are missing from most sites managed by mankind. This is very serious as Humic Acids are potentially the most important part of a healthy and productive soil, and have been described as “essential” in a recent paper published in the *Journal of Chemical Education* (Davies and Ghabbour, 2001).

While the theme of this conference is oak trees, the problem of soils can be exemplified by what has happened to our food quality and nutrient density over the past few generations. Whether a plant is a tree or a field crop, if it is failing to uptake minerals for any reason, it will not get what it needs in order to be healthy. The Kushi Institute findings on food nutrient density demonstrate this problem. The Kushi Institute analysis of nutrient data from 1975 to 1997 found that average calcium levels in 12 fresh vegetables dropped 27%; iron levels, 37%; vitamin A levels, 21%, and vitamin C levels, 30%. A similar study of British nutrient data from 1930 to 1980, published in the *British Food Journal*, found that in 20 vegetables the average calcium content had declined 19%; iron, 22%; and potassium, 14%. Yet another study concluded that one would have to eat eight oranges today to derive the same amount of Vitamin A as our grandparents would

have gotten from one. There are many more studies from all regions of the globe showing the same decline in the density of vitamins and minerals found in our food, including the food produced on organic farms.



1/ *Quercus hintoniorum* Nixon & C.H. Mull.

The Soil Food Web

Soil is the bridge between all life and the inanimate world, where the geosphere, the atmosphere, the hydrosphere and the biosphere meet, providing a fragile condition; “[w] here a thin blanket of air, a thinner film of water, and the thinnest veneer of soil combine to support a web of life, diversity and ongoing change” (Meléndrez, 2010). In recent years the industry of organic agriculture has become aware and supportive of the concept of a ‘soil food web’, which describes the flow of organic nitrogen from the smallest of microbes to a progressively larger and larger animal. In the process the excess nitrogen always leaks from the decay and consumption of the protein that was part of all those bodies of bacteria, protozoa, nematodes and other animals of soil. Each level of the process is called a **trophic level**. As we move up the levels to progressively larger and larger microbes, to multi cell animals, and finally larger animals such as earthworms, there is always an excess of nitrogen that becomes available to the vegetation growing on the site and this becomes the primary source of nitrogen in every ecotone on earth. It could also be the major source of nitrogen for our gardens, farms, mine reclamation sites, etc. Nitrogen may be the most emphasized of the big 3 major nutrients including phosphorus and potassium, called the N-P-K major nutrients, but there are many more

called the minor nutrients. Like your multiple vitamin mineral supplement A to Z formula, plants also need many elements such as iron, zinc, manganese, etc. These nutrients are present in the soil in the form of charged particles or ions, called **cations** when the charge is positive and **anions** when it is negative. All the minerals needed by a plant are expected to be provided in a natural ecosystem by decaying organic matter that is cycling. In this way, the decomposing Soil Organic Matter (SOM) is re-mineralizing the soil.

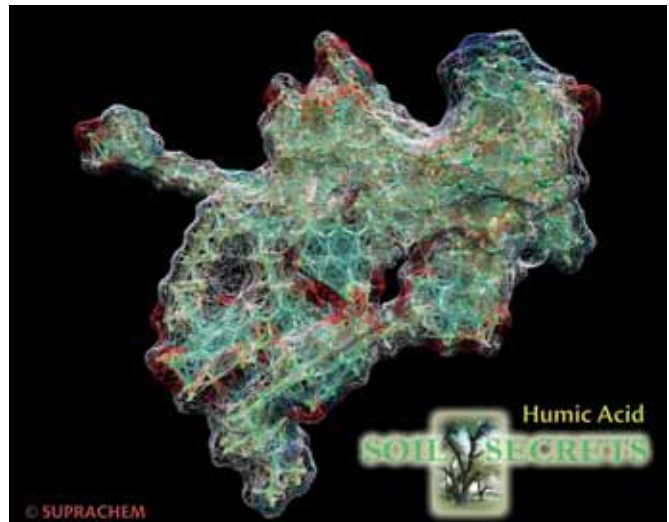
If the soil site is located where farming over many generations has been harvesting crops and consequently has shipped off many of the indigenous minerals of the site, or the soil pH is acidic, or the soil has a low cation exchange capacity, or thousands of years of high rainfall have washed away many of the plant nutrients, then it's likely that you will have a problem providing the nutrient density that your plant needs. This limiting factor is seen in the soil conditions of the managed forests of Europe, where generations of foresters have removed timber and destroyed the soil's structure, resulting in the depletion of soils! In agriculture and in urban horticulture, the question is, do you have enough minerals in organic form cycling in the soil and can your soil hold onto these mineral nutrients once they are no longer organic and have been liberated from the decaying organic matter? Agriculture and urban horticulture are haunted by disease pressure in the soil, caused by the overgrowth of soil disease microorganisms such as *Verticillium* wilt, *Phytophthora* blight, Texas root rot (cotton root rot), pink root disease, *Rhizoctonia*, and *Pythium*, a damping-off root rot. Modern agricultural fertilizers and soil fumigants have upset the balance of Nature, causing a decline in our beneficial soil microbes, particularly the mycorrhizal fungi, and stopping the competitive exclusion of disease!

For the purpose of describing the problem of sustainable soils, I'll cover two major bottlenecks in this paper. One limiting factor consists of the mutualistic mycorrhizal fungi that all oaks trees need for optimum nutritional uptake of many of the minerals that are not easily soluble in water. The other limiting factor is what I term the Carbon Connection, or the availability of carbon. Some carbon substances of the soil are simply decaying organic matter while other carbon fractions are powerful biologic chemicals that are doing many things that are critical to soil and plant health.

The Carbon Connection

To most plant professionals, landscape architects, nursery people, farmers and home owners, the concept of adding organic matter to soil as a method of improving the health of soil sounds reasonable. For most of us, the main defining characteristic of a top soil is the presence and the concentration of SOM that either accumulated over many centuries or was intentionally added. Organic matter can be in the form of actively decomposing dead things such as roots, leaves, wood or compost, or it can be in the form of complex molecular carbon-based chemicals that are not actively decomposing. It can be said that SOM is composed of a continuum of materials of varying chemical complexity with mean turnover times from days to years and even millennia (Davidson and Janssens, 2006). The discrete pools of soil carbon substances that make up the total SOM can be divided into more discrete pools that can be characterized by the turnover times they exhibit in soil (Parton et al., 1987, Jenkinson, 1990 and McCown et al., 1996). SOM pools are chemically divided into two categories, **labile carbon** which has a rapid turnover rate

and **recalcitrant carbon** which is slow to decay, lasting decades or longer. It is the accumulation of recalcitrant carbons that has the lasting benefit of building top soil! Due to the strong chemical bonds of the recalcitrant carbon substances, they are not easily consumed by the saprophytic microbes of soil, therefore they can accumulate and build a top soils' physical, chemical and biological characteristics. Labile carbon is any SOM that is in an active state of decomposition, turning rapidly



2/ Supramolecular Humic Acid Molecule.

back into CO₂ and includes dead roots, leaves, animals (large and small), along with soil amendments such as compost, manures, peat moss, worm castings, mushroom compost, etc. Within the recalcitrant carbon substances of soil may be found powerful biologic chemicals of Nature called **Supramolecular Humic Acids**, or humic acids for short. The common term **humus** refers to the scientific term **Humic substances**, another name for recalcitrant soil carbon. Humic substances may or may not contain a significant amount of Humic Acids, or the active fractions of Humic Acids called Humic acids, Fulvic acids and Humin. While soil amendment products are available that claim to contain Humic Acids, it's difficult for a manufacturer to prove that their Humic Acid product actually contains this active ingredient with the proper chemical characteristics since there is not a standardized method of analysis that commercial or university soil labs are capable of performing (Piccolo, 2002). Saying that the Humic Acids are Supramolecular is very significant because when any chemical is Supramolecular, the molecules of the chemical can find each other and self-assemble into giant clusters or chains called Supramolecular structures, where each molecule in the structure is not chemically bonded to the other molecules. It's this characteristic that really amounts to a powerful biologic chemical! In chemistry, **molecular self-assembly** is the process by which molecules adopt a defined arrangement without guidance or management from an outside source. At the 2013 IOS conference I showed a 3-D geospatial image of Humic Acids forming a Supramolecular structure and I also showed how Humic Acids, when supramolecular, attract and hold water molecules, preventing the water from easily evaporating. See next, an attached image of a Supramolecular Humic Acid molecule that was purified from a soil sample, described and characterized by the collaborative efforts of Soil Secrets LLC, SUPRACHEM Labs and the United States National Nuclear Security Administration laboratories.

In experimental studies, a variety of chemical, physical and biological fractionation procedures have been developed to characterize various pools of soil C and N and to study the distinction between labile soil carbon, recalcitrant soil carbon and Humic Acids and their impact on the carbon to nitrogen ratios (Olk and Gregorich, 2006). Recalcitrant soil carbons, also known as Humic substances, can be further described as potentially containing powerful biologic chemicals that are Supramolecular Humic Acids (Piccolo,

2002), (Meléndrez and Wood, 2011). While the general literature still concludes that there is considerable discrepancy between what is simply soil carbon, what is recalcitrant Humic carbon and what are the Humic Acids, the debate is caused by a lack of purification techniques that allow for the extraction of the Humic Acids without damaging or destroying them completely, therefore making it difficult or even impossible for typical commercial or university soil labs to perform true chemical analysis for modeling studies (Piccolo, 2002). Recently, however, Soil Secrets and a team of chemists at the National Laboratories of Sandia and Los Alamos in collaboration with the team of chemists from SUPRACHEM have developed the technique of purifying Humic Acids, for the objective of analysis, from a soil sample without changing them, providing the evidence of what the molecular description of Humic Acids really is and what benefits they can provide (Meléndrez and Wood, 2001).

Here's my laundry list of benefits provided by Supramolecular Humic Acids

1. Help the macro-aggregate formation of soil.
2. Help improve drainage, porosity and oxygen diffusion into the soil. All plants and all beneficial soil microbes need oxygen.
3. Have an extremely high cation exchange capacity allowing the chelation of plant nutrients so they won't wash away during high rainfall events.
4. Participate in microbial respiration, helping microbes to continue functioning when soils become saturated during high rainfall or irrigation events.
5. Can remove salts and sodium from soil.
6. Can accelerate the decomposition of petroleum hydrocarbons from soil, in the event of an oil spill.
7. Help to manage water in the soil and are particularly important in arid climates by helping to conserve water.
8. Help in the fluid transport of water up into a tree or taller plant by changing water into a semi water/gas state for improved uptake.
9. Help to hold plant nutrients in a water solution in the soil, so that plants can uptake the nutrient easier.
10. Stop virus replication in cells.
11. Reduce disease pressure in soil by changing the environment to one that is more supportive of beneficial microbes, causing competitive exclusion of the pathogen.
12. Help make indigenous minerals available to plants by creating a weak acid called carbonic acid, which will liberate minerals.

The Mycorrhizal Fungi Connection

The second bottleneck to providing optimum nutrition to crops or to urban landscapes is a fungus-plant relationship. Mycorrhizal fungi are best described as a partner with plants, where both fungus and plant are mutualistically benefited from the partnership. Research performed by several entities including the USDA Agricultural Research Service has proven that the 50 to 100 years of farming in the United States has taken a toll on the indigenous mycorrhizal fungi count in soil (Taheri, 2012). While many people will claim that mycorrhizal fungi are already in the soil and therefore don't need to be added, the research on this fact appears to dispute that claim. Research performed by the USDA Agricultural Research Laboratory for the upper Midwest measured how

many mycorrhizal fungi spores remained in a farm soil as compared to a native prairie soil that is not being farmed and the difference was huge. In addition, the farm soil was dominated by a different kind of fungus that was not mycorrhizal, so while the native non-cultivated site was dominated by arbuscular mycorrhizal (AM) fungi, the agricultural soil was dominated by non-mycorrhizal fungi. For example, the *Candida* yeast problem that may affect humans is a fungus that can dominate in a soil and which can cause disease pressure problems with crops. The same is true concerning urban landscapes that have a history of fertilizer use, compaction, and other practices that impair the plants' ability to maintain a relationship with mycorrhizal fungi. Mycorrhizal fungi can sequester minerals from the soil that the plant can either not reach or cannot harvest because the minerals are complexed into a chemical form that ties up the mineral preventing it from being put into solution for plant uptake. An example of this is the acidified phosphorus used in fertilizers. When acidified phosphorus comes into contact with iron in the soil, iron-phosphate is formed, a substance that will not oxidize and therefore cannot become soluble for a plant to sequester by itself. However, the hyphae tubes of mycorrhizal fungi are soil drills and they can explore the soil tenfold further than their host plant can with roots and they can make enzymes and chemical solutions that can liberate the iron and the phosphate, transporting those elements back to the host plant for feeding. The benefit of being supplied minerals and water by the mycorrhizal fungi is paid for by the plant as it will supply liquid carbon (glucose) that the mycorrhizal fungi needs for energy.

At the risk of over simplifying the many benefits of mycorrhizal fungi, here's a laundry list of benefits.

1. Nematode control, controlling harmful nematodes by eating them and their eggs for a nitrogen source. Remember the soil food web is all about nitrogen cycling.
2. Disease prevention, as mycorrhizal fungi protect plant roots from disease and also keep the host plant healthier so it can protect itself from disease.
3. Improved drought tolerance, as the mycorrhizal fungi's hyphae can sequester water from soil that the plant roots cannot reach.
4. Soil building, as the AM fungi (endotypes) in the genus *Glomus* make a glycoprotein called glomalin, a precursor chemical to recalcitrant soil carbons. This helps to glue the soil into a better macro-aggregate structure.
5. Improved water percolation into the soil, due to the improved macro-aggregate structure and the improved concentration of Humic Acids that also help soil structure and water management.
6. Improved uptake of soil minerals into the host plant, which will increase the nutrient density of that plant, therefore improving the health of the plant.
7. Improved tolerance of extreme pH conditions
8. Improved uptake of minerals that normally are tied up when the pH of soil is either too acid or too alkaline.

Finally, it has been demonstrated that in agriculture, mycorrhizal fungi can replace on the average 25% of the phosphorus we currently utilize without a decline in yield, on sites where adding phosphorus has always been needed because the indigenous phosphorus on the site is chemically tied up. However if there is plenty of phosphorus in the soil, but not available to plants, the mycorrhizal fungi can supply all the needs of the plant by harvesting what is native to the site. The key is to not wait for the native

mycorrhizal fungi to rebound once you begin a transition of appropriate mycorrhiza-friendly management techniques. Instead, it is very cost effective to inoculate your crop or your landscape with a mycorrhizal product that contains the proper species for the type of plant you are nurturing. There are plenty of good quality mycorrhizal products now on the market that provide what I call an “agriculturally applicable product” which means the product has a high spore count per pound of material and the manufacturer can show you evidence of the spore count provided by a certified 3rd party lab.

My Conclusion

I’ll hang my hat on the science and the benefits of mycorrhizal fungi and Humic Acids that are Supramolecular, because both play an active role in the Bio-Geo-Chemical process of plant nutrition and soil formation and without either the whole process is compromised. Over 90% of the Earth’s plants are dependent upon mycorrhizal fungi to successfully sequester the water and the minerals that plants need for optimum nutrition. While some plants may survive without that relationship, they may struggle, be easily infected by disease, grow poorly and yield a poor crop. Without Humic Acids and a mycorrhizal relationship, landscape plants such as trees may be prone to chlorosis, salt burn, drought, slow growth, poor health and a reduced life expectancy. Combined, Humic Acids and mycorrhizal fungi provide the environment for healthy soils, leading to the perpetuation of healthier plants.

Photographers. Title page: Béatrice Chassé (*Quercus macrocalyx* Hickel & A. Camus). Photo 1: Béatrice Chassé. Photo 2: Suprachem.

Bibliography

- Davidson, E.A. and I.A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440: 165–173.
- Davies, G. and E.A. Ghabbour. 2001. Humic Acids: Products of Soil Chemistry. *Journal of Chemical Education* 78 (12): 1609
- Jenkinson, D.S. 1990. The turnover of organic-carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society B* 329: 361–368.
- McCown, R.L., G.L. Hammer, J.N.G. Hargreaves, D.P. Holzworth, and D.M. Freebairn. 1996. APSIM: a novel software system for model development, model testing and Simulation in agricultural systems research. *Agricultural Systems* 50: 255–271.
- Meléndrez, M.M. 2010-2011. Only Healthy Soil Can Grow Healthy Plants. The Nursery Book. Unpublished personal studies.
- Meléndrez, M.M. and L. Wood. 2011. Describing the molecular structures and fractions of Supramolecular Humic Acids. Research and Molecular Data compiled by a Commercial Proprietary Study performed at Los Alamos National Laboratory and Sandia National Laboratories.
- Olk, D.C. and E.G. Gregorich. 2006. Overview of the symposium proceedings, “Meaningful pools in determining soil carbon and nitrogen dynamics”. *Soil Science Society of America Journal* 70: 967–974.
- Parton, W.J., D.S. Schimel, C.V. Cole and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51: 1173–1179.
- Piccolo, A. 2002. The Supramolecular Structure of Humic Substances: A Novel Understanding of Humus Chemistry and Implications in Soil Science. *Advances in Agronomy* Vol. 75.
- Taheri, W. 2012. Role of AM Fungi in Agricultural Ecosystems. *ACRES USA*. September 2012.



Botanic Collections: A Tool for Selecting Species Adapted to Climate Change

Hervé Le Bouler

Conservatoire National de la Biodiversité Forestière

La Pépinière

F-44290 Guémené-Penfao, France

Phone: +33 (0) 2 40 79 24 45

herve.le-bouler@agriculture.gouv.fr

ABSTRACT

It is very probable that many tree species currently in place in certain parts of the temperate world will not be able to survive in the face of current climate change. Increased periods and intensity of drought will be one of the principle causes of this and species important for forestry and horticultural alike will suffer. The genus *Quercus* is present in the Temperate Zone in a wide range of ecological niches including the dryer and warmer ones that are similar to what is expected in the future. Both the intra- and inter-specific genetic diversity of oaks is very high as is their capacity to hybridize. This would facilitate the natural transfer of genetic material, specifically, of genes that could confer drought resistance from one oak species to another, making oaks an interesting resource as replacement candidates or as “adaptation aids”. There is a large degree of phenotypic similarity between these oak species and this will ensure that while drought-resistant species become dominant the landscape will not be dramatically changed. Intended to be an aid to maintaining forests and landscapes, this “replacement” strategy requires a great deal of care, experimentation and further study. In this context, species introductions in botanic collections are an exceptional source of information. These collections are very varied, but they all have in common long-standing experience planting and growing species that are not in their natural habitat. The successes and the failures, if they can be correlated with climate, represent critical information concerning species’ adaptive capacity. New and even more precise information could be obtained by the selective introduction of key species in existing collections or in those to be created in future.

