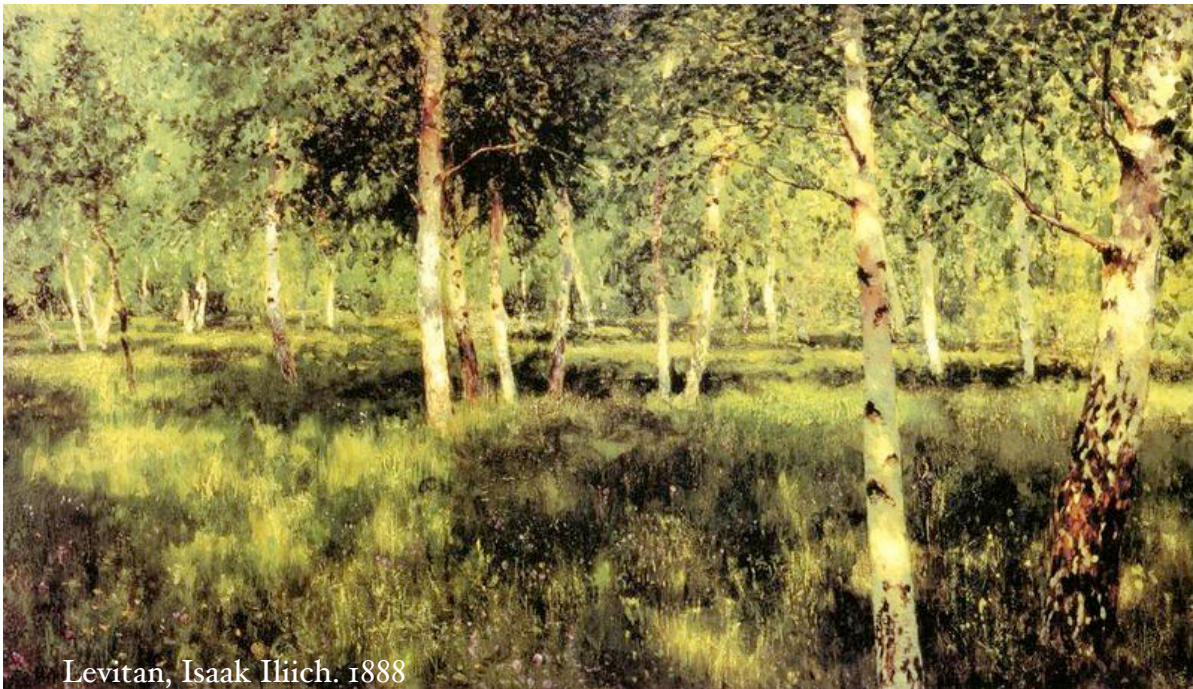


GENETICALLY MODIFIED POPLARS IN CHINA

A situation analysis



Levitan, Isaak Iliich. 1888

Xiao Song
Spring 2013

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Abstract

China has vast areas of poplar plantations serving as wind shelter, erosion control facility and industry resource. The intensive utilization of clonal forestry with its minimal genetic diversity has aroused serious pest infestation. To solve this problem and ultimately eliminate insect-caused losses, genetically engineered pest-resistant poplar has been introduced in a large scale planting. This made China the first and only country allowing genetically modified (GM) trees to be released into open environment.



Images of Populus spp.

However, the long life span of trees is likely to increase the chance in detecting transgene instability and increasing the danger to biodiversity, especially genetic diversity. It should be highlighted that the open-pollinated mating system of poplar would speed the gene dispersal of these GMO genotypes and issues related to potential environmental consequences and biosafety issues caused by gene flow and transgene escape need to be addressed in a comprehensive manner. In this article, I will analyze the condition of GM poplars released in China, review the major concerns and raise some proposals on how to eliminate the likelihood of transgene escape under the current situation. In my perspective, a prudent approach that considers the consequences of releasing GM trees, large-scale commercialization with a monitoring and risk assessing system is preferred, and corrections should not be hesitated to be made.

