

Ecological Studies, Vol. 194

Analysis and Synthesis

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Ecological Studies

Volumes published since 2002 are listed at the end of this book.

U. Lüttge (Ed.)

Clusia

A Woody Neotropical Genus
of Remarkable Plasticity and Diversity

With 111 Figures, 2 in Color, and 38 Tables

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Cover illustration: Male flower of Clusia hilariana Schlecht. (Photo Ulrich Lüttge)

ISSN 0070-8356

ISBN-10 3-540-37242-3 Springer Berlin Heidelberg New York

ISBN-13 978-3-540-37242-4 Springer Berlin Heidelberg New York

Library of Congress Control Number: 2006934618

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Editor: Dr. Dieter Czeschlik, Heidelberg, Germany
Desk editor: Dr. Andrea Schlitzberger, Heidelberg, Germany
Cover design: WMXDesign GmbH, Heidelberg, Germany
Typesetting and production: Friedmut Kröner, Heidelberg, Germany

31/3152 YK – 5 4 3 2 1 0 – Printed on acid free paper

Preface

From emotional attachment to the inherent beauty and diversity and the curiosity and thought provoking challenges of *Clusia* the plan to compose a book-monograph on *Clusia* emerged a number of years ago when it became evident that the research interests of several groups internationally focusing on studies of this remarkable genus of neotropical dicotyledonous shrubs and trees would develop a very broad picture comprising all aspects of tree life. *Clusia* displays unique features because it is the only dicotyledonous tree genus with crassulacean acid metabolism (CAM). *Clusia* species are extraordinarily flexible and plastic and in some cases all variants of CAM can even be expressed in one given species. This has raised special attention to this genus among the vast diversity of tropical tree genera and put *Clusia* in the limelight of international research interest. The scope of these studies embraces morphology, anatomy and plant architecture, phytogeographical distribution and community ecology, phylogeny and genetic diversity, physiology and metabolism, physiological ecology and functional diversity. Thus, *Clusia* can serve as a general example covering all facets of tree biology.

To present this was not possible without a close co-operation of a team of authors. I hope that the result bears up to the expectations of creating a comprehensive and integrated picture of *Clusia*, and thus produce a unique story of the biological history and topical impact of an outstanding tropical tree genus. I thank all co-authors of the book for the joint efforts and their patience with repeated editorial requests. I am grateful to the entire international scientific *Clusia* community including many members who are not co-authors of this book for much stimulating exchange. Particular thanks are due to Dr. ANNIE M. BORLAND, Newcastle upon Tyne, UK, for reading several chapters of the book during their preparation and for making important comments. I am most grateful to Professor Dr. Dr. h.c. mult. OTTO LUDWIG LANGE as member of the board of editors of Ecological Studies for his encouragement, support and valuable suggestions. I thank DORIS SCHÄFER, Darmstadt, Germany, for her care with many of the illustrations.

Continuous and long lasting internationally co-operative *Clusia* research in the field in South America and elsewhere over the years has been particularly supported by the following institutions: Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela; Brazilian Research Council (CNPq); the PROBRAL programme of the Brazilian Postgraduate Education Council (CAPES) and the German Academic Exchange Service (DAAD); and the international partnership programme of Volkswagen-Foundation, Hannover, Germany. Without their support much of the work reported in this book would not have been realized although in addition we must also remember support given by many other institutions to research groups whose work is quoted in this book from the published literature.

I am grateful to Springer-Verlag for taking up the idea to publish the book and I particularly thank Dr. Andrea Schlitzberger and Dr. Dieter Czeschlik for the wonderful cooperation in producing it.

Darmstadt, in October 2006

ULRICH LÜTTGE

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Section I Background

1 Historical Recollections

ULRICH LÜTTGE

*Entdecker sein ist nicht genug, man muss auch publizieren.
“It is not enough to discover, one also must publish.”*

CARL FRIEDRICH PHILIPP VON MARTIUS [1794–1868]