Keywords: climate change, oak collections, adaptation strategy

Introduction

Historically and to this day, the major challenge and obstacle for plant enthusiasts is “Will this plant survive in my climate?” For Temperate Zone inhabitants, winter cold and/or summer drought, represent the major obstacles and often – but not always – sad results for that “special” plant acquired with such high hopes. Nevertheless, it is by definition the nature of plant collectors to spend their time on risky introductions and in so doing furnish valuable information as regards species’ tolerance limits.



1/ *Quercus palustris*, from Eastern North America, growing in the private collection of Peter Laharrgue in Coronel Pringles (Argentina).

A time to take risks?

Obviously, foresters and horticulturists can not operate in the same manner: the important economic constraints within which they function oblige them to bet on “climate resistant” species and therefore choose those species or varieties that have proven hardy for a given location. In the face of current climate change and projected future scenarios, perhaps this “play-it-safe” strategy is not the most instructive and, further, should we be asking ourselves some new questions? If the climate changes, will currently adapted species remain so? In a different climate, can new species be introduced? And, if so, which ones?

For the following reasons, oaks represent a highly interesting group of candidates about which these questions can be asked in order to provide answers to both foresters and horticulturists:

1) Many species fulfill human/economic needs both in respect to timber production and landscape potential;

2) The genus covers nearly all climates where trees are present with the exception of the most northern forests;

3) Oak forests are host to enormous biodiversity;

4) Generic diversity is extremely high (more than 500 taxa) and interspecific genetic transfer is rampant, representing an extremely important asset for adaptation in any changing situation.

Answering the questions of changing bioclimatic envelopes and the consequences for species distribution as well as those concerning possible alternatives requires new concepts and scientific methods. This paper attempts to show that arboreta and botanic gardens have a specific and very important role to play in formulating those answers.

Climate change: perspectives and stakes

Current climate change is the result of the increase in the atmosphere of greenhouse gases. Because of this increase, solar energy remains trapped in the atmosphere and is reflected back on the Earth, thus inducing global warming. The mechanisms and principles of global climate are very complex and warming is neither spatially uniform nor linear in time. In addition, this warming affects all of the other components of climate: air humidity, rainfall, wind speed, etc. The consequences can be observed both on average and in the frequency and intensity of extreme phenomena, i.e., heat waves, drought, storms. Trees, like all plants, cannot get up and move and are therefore very dependent on their local climatic environment.

This dependency is related to several factors, amongst which:

1) The quantity of solar energy available determines growth and regeneration potential. Available energy can be estimated by taking the sum of maximum positive temperatures throughout the year. For each month an average maximum temperature can be calculated and thus the annual sum.

2) Winter cold can be responsible for general damage to the plant or to its vital organs (buds,



2/ *Quercus acutissima* Carruth., from Asia, at Starhill Forest Arboretum in Illinois (USA), founded by Guy and Edie Sternberg, and today part of Illinois College.

evergreen leaves, reproductive organs, seeds, young plants, etc.). A value for winter cold can be expressed by the average minimum temperatures of the coldest months of the year.

3) The water balance, taking into consideration the complex dynamics of water and soil is calculated per month with, on one side, the water deficit (taking into account water lost through evaporation) and, on the other, rainfall and seasonal variations in water availability (depending on type of soil, etc.).

For historical reasons, many botanic collections and arboreta are in the Temperate Zone. Winter cold and summer dry spells or drought are the determining factors in the success of new introductions.

A relational model for vegetation and climate

The following synthesis is based on research on the relationship between species and climate currently being investigated by AFORCE, a multi-disciplinary French initiative that regroups scientists from basic research, forestry management and development, as well as from different educational institutions. (For more information on AFORCE, see, www.foretriveefrancaise.com). The objective is to coordinate different approaches to the adaptation of forests to current climate change and to provide decision-making tools for forestry management policy.

The model that is being developed is based on the general hypothesis that there are limiting factors (for plants) based on climate, and these can be resumed as: for each species (or, for each geographic or taxonomic subset of trees in its natural range) there are climatic values that delimit the climates in which they can survive from those in which they cannot. The combined study of natural distribution and corresponding climatic values has led to the conclusion that the three determining factors are, as explained above, available solar energy, winter cold and the water balance. Today, values for these three climate factors are available with great precision (to 1 km/0.6 mi) for a great many regions and it is thus possible to map them together with natural range distribution (www.worldclim.org).

WorldClim was developed by Robert J. Hijmans, Susan Cameron, and Juan Parra, at the Museum of Vertebrate Zoology, University of California, Berkeley, in collaboration with Peter Jones and Andrew Jarvis (CIAT), and with Karen Richardson (Rainforest CRC).

A case in point : Hardiness Zones

The essential question remains, how can climate description based on these factors be related to species tolerance to new or changing climates? If the tolerance to these three factors is known then it should be possible to estimate species' climate tolerance at any given point. This is of course the approach used in the establishment of Hardiness Zones – but these are only based on tolerance to winter cold. Knowledge about the climatic limitations of each species, or of each population/provenance of a particular species, is obtained essentially through data collected in areas where that species is significantly present and therefore the natural distribution range is the best place to start. Nevertheless, factors other than climate can affect the presence or absence of a species in its “natural distribution range” (biotic, soil or altitudinal factors, for example). The absence of a species in a given location can thus lead to erroneous conclusions concerning its climate tolerance.

The usefulness and limits of arboreta

Knowing where species have been introduced (outside of their natural range) with success provides extremely useful information in the determination of climate tolerance. Conversely, knowing where these introductions have met with failure also provides information. But, the reasons for failure are often more complex, or not as straightforward, as the reasons for success and therefore difficult to interpret.

Introductions in the form of reforestation provide information but these are limited by economic considerations that limit the choices of what is tried. Introductions in botanic collections or arboreta offer a wider range of opportunity because, by definition, collectors are not as inhibited, their creed being, “try everything, everywhere!” This highly unreasonable behavior can provide precious information about the extreme limits of species’ climate tolerance.

Nevertheless, this empirical approach does have its limitations, principally based on the “representative” nature of the taxon in question. These limitations are related to the following points:

- 1) It is not rare to discover in collections that what has been planted does not in fact correspond to the label.
- 2) The use of grafted plants is obviously not conclusive because the host is used precisely for its greater climate tolerance.
- 3) Plants that are raised from non wild-collected seed may be phenotypically correct but because of the hybridization their genome may confer a greater climate tolerance. Clearly, only plants raised from seed collected in the range of the plant’s natural distribution can provide pertinent information.



3/ *Quercus dentata* Thunb. (Asia), *Q. phellos* L. and *Q. velutina* Lam. (Eastern North America) growing side-by-side in Henri de Brem’s private collection, the Quercetum du Hanouard (France).

4) Because of natural annual variation in climate, the length of time that an introduced plant lives in a new climate is crucial. Thirty years with no major problems is a reasonable time frame.

5) In collections, when plants are young they often receive “special care” to help them through this vulnerable period – care that would not be afforded them in a purely natural setting.

6) The mere fact of survival is not the ultimate criteria for determining climate tolerance. It is reproductive success that is crucial.

7) The last, and perhaps most important limitation is the “representative” genetic factor. Often, in collections, few plants are introduced and while they may be introduced into several different arboreta these often all come from the same source and are therefore not genetically representative of the species across its distribution.

Conclusion

To be significant in this context, introductions must be represented by many plants and raised from seed collected in the wild from different provenances. This is easier to accomplish in the context of scientific arboreta that have vaster surface areas and means at their disposal than in private collections.

Nevertheless this constraint of isolated introductions can be overcome through the creation of a collections/arboreta network that would cover a vast geographic area effectively increasing the size of the sample population. This network remains to be created but I am convinced that it is possible, especially for oaks, with the help of the International Oak Society and modern means of communication. Interpreting the resulting data requires specific scientific competence – but I am equally convinced that a network of scientists and plant enthusiasts is possible and desirable. The recent increased scientific interest in private collections/arboreta will contribute to this.

Photographers. Title page: Shaun Haddock (*Quercus hinckleyi* C.H. Mull.). Photo 1: Peter Laharrague. Photo 2: Guy Sternberg. Photo 3: Béatrice Chassé.

Further reading

Galbraith, David A. and William A. Rapley. 2005. *Research at Canadian zoos and botanical gardens*. Museum Management and Curatorship 20(4): 313-331.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.

Hulme, Philip E. 2011. Addressing the threat to biodiversity from botanic gardens. *Trends in Ecology & Evolution* 26(4): 168-174.

Jackson, Peter Wyse and Lucy A. Sutherland. Role of Botanic Gardens. *Encyclopedia of Biodiversity (Second Edition)*. Waltham: Academic Press, 2013.

Maxted, Nigel. In-Situ, Ex-Situ Conservation. *Encyclopedia of Biodiversity (Second Edition)*. Waltham: Academic Press, 2013.

Nageleisen, L.-M., D. Piou, F.-X. Saintonge, and Ph. Riou-Nivert. *La santé des Forêts – Maladies, insectes, accidents climatiques. Diagnostique et prévention*. France: Département de la Santé des Forêts, 2010.

Novacek, Michael J. and Suzann L. Goldberg. Role of Museums and Institutions. *Encyclopedia of Biodiversity (Second Edition)*. Waltham: Academic Press, 2013.

Oldfield, Sara F. 2009. Botanic gardens and the conservation of tree species. *Trends in Plant Science* 14(11): 581-583.



Pruning Oaks: Training the Young to Achieve Grandeur

Guy Sternberg
Starhill Forest Arboretum
12000 Boy Scout Trail
Petersburg, Illinois 62675 USA
e-mail: Guy@StarhillForest.com

ABSTRACT

Training young trees may be one of the most important, yet most neglected, procedures in growing oaks. These trees need to be pruned correctly when they are young in order to develop into the long-lived patriarchs that are their potential. We include discussion of the unique phyllotaxis of *Quercus*; growth hormone interactions; orthotropism versus plagiotropism; pruning seasons; basic ANSI A300 pruning standards; early correction of structural flaws such as parallel and crossing limbs, whorls, and codominant leaders; scaffold development; managing temporary branches and sprouts; root training; and aesthetic considerations for young trees that are in their first 7 meters (23 feet) of growth.

Keywords: *Quercus*, oak, pruning, phyllotaxis, tropism, auxin, cytokinin

Introduction

Training young specimens may be one of the most important yet most neglected procedures in growing oaks. Many young trees need to be pruned correctly when they are small in order to develop into the majestic, long-lived patriarchs that are their potential. Some need such attention much more than others, and some seem to do just fine on their own, but nearly every tree will be better if care is given to tweaking its structural development during the early years. One could debate for eternity whether bad pruning is worse than no pruning, but good pruning always will win.

I have learned much from successes I have had, and mistakes I have made, during my personal experience growing oaks, dating back to 1961. This has been supplemented with sound advice from some very good arborists and biologists, and from observations of the consequences of incorrect or neglected pruning. In a nutshell, there are some correct ways and some very incorrect ways to prune young oaks. Here is a summary of what I have found through a half century of oak culture, focusing upon the first seven meters of a young tree's development.

Goals of pruning young trees

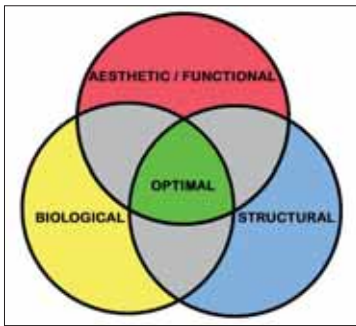


Figure 1/ A Venn diagram of pruning.

Pruning is done for three primary reasons. When it can be accomplished in a way that reflects all of those reasons, it is a job well done. Consider pruning strategies in the form of a Venn diagram with overlapping circles (Figure 1).

The first circle consists of **structural development**. This comprises elimination of codominant leaders, parallel branches, whorls, water sprouts, inward-directed growth, girdling roots, and damage. Without attention to these problems, your oak is less likely to persist into maturity and, gradually, attain the grandeur for which the genus is known. During structural pruning, we try to plan ahead to minimize the diameters of the present and future cuts to be made, and we cut just beyond the natural collars formed by that portion of the vascular system that bypasses the part of the tree being removed. We select competing vertical shoots, weak growth, clustered limbs, and misdirected branches that I like to say “have no future” for removal, leaving a strong, balanced scaffold of both permanent and temporary limbs.

The second circle represents **biological health**. This is at least as much a matter of knowing what (and when) NOT to prune as it is of knowing how to prune. We prune to increase, and in a way which will not diminish, the vitality and pest resistance of the tree. Managing existing or projected decay is a critical part of this, although that also is linked directly to the structure circle mentioned above. We prune in a way, and during a season, which will not expose the tree to increased pressure from insects – especially those that are known to vector diseases or cause significant damage. During pruning, we consider the production of auxins and cytokinins in the tree, and try either to minimize the disruption of their natural ratio or to tilt that ratio toward one or the other in a deliberate attempt to influence the growth balance of the tree. We prune to aid in stress recovery by removing decadent or suppressed portions of the crown, taking broken branches back to forks or

nodes, and re-forming the tree in its most effective, natural habit for future development. We do not prune excessively, following accepted American National Standards Institute (ANSI) A300 standards of limitation on the amount of meristematic tissue (number of buds) removed during any one annual cycle (in general, removing no more than 25% on a young tree).

The third circle is the top circle – the reason the other circles exist. We grow and maintain trees for ***aesthetic and functional values***, and pruning properly for structure and biological health helps us achieve this goal. In most cases, at least with oaks, the goal should be a future mature tree with a graceful, symmetrical habit characteristic of the species and without significant flaws. In some cases (certainly too many, in my view!), the functional goal might be a pollard, espalier, hedge, topiary, or utility clearance. Each of these goals requires a targeted approach.

Phyllotaxis

Meristems – the growing points of trees – are found in buds, root tips, cambial, and parenchymal tissue. The arrangement of buds (phyllotaxis) on oaks differs from that of most other trees, and this is critical to understanding how oaks grow.

An oak twig will have a dominant ***terminal (or apical) bud*** because oaks exhibit determinate growth. They flush and grow for a set time, then stop elongation to set buds and focus upon diameter growth and root extension. Terminal buds are the tree's primary Auxin producers. As the twig extends, lateral (axillary) buds are formed in the leaf axils. These lateral buds are arranged on oaks in a helical pattern with a repetition number of five. Every bud will be positioned 40% farther around the twig than the previous bud.



Figure 2/ Loss of the dominant terminal bud.

After making two complete revolutions of the twig, the fifth bud will be positioned in line with the first. This might not be apparent on horizontal twigs because the leaf petioles will bend to position the leaf blades in horizontal (diatropic) positions, but once the leaves fall the helical pattern can be seen in the buds. At the end of the growth cycle (called a “flush”), the last lateral buds are compressed together to form a ring of **subapical buds** surrounding the terminal bud. Often a vigorous twig will have five subapical buds (one complete helix cycle), with more or fewer being common as well (see photo, p. 151) This resembles the whorls of buds seen on pines (*Pinus* spp.), and functions similarly, except that oaks may produce more than one growth flush per season unlike most pines.

Apical buds are dominant, especially in young trees, and become the extensions of the stem and limbs. Loss of a terminal bud will stimulate the development of subapical buds (Figure 2; p. 153). Lateral buds are not dominant but some also can develop if enough light and nutrients are available; they tend to produce smaller branches that emerge at an angle acute to the axis of the branch. Subapical buds are intermediate in dominance, and produce several types of growth. A large subapical bud may produce a co-dominant leader, resulting in a structural problem for the tree. When several subapical buds in one ring develop, a whorl of branches is formed, also creating structural problems with scaffold development.

Tropism

Understanding the ways trees grow is crucial to guiding their growth. Trees, and other plants, follow stimulus-response rules known as **tropisms**. Several types of tropism combine to direct growth in oaks

Because direct exposure to sunlight reduces stem elongation and etiolation, trees bend toward light due to positive growth hormone action on the shaded side. The effect is called **phototropism**, or growth in the direction of light. Any oak tree that has been lit primarily from one side will exhibit this habit.

As acorns germinate and young oaks develop, their hypocotyls (future roots) grow downward and their plumules (future stems) grow upward, even in the absence of light. This phenomenon is a hormonal response to gravity, being positive in the hypocotyls and negative in the plumules, and it is called **geotropism**. It enables the seedling trees to establish themselves in an upright position (wise old nurserymen say “green side up”). Phototropism and geotropism combine to direct vertical growth.

As the young sapling develops, and throughout the life of the tree, other tropism effects can be seen. The primary stems of vigorous young trees and sprouts maintain apical dominance and grow vertically, exhibiting **orthotropism**. Having one orthotropic leader makes a strong, symmetrical tree; competing leaders usually should be subordinated or removed to avoid conflict. Conversely, lateral branches and twigs are most effective when their foliage is displayed in a horizontal plane normal to the mean direction of the sun, to intercept the maximum amount of insolation; this is called **diatropism**. As the tree or branch ages, or the topmost part of the tree reaches its physiological height limit (and beyond the focus of this paper), apical buds become less dominant and subapical buds may assume dominance, causing bends and kinks in the tree or branch. This oblique growth condition is known as **plagiotropism**, and it manifests as picturesque or even contorted growth in old trees.

Knowing how trees, and their parts, respond to external stimuli such as gravity, light, and damage is an important step toward understanding pruning.

Growth hormones

The following is a very simplified explanation of a very complex biochemistry. Think of an oak stem and limbs as a two-lane highway system. Terminal buds, and to a lesser extent other buds, and their associated leaves produce **auxins** that are sent to the roots. Root tips produce **cytokinins** which in turn are sent upward. As long as traffic is balanced on the stem highway, growth is normally balanced as well.

However, if roots are cut (as in transplanting), the hormone traffic is no longer balanced. The tree is triggered to direct more of its resources to restore the balance by generating more root growth. If the parts of the tree above ground are cut back severely or otherwise damaged, the imbalance is reversed, and the tree will direct its resources to replace the lost buds. This can trigger growth responses in buds that otherwise would remain dormant, and it can cause excessive, structurally unsound wood to form. This is how biology and structure are not always on the same page, as the tree struggles to fix itself. Heavy pruning during transplanting also will lessen the tree's restoration growth of its damaged root system because the hormone balance is artificially restored.

In addition, growth hormones induce the formation of wound-response callus (woundwood) by stimulating cell differentiation of phloem and xylem, regenerating damaged tissues. Beyond the stimulation or depression of root development and woundwood formation, auxins also cause apical dominance. This makes the central leader the most vigorous, orthotropic part of a young tree. Removal of the terminal bud, where the greatest production of auxin is located, will release subapical and lateral buds from inhibition and result in excessive branching and multiple leaders (good for hedges and pollards, bad for "real" trees). Maintaining a reasonable hormone balance in your tree by pruning properly will minimize such problems.