Key Words: Poplar; Genetic modification; Genetic diversity; Genetic Contamination

I. Introduction

I . I BACKGROUND

Forest harbours a great amount of the planet's biodiversity while serving significant ecological, social and economical functions, without which neither the ecosystem nor the social construction could last. During the industrialisation and population booming, China has experienced serious deforestation in the recently passed decades (Ewald et al. 2006). Poplar, with certain advanced characters against other tree species, majored the gigantic afforestation project in China, during which the massive plantation of artificial forests constructed with excessively used tree species cost severe pest infestation: 23.7% of the total forest plantation were under biotic disturbance resulting in an economic loss approaching 1 billion dollar (Ewald et al., 2006). In searching for the solution that would hopefully solve the problem efficaciously forever, Chinese forestal researchers employed the star of the biotech era — Genetic Modification. Thus, in the early 1990s gene transformation targeting trees within the *Populus* genus prevailed in China as well as across the world, and the goals were not limited within biotic disturbance resistance, but extended into aspects like environmental stress tolerance, wood quality modification and growth alternation (Tian & Tan, 2009).

As widely spread genus, *Populus* has an impressive natural distribution that covers from tropical to sub-polar climate zones in the Northern hemisphere and provides habitats for local and migrating wild lives as well as insects and micro-organisms, serves as air exchanging agents, water cycle tache and ecosystem holders. It also embraces great heterogeneity and includes many long cultivated and intensively used tree species across the world, which is both a virescence material, an industrial raw material and a conservation tool (Hu et al., 2010).

Poplars were broadly planted world-wide for wind shelters, erosion control / water-soil conservation, phytoremediation, landfill covers, biofuel production, pulp and logs (Acker et al. 2011; Marmioli et al., 2011; Zalesny & Bauer, 2007). Meanwhile, favoured by their simple clonal propagation, relatively rapid growth rate and considerably small genome size among woody spe-

cies, they are one of the major model plants used in both scientific and industrial forestal research (Bradshaw et al., 2000; Polle & Douglas, 2010).

China, with a rich flora of the genus and the biggest crop of poplars through the globe, has been using poplar plantation as an efficient approach several environmental and social issues arose along the industrialisation of the country (Weisgerber & Han, 2001). Historically, poplars have been closely associated with human civilisation and extensively utilised in agroforestry/silvopastoral systems on the land for hundreds of years, resulting in the overall present distribution of poplars, including native species, to be considerably transformed from its natural distribution (Sigaud, FAO). Hybrid clones are widely planted in China for their various functions mentioned above. One of the marked purposes lays in the protection against wind and desertification, poplar is one of the major material constructing the Three-North Shelter-belt, a massive shelter-belt grid horizontally across North China covering a 4480 km dimension east to west reserving planting area over 25 mil. ha., Figure 1-1.), while in the eastern provinces of the country the planting aims at commercial wood and biomass production (Sigaud, FAO). In the major afforestation programmes in China, poplar is estimated to occupy 60% of the total tree planting area (National Poplar Commission, 1996) and 80% of windbreak shelters of the Three North have been established with poplars (Sigaud, FAO). By 2006, artificial plantation area of poplars has exceed 7 million hectare in China, which is about 19% of its total artificial forest area (Lu & Hu, 2006), 5% of the total forest cover (Ewald, et al., 2006) and is steadily increasing. It is predictably hard for such enormous scale of artificial plantation constituted with clones from limited cultivars to perform well under the stress of insects and diseases. After witnessing great mortality under biotic disturbance, Chinese foresters took GM as a possible solution to eliminate the eco and commercial loss and overcome China's lack of pest resistant poplar germplasm resources (Hu et al., 2010), however, whether there is indeed a lack of pest resistant genetic resources remains to be discussed. The purpose of this paper is to interpret poplars breeding in China in an overall picture, given the situation of the rapid development in genetic modification and the already taken place commercialisation of GM cultivars, and provide a preventive, as well as remedial insight through the issue.