1.1 Namesakes: CAROLUS CLUSIUS and *Clusia*

CHARLES DE L’ECLUSE (Fig. 1.1), latinized CAROLUS CLUSIUS, son of a noble family, was the greatest botanist of his time (Hunger 1927; Veendorp and Baas Becking 1938; Mägdefrau 1992). He was born in Arras in 1526. He studied law at Lovain and Marburg and later medicine at Wittenberg, Montpellier and Paris and also lived in various other European cities including Frankfurt, Strasbourg, Montpellier, Antwerp and London. He travelled in Spain and Portugal, in the European Alps and in Hungary. In Vienna he founded a medical garden – *Hortus medicus* – in 1573. In 1592, at the age of 66, he was appointed director of the *Hortus medicus* in Leyden (Veendorp and Baas Becking 1938), one of the six oldest gardens in Europe founded in 1587, where he died in 1609. Due to his extensive travels in Europe he was intimately familiar with the European flora. He discovered many new species, which he described and depicted thoroughly. He introduced tulips to the Netherlands and was involved in the introduction of potato to European gardens providing its first detailed description in 1601 although at the time the great nutritional value of potato for large populations was not yet appreciated.

With CLUSIUS’ original descriptions of the alpine vegetation it is evident why one of the most beautiful alpine plants, the large flowered gentian *Gentiana clusii* Perr. et Song. was named after him. However, we do not know the background of the motivation to name the genus *Clusia* after him. *Clusia* L. is a genus of 300–400 neotropical woody plants in the family Clusiaceae (alternatively Guttiferae or Hypericaceae) in the order Malpighiales of the Rosidae (Eudicotyledoneae). The name *Clusia* was coined by the Franciscan CHARLES PLUMIER who was born in 1646 in Marseille and died in 1704 in Cadiz.



Fig. 1.1. Sculpture of CAROLUS CLUSIUS in the Botanical Garden of Leyden in the Netherlands, where also a historical reconstruction of the *Hortus medicus* of CLUSIUS can be seen

PLUMIER was one of the most outstanding scientific explorers of his time (Mägdefrau 1992). He travelled widely in America and the West Indies and knew *Clusia*. LINNAEUS adopted the name for the genus from PLUMIER who cannot be named as authority for some rules of nomenclature. LINNAEUS distinguished two species of *Clusia*, namely *C. major* with three “varieties” and *C. minor* (Bittrich and Stevens 1998).

1.2 ALEXANDER VON HUMBOLDT: The First Ecophysiological Studies of *Clusia*

In the February of 1800 ALEXANDER VON HUMBOLDT performed ecophysiological gas-exchange measurements on *Clusia rosea* Jacq. at Lake Valencia in Venezuela (Alexander von Humboldt’s diaries; Faak 2000). At the time photosynthesis was measured observing gas bubbles emerging from green tissues submerged in water. HUMBOLDT wrote:

In keiner Pflanze zirkuliert vielleicht eine so ungeheure Menge an Luft als in der Clusia rosea. Wenn man die Blätter dem Sonnenlicht aussetzt, so geben sie ... nicht eine einzige Luftblase.

< In no other plant perhaps as much air is circulating than in the Clusia rosea. If one exposes the leaves to the sunlight, they produce ... not a single air bubble.>

This implies that there is no obvious gas exchange in the light via the leaf surface. We now know that *C. rosea* is a plant with Crassulacean acid metabolism (CAM) (Ball et al. 1991a, b) where stomata remain closed during the light period and CO₂ from internal sources, i.e. organic acids, accumulated after dark fixation of CO₂ in the night, is assimilated (Chap. 8) in the light. HUMBOLDT goes on writing:

Aus dem verwundeten Teil des Stengels fährt aber mit ungeheurer Geschwindigkeit ein Strom von perlartigen Luftbläschen aus; ... Zerschneidet man das Blatt selbst, so bemerkt man zahllose ähnliche Luftströme. Das Blatt hat Gefäßbündel, die transversal verlaufen. Es scheint als fahre die Luft aus jedem dieser Gefäßbündel aus – ein herrliches Schauspiel.

<However, at the cut end of the petiole with an immense velocity a stream of pearl-like gas bubbles is released; ... When one cuts the leaf itself one observes numerous similar air streams. The leaf has transversely arranged veins. It appears that the air is released from each of these vascular bundles – a magnificent spectacle.>

We now know that in the CAM cycle in the light period a high internal gas pressure of CO_2 and O_2 is building up behind closed stomata explaining HUMBOLDT's observation of a vigorous gas flow via wounds of the leaves. HUMBOLDT also made the appropriate control to show that his observations were due to photosynthesis:

*Setzte ich den Apparat in den Schatten, so hörte der Luftstrom auf.
Der Reiz des Sonnenlichtes fehlt.*

<Did I place the apparatus in the shade, the gas stream ceased. The stimulation by the sun light is missing.>

He then tried to determine the chemical composition of the gas stream. He could not determine CO_2 , but by using chemical reactions he could measure oxygen and nitrogen:

Diese Luft aus dem Innern der Clusia rosea besteht aus 0,35 Oxygen und 0,65 Stickgas.