Seasonal considerations

In the late 1800s, fruit tree research suggested a seasonal distribution of growth versus reserve energy now called the **Askenasy Potential Energy Curve**. Much of this work is applicable to oaks as well. Basically, trees carry their maximum reserve energy level when dormant. As new root growth begins in late winter, some of this energy is consumed. Initiation of springwood (early, very porous wood) formation in oaks, pre-budbreak, takes more stored energy. New leaf and twig formation in spring then consumes much more energy. As the first growth flush hardens and the leaves reach peak photosynthesis, some energy restoration is accomplished; but this is offset by additional growth, both as elongation of supplemental flushes and as diameter growth during summerwood formation. Fruit development in late summer consumes large amounts of energy. Finally, as all of this growth comes to an end toward autumn while photosynthesis continues, the energy level is restored to its peak level at the close of the growing season.

The relevance of this to pruning is that removing live branches during dormancy results in little metabolic cost, whereas pruning during the growing season has variable costs depending upon the growth stage. Dead branches may be removed at any time, and damaged or diseased branches usually should be removed as part of sanitation despite the season. Rapid wound closure also is enhanced by pruning during the peak summerwood growth season if pruning is very light and does not remove much photosynthetic tissue. However, significant removal of healthy branches usually should be deferred until the

dormant season to conserve maximum levels of energy in the tree and to prevent disease.

In much of North America, and in other regions where pathogenic fungi or bacteria are vectored by insects attracted to fresh wounds, no pruning of live wood should be done during active stages of those vector species. If damage dictates such pruning, non-phytotoxic wound dressings should be applied to discourage the access of these vectors to the wound. The most serious widespread problem is oak wilt, *Ceratocystis fagacearum* (T.W. Bretz) J. Hunt, but other diseases or opportunistic phytophagous insects could become part of the equation as well.

Pruning during the dormant season also affords a better view of the habit of the young tree and the possible presence of incipient structural problems that, if ignored, will become larger problems. The bottom line is that for reasons of architecture and physiology as well as pathology, we usually should avoid pruning live wood on young oaks during the growing season.

Collar formation and compartmentalization

As trees branch, part of the vascular system follows the branch and the remainder continues around the base of the branch to serve other branches. The overlap zone where this happens creates a swelling at the base of the branch, called the **branch collar**. In some cases the collar is very noticeable, and in others it is hardly detectible. Often, this swelling can be more easily felt than seen. A procedure called **target pruning** is followed to prevent cutting through the portion of the wood connected to the distal portions of the main branch by cutting just outside of the collar. This leaves a slight swelling of active tissue at the cut, and minimizes the size of the wound and the damage done to the remainder of the tree. Such cuts close over rapidly from all directions via **callus formation** if the tree is vigorous.

Cuts made flush with the main branch or trunk do not seal uniformly or quickly, increasing the window of entry for decay fungi and phytophagous insects and disrupting vascular flow along the stem. Conversely, leaving long stubs places the cut beyond the quick reach of callus formation, resulting in a long exposure of the open wound. Following Shigo's principles of **compartmentalization of decay in trees** (CODIT), stubbing is still better than flush cutting. Because the likelihood of ultimate decay advance in oaks is generally limited to the old wood present at the time of the pruning, and because small wounds surrounded by active cambial meristematic tissue which is supported by strong distal growth close most quickly, small wounds are better than large ones. In this discussion, "small" is a proportionate term meaning the wound is much smaller in diameter than the remaining part of the tree at the wound location. A 2 cm (.78 in) wound on a 3 cm (1.2 in) branch will close more slowly than a 3 cm wound on a 10 cm (4 in) branch because of the increased callus energy available from distal portions of the larger branch. If absolutely necessary, usually due to storm breakage, heading (stub cutting) should be done distal to nodes to encourage regrowth from latent subapical buds. Such growth sometimes is described as endocormic, versus the typical epicormic, weakly attached sprouts formed from adventitious internodal buds. This situation is more likely to be important with larger trees than with the young trees being discussed here.

Observations of natural branch shedding confirm that target pruning mimics how trees have evolved to eliminate lower, shaded, unproductive branches that otherwise would be metabolic sinks. Branches that break off leaving long stubs mimic internodal heading cuts,

and they often resprout vigorously to try to close the wound, resulting in weak multiple branches and setting the stage for future failure. Tear-outs, where large limbs are ripped away down the trunk, mimic flush pruning. Trees with tear outs usually become hollow at best, and fail very prematurely at worst.

Structural elements

Pruning young oaks should address a series of potential problems with the goal of developing a young tree with a bright future:

1. **Codominant leaders** must be eliminated during the dormant season as soon as they are found (Figure 3). If they are noticed as they first begin to form, they may be snapped off by hand as they begin to develop in spring. Leaving codominant leaders for future resolution will result in unnecessarily large pruning wounds in immediate proximity to the remaining leader. Due to their codominance, these double leaders do not form branch collars, so their removal when large causes excessive damage to the tree.

2. If a codominant leader was missed early in the pruning cycle, the next best approach is to subordinate it heavily so that it will be outgrown by the selected leader. **Subordination** (also called suppression) is the removal of a large portion of the main (distal) end of a branch back to a smaller, diatropic side branch or abaxial fork. This is severe pruning and often involves removing roughly half or more of the codominant leader being treated. If it is necessary, it should be done when the tree is as small as possible.

3. Branches which are parallel, crossing, clustered, damaged, or directed back toward the trunk will cause structural problems as they grow. They should be removed during each pruning cycle.

4. **Low branches** on the trunk can serve a useful, if usually temporary, function in development of a strong taper, and they can discourage antler rubbing by deer and damage from close mowing or cultivation by careless workers. Their removal should be delayed, and then done gradually once the base of the tree reaches a non-vulnerable size and can resist deer damage. However, permitting them to grow unchecked may result in their development of a large caliper that will cause an unnecessarily large pruning wound if they are removed later. Subordinate them by cutting back to small, outward- or downward-growing side branches. This process keeps their diameter growth in check while the trunk continues to expand, making the eventual pruning wound proportionately smaller and quicker to callus over and seal.



Figure 3/ Target line for pruning a weak secondary leader.



Figure 4/ Phased thinning and subordination of an orthotropic branch.



Figure 5/ Phased removal of a whorl.

5. **Crown raising** for traffic clearance and opening views should be phased in, with some cuts being made gradually throughout the height of the portion of the trunk being cleared and other branches being subordinated to retard their diameter growth pending future removal (Figure 4).

6. **Whorls** formed by subapical buds should be thinned to no more than one or two branches by staging pruning over several years in order to prevent a bottleneck girdling effect at the whorl site, thereby discouraging water sprout formation. If crown raising is complicated by a whorl consisting of more than two branches emerging from the same level at the trunk, remove branches one and three or one and four this year, then subordinate the remainder for removal over the following one or two years (Figure 5). Choose the largest or most orthotropic branches for subordination or removal first.

7. When pruning requires removal of a significant branch, **resprouting** due to hormone disruption sometimes cannot be avoided. The sprouts which develop from the lower side of the cut may be desirable if they can be kept growing in a comparatively diatropic direction, but those originating from the top of the cut frequently are orthotropic and must be redirected or removed (Figure 6). Such removal can be accompanied by a **hormone application** on the cut surface to discourage recurrence. The most effective chemical treatment I have used

is dithiopyr, 3, 5-pyridinedicarbothioic acid, 2-(difluoromethyl) -4 - (2-methopropyl) -6-(trifluoromethyl) -S, S-dimethyl ester (available commercially). Another product, useful mostly to treat new sprout growth after it begins to expand, is Ethyl 1-naphthaleneacetate, (available commercially). Neither is inexpensive!

8. **Circling or girdling roots** can strangle the tree and must be cut while they are still small to prevent heavy damage to the remainder of the buttress (Figure 7; p. 160). Sometimes this requires careful excavation (with a brush, or a water blast or air gun) at the base of the tree to determine if such roots are present. Removal is best done with a chisel, lopper, or chain saw, positioned with the cut parallel to the direction of the primary flare root being released in order to minimize vascular disruption of that primary root from accidentally cutting past the intended area. Girdling roots often result from



Figure 6/ Removal of orthotropic shoots.

planting container-grown trees without spreading or pruning the roots at planting, or from planting too deeply. All too frequently, girdling roots go unnoticed for many years until the tree begins to decline, or the buttress flare becomes conspicuously one-sided due to strangulation, or the tree simply falls over. Spontaneous seedlings seldom develop girdling roots.

Experts and professionals

Tree experts are certified by the *International Society of Arboriculture* (ISA) or a similar organization or agency. They must pass examinations and accrue continuing education in order to remain current and stay certified. These are the people who should be looked to for examples of proper tree care. Find them through the organizations that foster development of skills and knowledge among arborists. In Europe, see the web site of the European Arboricultural Council (www.eac-arboriculture.com); and worldwide, seek out the ISA (www.isa-arbor.com).

When pruning your young oaks, always remember that you are creating the potential for them to become grand trees that will give lasting benefits in terms of aesthetics and function far beyond your lifetime. Pruning oaks is not mowing turf! Take the time, and the care, to do it right.



Figure 7/ A badly girdled root system.

Acknowledgements

I would like to thank ISA Board Certified Master Arborist Guy Meilleur of HistoricTreeCare.com for his review of the first draft of this paper.

Photographers. Title page: Guy Sternberg (terminal and subapical buds). Photos in Figures 2-7: Guy Sternberg.

Further reading

American National Standards Institute. *American National Standard for Tree Care Operations - Tree, Shrub, and other Woody Plant Maintenance - Standard Practices (Pruning) (A300, Part 1)*. New York, New York: ANSI, updated periodically.

Brickell, Christopher and David Joyce. 2011. *Pruning & Training: The Definitive Guide to Pruning Trees, Shrubs, and Climbers*. American Horticultural Society, DK Adult.

Free, Montague. *Plant Pruning in Pictures*. 1961. Garden City, New York: Doubleday & Company Inc.

Gilman, Edward F. *An Illustrated Guide to Pruning - 3rd Edition*. 2011. Delmar Cengage Learning.

Gilman, Edward F. and Sharon J. Lilly. 2008. *Best Management Practices: Tree Pruning. Companion publication to ANSI A300 Part 1: Tree, Shrub, and Other Woody Plant Maintenance - Standard Practices, Pruning*. Champaign, Illinois: International Society of Arboriculture.

Harris, Richard W. 2003. *Arboriculture: Integrated Management of Landscape Trees, Shrubs, and Vines - 4th Edition*. New York, New York: Prentice Hall Press.

Pirone, Pascal Pompey. 1978. *Tree Maintenance*. New York, New York: Oxford University Press.

Pleninger, Andrew G. and Christopher J. Luley. 2012. *The ABCs Field Guide to Young and Small Tree Pruning*. Naples, New York: Urban Forestry LLC.

Shigo, Alex. 1991. *Modern Arboriculture: A Systems Approach to the Care of Trees and their Associates*. Shigo & Trees Assoc.

Shigo, Alex. 1990. *Tree Pruning: A Worldwide Photo Guide*. Published by the author.

Steffek, Edwin F. *The Pruning Manual. Second Revised Edition*. 1986. New York, New York: Prentice Hall Press, Simon & Schuster, Inc.

Sternberg, Guy. 1991. Pruning. In *Taylor's Guide to Gardening Techniques*, edited by Roger Holmes, 292-335. Boston, Massachusetts: Houghton Mifflin Company.

Sternberg, Guy. *Pruning*. 1994. In *Taylor's Master Guide to Gardening*, pp. 559-566. Frances Tenenbaum, Editor in Chief. Boston, Massachusetts: Houghton Mifflin Company.



New and Recently Described Oak Cultivars

Eike J. Jablonski

LTA, Dept. Horticole, Arboretum
72, Avenue Salentiny
L-9001 Ettelbruck, Luxembourg
Phone: +352 691 864079
eike.jablonski@education.lu

ABSTRACT

The International Oak Society was appointed by the International Society for Horticultural Science (ISHS) as International Cultivar Registration Authority (ICRA) for the genus *Quercus* in 1998. The system of ICRA aims to promote stability in the naming of cultivated plants by promoting lists of authenticated names in a number of important groups of plants which are commonly cultivated. New and recently published oak cultivars will be described. The new cultivars have been released into cultivation from various countries, such as the United States of America, Poland, Belgium, The Netherlands, and Germany.

Keywords: new oak cultivars, oak cultivar registration, ICRA

Introduction

The International Oak Society was appointed by the International Society for Horticultural Science (ISHS) as International Cultivar Registration Authority (ICRA) for the genus *Quercus* in 1998. The system of ICRA aims to promote stability in the naming of cultivated plants by publishing lists of authenticated names in a number of important groups of plants which are commonly cultivated (Trehane, 2007).

A selection that is represented by a single plant in a collection or nursery is not a cultivar; it is just a single specimen. A cultivar is a taxonomic unit made up of a number of plants with the same set of characters. Therefore, a single selected plant needs to be (vegetatively) propagated to obtain a certain number of identical plants. The number of new oak cultivars selected or raised by nurserymen and collectors or those originating in botanical collections has risen rapidly over the last few years. The ICRA registers cultivar or Group names, describes the new cultivar and maintains records of the origin, characteristics, and history, without judgment of the value or distinctness of the cultivar. This is up to the breeder or finder of the cultivar.

A searchable database of registered names and Group names as well as guidelines for oak cultivar registration can be found in the International Oak Society's database www.oaknames.org (also accessible from the IOS homepage at www.internationaloaksociety.org).

The cultivars described here are accompanied by herbarium specimens, all of which have been deposited as Standard Specimens in the Harold Hillier Herbarium (HILL) at the Sir Harold Hillier Gardens, the official herbarium of the International Oak Society. The holdings of that herbarium, as well as the living collections, can be consulted online using the search facility from the garden's homepage at www.hilliergardens.org.uk. Duplicates of the Standard Specimen sheets are also deposited at the herbarium in the Missouri Botanical Garden (MO).

The oak cultivars described here represent many, but not all, of the recent introductions to the trade which have come to my knowledge. The cultivars are sorted by country of origin or source of commerce.

United States of America

Within the last decade many of the recent oak introductions originate from the United States. Besides the great number of natural oak taxa in North America, good selections for different purposes are getting more and more attention.

Ryan Russell, Fulton, Missouri

Ryan Russell, elected member of the IOS Board in 2012, is an ISA Certified Arborist at the University of Missouri-Columbia. He has selected some interesting forms of native oaks, which are now in cultivation both in the USA and in Europe.

1. *Quercus coccinea* Münchh. 'Crimson Cloud'

New cultivar. A deciduous tree, selected for the large leaves (up to 33 × 20 cm)* that have very deep sinuses. Bright red fall color, coloring later than surrounding *Q. coccinea*. Superior fall color. Color lasts well into winter, until January. The tree has large acorns and cups but does not fruit abundantly despite adequate pollinators nearby. Over the last

* Due to the quantity of measurements in this article, only altitude is given in both metric and imperial units in the text. Please see the table p. 123, if needed, for converting other measurements.

10 years no good acorn crop was observed. Ryan Russell found this oak (USA, Missouri, Boone Co., on the University of Missouri Campus) and named it in 2009. The name, ‘Crimson Cloud’ describes the impression this plant gives in fall. Standard specimen: Harold Hillier Herbarium (HILL) No. 7388. Specimen from original plant, ca. 45 years old in 2010, with a height of ca. 20 m, and a crown width of 15 m. A possible replacement for popular *Q. palustris* Münchh. with better fall color and more suited to calcareous soils. Limited acorn set may be useful near streets and parks. The large leaves are very ornamental and could serve collectors’ purposes.

2. *Quercus alba* L. (Pinnatifida Group) ‘Marcell’

New cultivar (Plate 1). A deciduous tree selected for the diminutive leaves, good fruiting, and leaf shape with very deep sinuses and forked lobes. Leaves to 11 (13) × 6 (8) cm. The small, nicely cut leaves are consistent through entire canopy. Acorns are smaller than typical. Reddish-orange fall color. The ortet (= the original plant from which the members of a clone have descended) was possibly more than 100 years old in 2010 and approx. 26 m high, with a crown spread of also approx. 26 m. Standard specimen from original plant: Harold Hillier Herbarium (HILL) No. 7389. Ryan Russell found the tree in 2008 (USA, Missouri, Callaway Co.). ‘Marcell’ is named after the grandfather of the originator, who found this oak on his grandfather’s property.

3. *Quercus palustris* Münchh. ‘Betty Jean’

New cultivar (Plate 1). A deciduous tree selected for its unusual leaf form and good dark green color of the leaves, which have very deep sinuses (can extend to the midrib), giving the tree a cut-leaf appearance. Leaves up to 20 × 16 cm. No sign of chlorosis which is unusual for *Quercus palustris* at the site. Ryan Russell selected the tree in 2007 (USA, Missouri, Boone Co., University of Missouri Columbia (UMC) property). The mother tree was ca. 50 years old in 2010, with a height of approx. 22 m and a crown spread of 20 m. It is unclear if the tree is from cultivated stock or a chance seedling. The tree is part of the accessioned inventory [give accession number] of the Mizzou Botanic Garden on the UMC Campus. Standard specimen from the ortet: Harold Hillier Herbarium (HILL) No. 7390. ‘Betty Jean’ was the name of the originator’s grandmother, a retiree from UMC with a great affinity with trees and plants.

Guy Sternberg, Petersburg, Illinois

Guy Sternberg, past President of the International Oak Society, and Director of Starhill Forest Arboretum, with one of the reference collections of oaks in the US has introduced several selections to the trade both in Europe and North America.

1. *Quercus nigra* L. × *Quercus coccinea* Münchh. ‘Fire Water’

New cultivar. A deciduous to semi-deciduous tree found by Guy Sternberg at the Starhill Forest Arboretum (USA, Illinois, Menard Co.). Leaves leathery, size up to 17 × 11 cm, with 2-3 mucronate lobes on each side, reaching 2/3 of the way to the midrib, rounded to truncate base, petiole 20-25 mm. The leaf outline is intermediate between those of the parents. F₁ seedling from *Quercus nigra* Kentucky state champion at Kentucky Dam St. Park pollinated by nearby *Quercus coccinea*. Selected for its good habit and bright fall color. The cultivar epithet ‘Fire Water’ derives from the fiery color of scarlet oak and the common name of water oak, which has long-lasting (from *Q. nigra*) brilliant red (from *Q. coccinea*) fall color and good form (from *Q. coccinea* rather than from *Q. nigra*). “Firewater” is also an American colloquial term applied to Kentucky whiskey and other strong alcoholic drinks. Herbarium specimen seen at the Herbarium of Illinois College (specimen 4 of 4), hybrid origin determined and specimen collected (21 August 2011)

from ortet tree by G. Sternberg. Standard specimen: Harold Hillier Herbarium (HILL) No. 7391.