1.2 TAXONOMY, DISTRIBUTION, BASIC BOTANY AND MOLECULAR PHYSIOLOGY OF POPLARS

The Taxonomy Lineage of poplars (Chao et al., 2009):

Kingdom: *Plantae*

Phylum: *Angiosperms*

Class: *Eudicots*

Order: *Malpighiales*

Family: *Salicaceae*

Subfamily: *Populoideae*

Genus: *Populus*

Populus is a genus of six sections (*Leuce*, *Tacamahaca*, *Aigeiros*, *Turanga*, *Populus* and *Leucoides*), a member of *Salicaceae*, which have been placed under the *Malpighiales* in the recent cladistic analysis of the angiosperms, while various classifications still exist (FOC, 1999; Bradshaw et al. 2000; Sterck et al., 2005). It is naturally distributed through most terrestrial areas within the Northern Hemisphere and has a small representation in tropical Africa (FOC, 1999; Polle & Douglas, 2010). There are about 100 species worldwide, including species applied with various common names such as poplar, aspen, and cottonwood (FOC, 1999; URGI, 2010).

China is among countries with a highly multifarious indigenous flora; based on its ample genetic variation of poplar species, there are germplasm resources with the conserved ability to survive, reproduce and settle in divergent habitats after long periods of adaptation processes (Weisgerber & Han, 2001). Out of over 100 *Populus* species found in nature, 71 species (47 endemic) are distributed in China, including at least nine hybrids (FOC). Among them, 37 are distributed in North China (Sigaud, FAO, Table 1.), which have been intensively researched and utilised through the history of Chinese agroforestry. Meanwhile, comprehensive contemporary studies of the genus *Populus* looked into the mountain ranges of the Qinghai-Tibet Plateau, and uncovered concentrated genetic diversity of poplars in the subtropical mountainous regions of Southwest China: 3 sections, 17 species and 15 varieties have been recorded, described and taxonomically classified there. They grow within board altitudes between 1500 m and 4300 m above sea level. Many of these poplar sources are notable for their remarkable site adaptation potential in harsh habitats

and vigorous growth under acceptable conditions (Weisgerber & Han, 2001). As summarised by Bradshaw et al. (2000), with the capability of rapidly invading disturbed sites, many poplar species occupy habitats in the dynamic environment of riverine floodplains, where they form a key component of riparian forests (Braatne et al., 1996). Others, such as the aspens, commonly colonise upland areas after intense, initialising fires (Burns & Honkala, 1990).

Populus plants are deciduous broadleaf trees that can grow from 15 to 50 meters in height, with trunk diameters up to 2.5 meter (URGI, 2010). The majority species under the genus are dioecious with pendulous catkins formed by flowers of neither calyx nor corolla, which is adapted to wind pollination; the female plants produce tiny capsules with filament around the bottom, a typical seed structure established for wind and water dispersal (FOC, 1999; Chao et al., 2009).

The heteromorphic plants' fertilisation method is typical chalazogamy, and they perform an obligate outcrossing mating system with self-incompatibility mechanism and interspecific recognition, thus inbred strains rarely occur and haplotypic polymorphisms were expected (Knox et al., 1972; Valda & Murray, 1981; Tuskan et al., 2006). Certain proteins in its pollen grain walls are essential for pollen germination and altering the interspecific incompatibility system, which determines whether pollen tubes develop sufficiently. This system lays barriers in the hybridisation between some poplar species, for instance, between the section *Leuce* and *Aigeiros* (Knox et al., 1972).

Also, plants in *Populus* are all capable of reproducing asexually, often by sprouting from the root collar of killed trees or from detached branches that have been kept in moist condition and become embedded in the soil; some species propagate through sucker shoots that arise from horizontal roots, mostly after clear-cut and abiotic disturbance, especially fire (Bradshaw et al., 2000; Ghazoul, 2004). This property of poplars would typically result in clonal stands up to a few hectares, and recurrent fires can maintain the generation of such clones for centuries (Bradshaw et al., 2000). Such eco-association with fire made it a good choice for regenerate and conserve fire damaged forest land.