<The air from the interior of Clusia rosea consists of 0.35 oxygen and 0.65 nitrogen gas.>

This means that the gas in the leaf air spaces had 35 % O_2 and 65 % N_2 . As measurements in the field are always difficult, HUMBOLDT was prudent to check his chemical O_2 -determinations later in the laboratory of L.J. GAY-LUSSAC in Paris and found them to be too high by a systematic error of 5 % (HUMBOLDT-quotations from Faak 2000; see also Krätz 2001; Lüttge 2002). The measurements of HUMBOLDT were confirmed much later by Spalding et al. (1979) using gas chromatography, and we now know that it is a feature of CAM that high internal O_2 pressures are building up in the light period during CO_2 assimilation behind closed stomata.

Thus, HUMBOLDT correctly described many aspects of the CAM cycle and we might consider him the discoverer of CAM in the trees of *Clusia*. However, he did not interpret his observations far enough and had no idea of the functions of the CAM cycle.

1.3 The Discovery of Crassulacean Acid Metabolism (CAM) in *Clusia*

Another researcher who made the right observations but did not realize that they were features of CAM was Hartenburg (1937), a Ph.D. student of the famous German ecophysiological OTTO STOCKER. He studied gas exchange of *Clusia mexicana* Vesque in a glasshouse in summer and found that after an

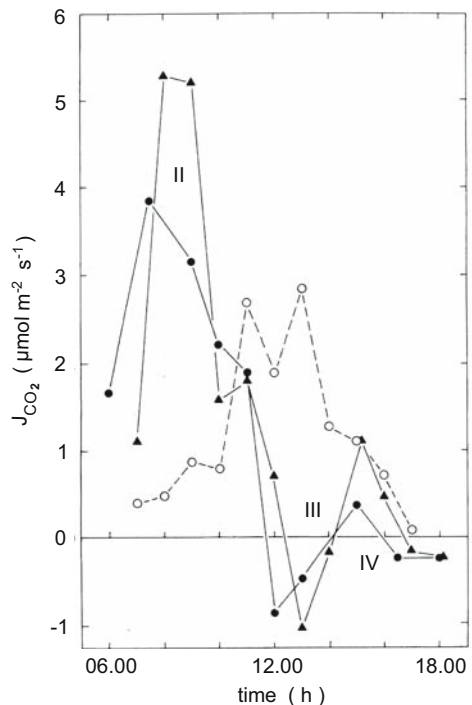
early peak in the morning CO_2 -uptake ceased during the day and there was even a small CO_2 release from the leaves around midday (Fig. 1.2). He discussed in detail whether the latter was due to respiration but discarded this possibility:

Dass es sich um Atmungskohlensäure handelt, ist wenig wahrscheinlich. Eher kann an die Entbindung von CO_2 gedacht werden, das im Clusia-Blatt spezifisch irgendwie physikalisch oder chemisch gebunden ist.

<It is unlikely that this is respiratory CO_2 . More likely it is due to CO_2 specifically bound either physically or chemically in the Clusia leaf and set free.>

Current work shows that in CAM during the day indeed so much CO_2 is released from malic acid, in which it is chemically bound during the night, that very high internal CO_2 -concentrations may arise in the leaves (Chap. 8) so that some CO_2 can diffuse out along a steep downhill concentration gradient to the atmosphere via the epidermis despite closed stomata. Hartenburg (1937) discovered even another facet of CAM in *Clusia* that currently is exciting physiological ecologists (Chap. 9). The strange behaviour described