2. *Quercus macrocarpa* Michx. 'Big John'

New cultivar (Plate 1). A deciduous tree selected by G. Sternberg for its fastigate growth. Leaves similar to typical forms of the species, up to 25 × 16 cm. Possibly seedless but needs more observation. Original specimen is ca. 20 m height, with 5 m crown spread, and was about 50 years old in 2010. Found in Nov. 2009 by G. Sternberg and John Benedict in Springfield, Illinois (USA) on a public right-of-way along Glenwood Street. 'Big John' is named to honor a tall friend of the originator, John Benedict, who brought this particular tall tree to the attention of Guy Sternberg. The new cultivar is similar to the upright *Quercus macrocarpa* 'Anton de Bary', from Strasbourg, France, but differs in the origin and in form, and the possible sterility (no acorns observed yet). It is also different from the upright *Quercus macrocarpa* 'JFS-KW3' (Urban Pinnacle[®]), introduced by Schmidt Nursery, Oregon, USA, which is a chance seedling with remarkably small acorns. Standard specimen collected June 9, 2010 from ortet tree by G. Sternberg: Harold Hillier Herbarium (HILL) No. 7392.



Plate 1. New oak cultivars from the USA and Europe. 1. *Quercus palustris* 'Betty Jean'; 2. *Q. alba* 'Marcell'; 3. *Q. macrocarpa* 'Big John'; 4. *Q. petraea* 'Rzepin'.

Allan Taylor, Boulder, Colorado

Allan Taylor is a long-standing member of the International Oak Society and was Editor of Oak News & Notes, the IOS newsletter from 2009-2012. He travels widely in Colorado, New Mexico, Arizona and adjoining states selecting oaks from this area, searching for unusual or interesting features. Many of his introductions are selections from *Quercus ×undulata* Torr. (syn.: *Quercus ×pauciloba* Rydb.), a widespread hybrid

complex of that area with a lot of variation between individuals (sensu stricto this hybrid complex is restricted to *Q. gambelii* Nutt. × *Q. grisea* Liebm. forms; sensu lato *Q. gambelii* crosses with any other white oak species with which it is sympatric now or at an earlier historic period e.g., *Q. grisea*, *Q. turbinella* Greene, *Q. muehlenbergii* Engelm., *Q. mohriana* Buckley ex Rydb. or *Q. arizonica* Sarg.). All of the selections show more or less the range of this natural variation. The selections made by Allan Taylor are in cultivation at Pavia Nursery, Deerlijk, Belgium. The owner of this nursery, Dirk Benoit, has traveled with Allan in southwestern USA, discovering some of the new cultivars mentioned here.

1. *Quercus grisea* Liebm. ‘Encinosa’

New cultivar (Plate 2). Small graceful, short and spreading evergreen tree approximately 5 × 5 m, narrow, gray, entire, evergreen leaf (up to 5.5 × 2.5 cm). Growing on the east side of Highway 246 approximately 12 miles NE of Capitan, New Mexico (one mile south of the village of Encinosa, New Mexico), in Lincoln County. 6400’ altitude, GPS N 35 degrees 40.676’, W 105 degrees 30.763’. Standard specimen collected by Allan Taylor from the original plant: Harold Hillier Herbarium (HILL) No. 7393.

2. *Quercus grisea* Liebm. ‘Hondo Valley’

New cultivar (Plate 2). Evergreen tree, the original tree 12 × 10 m, forms a large tree with very elegant, light green, willow-like leaves, tolerates poor soil and drought. Leaves oblong to elliptic, margins minutely revolute, entire, up to 7 × 3 cm, apex acute, petiole 2-4 mm, base rounded to subcordate; leaves growing in whorls on twigs. The original tree is growing in a corridor called Hondo Valley beside Hwy. 380 in Lincoln Co., New Mexico, about 5 miles east of Lincoln, at 1,800 m altitude (5,400 ‘) N33°25.309 W 105° 18.219. Found by Allan Taylor in 2009, standard specimen collected by him from the original plant: Harold Hillier Herbarium (HILL) No. 7394.

3. *Quercus havardii* Rydb. × *Quercus stellata* Wangenh. ‘Blue Shamrock’

New cultivar (Plate 2). A form selected for the very blue leaf. Deciduous or semi-deciduous tree ca. 7.5 × 3 m. Leaves oblong, 9 × 3.5 cm, petiole 5 mm; base rounded to cuneate, at least some rounded teeth on each side. Tolerates dry, limey soil. Putative *Q. havardii* × *Q. stellata* backcross. Found by Allan Taylor in 2008 east of Shamrock, Texas, Wheeler County, about 1 mile north of I-40 and 70 m west of Farm Road 2168 (Daberry Road) growing in a thicket of hybrid trees. Tree about 7 m high, deciduous. Standard specimen collected by Allan Taylor from the original plant; 700 m (2,296 ft) altitude, N 35° 14.455’, W 100° 09.970’: Harold Hillier Herbarium (HILL) No. 7395.

4. *Quercus ×undulata* Torr. ‘Azul de Salinas’

New cultivar (Plate 2). Evergreen shrub. The mother plant after ca. 25 years is only 1 m high; leaves evergreen, leathery, prickly and bright blue, up to 3.5 × 2 cm. Very drought tolerant. Putative hybrid *Q. gambelii* × *Q. turbinella*. Standard specimen from the original plant collected in 2008, by Allan Taylor in Socorro Co., NM, USA, uphill from Hwy. 60, just before mile marker 185, at ca. 1,900 m (6,232 ft) altitude, N 34°24.935’ W 106°30.926’: Harold Hillier Herbarium (HILL) No. 7396.

5. *Quercus ×undulata* Torr. ‘Blue Hole’

New cultivar (Plate 2). Evergreen, slender tree, approximately 3 m tall, narrow growth habit with 1.5 m width; leathery, prickly, bluish leaves up to 4.2 × 2.5 cm; most others trees in the grove are deciduous. Does not sucker. Vigorous grower and very drought tolerant.



Plate 2. New oak cultivars from the USA. 1. *Quercus grisea* ‘Encinoso’; 2. *Q. grisea* ‘Hondo Valley’; 3. *Q. havardii* × *Q. stellata* ‘Blue Shamrock’; 4. *Q. ×undulata* ‘Azul de Salinas’; 5. *Q. ×undulata* ‘Blue Hole’; 6. *Q. ×undulata* ‘Mesa de Maya’; 7. *Q. ×undulata* ‘Tinnie’; 8. *Q. ×undulata* ‘Toll Gate Canyon’; 9. *Q. ×undulata* ‘Picture Rock’; 10. *Q. ×undulata* ‘Placitas del Rio Bonito’; 11. *Q. ×undulata* ‘Spring Ranch’.

Putative hybrid *Q. gambelii* × *Q. turbinella*. Collected at Santa Rosa, New Mexico, Guadalupe County, in a municipal park called Blue Hole, east of the parking lot in a stand of native oaks, all *Q. ×undulata*, at ca. 1,850 m (6,068 ft) altitude, GPS N 34°57.845’, W 104°44.539’. Standard specimen collected by Allan Taylor from the original plant: Harold Hillier Herbarium (HILL) No. 7397. ‘Blue Hole’ is named for the locally famous deep, bell-shaped artesian spring in Santa Rosa, NM, in the Municipal Park.

6. *Quercus ×undulata* Torr. ‘Mesa de Maya’

New cultivar (Plate 2). A dense, upright tree, tardily deciduous, 7.5 × 8 m. Selected for the unusual long, blue leaves and vigorous growth. Leaves up to 9 × 4.5 cm, entire or toothed or with 2-3 short mucronate lobes on each side, base rounded, petiole 6-8 mm. Chance seedling grown from acorns collected in southeastern Colorado, and propagated at the Denver Botanic Garden, Denver, Colorado, by James Bowland, in the 1970s. The tree is growing in a private garden in Boulder, Colorado, Boulder County. Putative hybrid of *Q. gambelii* × *Q. grisea* × *Q. turbinella*. Vigorous grower, heavy fruiter, very drought tolerant. ‘Mesa de Maya’ derives from a local landmark in Baca County, Colorado. Standard specimen collected by Allan Taylor from the original plant in Boulder, Colorado: Harold Hillier Herbarium (HILL) No. 7398.

7. *Quercus ×undulata* Torr. ‘Tinnie’

New cultivar (Plate 2). Spreading shrub or clumping tree of 3 × 7 m, putative hybrid of *Q. gambelii* × *Q. oblongifolia* Torr. × *Q. grisea* Liebm. Oblong, gray leaves (up to 8 × 2.5 cm), margin entire or dentate with 2-4 mucronate teeth, base cuneate to rounded, petiole 3-5

mm. Very drought tolerant. Growing at western edge of Highway 368 approximately four miles north of Tinnie, in Lincoln County, New Mexico. Standard specimen collected by Allan Taylor on Dec. 15, 2011, from the original plant: Harold Hillier Herbarium (HILL) No. 7399.

8. *Quercus* ×*undulata* Torr. ‘Toll Gate Canyon’

New cultivar (Plate 2). Deciduous tree, 8 × 5 m; selected in 2004 by Allan Taylor for its large undulate leaves and good, red fall color. Large leaf for this taxon (up to 14 × 7 cm), with 4-5 pointed lobes, base rounded to subcordate, petiole 8-10 mm, one single pedunculate fruit observed: peduncle 22 mm. Leaf adaxial dark green, abaxial paler green. Leaves turn a bright red in fall. Putative hybrid *Q. gambelii* × *Q. turbinella*. A selection of a tree growing in a grove of around 10 individuals, all about 7 m high, growing on the high bank of a creek east of Highway 551, around a half mile south of the picnic area in Toll Gate Canyon, in Union County, New Mexico, at ca. 2,000 m altitude (6,100 ft) at N36° 55.489' W103° 51.678'. Cultivar epithet after collection site. Standard specimen collected by Allan Taylor on Dec. 15, 2011, from the original plant: Harold Hillier Herbarium (HILL) No. 7400.

9. *Quercus* ×*undulata* Torr. ‘Picture Rock’

New cultivar (Plate 2). Deciduous small, compact, tree or large shrub, with long elegant acorns. Cold and draught tolerant. Original plant ca. 3 × 1.7 m. Leaves up to 5 × 2.2 cm, base obtuse to truncate, petiole 2-4 mm. No special fall color observed; chestnut brown leaves after frost. Putative hybrid *Q. gambelii* × *Q. turbinella*. From the original plant discovered in 2001, in Union Co., NM, USA, just north of Hwy. 456, between mile markers 10 & 11, a few feet away from a large boulder which has an Indian petroglyph on it, at 1,930 m (5,800 ft) altitude, N 36°54.543' W 103°47.802'. Standard specimen collected by Allan Taylor from the original plant: Harold Hillier Herbarium (HILL) No. 7401. ‘Picture Rock’ was named after the nearby Indian petroglyph. Name first appeared in Pavia Nursery catalogue in 2010 without a description.



1/ *Quercus* ×*undulata* ‘Picture Rock’.

10. *Quercus* × *undulata* Torr. ‘Placitas del Rio Bonito’

New cultivar (Plate 2). Evergreen, small tree, selected for its glossy, narrow, willow-like leaves. Draught tolerant, withstands temperatures to at least -28 °C; leaves up to 4 × 3 cm but mostly smaller, greenish-bluish. The original plant, 6 × 3.5 m. Probably *Q. grisea* × *Q. turbinella* hybrid. From the original plant discovered in 2001 by Dirk Benoit, growing just north of the Lincoln cemetery, 1 mile east of Lincoln, NM, down Hwy 380, at ca. 1,900 m (5,670 ft) altitude, N 33°29.129' W 105°22.529'. *Placitas del Rio Bonito* is the original name of the town of Lincoln, NM. Standard specimen collected by Allan Taylor from the original plant: Harold Hillier Herbarium (HILL) No. 7402.

11. *Quercus* × *undulata* Torr. ‘Spring Ranch’

New cultivar (Plate 2). Deciduous tree, selected for its very large blue leaves and dense canopy. Leaves up to 15 × 5.5 cm, base rounded to obtuse, mostly with 1-4 pointed lobes on each side, petiole 8-15 mm. Bark dark grey. The thick canopy of leaves appears to be evergreen until the leaves turn brown in fall. Putative hybrid of *Q. gambelii* × *Q. grisea* × *Q. oblongifolia*. Standard specimen collected by Allan Taylor from the original plant discovered by Michael Meléndrez (Albuquerque, New Mexico, USA) - no date mentioned - in a grove of trees 7 miles east of the village of Lincoln, Lincoln Co., NM, USA near Spring Ranch, at ca. 1,800 m (5,350 ft) altitude, N 33°24.606' W 105°17.240': Harold Hillier Herbarium (HILL) No. 7403. Name first appeared in the Pavia Nursery catalogue in 2010 without a description.

Europe

From Belgium, England, Germany and Poland, interesting new cultivars from Europe have also been selected.

Timothy Whiteley, Evenley, Northamptonshire, England

Timothy Whiteley is a British amateur dendrologist and long time Vice President of the International Dendrology Society for England. On his estate, Evenley Wood Garden, he has established a rich dendrological collection and a remarkable collection of snowdrops as well.

1. *Quercus rubra* L. (Aurea Group) ‘Evenley Gold’

New cultivar. Deciduous tree. Leaves typical for the species, with a good yellow color still in August. Original tree growing in Evenley, Northamptonshire (England) at Evenley Wood Garden, property of Timothy Whiteley. Colin Crosbie, the curator at Wisley, spotted that it was still golden in August. Timothy Whiteley and Colin Crosbie watched it for some years and also noticed that it didn't burn in the sunshine; they think that it is slightly better than most of the other golden red oaks available. Also colors well in autumn. Originated as a chance seedling from seed collected ca. 1985 from the well know *Quercus rubra* ‘Aurea’ at Arboretum Wespelaar, Belgium. The name was first published in the catalogue of Evenley Wood Garden in 2008, and by Jablonski (2010). The form is propagated and in the trade in England. ‘Evenley Gold’ was named by T. Whiteley after Evenley Wood Garden. Standard specimen collected in July 2011, from the original tree, by Timothy Whiteley: Harold Hillier Herbarium (HILL) No. 7387.

Gerhard Dönig, Erlangen, Germany

Gerhard Dönig is a well known German amateur dendrologist specializing in *Fagus* and, together with his wife Gisela, owner of the Arboretum Altdorf with the reference collection of *Fagus* species and cultivars. He is also the author of four books about

Fagus. He collects a wide range of plants including his own selections.

1. *Quercus ilex* L. ‘Ditha Jung’

New cultivar (Plate 4). Evergreen small shrub, selected for its dwarf pyramidal habit and very small leaves. Leaves small, up to 3×0.5 cm, margins spinose-dentate, base obtuse, petiole 1-3 mm. Leaves glossy dark green above, paler beneath. No fruits observed. Original plant a chance seedling from acorns collected in 1989 by Gerhard Dönig from *Q. ilex* growing next to the road from Arco to San Giovanni north of Lake Garda, Trent/South-Tyrol, Italy, at ca. 600 m altitude. The original plant, still in a pot, is only 85 cm high and 25 cm wide after 23 years. The thin twigs cause a very filigree appearance. Standard specimen (EJ 111101) collected 11 Nov. 2011 from the original tree, at Altdorf Arboretum, by Gerhard Dönig: Harold Hillier Herbarium (HILL) No. 7375. Named by G. Dönig after his mother-in-law.

Dieter Döring, Ahnatal, Germany

The nurseryman Dieter Döring has a wide range of oaks in cultivation in his nursery, including some old cultivars. His nursery is situated in central Germany, in Ahnatal near Kassel.

1. *Quercus petraea* (Matt.) Liebl. ‘Steigerwald’

New cultivar. Deciduous tree, selected for its narrow upright growth habit. A tree originally found in the Steigerwald forest in Bavaria by the retired forester Franz Muhl, who selected some interesting cultivars of native trees found by him in the forest. Leaves are of typical shape for the species, but leaf blade smaller, up to 8×4 cm in the material seen, dark green above, light green beneath; petiole 5-11 mm. Standard specimen (EJ 12073001) collected by Eike Jablonski together with Dieter Döring, from a grafted tree at Döring nursery, Ahnatal, Germany, on July 30, 2012: Harold Hillier Herbarium (HILL) No. 7379. Named by D. Döring after the Steigerwald forest.

2. *Quercus robur* L. ‘Kobold’

New cultivar (Plate 4). Deciduous shrub, selected for its dwarf growth. Found as a chance seedling by Dieter Döring, the original plant is only 0.7×0.5 m in 12 years. Leaves in shape typical for the species, but smaller: up to 8.5×4.5 cm, petiole 1-3 mm. Susceptible to powdery mildew (*Microsphaera alphitoides* Griffon & Maubl.). Standard specimen (EJ 12073002) collected by Eike Jablonski together with Dieter Döring, from the original plant at Döring nursery, Ahnatal, Germany, on July 30, 2012: Harold Hillier Herbarium (HILL) No. 7380. Named by D. Döring, the German word “Kobold” means troll or goblin.

3. *Quercus robur* L. subsp. *estremadurensis* (O. Schwarz) A. Camus ‘Andenken an Prof. Otto Schwarz’ (*Quercus robur* L. ‘Andenken an Prof. Otto Schwarz’)

New cultivar. Deciduous to tardily deciduous tree, selected for its botanical and horticultural value; it is the vegetatively propagated form of the tree from which the type specimen of the subspecies was taken. The name is given here to vegetative propagations from the original tree of this subspecies, which is growing at the Berlin-Dahlem Botanical Garden. This distinguishes them from other plants that have been raised from seed and that may show some differences. Leaves lanceolate to oblanceolate, up to 14×4 cm, edged with 6-8, mucronate, slightly undulate lobes on each side, sinuses to 1/3 of the midrib, dark green above, grey-green beneath, petiole 5-10 mm, yellow-reddish, base rounded to subcordate. The original tree in Berlin was planted ca. 1930 by Dr. Otto Schwarz, who described the subspecies (Schwarz 1939). Named by E. Jablonski to honor Prof. Dr. Otto Schwarz, who wrote several taxonomic abstracts and a monograph about



Plate 3. *Quercus petraea* 'Rzepin'.

the oaks of Europe and the Mediterranean. He worked in Berlin until 1936, after which, because he was a communist, was banned from employment and could not finish his oak taxonomy. After 1946 he was appointed Professor of Botany in East Germany at Jena

University, but did not continue his work on oaks. He was also elected deputy of the East German People's Parliament. Standard specimen (EJ 12082201) collected by Eike Jablonski at Kruchten Arboretum, Germany, from a cultivated plant (a graft from Döring nursery who obtained the propagation material from the original tree: Harold Hillier Herbarium (HILL). [Nomenclatural note: according to ICNCP (2009) a cultivar epithet may contain abbreviations, when they are in common use (such as Prof.), and they may consist of 10 syllables and not more than 30 characters, not including spaces.]