All species within this genus are diploids ($2n=38$) and can be breed for many fertile hybrids with highly targeted characteristics that enrich the diversity of the natural germplasm and benefits the human society (Marmioli et al., 2011). As suggested by Marmioli et al., the small size of the haploid *Populus* genome (ca. 480 to 550 Mbp, only four times that of *Arabidopsis*, and 400 times smaller than that of *Pinus*) has favoured the creation of 25 genetic maps and the development of various molecular resources in different species (Cervera et al., 2004; Tuskan et al., 2006; Markussen et al., 2007; Gaudet et al., 2008; Polle & Douglas, 2010), which forms an efficient complement to plant researches based on *Arabidopsis*, since many plant species found in nature are more similar to *Populus* than to *Arabidopsis*, life-historically and genetically (URGI, 2010).

2. Experimental approach towards poplar breeding

2.1 THE GENOME SEQUENCING PROJECT AND GENETIC MAPS OF *POPULUS* SPECIES

The genome sequencing of *Populus trichocarpa* conducted by Tuskan et al. (2006) is a milestone of forest sciences' successfully employing biotechnology, which opened doors and paved the way for molecular-scope breeding and research on and around poplars. With the sophisticated biotechnical tools, the detailed interpretation of its genomic information and its favoured nature, *Populus* has become a well accepted model system (Polle & Douglas, 2010). During the sequencing, a wealth of biotechnics and several genomic databases are adhibited to draft the *P. trichocarpa* genome, which enabled and facilitated the investigation of cellular and molecular mechanisms in long-lived forest trees by providing a thoroughly studied model system (Tuskan et al., 2006, Polle & Douglas, 2010).

The research group adopted whole-genome shot gun strategy for sequencing and assembling, and augmented it by constructing a physical map “based on BAC restriction fragment fingerprints, BAC-end sequencing, and extensive genetic mapping based on simple sequence repeat (SSR) length polymorphisms” (Tuskan et al., 2006). In order to assemble as many of substantial frac-

tions derived from the shotgun reads as possible and assess the nature of the sequences in the fraction of the genome, the group performed BLAST searches against online databases (eg. NCBI, etc.). After that BAC clones were fingerprinted with an agarose gel based method and the BAC-end sequence were compared with the shotgun assembly through BLAST. With the linkage groups already discovered by previous researchers added in, the map was drafted (Tuskan et al. 2006). After getting the map, the research group constructed genome-wide pairwise DNA alignments between *Populus* and assemblies of *Oryza* and *Arabidopsis* with VISTA pipeline infrastructure for detailed information. Thus, with following refinement, further prediction and annotation, whole-genome microarray analyses, related RNA verification and statistic analysis, the millstone project that laid the foundation of transgenic tree breeding was carried out (some major results demonstrated in figures are attached in Appendix II). This initiative approach did not only answered the questions on how perennial plants are different from annual ones, what makes a tree to have the unique biology and how should the future breeding of trees be conducted, but set a completely new agenda for forest research (Bhalerao et al., 2003).

2.2 CURRENT COMMERCIAL BREEDING OBJECTIVES AND PERTINENT BREEDING APPROACHES

Currently the breeding of poplars mainly aims at insect and disease resistance, environmental adaptation, biotic and abiotic stress tolerance, lignin and cellulose content modification, rapid growth with high biomass production, phytoremediation and aesthetic value for virescence (Hu et al., 2010; Marmioli et al., 2011; Weisgerber & Han, 2001). The classical breeding programmes are continued while molecular methods start to draw growing attention (Weisgerber & Han, 2001).

For classical breedings, the major approaches are domestication of plants, deliberate crossing and targeting properties selecting, which relies on homologous recombination between chromosomes and mutants to generate genetic diversity that allows for desirable traits to occur (Kingsbury, 2009). Since we entered the biotech era, classical breedings are no longer limited in nurseries and fields; procedures could also take place partially or entirely in the lab, benefiting from bio-

technics such as hormonal regulation, tissue culture, hydroponic culture, protoplast fusion and mutagenesis, etc. One of the major achievement in classical poplar breeding is the recognition pollen method developed for successful interspecific breeding. As mentioned previously, some species within the *Populus* genus are interspecific incompatible, thus one species' pollen might not sufficiently germinate on a stigma from another species even though they are within the same genus. To come across this barrier and breed hybrid poplar cultivars, conventional tree breeders used recognition pollen technique to overcome the barrier (Knox et al. 1972): by mixing viability reduced compatible pollens achieved by repeated freezing and thawing, gamma-radiation or chemical treatment into the viable incompatible pollens and bringing in the proteins that enables them to germinate, Knox et al. obtained highly successful hybridisation from the cross *P. alba* x *P. deltoides* repeatedly.