Fig. 1.2. Three gas exchange curves of *C. mexicana* after measurements of Hartenburg (1937) on a sunny day (closed circles, 29 June 1935), a partially cloudy day (closed triangles, 24 August 1935) and an overcast rainy day (open circles, 27 August 1935) in a glass house of the Botanical Garden of the Technical University Darmstadt. The solid lines (closed symbols) correspond to a CAM-gas exchange with phases II, III and IV, the dashed line (open symbols) represents C_3 gas exchange. (Net CO_2 -uptake positive values, net CO_2 -release negative values.) (See Lüttge 1995)



above, and which he could not explain, was only observed on a sunny day and on a partially cloudy day but not on a totally overcast rainy day, when he found quite conventional CO_2 uptake all over the day as in normal C_3 -photosynthesis (Fig. 1.2). Thus, he saw the reactions of a plant that was intermediate between CAM and C_3 -photosynthesis and could switch between the two modes in response to external conditions.

HARTENBURG, unlike ALEXANDER VON HUMBOLDT, could have much more advanced the interpretation of his observations. Since 1804 it has been known from experiments of DE SAUSSURE that some plants have a CO_2 gas exchange with nocturnal CO_2 uptake and largely suppressed gas exchange during the day. The associated acid rhythm with a nocturnal accumulation of acids and a remobilization during the day had been known since the early nineteenth century (see Wolf 1960). However, it remained left to the Mexicans Tinoco Ojanguren and Vazquez-Yanez (1983) to describe, explain and establish firmly the performance of CAM in trees of *Clusia*, and after a seminal publication of Ting et al. (1985) this then became general knowledge.

Why is it so important for the history of *Clusia* research that *Clusias* perform CAM? There are several sizeable and tree-like plants which perform CAM. Among the monocotyledons these are the *Yuccas*, and among the dicotyledons giant stem succulent cacti and euphorbs and the Didieraceae of Madagascar exhibit CAM. One may range such species among the trees (Menninger 1967) although they either have no secondary growth at all or the special type of secondary growth of monocotyledons. *Clusias* are the only "real" CAM-trees with a typically dicotyledonous secondary growth based on the activity of a circumferential cambium (Chap. 2). Without the reported occurrence of CAM *Clusia* most likely would have remained just one of many other taxa in the large diversity of tropical trees. It is an open phylogenetic question why there are not more CAM plants among trees. However, it certainly was the unique performance of CAM in these trees that raised very pronounced interest in *Clusia* following the publications of Tinoco Ojanguren and Vazquez-Yanez (1983) and Ting et al. (1985), and it explains the burst of research activities in the last 20 years that now allows us to survey a large body of literature in this *Clusia* monograph.

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Section II Phylogeny, Diversity and Ecology

Introduction

ULRICH LÜTTGE

On 26 March 1983 we climbed the highest elevation of the island of Trinidad, Cerro del Aripo, 941 m a.s.l. We were studying epiphytic C_3 and CAM bromeliads. It was the same year when Tinoco Ojanguren and Vazquez Yanes (1983) published their discovery of CAM in *Clusia*. However, at that time we did not know about it. Later we discovered that we even had a branch of *Clusia* in the cover photograph (Fig. II.1) depicting *Aechmaea aripensis* in the special issue number 5, vol. 9, Plant Cell and Environment (1986) with our bromeliad work. One other member of the Cerro del Aripo crew of 1983, HOWARD GRIFFITHS, Cambridge, UK, later also became a *Clusia* enthusiast, and therefore we now know that on Trinidad – in addition to the ubiquitous *Clusia minor* L. – there are three endemic *Clusia* species, namely *C. tocuchensis* Britt., *C. aripoensis* Britt. and *C. intertexta* Britt. (Borland et al. 1992, Sect. 9.4.2.9). In view of the endemism of the *Clusia* species in Trinidad it is interesting to note that in the phylogenetic tree of Fig. 6.1 (Chap. 6) the three branches which have *C. minor*, *C. tocuchensis* and *C. aripoensis* in them are separated at the very base of the tree. (*C. intertexta* is not contained in this tree.) Thus, the endemic species must have evolved separately from a basic original *Clusia* ancestor on the island.

In the six chapters of this Section we present a broad coverage of aspects of the plant life and organismic biology of *Clusia*. We begin by describing anatomy and morphology of *Clusia* life forms to introduce its physical constitution. However, this also leads us already into some considerations of function, especially where the hydraulic architecture is considered as a basis of some intrinsic aspects of water relations combining structure-function assessments (Chap. 2).