Joanna and Bronislaw Szmit, Ciechánów, Poland

The Szmits manage the Szmit nursery in central Poland, introducing new cultivars including some of their own selections

1. *Quercus petraea* (Matt.) Liebl. (Mespilifolia Group) 'Rzepin'

New cultivar (Plates 1 and 3). Deciduous, vigorous tree selected for its lanceolate foliage. Leaves up to 15 × 2.5 cm, entire or sometimes shallowly lobed with 2-5 shallow, rounded lobes on each side; base acute to attenuate, glossy, dark green above, paler underneath, petiole 17-25 mm. Named by B. Szmit after Rzepin, a town in northwestern Poland. Standard specimen (EJ 11092003) collected by Eike Jablonski together with Bronislaw Jan Szmit and Piotr Krasinski, from a grafted tree at Szmit nursery, Ciechánów, Poland, on 20 Sept. 2011: Harold Hillier Herbarium (HILL) No. 7381.

2. *Quercus petraea* (Matt.) Liebl. 'Włodzimierz Seneta'

New cultivar (Plate 4). A selection of *Q. petraea* with variegated leaves. Name published in 2011 in the Szmit nursery catalogue. Tree of relatively strong growth, but much slower than normal for the species. Shape typical for the species. Leaves large (15 × 5 cm, but occasionally up to 25 cm), regularly lobed, intensely yellow-white speckled and marbled. New growth has a decorative pink color. Splashing variable, depending on the year. Fully hardy (Zone 3). Tolerant as to substrate, though it grows best in fresh, deep and fertile soils with moderate moisture and a neutral or alkaline pH. Should be planted in sunny or semi-shady locations. Suitable for gardens, parks and estate plantings. This is the first variegated foliage variety of the sessile oak. Cultivar selected by Bronislaw Jan Szmit, first described in 2011, released to the market the same year by the Szmit nursery. Named by B. Szmit in honour of the eminent Polish dendrologist – Włodzimierz Seneta (1923-2003), author of many dendrological books. Standard specimen (EJ 11092001) collected by Eike Jablonski together with Bronislaw Jan Szmit and Piotr Krasinski, from a grafted tree at Szmit nursery, on 20 Sept. 2011: Harold Hillier Herbarium (HILL) No. 7382.

3. *Quercus robur* L. 'Jan Zamoyski' (Plate 4). (*Quercus robur* 'Jan Zamorski' Jablonski 2004)

The older Polish oak cultivar is correctly spelled 'Jan Zamoyski' and not 'Jan Zamorski'. It is named after the renowned Polish statesman Jan Zamoyski (1542-1605), and not after Władysław Zamoyski (1853-1924), who was the founder of Kórnik-Arboretum in 1924. Standard specimen (EJ 11092005) collected by Eike Jablonski together with Bronislaw Jan Szmit and Piotr Krasinski, from a grafted tree at Szmit nursery on 20 Sept. 2011: Harold Hillier Herbarium (HILL) No. 7383.

4. *Quercus robur* L. (Heterophylla Group) 'Posnania'

New cultivar (Plate 4). Name published in 2009 catalogue of Szmit nursery, Ciechánów, Poland. Selected for the large, very deeply cut leaves, which can be as long as 30 cm × 15 cm wide, 4-9 lobes on each side deeply cut, often until the midrib; petiole 8-12 mm. The large leaves hang downwards, giving the tree a very elegant appearance. Standard



Plate 4. New oak cultivars from Europe. 1. *Quercus ilex* 'Ditha Jung'; 2. *Q. petraea* 'Włodzimierz Seneta'; 3. *Q. robur* 'Kobold'; 4. *Q. robur* 'Posnania'; 5. *Q. robur* 'Siedlec'; 6. *Q. robur* 'Jan Zamoyski'.

specimen (EJ 11092002) collected by Eike Jablonski together with Bronislaw Jan Szmit and Piotr Krasinski, from a grafted tree at Szmit nursery on 20 Sept. 2011. Named by B. Szmit after the old Polish (Latin) name for Poznan, a historical city in Central Poland: Harold Hillier Herbarium (HILL) No. 7384. [Nomenclatural note: Name first rejected because "Posnania" is the old Latin name for the Polish city of Poznan, and the Latin form is not current in a language other than Latin (ICNCP 21.11.), but later I noticed that it is valid according ICNCP 21.12 (Latin form may be used when it can be demonstrated that it is current in language, e.g., common phrases, terms, etc. The name "Posnania" is today used for certain terms, e.g., a local soccer team.)]

5. *Quercus robur* L. (Fastigiata Group) 'Siedlec'. (Plate 4). Name published in the 2005 Szmit nursery catalogue and by Houtman (2005). Selected for the narrow fastigiate growth. Standard specimen (EJ 11092004) collected by Eike Jablonski together with Bronislaw Jan Szmit and Piotr Krasinski, from a grafted tree at Szmit nursery on 20 Sept. 2011: Harold Hillier Herbarium (HILL) No. 7385. Named by B. Szmit after the village of Siedlec in western Poland.

Vicomte Philippe de Spoelberch, Herkenrode, Belgium

The well known dendrologist, Vicomte Philippe de Spoelberch, President of the Belgian Dendrology Society and owner of Herkenrode Gardens and Arboretum Wespelaar has unique collections of woody plants, many of them wild collected. He also grows the *Magnolia* reference collection in Belgium. Together with the director of Arboretum Wespelaar, Koen Camelbeke, he has named some fine selections with interesting features, always after careful observation and study, documented with meticulous notes.

1. *Quercus serrata* Thunb. ‘Herkenrode’

New cultivar. Deciduous tree, selected for the regular, good red autumn color. The name first appeared in the *Catalogue of Woody Plants of the Arboretum Wespelaar* in 2009. The tree has a sprawling habit, 5 × 7 m after 18 years. Leaves in shape like the species; variable in size, up to 18 × 7 cm, oblong-obovate to ovate-lanceolate, margined with gland-tipped teeth, bright green above, grayish-white beneath; leaves fall very late in the year. This selection shows a good, deep red autumn color every year. The tree was raised from a seedling (seedling No. 4388), wild collected by P. de Spoelberch in 1992 on the IDS Japan tour in Tono Hetsuri, Honshu, Japan and is now growing at Arboretum Wespelaar (accession No. 97037). Standard specimen EJ10102301 collected by Eike Jablonski on Oct. 23, 2010, from original tree at Herkenrode, named by P. de Spoelberch after the name of the Arboretum & Garden: Harold Hillier Herbarium (HILL) No. 7386.

Conversion table

1 mm = 0.039 in	1 cm = 0.39 in	1 m = 3.28 ft	1 km = 0.621 mi
5 mm = 0.195 in	5 cm = 1.95 in	5 m = 16.4 ft	5 km = 3.1 mi
7 mm = 0.273 in	7 cm = 2.73 in	7 m = 22.9 ft	7 km = 4.34 mi
12 mm = 0.468 in	12 cm = 4.68 in	12 m = 39.4 ft	12 km = 7.45 mi
20 mm = 0.78 in	20 cm = 7.8 in	20 m = 65.6 ft	20 km = 12.42 mi

Acknowledgements

My sincere thanks go to Ryan Russell, Guy Sternberg & Allan Taylor (USA), Dirk Benoit, Philippe de Spoelberch & Koen Camelbeke (Belgium), Dieter Döring & Gerhard Dönig (Germany), Brunislaw Jan Szmit & Pjotr Krasinski (Poland) and Timothy Whiteley (England) for sending original specimens, supplying valuable information and participating in various discussions.

Photographers. Title page: Guy Sternberg (*Quercus nigra* × *Quercus coccinea* ‘Fire Water’). Plates 1-4: Eike Jablonski. Photo 1: Allan Taylor.

Bibliography

- Houtmann, M. 2005. Naamlijst van Houtige Gewassen. ENA 2005 - 2010. APR, Wageningen, The Netherlands.
- Jablonski, E. 2004. European Oak Cultivars, Collections and Collectors. Proceedings Fourth International Oak Society Conference, Winchester, England. *International Oaks* 15: 103-118.
- Jablonski, E. and V.A. Bouffier. 2010. *Quercus rubra* ‘Aurea’ im Arboretum Herkenrode/Belgien, und andere gelbblauige Eichensorten (*Q. rubra* ‘Aurea’ in Herkenrode Arboretum, Belgium, and other yellow oak cultivars). *Beiträge zur Gehölkunde* 19: 267-269. Szmit (Johanna & Bronislaw Szmit Nursery, Poland), catalogues 2009 - 2012
- Trehane, P., ed. 2005. *International Code of Nomenclature for Cultivated Plants - 1995*. Regnum Vegetabile 133. Wimborne, UK: Quarterjack Publishing.
- The Oak Names Checklist* of the International Oak Society. Accessible at <http://www.oaknames.org>. or through the IOS home page internationaloaksociety.org.



Quercus ilex in the Madres-Coronat massif.



Highest Altitude Population of *Quercus ilex* L. in France

Thierry Lamant¹ and Vincent Parmain²

1. Association des Parcs Botaniques de France
15 bis, rue de Marignan
75008 Paris
thierry.lamant@orleans.inra.fr

2. Office National des Forêts
Bureau d'Etudes des Pyrénées Orientales
Vincent.parmain@onf.fr

ABSTRACT

In the valley of the upper Conflent, in southwestern France not far from the Spanish frontier is the Madres-Coronat massif. With an area of 600 hectares (1,500 acres), it harbors a small, three-hectare (7.5 acres) population of holm oak (*Quercus ilex* L.), the highest occurrence (1,840 m/6,035 ft) of this species in France and indeed in Europe. This article describes the growing conditions of this exceptional population, which because of its dynamism is increasing in size from year to year.

Keywords: holm oak, *Quercus ilex* L., Madres-Coronat, altitude, hardiness

In a paper presented at the 6th International Oak Society Conference in Puebla, (Mexico) in 2009, I described several marginal French populations of holm oak, either natural or naturalized. At the time I had to postpone consideration of a population that is noteworthy because of its altitudinal location, being the highest in France and indeed in Europe. It is located in the department of the Pyrénées-Orientales, which unites the Pyrénées and the Mediterranean Sea at the edge of Spanish territory. These trees are located in the massif of Madres-Coronat, which varies from 400 to 2,469 m (1,300 to 8,000 ft) in altitude, located only 60 kilometers (35 miles) from the ocean.

This forest harbors a community where *Quercus ilex* is associated with Scots pine (*Pinus sylvestris* L.), downy oak (*Quercus pubescens* Willd.), common juniper (*Juniperus communis* L.), savin (*Juniperus sabina* L.), and the slender broom (*Genista cinerea* (Vill.) DC.)

These dominant evergreen forests constitute only 3% of the total area of the massif, which is to say 600 hectares (1,500 acres), and stand on south-facing slopes with calcareous soils. *Q. ilex* occurs up to 1,840 m (6,035 ft) in altitude; this exceeds the altitude given three years ago (1,560 m) by 300 meters (985 ft).

On rocky calcareous soils, but also on schists in another sector of this forest, other old-growth or post-pastoral populations can be observed up to 1,300 meters (4,500 ft) in altitude. At higher altitudes, these populations encounter heaths of secondary, pastoral origin dominated by Andorra broom (*Cytisus purgans* Spach). The high cliffs harbor a Pyrenean endemic plant, the Pyrenean alysum (*Alyssum pyrenaicum* Lapeyr.).

This site is also of remarkable interest due to the presence of the bearded vulture (*Gypaetus barbatus* L.); a breeding pair of this species has been living in the area for the past three years. This raptor has a very specialized dietary regime, feeding on marrow from the bones of dead animals once they have been dissected by other vultures. The Pyrenean desman (*Galemys pyrenaicus* E. Geoffroy) and the Spanish moon moth (*Actias isabellae* Graells) are also found here.

The utilization of this forest consists since time immemorial, of both grazing and harvesting of forest products. Vestiges of these practices can still be found in the form of watering troughs for sheep. Administrators in fact tend to favor forestry and pastoralism, which allows the maintenance of open areas appropriate for certain plant and animal species.

The geology is distinctive: old mines of red marble can still be found. This was used regionally for ornamentation of the portals of religious edifices between the eleventh and fourteenth centuries.

As regards climate, average annual rainfall where these holm oaks are located is 780 mm (30.7 in) at an altitude of 1,560 m (5,120 ft). At 1,640 m (5,380 ft) it is 850 to 900 mm (33.5 to 35.4 in) annually.

In this massif there is a kind of climatic corridor that is dried by a north wind, and which endures a weak moisture regime in the path of the wind. The clouds hardly linger there and the average annual rainfall in this sector is only 550 mm (21.7 in) at 1,060 m (3,480 ft), which makes it one of the driest places in France. By way of comparison, Colmar, in Alsace (Northeast France), is the French city with least precipitation, having only 530 mm (20.9 in) average annual rainfall.

The average annual temperature here is 10.15 °C (50.27 °F); the average of the minima for the coldest month is 0 °C (32 °F), while that of the maxima of the warmest month is 24 °C (75 °F). As a side note, the maxima exceeded 40 °C (104 °F) in 2003.

The forested massif has not always had its present aspect. The restoration of the mountain terrain undertaken by the forestry service was a result of laws passed in 1860 and 1862, during the Second Empire. It consisted, and still consists, of a struggle against erosion and for regularization of water regimes, accomplished by methods of reforestation and means for channeling excessive rain. The Pyrénées-Orientales were affected by these measures following the recognition of intense deforestation and violent erosion, from the high demand for firewood and industrial fuel, which reached its apogee during the nineteenth century.

The holm oak populations of this massif were cut back in short cycles during the nineteenth century. Later, law ensured protection of these trees, allowing them especially to bear seed and hence to recolonize the territory.

Lately, the dynamism of the holm oak populations has been particularly noteworthy. The climatic conditions, which are basically arid, but depending on the time of year can be somewhat moist, put the oak in a position of virtually no competition; the relatively weak cover of Scots pine does not hinder its dissemination by the local fauna.

The holm oak was formerly very much esteemed for charcoal, and its heavy, hard wood was hardly ever used for other purposes. Climate changes observed for several years now argue in favor of using this oak to stabilize Mediterranean soils as well as for higher purposes (turnery, paneling, and parquet flooring). It is difficult to season, but this problem can be remedied by curing after two years of soaking; it then assumes a lovely aspect comparable to marble.

It also has a role in ornamental horticulture. Thus, urban forestry in French cities is making greater and greater use of the holm oak. Most of these come from Italian nurseries, sometimes with problems of winter susceptibility to frost stemming from the location of the propagation site and/or of provenance. The horticultural profession would do well to follow practices of American nurserymen, who pay attention to provenance for adaptation as much as to the conditions of the planting site.

This high altitude Pyrenean origin, as well as that in the Cévennes (at 900 m/2950 ft, beneath the Aigoual massif, also mentioned at the 6th IOS Conference in Mexico in 2009), constitute an excellent reservoir of hardy holm oaks.

During the winter of 2010, a holm oak from the Cévennes planted in a one liter container, in the middle of a garden without protection, survived a temperature of -15 °C (5 °F) with nightly frosts for a whole week without the slightest damage.

With ongoing climate change, the holm oak seems to offer a paragon of adaptability in France, most evident in the Rhone corridor and in the Cévennes. A detailed study of its dynamics should be undertaken and it could constitute an excellent indicator of the evolution of our vegetation under a climate which tends, on average, towards increasing heat, with potentially greater and greater irregularities in the moisture regime throughout the year.

Acknowledgements

Many thanks to Allan Taylor for the translation from French.

Photographers. Title page: Thierry Lamant (*Quercus ilex*). Photos p. 174: Thierry Lamant.



1



2



3



4



5

1/ Pre-Conference Tour participants. 2/ *Quercus phellos*, Arboretum de Chèvreloup. 3/ *Quercus macrocarpa*, Jardin des Plantes. 4/ *Quercus robur* Haas Group, Jardin des Plantes. 5/ *Quercus pyrenaica* 'Pendula', Arboretum de Chèvreloup.

Pre-Conference Tour September 26-29, 2012

Peter Laharrague
Estancia San Miguel
7530 Coronel Pringles C.C.64
Argentina



On the 26th September 31 IOS members gathered at the entrance of the Jardin des Plantes in Paris. We were welcomed by our Pre-Tour leader, Thierry Lamant. The Jardin des Plantes, the largest (28 ha/69 ac) and one of the most famous botanic gardens in France, is also one of the oldest, founded in 1635. Originally called the Jardin du Roi, it was renamed the Jardin des Plantes in 1793 when the Muséum national d'Histoire naturelle was instituted. Today the Muséum comprises many different gardens and institutions. We walked in along the Grand Parterre towards the *Quercus macrolepis* Kotschy planted in 1814 by René Desfontaines. It now stands 20 m (65.6 ft) tall, with a 3.15 m (10.3 ft) girth and 17 m (55.7 ft) crown spread. We passed by *Ehretia dicksonii* Hance, a *Boraginaceae* from East Asia with a corky bark, and near the statue of Bernardin de St. Pierre we saw a splendid *Platanus orientalis* L. with a 24 m (78.7 ft) crown spread, planted in 1785 by the Comte de Buffon. The historical *Quercus macrocarpa* Michx., planted in 1811 from acorns brought from the United States by André Michaux, with its magnificent shape, featuring a 4 m (13.1 ft) girth, and the famous *Cedrus libani* A. Rich., planted in 1734 by Bernard de Jussieu, were also on our way. We saw the first *Styphnolobium japonicum* (L.) Schott (formerly *Sophora japonica*) planted in Europe, known as the “Sophora de Jussieu”. The seeds were sent from China in 1747 by Père R.P. d’Incarville, a Jesuit priest, to Bernard de Jussieu. It now stands 21 m (68.8 ft) tall and was designated an Arbre Remarquable de France (Remarkable Tree of France) in June 2001. We stopped to admire the oldest tree in Paris, the “Robinier de Robin”, a *Robinia pseudoacacia* planted in 1635 by Vespasien Robin. Crossing towards a section of the Jardin des Plantes not open to the public, we met the huge *Quercus haas* Kotschy (now considered *Q. robur* Haas Group) from 1855, a historic tree introduced by Benedict Balansa. It was a pity there were no acorns for the amateur oak collectors. Having left the Jardin des Plantes bound for Versailles, our coach drove us by the *quais* of the Seine; unable to stop, we had a brief glimpse of the famous “vertical wall garden” of the Musée du Quai Branly near the Tour Eiffel.