For modern breedings, molecular biotechnics are involved in enlarging the gene pool, desired trait selecting for desired traits and eventually enhancing the efficiency of breeding (Kingsbury, 2009). The major approaches are marker assisted selection, reverse breeding, doubled haploidy and genetic engineering (Gepts, 2002, Kingsbury, 2009). With decades of endeavour of the scientists and breeders, molecular markers and genetic maps are available for most important crop plants and marker-trait association have been establish for a diverse array of traits (Dwivedi et al., 2007), which provides information and visions for poplar breeding nowadays. Main attempts in genetic modification in poplars includes transfer of single genes into poplars and transformation of combined multi-genes for targeted traits (Ewald et al., 2006). The transferred sections came from a wealth of sources, from the bacteria to insect, and got engineered into certain poplar cultivars' gene pool with molecularized methods. The two most common transformation methods are *Agrobacterium*-mediated DNA transfer, and bombardment with DNA-coated micro-projectiles, so-called "biolistic" transformation. By the beginning of this century, transformation systems were further developed, but progress was mostly limited to a few poplar hybrids that were selected for ease of transformation. Nowadays, routine transformation procedures utilising *A. tumefaciens* or *A. rhizogenes* are conducted on most poplar species and hybrids even for recalcitrant genotypes such as cottonwoods (Frankenhuyzen & Beardmore, 2004).

Wu and Fan (1991) carried out the first gene transfer project in China inserting single Bt genes into poplars and created anti-defoliator poplars, following which various of genetic engineering took place in China. Meanwhile, genetic modification of crop plants, fruits and vegetables as well as trees are happening as a new way towards food security and biomass mass sufficiency to satisfy the world with booming population (Dwivedi et al., 2007). By now, genetically modified poplar cultivars have been processed to have many purposeful customised novel traits, which will be introduced in the following section.

3. Genetically Modified poplars

3.1 EVOLUTIONARY BACKGROUND AND PHYLOGENETIC RELATIONSHIP WITH ITS RELATED WILD / CULTIVATED SPECIES

Although *Populus* has been cultivated and studied for a long time, the exact phylogenetic information about the genus is still under discussion; the classification sections was majorly relying on morphological, reproductive characters and interspecific crossability (Hamzeh & Dayanandan, 2004; Cervera et al., 2005): members of the same section can hybridise with each other naturally or artificially (Zsuffa, 1975; Cervera et al., 2005). Classic taxonomic analysis, has been under great difficulties posed by high intraspecific diversity, wide natural crossability, and the convergent morphology shown by hybrids and their parental species (Cervera et al., 2005).

To overcome the difficulties, molecular methods was brought in. Cervera et al. (2005) tried to determine the intergeneric, intersectional, interspecific, and intraspecific genetic and phylogenetic relationships among species and hybrids of the *Populus* genus molecularly by using AFLP markers, and concluded *Populus* species generally group along their classical section lines, with markable exceptions observed, such as the placement of *P. nigra* in the *Aigeiros* section (Fig. 3-1-4). Meanwhile Hamzeh and Dayanandan (2004) approached the phylogeny by nucleotide sequences of certain chloroplast and nuclear genes (chloroplast *trnT-trnF* region and rDNA), and

proposed a phylogeny trees of the genus which fits into the molecular interpretations towards the interspecific phylogenetic relationship of the genus from three different angle (Fig. 3-1-3). Combining the molecular analysis with the traditional evolutionary analysis, the researches conducted by Cervera, as well as Hamzeh and Dayanandan proved the suggestion of Eckenwalder: since the progenitor species are generally of higher genetical diversity than the derived species do, *Populus* species under the *Leuce* and *Aigeiros* section are reckoned to be the oldest and the most recent poplar species, respectively (Eckenwalder, 1996).