The following three chapters constitute a unit dealing with the occupation of space by *Clusia*. As an exclusively neotropical genus *Clusia* is spread widely in Central America and on the South American continent and Chap. 3 takes us on a journey around its phytogeographical locations. Seeds of *Clusia* may germinate terrestrially or epiphytically and in the latter case eventually reach the ground via adventitious aerial roots to become independent trees. Seedlings



Fig. II.1. *Aechmea aripensis*, an epiphytic CAM-bromeliad in the upper montane rain forest at about 850 m a.s.l. on Cerro del Aripo, Trinidad, with a branch of *Clusia* in the lower right hand corner of the photograph

Fig. II.2. Seedling of *Clusia amygdioi* Silva et Weinberg growing in the tank of a bromeliad on rock outcrops in the Atlantic rain forest of Estação Biologica de Santa Lucia, Santa Teresa, Espírito Santo State, Brazil



are also often found in the water and humus filled tanks of both terrestrial and epiphytic bromeliads (Fig. II.2) and are thus protected in their early stages of life by the bromeliads as their nurse plants before they grow out of the tanks to become independent trees. However, *Clusias* themselves are often functioning as nurse plants where free standing shrubs and trees of *Clusia* allow the establishment of a diverse vegetation underneath their canopies. Thus, *Clusias* are often pioneer species starting vegetation islands, e.g. on the bare sandy ground of coastal restingas in Brazil (Chap. 4). Most likely it is the enormous ecophysiological plasticity and flexibility of *Clusias* as described below in Chaps. 8 and 9 of Sect. III, which make them particularly fit for such a function. Reproductive biology plays a central role in the conquest of space by plants which are firmly rooted in their substrate and need to combine distribution with reproduction. *Clusias* have developed several unique features in their reproduction, such as dioecy, resin production as an award for polli-

nation by bees, and a partially dominating asexual propagation. These are described and assessed in Chap. 5.

Chapters 6 and 7 form another unit, where the latest molecular approaches are applied to fathom species diversity, phylogeny and classification, and genetic variation in a defined geographical range. We realize that there is a very high speciation rate in the genus. The genotypic plasticity studied in these chapters is revisited again at the end of Chap. 9 in Sect. III, i.e. after eco-physiological plasticity has been described and when some more theoretical thoughts on the relations between genotypes and phenotypes in relation to diversity can be developed.

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2 Morphology, Anatomy, Life Forms and Hydraulic Architecture

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2.1 Hundreds of Species of One Morphotype

The 300 to 400 woody species of *Clusia* all display one typical morphotype (Lüttge 2000). *Clusias* are branched shrubs and trees with dichasial cymes and opposite leaves (see also Sect. 6.1). Among the various species leaves vary in absolute size. However, the leaves of all species are morphologically and anatomically very similar, always entire, leathery and somewhat succulent (Fig. 2.1). In view of the important effects of leaf form and structure on photosynthesis and ecophysiological performance (Niinemets and Sack 2005), this is remarkable particularly with respect to the large photosynthetic flexibility of some species of *Clusia*. However, this has not been much explored for *Clusia*. On the other hand, floral morphology of *Clusias* is rather variable (Sect. 6.5).

Leaf succulence of *Clusia* species is indicated by comparatively high fresh weight/dry weight and fresh weight or plant water/area ratios (Table 2.1). Although the data reveal some developmental influences (mature plants versus seedlings of *C. rosea*) and effects of nitrogen supply and irradiance (*C. minor*), the values obtained are rather homogenous. Two important exceptions are the conspicuously succulent *Clusia alata* Pl. et Tr. and *Clusia hilariana* Schlechtendal. These are obligate Crassulacean acid metabolism (CAM) plants. Succulence with highly vacuolated photosynthetically active cells is a general feature of CAM plants, which fix CO₂ in the dark period forming malate that is nocturnally accumulated in the vacuoles (see Chaps. 8 and 9). Another species, where comparatively high values of leaf succulence were obtained is *C. rosea*, which is also a CAM species.

Zotz et al. (1997) compared the leaf succulence attributes of *Clusia minor* L. with six other woody plants. *C. minor* is a C₃-photosynthesis/CAM-intermediate species. The ratios of fresh weight/dry weight of 4.7 and of plant water/area of 580 g m⁻² measured by Zotz et al. (1997) in *C. minor* (Table 2.1)