After a light lunch in Versailles, we went to the Arboretum de Chèvreloup, a 200-ha (494 ac) domain acquired by King Louis XIV in 1669, adjacent to the park of the Petit Trianon, a section of the Château de Versailles. This arboretum is today, like the Jardin des Plantes, part of the National Museum of Natural History. During World War II, the arboretum was badly spoiled, particularly by farmers who grazed their cattle there. It was replanted in 1967, and since 1979 50 ha (124 ac) are open to the public. The fierce storm of 1999 uprooted many trees, including a famous *Styphnolobium*, also planted by Jussieu. Fortunately a cutting, taken from the root of the felled, was successfully grown and is now thriving in the same place as the original. On our way to the Quercetum we crossed a superb 60-year-old *allée* of *Juglans nigra* L., a special feature of the arboretum.

We saw a *Quercus libani* G. Olivier, (with acorns), a *Q. castaneifolia* C.A. Mey. (acorns not guaranteed to be “true”), a *Q. crispula* Blume (formerly *Q. mongolica* subsp. *crispula* (Blume) Menitsky), a *Q. Pondaim* Group with its large leathery leaves, a nice 16-meter-tall (52.4 ft) specimen of *Q. aliena* Blume and a *Q. phellos* L. ‘Latifolia’, whose leaf is very similar to *Q. imbricaria* Michx.

From Chèvreloup we took the highway towards the city of Angers (our first night’s stop), crossing the flatlands of the rich agricultural department of the Beauce, and then passing through the cities of Chartres and Le Mans.

On the morning of the 27th we visited the Arboretum Gaston Allard. Created by Mr. Allard in 1880, the arboretum was later taken over by the Institut Pasteur and at present

is owned by the City of Angers. Among other distinctions, the arboretum holds one of the French National Collections of *Hydrangea*. We entered along an avenue of oaks, including old specimens of *Q. cerris* L., *Q. frainetto* Ten., *Q. canariensis* Willd. and *Q. afares* Pomel (from Algeria). This last had a girth of 4.35 m (14.2 ft), stood 19 m (62.3 ft) tall and, most importantly, had shed a plentiful supply of acorns! The former national champion of *Q. ×schochiana* Dieck. (*Q. phellos* Münchh. × *Q. palustris* L.), which had a codominant stem, had collapsed some time ago: a sad spectacle for all of us oak lovers. The group wandered around the arboretum where conifers were omnipresent: *Sequoia sempervirens* (D. Don) Endl. ‘Prostrata’, *Pinus bungeana* Zucc. ex Endl. (its bark resembles that of a plane tree), *Torreya nucifera* L., *Torreya grandis* Fortune ex Lindley (with a bountiful crop of seeds on the ground) and *Keteleeria davidiana* (Bertrand) Beissn. Our morning ended with lunch at Angers.

The afternoon was spent visiting the well-known Forêt de Bercé in the Sarthe. This forest was planted during the reign of Louis XIV by his minister Colbert. It now consists mainly of *Q. petraea* (Matt.) Liebl., but originally it was a mixed forest of *Q. robur* L. and *Q. petraea*; as the latter is more resistant to drought they have survived, while almost all the *Q. robur* have disappeared. *Fagus sylvatica* L. were planted with the oaks and some now reach a majestic height of 30 m (98.4 ft), as tall as the *Quercus*. Bercé is managed by the ONF (Office National des Forêts). The local forester who welcomed us immediately informed us there was no acorn mast this year. Sad, long faces were our only reply to this announcement! We went to a stand of old giant oaks and saw the “Chêne Boppe”: a 350-year-old *Q. petraea* with a girth of 3.45 m (11.3 ft) and standing 36 m (118 ft) tall. It was the highlight of the visit.



6/ *Quercus afares*, Arboretum Gaston Allard.



7/ *Quercus petraea*, Forêt de Bercé.

Many other species are to be found in this magnificent forest, including *Pinus sylvestris* L., *Pinus pinaster* Aiton, *Pinus nigra* subsp. *laricio* (Poir.) Maire, *Carpinus betulus* L., *Acer pseudoplatanus* L., *Sorbus torminalis* (L.) Crantz, *Betula pendula* Roth (syn. *B. verrucosa* Ehrh.), *Prunus cerasus* L., *Crataegus monogyna* Jacq., *Ilex aquifolium* L. and *Frangula alnus* Mill. (syn. *Rhamnus frangula* L.).

It was dark when we arrived at our hotel in Orléans, a modern and comfortable golf resort where we would spend the next two nights.

Friday 28th: As we did not have to pack we were prompt to depart at 8am sharp. Thierry surprised us by taking us to his charming home to visit his garden, where we saw *Q. pacifica* Nixon & C.H. Mull. (endemic to Santa Cruz Island off the coast of California), grown from seeds he collected himself in 1997 during the 2nd International Oak Society Post-

Conference Tour. Other species of interest were: *Q. gravesii* Sudw., *Juglans microcarpa* Berland., *Heptacodium miconoides* Rehder (from China) and *Pinus johannis* M.-F. Robert (from Mexico), a very rare pine with stomata restricted to the adaxial sides of the needles.

Our next destination was the Arboretum national des Barres in Nogent-sur-Vernisson. In 1821 Philippe de Vilmorin bought the estate and in it he began planting tree collections grouped according to provenance. The Vilmorin family kept les Barres until 1936 when the French state assumed ownership. The arboretum now holds over 2,800 species from the world's temperate regions.

The quercetum was the main purpose of our visit. We admired the rare specimen labeled for a very long time *Q. oxyodon* Miq. that was then identified by Zhou Zhekun in 1998 as *Q. liboensis* Z.K. Zhou. This name was then considered in the *Flora of China* to be a synonym of *Cyclobalanopsis gracilis* (Rehder & E.H. Wilson) W.C. Cheng & T. Hong, the correct name for which as a species in the genus *Quercus* is *Q. ciliaris* C.C. Huang & Y.T. Chang. Finally Min Deng, who gave a presentation at the conference and who has revised the *Cyclobalanopsis* group, is of the opinion that this taxon is now considered to be *Quercus glauca* var. *gracilis* (Rehder & E.H. Wilson) A. Camus (evidently botanists have a difficult time sorting out these complicated questions!). *Q. sartorii* Liebm. (from Mexico) with nice long dentate leaves thrives here, as does an old *Q. dentata* Thunb., the parent tree of the hybrid named in honor of Vilmorin: *Q. ×vilmoriniana* A. Camus (*Q. dentata* × *Q. petraea*). *Q. variabilis* Blume and *Q. aliena* Blume were some of the Asian oaks we saw at les Barres. I asked Thierry about a lovely, huge *Q. frainetto* Ten. with a 3 m (9.8 ft) girth I had seen at the arboretum in 1999; it had recently died—another tree for our reminiscences... As is often the case, we were running short of time as we had to be at Ingrannes for lunch prior to our last Pre-Tour visit: the Arboretum des Grandes Bruyères.

This lovely arboretum owned by the Comte and Comtesse de la Rochefoucauld, situated in the heart of the Orléans forest, has earned the designation “Jardin remarquable” awarded by the Ministère de la Culture. Over 2,500 taxa are represented, while 7,000 labels correctly identify each specimen, providing the visitor an opportunity to learn botany. The arboretum is laid out according to the geographical origin of plants, Asia and America being the most important areas. Les Grandes Bruyères holds three French National Collections: *Magnolia*, *Cornus* and oaks of Northeast America.

We were welcomed by the hosts, Bernard and Brigitte de la Rochefoucauld, and split in two groups, each to be led by one of the hosts. Brigitte explained that no chemical pesticides or fertilizers are allowed at les Grandes Bruyères: only compost and manure which are spread around the plants. The soil is sandy with subsoil of clay and a pH of 5-6. The arboretum is very pleasant to visit, with meandering lanes connecting the borders and charming ponds that enhance all the vistas. A list of plants seen would be overwhelming; in my opinion, the most important feature of les Grandes Bruyères is the great enthusiasm that the owners have for taking care of their arboretum, which encompasses new projects for the near future! In a nutshell, it is truly a *jardin remarquable*. A farewell cup of tea was kindly offered by our hosts under the canopy of a splendid *Q. robur*.

Saturday 29th was dedicated to traveling from Orléans to Bordeaux by way of Tours, Poitiers and Angoulême. We arrived in the magnificent architectural city of Bordeaux just in time to get ready for the conference reception cocktail party.

Thanks to Thierry Lamant our leader who organized this IOS Pre-Conference Tour so well in this our beloved France!



8



9



10



11



12



13

8/ *Quercus robur*, Arboretum des Grandes Bruyères. 9/ *Quercus dentata*, Arboretum national des Barres. 10/ *Quercus baronii*, Arboretum national des Barres. 11/ *Quercus glauca*, Arboretum des Grandes Bruyères. 12/ Le Chêne Boppe, Forêt de Bercé. 13/ *Quercus* × *schochiana*, Arboretum Gaston Allard.

Photographers. Title page: Lloyd Kenyon (*Quercus glauca* var. *gracilis*). Photo 1: Guy Sternberg. Photos 2, 4, 5, 6, 7, 9, 11: Roderick Cameron. Photos 3, 10, 12: Lloyd Kenyon. Photo 8: Joyce Lee. Photo 13: Thierry Lamant.

Post-Conference Tour October 3-7, 2012

Allan R. Taylor
787, 17th Street
Boulder, Colorado, 80302
USA
tayloralro@comcast.net



Introduction

“You will see trees!” trumpeted a brochure from one of the hosts of the Post-Conference Tour of the 7th International IOS Conference. Great! That’s what the 52 Post-Conference Tour participants, from eight countries, had signed up for. But the bus load of quercophiles saw much more than trees, all of it interesting, in five event-packed days in two countries (with apologies to Basque separatists): France and Spain. I will try to give an indication here of the trees and other exciting things that tour participants saw and did during those five unforgettable days in early October, 2012.



1/ Post-Conference Tour participants, Forêt communale de Sare.

A Little History and Geography

The Aquitaine Region, home of Eleanor, the mother of Richard the LionHeart, lies in the southwest part of France and includes, amongst others, both Gascony and the Basque country and is where the first two days of the Post-Tour were spent. The term ‘Gascony’ (in French Gascogne, which has the same origin as the word ‘Basque’) designates an area that goes from the Garonne River down to the Spanish border and, to the east, to the cities of Auch and Tarbes.

From Roman times until less than two hundred years ago, the *landes* were sparsely populated, inhabited by shepherds and their families who pastured their sheep on the sandy, low-lying heaths (called *landes* in French and whence comes the name of that department, the Landes). During this long period there was almost no forest cover, due probably to regular burning by the pastoralists seeking to provide more forage for their animals. During the last half of the 19th century an ambitious program of forestation was undertaken by the Emperor Napoleon III, in part in order to halt erosion in the Garonne drainage which was silting up the estuary and threatening the important shipping industry of Southwest France.

Wednesday, October 3rd: Off we go!

After a quick breakfast on October 3rd, we got an early start (this would become a rule!); we soon left Bordeaux behind, as we headed towards the southwestern area of the Gironde, as the estuary of the Garonne River is called. Making our way through commuter traffic in and near the city, then along rural roads, we soon reached the town of Belin-Béliet, the site of our first scheduled activity of the day, Le Centre de Graoux in the Parc Naturel Régional des Landes de Gascogne where our guides from the Conservatoire Botanique du Sud-Atlantique, Anthony Le Fouler and Aurélien Caillon, were awaiting us.

The Centre de Graoux in the Parc Naturel Régional des Landes de Gascogne

The *landes* today—as represented by this park which we visited and at the heart of which is the Centre de Graoux—would be unrecognizable to the earlier inhabitants, since it is now largely covered with planted forests of maritime pine (*Pinus pinaster* Aiton) and oaks (*Quercus petraea* (Matt.) Liebl., sessile oak; *Q. robur* L., English oak; and *Q. pyrenaica* L., Pyrenean oak). Also present in the forest are many other trees, such as *Populus tremula* L., European aspen, *Castanea sativa* L., common or sweet chestnut, and *Fraxinus excelsior* L., European ash, among others. North America is represented by expatriates such as *Quercus rubra* L., red oak, *Taxodium distichum* (L.) Rich., bald cypress, *Robinia pseudoacacia* L., black locust, and *Prunus serotina* Ehrh., black cherry. The understory is composed of such native European plants as *Ilex aquifolium* L., English holly, *Viburnum opulus* L., snowball bush, *Erica arborea* L., tree heath, and *Frangula alnus* Mill., an important source of nectar for honeybees. Also common in the boggy soil are the largest French fern, *Osmunda regalis* L., European royal fern, *Hedera helix* L., English ivy, and *Iris pseudacorus* L., European yellow flag, the prototype for the fleur-de-lis which is so prominent in French and European heraldry generally. On better drained sites are found profuse banks of *Pteridium aquilinum* (L.) Kuhn, the bracken fern of European moorlands.



2/ The Leyre River, Centre de Graoux.

A curious plant that I had never seen before was *Ruscus aculeatus* L., butcher's broom, a shrubby, evergreen Eurasian plant that has cladodes rather than leaves. (A cladode is a flattened green stem that looks like a leaf; think prickly pear cactus, whose "pads" are also cladodes.) That these are stems rather than leaves is shown by the fact that plants that have this morphology also have inconspicuous ephemeral leaves. Since the flattened stems also have chlorophyll, the true leaves are redundant and normally they are shed

early in the season. In *R. aculeatus*, small greenish flowers appear on the surface of the "leaf" (cladode), followed by a red berry that also sits on the "leaf."

This low-lying district is extremely wet and poorly drained. Moss is everywhere, and many tree-trunks are covered with lichens. The area receives 900 mm (35-36 in) of rain per year; some areas have over four feet (1.5 meters) of standing water in the winter.

While we were there it was dry, although there was abundant water in streams flowing through the area we visited. *Quercus robur* L. is abundant in the low-lying areas whilst beautiful clumps of *Q. pyrenaica* Willd. start to appear as we move higher up.



3/ *Quercus pyrenaica*, Centre de Graoux.

Clearly, many of the plants growing here were not planted: they simply moved in once a forest environment, with appropriate niches, had been established. This applies both to native Eurasian and exotic species.



4/ *Boletus edulis*, Centre de Graoux.

Recent years have seen some weather events that were unusual if not unprecedented. Hurricanes in 1999 and 2009, with winds of 200 km (120 mi) per hour, knocked down large areas of trees. Recent winters have also been harsher than usual. It is assumed that this change in weather conditions is due to world-wide climate change. Time will tell if nature returns this area to moorland...

A very interesting addition to the pleasure of botanizing in the park were our encounters with mushroom gatherers. Large quantities of *Boletus edulis* Bull., often known by the Italian name *porcino* (piglet), are gathered in this park each autumn. (We're talking hundreds of kilos here!). We saw them growing among the leaves and nestled in the collecting baskets of people gathering them. Some were large, many were small, and almost all had already been discovered, and grazed, by snails. What the snails don't eat is still good, and so both people and snails



5/ *Quercus suber*, Réserve naturelle Nationale du Courant d'Huchet.

get to enjoy the delicious fungus. One lady I spoke to even told me how she prepares the mushrooms for dinner. (“Wash, slice, sauté in butter, add salt, pepper, a touch of garlic and parsley when the mushrooms are golden...”)

We finished the afternoon with a visit to the Réserve naturelle Nationale du Courant d’Huchet, not far from the regional park just described, guided by Hervé Le Bouler. This reserve consists of sand dunes stabilized by pine and curious *Q. robur* clumps growing in the dunes. The Atlantic Ocean (Bay of Biscay) was not far off. In fact, several of the tour members hiked over to the beach, past beach houses, to see the breakers. Here in this reserve we saw some of the freshwater lakes, common in the flat terrain of the *landes*, into which drain many of the streams in the area.

As is usual for this part of France, there are remnants of the native forest mixed together with plantations of maritime pine, oak and others. Growing here is *Quercus suber* L., the famous evergreen cork oak

endemic to southwest Europe and North Africa, whose thick, knobby, impermeable bark is used for the manufacture of corks for bottles. We saw many of these trees, including some from which the bark had been harvested at some time in the past.

Bark is first harvested from a cork oak when it is about 25 years old. The first harvest of the knobby “male” bark is usually of poor, unusable quality, but subsequent harvests of smooth regrown “female” bark are used commercially for bottle stoppers and many other uses. Bark is carefully stripped from trees during the summer by skilled workers using special axes; the workers must be very careful not to damage the phellogen (cambium) which lies just under the bark and which will regenerate the desirable smooth bark. Bark is harvested every 12-15 years.

That evening, in Saint-Paul-les-Dax, we enjoyed a Basque-style dinner. Basque cuisine uses more tomatoes in sauces than is common in either Spanish or French cuisine; Basques consider their culinary traditions better than those of either of these neighboring cuisines, and as a tomato-lover, I have to agree! This was our introduction to the next chapter of the tour.

The Basque country of France and Spain: Labourd and Gipuzkoa

The Basque country, in France, designates a very small area in the most southwestern corner of the Aquitaine region; in Spain, the Basque country includes four provinces: Gipuzkoa, Alava, Biscay and Navarre. It is a distinct region, regardless of which modern state governs the area united as it is by such things as language, rural economy and lifestyle as well as material culture. The Basques’ desire for freedom has unfortunately spawned

an often violent separatist movement in Spain, with the ultimate aim of establishing an independent Basque nation formed from the Spanish and French territories inhabited largely by Basque people. The separatist formula is $3 + 4 = 1$, which means the 3 French Basque provinces plus the 4 Spanish ones equals one nation. Basque nationalism is not so evident in France, where state centrism has always disfavored ethnic and linguistic minorities such as Basque, Breton, Catalan, Corsican and Alsatian. But French Basques do not hesitate to identify themselves as Basque, even without the state sponsorship of regional entities (*autonomías*) that exists in the present Spanish federation.

You know that you are in Basque country when you see flocks of grazing white sheep and large, beautiful stone two-storey houses with red window shutters and red tile roofs, so different from houses elsewhere in France and Spain.

The region today is vibrant with self-confidence, largely due to the demise of repression in Spain after the death of the Spanish caudillo Francisco Franco. Under Franco, Basque (and also Catalan) ethnicity was ridiculed and speaking Basque in public was forbidden and punished. Today in Spain there is a thriving school system with instruction in Basque; we saw a large group of school children on excursion at *the Jardín Botánico de Iurraran* in Zarautz, Gipuzkoa, all chatting happily in Basque. Among them were Oriental and African children.