With the refined information evolutionary back ground and phylogenetic relationship provided, the breeding within the species and the genetic modification targeting species within the genus are under going a way with more directions. It would provide information for both traditional and modern poplar breeding. One example of phylogenetic background knowledge helps throwing light upon poplar breeding is the developing and utilisation of Poplar 741. For many poplar transgenic experiments conducted in China, hybrid-clone 741, which is a complex cross of several poplars [*Populus alba* L. $\times$ (*P. davidiana* Dode + *P. simonii* Carr.) $\times$ *P. tomentosa* Carr.], is used to diminish gene flow of transgenes into the environment and natural population, since the formation of seeds in 741 Poplar is restricted and these seeds possess no capability to germinate under natural condition (Ewald et al., 2006). Finding this base material, increased the efficiency and reduced the cost of the experiments on transgenic poplars.

3.2 WHY DO CHINESE FORESTERS CREATE AND RELEASE GM POPLARS?

With such improved technology to facilitate breeding, and the public concerns on genetic engineering both scientifically and ethically, why are GM poplars still created and why is it even developed with considerably or even concernably high pace?

Improvement of trees through conventional breeding is constrained by the long reproductive cycles and complex reproductive characteristics of woody plants, even with the help with *in vitro* technologies, it takes a relatively long period to stable or maintainable cultivars with favoured

characteristics (Fladung, 2006), especially with the interspecific incompatibility system in some poplar species. Thus, when genetic engineering offers an attractive addition to conventional breeding by permitting the transfer of genes coding for preferred traits into selected cultivars without compromising their desirable genetic background, while taking the waiting through several life cycles out of the breeders way (Frankenhuyzen & Beardmore, 2004), the industry jumped for it.

Genetic engineering is expected to bring great traits into poplar cultivars, which will majorly benefit the intensively managed short-rotation plantations with clonally propagated species, in contrast to conventional breeding, which is limited to sexually accessible variation with complex, sometimes combined traits that typically depend on a large number of interacting genes, recombinant-DNA technology presented an almost infinite gene pool for breeders' to find and use genes coding for favourable traits. Concluded by Frankenhuyzen and Beardmore, endogenous genes already present in the tree genome can be modified to improve certain traits, such as fibre content and wood quantity, while exogenous genes can be transferred from unrelated organisms to provide entirely novel traits, such as resistance to herbicides, diseases or pests. The targeting traits are expected to positively affect the economics of plantation forests (improved growth, reduced rotation, promoted wood yield and quality, lowered cost of pest control), or confer various environmental benefits associated with forestry production (reduced pesticide and herbicide use) or processing (improved pulping, reduced inputs of hazardous chemicals and energy). (Frankenhuyzen & Beardmore, 2004)

By reducing the harvesting pressures on natural forest and meeting the industrial demands, GM tree breeding is now seen as an important future forest conservation strategies by its supporters (Adams et al. 2002).

3.2.1 MODIFICATION OF WOOD PRODUCTION

The same as in most areas in the world, there is an urgent demand in wood and wood products to be met in China. The country is now, the largest importer of industrial logs and the second largest

importer of forest products globally, reported by FAO (Lu, 2004). At the same time, the protection of natural forests, which had become necessary because of the severe deforestation caused by industrialisation and environmental degradation, contributed to a shortage in wood production (Ewald et al., 2006).

To achieve maximised economic benefits, there are two basic directions in modifying wood production: quantitatively and qualitatively. The first one is usually achieved by altering the plant metabolism and increase the growth rate thus to obtain increased biomass production. The latter could be achieved by modifying the lignin / cellulose synthesis mechanism (Fladung, 2006). While modification of wood parameters and growth are traditionally a major goal in forest breeding programs, the material is as complex as the formation process, thus targets are extremely hard to be accomplish through the time and resources consuming methods of conventional breeding; even when cultivars are established, their performance is largely dependent on ambient conditions (Fladung, 2006).

Genetically modified trees with reduced lignin composition have been proposed as a strategy to potentially reduce environmental impacts from chemically harsh pulping practices, maximise operation efficiency and minimise the environmental footprint in the paper industry (Sponza, 2003).

3.2.2 ABIOTIC STRESS TOLERANT

Along with the megatrend of global climate change, desertification, salinization and accumulation of toxic substances in soils (Frankenhuyzen & Beardmore, 2004), one of the serious problems confronting Chinese forestry is soil salinity (Ewald et al, 2006), as well as dry out and pollution of the limited water supply, which makes the already limited land resources for forest habitat conservation and industrial plantation even more stretched. Poplars as tested phytoremediating and water-soil conserving species (Marmioli, 2011), are propagated as a fixation of the situation, which will make the primary salinized land productive, put the secondary salinized land on the way of recovering and becoming arable and detoxify the polluted soil to a certain

degree. However, the mechanism is very complexed and only by transcriptomes comparison and pathway analysis can scientists understand the establishment of such stress tolerance mechanisms through evolutionary adaption (Janz et al., 2010). Thus, genetic engineering becomes the most efficient way to combine preferred traits and realise them in single cultivars, so as to keep the land productivity within salinised areas, or with the plantation still functioning in phytoremediation, which is considered an approach towards ease the dilemma of mitigating the shortage of land resource contradicting the unfulfilled huge forest biomass demands in China.

Another main abiotic stress affecting poplar plantations in China is frost. To overcome this issue, alternations in poplar phenology were often conducted. Usually, breeders try to put back the budding time to avoid cold damage to the newly germinated parts. With conventional breeding, the goal of achieving cold hardness as well as high productivity is constrained by limited germplasm resources within the genus and interspecific incompatibility. To remove frost as a growth limiting factor for plantations and to adapt to the capricious weather under the influence of global climate change, as well as to meet the urgent need of forestry product by the booming population, gene transfer became the most economic solution.

3.2.3 BIOTIC DISTURBANCE RESISTANCE

Insect attacks and diseases are the main factors for economic losses in forestry. According to incomplete statistics dating back to the 1950s, the 1960s and the 1990s, an annual increase of losses of 25% was calculated in Chinese forestal economy (Su et al. 2003).

Insect resistance is among the major goal, if not the most important one, of Chinese modern forestry, since pest infection is one of the main causes of forest damage, especially in artificial plantations and the insects are often a limiting factor for tree growth and biomass production (Ewald et al., 2006). The control of forest pests with insecticides is only capable on smaller scales, such as in nurseries, but has detrimental ecological effects (Ewald et al., 2006). The Three North Shelterbelts Project, which, as mentioned previously, is established with intensely duplicated clones of very limited cultivars, has already been threatened by insect attacks. The reduction in timber

production of Chinese forestry due to pests has been estimated to be around 17 million cubic metres per year that results in a huge economic loss. A spread of these insects from plantations into natural forests, causing a loss in both forest coverage and biodiversity in the surrounding ecosystem is of great possibility (Su et al. 2003).

Meanwhile, the resistance and resilience against diseases caused by virus, fungus and bacteria are attracting increasing attention in China. The diseases do not only cause forest mortality, damaged wood quality and reduced aesthetic value, but often spread around fleetly and tend to be associated with insects, which made it extremely hard to be taken under control once happened, usually requiring intense chemical treatment that potentially do harm to micro-organisms, the rhizosphere, the local environment and affects broader area through the water-soil system.

Therefore, efficient solutions for overcoming the problems in an economic way is under urgent call and biotechnology offers a real and fast solution (Ewald et al., 2006), both the breeders and the stakeholders jump at having the insect resistant genes engineered into poplar and have the cultivars commercialised to take the severe loss under control, and maybe make some benefit within the shortest time. This would not only ease the economic issue, but will also approach towards solving the biomass resource security issue of the nation, since it is not a secure way for long term operation to rely that much on imported wood.