On this tour I was pleased to learn that the famous missionary-naturalist Father Armand David was from the French Basque country. Born at Ezpeleta, near Bayonne in 1826, he entered holy orders and went to China as a missionary. While in China he collected a number of specimens of plants and animals unknown until then, including the giant panda, Father David's deer, the dove tree (*Davidia involucrata* Baillon), and the Chinese white pine (*Pinus armandii* Franch.), both named for him.

Thursday, October 4th and Friday, October 5th

In order to describe the activities of the 4th and 5th of October, it is better to rearrange the order of the schedule. This is because the afternoon of the 4th had a great deal in common with the afternoon visit of the 3rd, and the morning visit of the 4th likewise shares many features with the morning visit of the 5th. I will therefore describe the afternoon visit of the 4th before the morning visit, which will be followed by a description of the morning visits of the 4th and 5th of October.

October 4th afternoon: the Forêt communale de Sare

The Sare region is right on the Spanish frontier; the village of the same name is 15 km (around ten miles) east of the picturesque fishing village of Saint-Jean-de-Luz, where we would spend the night of October 4th. Both are only a few kilometers north of the Bidasoa River, which marks the border with Spain. The terrain is quite mountainous, as would be expected in the foothills of the Pyrenees.

Forêts communales are forests that are privately or communally owned and are the responsibility of local jurisdictions rather than the State. As such, there are interesting differences of attitude between the local and national organs responsible for forest management. In forests administered by local government there is much more sympathy for traditional uses, such as grazing and wood collecting. In forests administered by organs of the national government, there is far greater emphasis on management for commercial production and for sustainability. The two are often in conflict, as can be imagined. It

is ironic that the survival of communal forests is often attributed to the expedient use of the forests rather than from planned uses: planned uses tend to eliminate the resource over time, while expedient uses, by definition far less efficient, tend to preserve the forest willy-nilly. In a sense, it is the classical conflict of the cowboys and the farmers: cowboys being represented in this part of France by those advocating *élevage* (stockraising), and farmers by *forestiers* (foresters). (Thank you Chris Carnaghan, for the apt analogy!)

Guided by Cryille Van Meere from the Office Nationale des Forêts, the visit to this forest necessitated a good bit of uphill climbing. The climb was well worth it however, for it brought us to the zone where the forest is dominated by pollarded oaks (mostly *Q. robur* L.), called



6/ *Quercus robur* pollard, Forêt communale de Sare.

tétards in certain parts of France (more than a dozen words exist for pollard, depending on what region of France you are in). We had heard a good paper on this subject during the conference by Dominique Mansion. Pollarding is the custom of chopping significant new growth on a tree back to the main trunk. This is done periodically, so that the tree never attains much height as long as the pollarding continues, while the trunk continues to expand in girth. This practice used to be done all over Europe in order to obtain stock feed or fuel without killing the tree. In this forest, pollarding was done every 15-18 years to trees which were selected by a communal official. The result of pollarding is huge trunks topped by puny growth of only a few seasons.

Pollarding in this region was directly connected to charcoal manufacture up to around 100 years ago, for use in smelting iron. The iron ores, and the smelters, were located in the Spanish Basque province of Gipuzkoa. The charcoal was produced *in situ* in France, hauled the short distance to the coast by oxcart, then shipped by boat to Spain, where it was utilized. The use of charcoal for fuel at the smelters was gradually superseded by the use of coal, so that by the late 19th century, pollarding of French oak trees had ceased. After that, the trees were no longer chopped back, so that a visitor today sees pollarded trees that have produced a significant new canopy atop a huge, much older trunk. Not surprisingly, many of these trees are quite grotesque, a veritable goblin forest.

Thursday, October 4th and Friday, October 5th, morning

Both mornings were spent visiting arboreta that contain significant oak collections, particularly of subtropical and tropical American oaks. The visit of October 4th was to the Arboretum de Chocha in Ustaritz. This arboretum, founded in 1975 by Michel Duhart, is the National Collection of Mexican oaks in France. Mr. Duhart, despite being past



Arboretum de Chocha. 7/ *Quercus phellos* L. 8/ *Quercus crassifolia*. 9/ *Quercus glauca* var. *gracilis* Rehder & E.H. Wilson. 10/ *Quercus rysophylla*. 11/ *Quercus variabilis* Blume.

80, is still an avid and active plant explorer, making collecting trips each summer. The collection at the Arboretum de Chocha emphasizes the *Fagaceae*, with more than 150 species of oaks, most from North and Central America. Also at the arboretum is a notable collection of plants from southern Chile. The arboretum covers 3 ha/7.4 ac, so it was possible to see the entire collection in the time allotted.

The visit of October 5th was to the Jardín Botánico de Iturraran, (in Basque, Iturrarango Lorategi Botanikoa) near Zarautz. The garden belongs to the provincial government of Gipuzkoa. Our host at this visit was Francisco Garin García, manager of the garden; he is also a close friend and collaborator of Michel Duhart. This garden of 10 hectares (25 acres) is situated within the Parque Natural de Pagoeta at an altitude between 100 and 200 meters (300-600 feet) above sea level. The climate is humid (up to 1600 mm/64 in) rainfall per year and mild, with winter low of only -5 °C (23 °F). Thanks to the situation and the mild climate it is possible to grow plants from both warm and cold regions in the Temperate Zone.

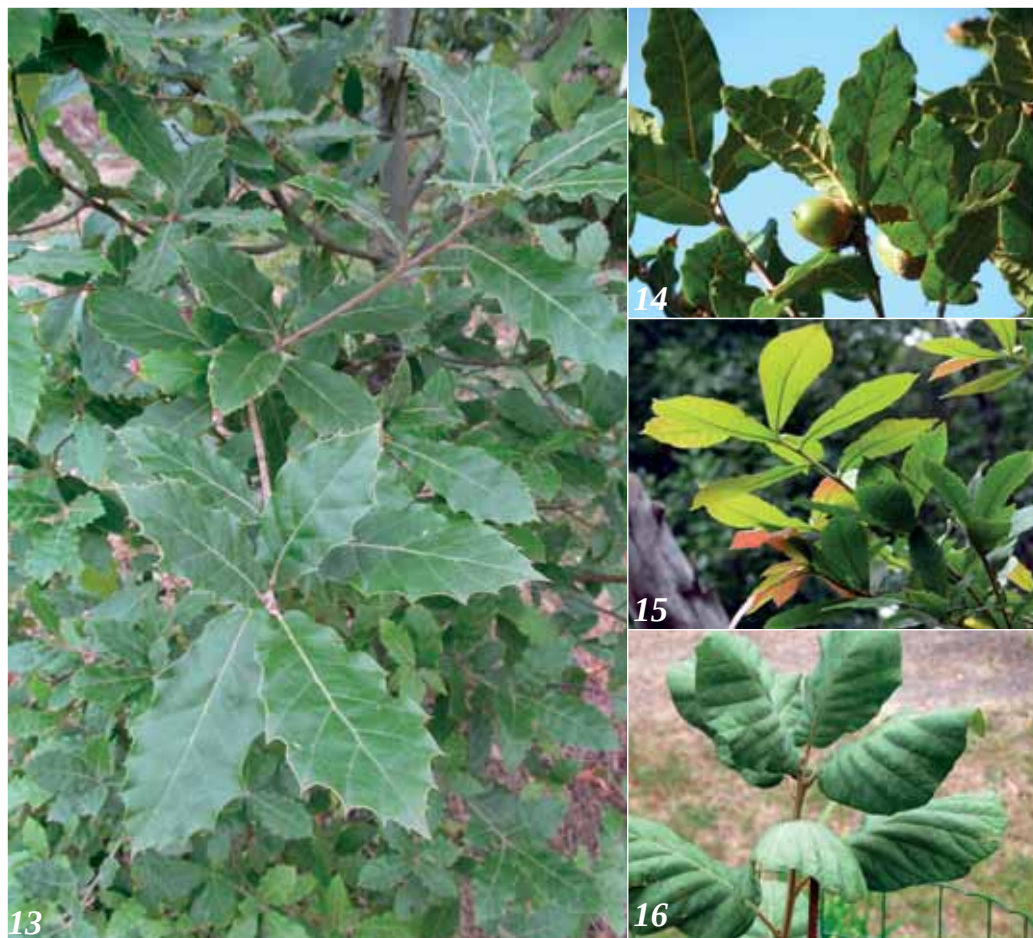
Plantings in Iturraran were first made in late 1986, on what was formerly a farm. (The reception center for the botanic garden is the former farmhouse, a beautiful example of Basque rural architecture.) The botanical collection now includes more than 5,000 taxa belonging to 3,000 species from 130 families. Included are 300 oak taxa, including 160 species, around 100 from Mexico and Central America. (See *International Oaks*, No. 22, 2011, pp. 48-53, for a list of the Mexican and Central American oaks in the Iturraran collection.) The garden also has extensive collections of maples, dogwoods, magnolias, rosaceous plants, conifers, rhododendrons, palms, bamboos, and herbaceous perennials. There are also some regional collections, such as Mediterranean plants, winter blooming plants, and plants from the Southern Hemisphere. It is a working garden, with a regular program of propagation of plants in the collection, including endangered species of the Iberian Peninsula.



12/ Part of the Jardín Botánico de Iturraran's oak collection.

In both gardens, most of the plantings are on hillsides, with south, southeast, and northwest exposure. Equally, in both gardens, all specimens are labeled with their Latin binomial, and an indication of their country or continent of origin (the latter often in Basque). At Iturraran, the plantings are in eight zones, with a network of paths which wind along and through them. Most of us concentrated our time in Zone 1, where the oaks are planted, but since we had adequate time, we enjoyed checking out the other zones as well.

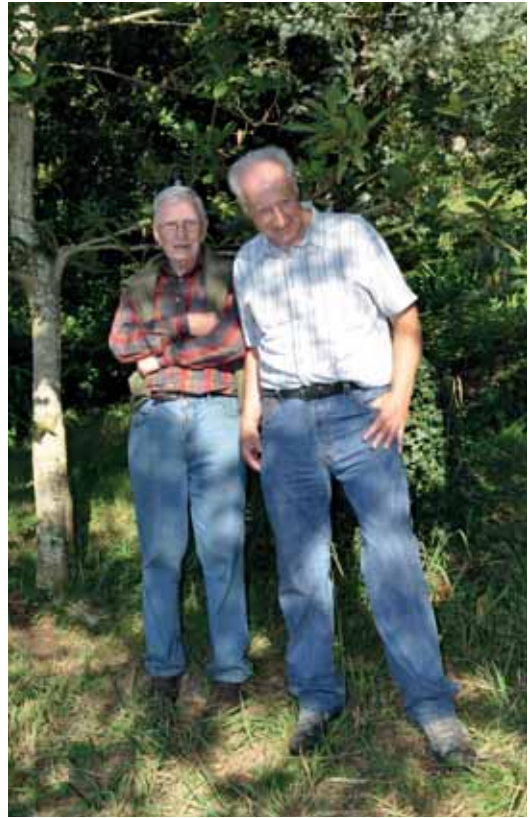
I took many photographs in the two gardens, mostly of oaks that impressed because of their interesting leaf morphology or growth habit. Probably not by accident, all of these belong to section *Lobatae*, red oaks, which I especially like. There are too many of these to list all of them, but I especially liked *Q. hintonii* E.F. Warb., *Q. xalapensis* Bonpl., *Q. candicans* Née and *Q. crassifolia* Bonpl. Another very interesting oak which caught my eye is *Q. leiophylla* A. DC. Although this oak belongs to the white oak section, it also has red juvenile foliage. The outstanding oak species in both gardens in my opinion, however, is the lovely evergreen Mexican oak *Quercus rysophylla* Weath., loquat-leaf oak. This red oak from Northeastern Mexico is too tender for me to grow in the interior of North America where I live at 6,000 ft altitude (1,800 meters), but I can dream, can't I?!



Jardín Botánico de Iturraran. 13/ *Quercus hintonii* 14/ *Quercus costaricensis* Liebm. 15/ *Quercus insignis* Mart. & Gal. 16/ *Quercus tarahumara* Spellenb.

Widespread natural hybridization between sympatric species of red oaks has been reported for such oaks in both the eastern U.S. and in California. Similar hybridization has also been reported for some red oak species in Mexico. But have any Mexican red oaks ever been deliberately hybridized with much hardier North American red oaks? (A cursory check of the internet did not return any answer to this question.) This seems to me to be a likely area of concentration for oak breeders and oak hobbyists, since hybrid offspring of these Mexican red oaks with very hardy red oaks from the U.S. could not fail to be stunning.

Our visit to the Arboretum de Chocha ended with a lovely outdoor lunch of Basque specialties, buffet-style and our morning at the Jardín Botánico de Iturarran was drawn to a close with lunch in a nearby restaurant where we enjoyed a well-known Spanish (well, actually Catalan) dish: paella. Although it lacked the usual chicken and sausage, the *almejas* (mussels) were there, and I, at least, enjoyed it...



17/ Michel Duhart (left) and Francisco Garin, long-time partners in acorn collecting.

Friday afternoon October 5th: back to France and on to the Languedoc

The drive to our next stop, Labourgade, 45 kilometers (28 miles) from Toulouse, was a long one. At first our route paralleled the Pyrenees, and a glance out the window toward the south encountered high peaks partly shrouded in clouds or shining in bright sunlight. But in the late afternoon the mountains faded into the distance, and we traveled through agricultural lands. As darkness approached we entered the outskirts of Toulouse, the fourth largest city in France.

Labourgade, it turned out, was not easy to reach. It seems that there was a bridge on the projected route that was problematic for our large tour bus, so we had to take a long and tiring detour. The result was that our arrival at our lodgings, in the imposing medieval Château de Terrides, was long after dark. But our late arrival was more than compensated for by a meal whose centerpiece was a delicious *cassoulet* (duck and pork with white beans baked in a casserole), washed down by a rich red wine from the region.

As we were eating, several of us at my table were speculating on the original use of the large, high ceilinged room we were sitting in. A refectory? A stable? Uses obviously change through time...

It is a real pity that we arrived too late to permit exploration of the chateau and its grounds, 97 hectares (240 acres) of forest and prairies. The chateau has had a colorful history. Though serving as a tourist hotel since 1987, it began its career in 1320 as a

hunting lodge for the Viscounts of Terrides, vassals of the Counts of Toulouse. The castle has survived numerous wars, including the Hundred Years' War, 1337-1453; the religious wars of the 16th and 17th centuries; and the French Revolution at the end of the 18th century: 700 exciting years and still going strong!

Saturday, October 6th: the trees of the little shepherdess

Shaun Haddock is a long-time member of the IOS and a newly elected member of the IOS Board. Since his retirement in 2006 from British Airways, where he was a pilot, he has lived in southern France, where he has created a beautiful arboretum, the Arboretum de la Bergerette, near the village of Saint-Sardos, a short distance away from Labourgade. The arboretum includes 14.5 hectares (35 acres) of gently rolling land. Shaun has owned half of the land since 1989, with an additional purchase in 1996, and he has been actively developing it as an arboretum since he acquired the first parcel.



18/ Arriving at the Arboretum de la Bergerette.

Shaun describes his location as “difficult.” This has to do with the weather in this part of the Languedoc. The average annual rainfall, measured by weather-measuring equipment on site, is 600 mm (24 in), which would certainly be regarded as dry in most parts of the world, and some years at la Bergerette, e.g., 2003, have been even drier. Normal winter lows here are an occasional -7 to -8 °C (19-20 °F), but 2011 had a harsh winter, with the temperature dropping to -13 °C (8 °F) with constant below freezing temperatures for nearly two weeks, which caused tissue damage to all of the trees in the collection or killed them outright. Summer temperatures are high, with average temperatures above 32 °C (90 °F), going at times as high as 40 °C (104 °F). This heat, combined with drying prevailing winds, (the so-called Vent d’Autan), brings desiccation to leaves even when the soil is not overly dry. As Shaun puts it “The trees have a hard life.”

We arrived fairly early in the morning at the rural site, the sun just coming up, to find preparations in full swing for an over-the-top celebration. Anke Mattern, Shaun’s partner, and he himself had been hard at work for weeks getting ready for this event, and everything was coming together beautifully.

The visit began, of course, with a tour of the arboretum. Due to a lucky (for us) accident on a neighbor’s property (a broken water pipe), the now dry watercourses in Shaun’s arboretum were full of water, as if it were spring. We looked first at the oldest plantings, which were trees of various families, including conifers, some of which were quite large. These trees grow at stream level, i.e., the lowest (and wettest) part of the arboretum. The bulk of the plantings lie above this level, eventually culminating in what Shaun calls the “plateau,” which is the driest of his areas.

Shaun is a true plantsman, i.e., one interested in, and knowledgeable about, all kinds of plants. But he has been especially interested in oaks, both because many species of the genus do well in this part of France, but also due to the fact that good seed of a variety of oak species is available through contacts, IOS collecting trips, and the IOS

seed exchange. Thanks to all of these sources, Shaun is now growing a large number of oak species from all over the world that are both rare in cultivation and new to France. He has already planted 200 species of *Quercus*, and has 50 more which will eventually be planted out.



19/ *Quercus baloot* Griff., Arboretum de la Bergerette.

In his article, Oaks in a Difficult Climate (*International Oaks*, No. 23, 2011, pp. 27-40, and posted on the IOS website under “Articles”/”Gardens and Arboreta”), he gives a detailed rundown of some of the results to date of his plantings in the arboretum. The article is an extremely valuable contribution to the subject of oaks and drought, and is written in Shaun’s inimitable wry style, as anyone who knows him might expect. (He is a textbook example of the self-effacing Brit, with a seemingly inexhaustible supply of sangfroid.)

One finding, which surprised both him and me, is that most of his American oaks (oaks from the east and Midwest of the United States) have proved to be remarkably drought-tolerant. The same is largely true of the oaks from western North America, although many of these are unluckily planted in the driest part of his arboretum, and are not thriving as well as he had expected. He mentioned *Q. douglasii* Hook & Arn. in this connection.

Two oaks which I remember in particular were an oak labeled *Q. hinckleyi* C.H. Mull., sent as an acorn by Texas IOS member David Richardson, and *Q. ×bushii* Sarg., a hybrid between *Q. marilandica* Münchh. and *Q. velutina* Lam. *Q. hinckleyi* is a threatened dwarf oak from the Big Bend area of Texas. Richardson has a



20/ Shaun Haddock, telling a tree tale in his inimitable style.



21/ *Quercus marilandica*, Arboretum de la Bergerette.

plant originally grown by the famed Texas plantsman Benny Simpson. It is growing in his (Richardson's) garden, and the flowers are consistently pollinated from other white oaks growing in the area, many *Q. virginiana* Mill. The plant in Shaun's arboretum appears to me to be hybrid: it is two meters (six feet) or more high, whereas true *Q. hinckleyi* is not that tall, and this plant does not have the tiny blue leaves of true *Q. hinckleyi*. I also have seedlings from Richardson, all evident hybrids, growing in Boulder, Colorado. One planted outside will face its first winter outside this year, 2012-2013. (I am resigned to losing it, as it will quite likely prove to be too tender to survive here in Colorado. But it has to be tried...)

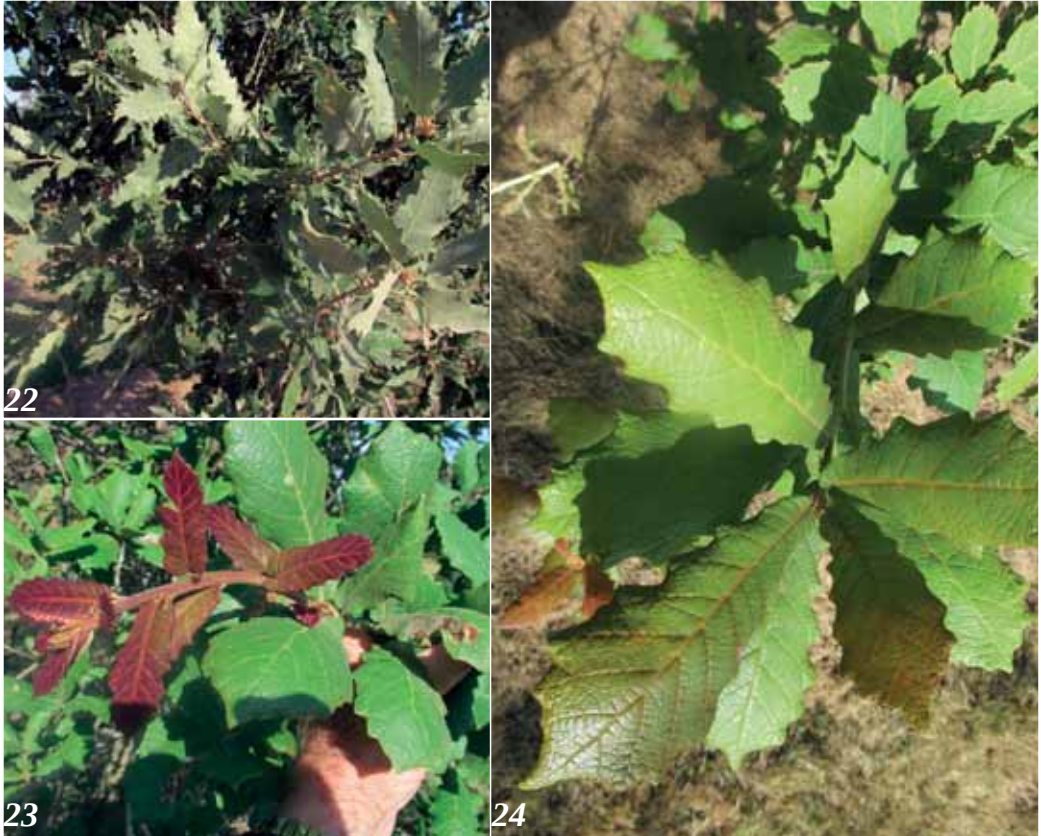
Q. ×bushii is a cross I had never seen before, and it is a stunningly beautiful plant, with great morphological variation in the leaves. (*Q. marilandica* has a leaf which lacks lobes and is typically club-like at the apex—"duck's foot leaves," as Shaun describes them—whereas the leaf of *Q. velutina* has the typical deep lobing of a North American red oak. Shaun's plant came from Guy Sternberg at Star Hill Forest Arboretum in Illinois. These two are also among Shaun's favorites.

Other oaks, some of which I was already familiar with from their natural habitat, were doing very well in Shaun's garden: *Quercus dentata* Thunb., the (Japanese) daimyo oak, in Section *Quercus*; *Quercus ithaburensis* subsp. *macrolepis* (Kotschy) Hedge & Yalt., the Valonia oak from the eastern Mediterranean, in Section *Cerris*; *Quercus obtusata* Bonpl. and *Q. tuberculata* Liebm., both Mexican white oaks in Section *Quercus*.

The Arboretum de la Bergerette now enjoys French National Collection status for its American oaks.

After viewing his trees, our party congregated in the area in front of his house, which had been set up as an outdoor

kitchen/dining room. Food preparation was underway, and mouths were watering at the prospect of regional delicacies. While awaiting the dinner bell, we admired some large wooden acorns that were lying here and there around the dining area. Larger than basketballs, the ‘corns were sculpted from wood from a tree knocked down in the 2009 cyclone, Hurricane Klaus. That cyclone knocked down nearly forty large trees, mostly pines, eucalypts, and some evergreen oaks. (Deciduous oaks were not affected.) It proved possible to straighten some of them up again, but not all. The successfully straightened trees are still held upright and firm by guy wires.



Arboretum de la Bergerette. 22/ *Quercus ithaburensis* subsp. *macrolepis*. 23/ *Quercus tuberculata*. 24/ *Quercus obtusata*.

In preparation for the noon meal, tables had been set up throughout the area, and also in a nearby shed, and soon we were invited to fill our plates with the food that was now ready. Barbecued pork, stewed mussels, crudités (fresh vegetable tidbits such as bell peppers, onions, cauliflower, cured olives of several kinds, *cornichons* [gherkins], etc), lovely salads, a variety of cheeses, an endless supply of fresh French bread and local wines...Would any of us ever be hungry again?! Fantastic job, Anke and Shaun and all your volunteer helpers!

I have to mention a final delicate touch: colorful place mats prepared especially for this feast featuring representations of oak leaves of different species, many represented in the arboretum collection. I brought several of these mats home with me; I intend to have them laminated so that I can share them with guests at future dinners of my own. They

will be a lasting reminder of a wonderful day in an impressive young arboretum, hosted by two of the most charming people I have met through the International Oak Society.

All too soon it was time to get on the bus again for the drive to our overnight lodgings in Périgueux, a fair distance away. It was past sundown when we pulled into the city, with its huge cathedral looming over it in the light rain and fading light. “It looks like a mosque”, I thought to myself, remembering the skyline of the old city in Istanbul. And in fact, it does look very oriental in a way, since its cupolas and domes give it a kind of Byzantine look. This was deliberately emphasized in a 19th century remodeling of the church. Too bad it was too late in the day for a closer inspection. (One more place to visit again, with enough time to look around. The Post-Conference Tour provided several of those...)



25/ La Bergerette, in the oldest part of the arboretum.

Sunday, October 8th: The green Périgord (or is it one of the other colors?)

Most tourists visit the Périgord for such things as the stunning Magdalenian painted caves from the Upper Paleolithic period 20,000 years ago, medieval castles dating from the time of the 100 Years War, charming rural villages and landscapes, or in order to stuff themselves on truffles and foie gras.

But we were not ordinary tourists (although we appreciate all of those other things); we came to visit the ambitious young Arboretum des Pouyouleix, located 50 km (30 miles) northeast of Périgueux, in the Green Périgord, near the village of St.-Jory-de-Chalais. The arboretum, which dates only from 2003, was created by Béatrice Chassé, the current President of the International Oak Society and her partner, Gérard Lionet. Abundant information about this arboretum is available online. (See also *International Oaks*, No. 22, 2011, pp. 23-26).

The arboretum is in a beautiful rural setting, located on a 25 ha (60 ac) parcel of land with varying soils (pH 7 or less) and topography. The climate is mild, comparable to U.S. Hardiness Zone 8, but unpredictable. (Is there any climate zone in the Temperate Zone which is not unpredictable?!) Bordered on one side by the river Côte, the altitudinal variation is from 270 to 210 m (688-885 ft) above sea level. Situated between the Aquitaine basin and the Massif Central, it is a metamorphic region in which the soils are



26/ The Arboretum des Pouyouleix looking out over the North American oaks.

largely the product of mineral decomposition. Over the past eight years rainfall – that Gérard records scrupulously along with temperature – has varied from 716 mm to 1021 mm (30-40 in). It is rare that winter night temperatures fall below -8°C (17.6°F) and more habitually they are between -2 and -5°C (28.4 to 23°F). Before February 2012, through eight winters, there have only been half a dozen days where diurnal temperatures did not rise above 0°C (32°F).

The 25 ha arboretum is about an equal mix between prairie and forest, with a slight advantage for the former. A major effort at the arboretum since its inception has been clearing the forest parts severely damaged in the great storm of 1999 followed by replanting. Throughout the newer planted areas are stacks of chopped wood from the clearing. No use of any type of chemical product, be it for clearing, weeding or planting, is made.

The plantings are mostly very young seedlings, since it is axiomatic for the founders that trees in the collection must be of known provenance and that the less time a tree spends in a pot the better. For the past three years, when there have been sufficient acorns, attempts at sowing directly in place have been made with encouraging results for *Q. saltillensis* Trel., *Q. acerifolia* (E.J. Palmer) Stoyneff & Hess, *Q. flocculenta* C.H. Mull., to name but a few.

In most cases the trees are grown from seed specially collected from the wild. This explains Béatrice's zeal for seed collecting expeditions (sponsored by a group of oak collectors that includes Shaun Haddock), the most recent example of which was to Mexico in the autumn of 2010. (See: 9490 Kilometers Across Mexico, in *International Oaks*, No. 22, 2011, pp. 70-88; or at www.internationaloaksociety.org, under "Articles" / "Trip Reports".) Seed and plant exchanges with other arboreta and seed collectors is another very valuable source of plant material. With nearly 300 botanical taxa, and a dozen or so new species waiting to be planted, the Arboretum des Pouyouleix is, since March 2012, with the Arboretum national des Barres, one of the two National Collections in France for the genus *Quercus*,

The collection emphasizes but is not limited to oaks (total number of taxa planted is about 800). Gérard is also interested in conifers (a small collection of nearly 80 taxa is already growing in the arboretum, as well as maples with 50 taxa – and there are plans to add many more) again as young seedlings. *Cornus florida* L., an unidentified *Stewartia* near the residence, and a stunning *Parrotia persica* (DC.) C.A. Mey. in full autumn color out in the arboretum, amid young oaks, were observed.



Arboretum des Pouyouleix. 27/ *Quercus greggii* (A. DC.) Trel. 28/ *Quercus wislizeni* var. *frutescens* Engelm. 29/ *Quercus ilicifolia* Wangerh. 30/ *Quercus miquihuanensis* Nixon & C.H. Mull.

Béatrice personally escorted us through the arboretum, stopping often to tell us something about a particular tree. For example, as we looked at a seedling of *Q. salicina* Blume, Beatrice told us “If you can grow only one oak, this is the one: the new spring growth is wine colored, which turns to green in summer and fall. It is very frost hardy (-7 to -18 °C, (19-0 °F) coming through February 2012’s fifteen day freeze to -18 °C absolutely unscathed.” Advice duly noted... but only applicable in mild winter climates!

Other oaks that were not at all bothered by the length and duration of this cold, include 5 *Quercus myrtifolia* Willd. (planted in 2008); 3 *Q. geminata* Small (planted in 2005 and 2011). You never know what plants are capable of...

In front of two quite different *Q. dolicholepis* A. Camus, Béatrice also commented on, and pointed out, morphological variation within a species, a result of which is that no two members of a species look exactly alike. “You have to have seen a whole lot of *Q. dolicholepis* in your life to be able to walk up to one and say, you’re not what the label says!!” For this reason, you cannot expect your tree to look just like the picture of it in a reference book.

The most interesting aspect of visiting this arboretum, which has the oak collection segregated by continent of origin, is to see the great diversity of the collection and to learn of the rigors of establishing the plants on the site. Last winter was very mild but was punctuated by particularly harsh February cold, and 600 young plants in the nursery were lost. Not surprisingly, individuals of certain species that had been planted out in fall 2011 survived while those of the same species (same size, same age) left in the greenhouse did not (for example, *Q. invaginata* Trel., *Q. durifolia* Seemen ex Loes., *Q. viminea* Trel.). *Q. tarahumara* Spellenb. and *Q. resinosa* Liebm. survived in the nursery, *Q. urbanii* Trel. did not (unfortunately none of those had been planted out to provide a comparison). Many trees were damaged again by frost in April 2012 after growth had

commenced. Nevertheless, all of the trees that did suffer in February (Mexican, Asian, North American or European) are alive and thriving today – with no visible or lasting damage (even a *Q. germana* Schltdl. collected in Veracruz, Mexico and planted in 2010, given up for dead in March!). See *Oak News & Notes*, Volume 16, No. 2, Summer 2012, pp. 6-8, for an account of the dramatic February 2012 at the Arboretum des Pouyouleix.

Very few arboreta start from scratch with seedlings – and truth to tell the first two years' plantings were with nursery trees. Records here, on the other hand, begin with the day the seeds were collected and include a complete map with GPS coordinates for all of the trees, labels with accession details and a very large accessions file that includes date planted, age and height at planting, origin, comments and how to find the tree on the map. Presumably, descriptive records will continue as long as the arboretum exists. Certainly none of the tour participants, nor the creators of this interesting collection, will live to see it when it has matured. This is an arboretum which will be at its prime in 100 or 150 years. Let us hope that it will continue to enjoy love and enthusiasm comparable to that of Béatrice and Gérard throughout what one hopes will be many lifetimes.



31/ *Quercus bicolor* Willd. (center) and *Q. xcapesii* W. Wolf (right), Arboretum des Pouyouleix.

A rip-roaring country festival and more food

About noon we again boarded our bus to drive to a nearby village, Saint-Saud-Lacoussière, where a country festival and fair were taking place. Called La Fête du Cèpe et du Veau Sous la Mère (The Festival of Mushrooms and Suckling Calves), it featured local products as in a farmers market, local crafts, French country music (you all knew, I assume, that an accordion can blast out country music?), dancing, and an endless stream of mushroom omelets and golden French fries. It goes without saying that there was



32/ *Quercus salicina* (center); *Q. glauca* Thunb. (right), Arboretum des Pouyouleix.

plenty of red wine to assist in swallowing and to promote the gala spirit of the occasion. We all sat together at tables reserved for us inside the huge tent which served as the communal dining room. What can I say? A good time was had by all, and it was interesting to encounter here the roots of Cajun music and chivarees. Once again, however, we doubted that we could ever be hungry again...

Nearing sensory overload...

But our hosts for the day, Béatrice and Gérard, had more in store for us. Into the bus, and off we went to visit a small private collection of trees in the nearby hamlet of Montagnac. Our host in this garden visit would be Mr. Laurent Lautier, a retired dairy farmer. According to a recent article in Sud-Ouest, a regional newspaper, “Cet homme chuchote à l’oreille des arbres” (“This man is a tree-whisperer.”). Seems like we’ve met a lot of those on this tour.

Mr. Lautier’s collection is housed at his home, and is known as the Arboretum de Montagnac; this small arboretum represents plantings of 140 species which are personal favorites of Mr. Lautier. There was no particular theme in the collection, with some oaks, but also many other deciduous species as well as conifers such as *Picea abies* (L.) H. Karst



33/ Arboretum de Montagnac.

and *Cedrus atlantica* (Endl.) Batt. & Trab. The trees were in long rows, like an orchard really, along one side of which was an entire row of the blue form of *Cedrus atlantica*.

One of the more interesting aspects of this visit was the setting: rural, with pastures and patches of woodland here and there, livestock grazing quietly nearby. The farmhouse itself was also very interesting: an 18th or early 19th century structure, it was really a compound, with a central courtyard; it was an authentic *périgourdine* farmstead. Entrance was through a stonewall, which closed off the fourth side of the courtyard. There was a large gate, which could be securely bolted with a heavy iron bar. The two-storey residence was along one side of the courtyard, while sheds and other outbuildings occupied the other two sides. A passageway through the central wing opposite the gate led to another smaller residence outside and behind the courtyard, which is where Mr. Lautier now lives. At its back were trees, and under them a deep carpet of blooming *Cyclamen hederifolium* Aiton, an absolutely stunning sight. Pale pink, dark pink, white – I have never seen so many blooming cyclamens, all at their peak, since all of the buds on a plant open at the same time.

Back inside the courtyard there were tables under a long shed opposite the manor house. On these tables were spread a myriad of finger foods and beverages, prepared for our farewell cocktail. Music was provided by an accordionist who kept up a constant stream of traditional popular music from all over the Western world: *Un Gamin de Paris*, *La Paloma*, *Dark Eyes*, an Argentine tango... In the waning light of the afternoon we snacked (couldn't do more, after the lunch we had had!) and visited among ourselves and with local dignitaries in attendance, including the mayor of Saint-Saud. There were lots of thanks to the host and to the organizers, tearful hugs, and promises to keep in touch as strains of *Auld Lang Syne* filled the cool air of early evening. And so, after five exciting days, we went our separate ways, some to Paris, some back to Bordeaux, all headed back home with wonderful memories.

Future IOS conferences are going to have a difficult time matching this one, especially because of the richness of the associated tours. I wouldn't have missed the 7th International Oak Society Conference and the two associated tours for anything in the world, since they combined so many things which fascinate me: trees, tree-lore, science, good company, good food, and abundant international cultural experiences.



34/ Saying good-bye to Laurent Lautier (center).

Photographers. Photo 1: Guy Sternberg. Photos 2, 4, 6, 8, 10, 13, 18, 22-24: Allan Taylor. Photos 3, 7, 9, 11: Lloyd Kenyon. Photos 5, 20, 21, 32: Jo Bömer. Photos 12, 17, 25, 33, 34: Charles Snyers d'Attenhoven. Photos 14-16: Francisco Garin. Photo 19: Shaun Haddock. Photos 26, 28, 31: Marie-Paule Thuaud. Photos 27, 29, 30: Béatrice Chassé.



MISSION

To further the study, sustainable management, preservation, appreciation, and dissemination of knowledge to the public about oaks (genus *Quercus*) and their ecosystems.

GOALS

To advance the state of scientific knowledge regarding oaks and oakland ecology

To locate, preserve and catalog significant oak-related literature

To facilitate the location and distribution of living material for propagation of oaks

To foster communication among members via a journal, newsletter and website, and periodic meetings

To promote the study, development, naming, and distribution of superior cultivars and cultivar groups for horticultural use, and the study of oaks for the production of timber, mast, and other useful products

To sponsor the preservation, display, and interpretation of oak-related traditions, art, and lore; and encourage the development and curation of appropriate and useful collections of oak-related pieces, such as wood samples, taxonomic specimens, or historic oak artifacts

To develop the capability and to serve as a registrar authority for oak cultivars, historic and champion oak trees, ancient oak groves, unusual or rare oak specimens, or objects of significance involving oaks

To provide information regarding the use, preservation, and appreciation of oaks, and successful techniques for oak culture and management

To encourage, recognize and honor outstanding achievements by individuals and organizations, members and non-members, in advancing these goals of the International Oak Society



www.internationaloaksociety.org