3.3 IMPACTS AND CONCERNS IN BOTH LONG- AND SHORT-TERMS

3.3.1 GENETIC CONTAMINATION

Since poplars have a relatively long life span, and the metabolism and reproduction process of GM poplar will leave tissues and secretions containing novel genes in the local ecosystem to be accumulated through their life cycle. Suggested by Li (unpublished), the transferred genes left in the rhizospheric soil system is testable and stable for approximately three years, while the metabolism of the trees is always happening. Also, routes of novel gene transfer and exotic protein

obtain could be established in the forest soil system, which links litter decomposition and nutrient cycling dynamically, and where novel proteins could be transmitted through the network constructed by soil, soil microflora, mycorrhizal and plant root (Frankenhuyzen & Beardmore, 2004). Thus, with the continually inflow of engineered DNAs and novel proteins into the soil, concerns on the direct and indirect effects of novel gene leftovers are rising from the very beginning of tree genetic engineering, which are mainly addressed on impacts of toxin-encoding transgenes on population levels of competitors, preys, hosts, symbionts, predators, parasites, pathogens and soil microbes, as well as the influence of novel genes and toxic proteins on non-target organisms (Lu, 2008).

Apart from this, the invasive escape and vertical gene flow from GM clones towards their non-GM counter-species, varieties, cultivars, landraces, as well as wild relatives has intimidated tremendous debate worldwide (Snow, 2002). Transgenic species and their offsprings are concerned to turn into weeds, since the super competitive characters brought in by the transgenes greatly increased the invasiveness of its carrier, for instance by conferring early stage herbicides resistance into certain cultivar (Frankenhuyzen & Beardmore, 2004). Then, they might take over the habitat of the wild species or traditional varieties resulting in biodiversity losses and increased conservational cost. The concern is not a presumption but a lesson learned from the history of exotic tree species cultivation and plantation, for example, more than 19 species of pines have escaped cultivation and become invasive weeds in the southern hemisphere during the last decades costing huge losses in economic and ecological values (Richardson, 1998; Frankenhuyzen & Beardmore, 2004). Moreover, the novel genes could flow to nontransgenic individuals within the same species through sexual reproduction, such as pollination, which is already observed by Stewart et al. (2003) and many other scientists in GM annual crop plants, and as stated by Smouse et al. (2007), transgene flow by propagules was seen in GM forest trees. In addition, transgenes could be passed on to the wild relatives without interspecific incompatibility through out-breeding and gene introgression (Snow, 2002; Stewart et al., 2003).

Concerns have also been addressed on horizontal novel gene transferring from GM plants to unrelated organisms, sometimes even a cross-kingdom gene transfer, through nonsexual means, like feed and digestion or biosynthesis. The most common example is from plants to parasite or micro-organisms (Lu, 2008; Frankenhuyzen & Beardmore, 2004). A recent research conducted by Zhang et al. (2012) found out that exogenous plant miRNAs were present in the sera and tissues of various animals, which were primarily acquired orally through food intake; they stated that their findings demonstrated that exogenous plant genetic material in food can regulate expression of target genes in mammals. Suddenly, the discussion of biosafety risks brought by commercialising GM crops and trees reached a new peak in vehemence.

3.3.2 ECOLOGICAL PRESSURE

Even if transgenes are well restricted within the carriers, they might still have its influence on the holding environment (Frankenhuyzen & Beardmore, 2004). The large existence of transgenic trees with engineered traits and a long life span draws significant ecological pressure on its living habitat, which includes the selection pressure on both targeting and non-targeting organisms in the local habitat and the ecosystem and the possible niche shift caused by their over-competing surrounding plant species and the influence on their associated species. All of these implicate a predictable loss in biodiversity, especially genetic diversity both within the species and among the ecosystem. Thus, they might as well affect critical ecosystem processes like decomposition and nutrient cycling (Frankenhuyzen & Beardmore, 2004).

Insects and pathogens have extremely short life cycles comparing with trees, thus within a pest or disease resistant GM poplar site, the evolution of resistant pest or pathogen biotypes stand a great chance of exceeding both the sustainability of the habitat and the function of the engineered traits (Strauss et al., 1991; Brunner et al., 2007). Selection pressures resulting from GM trees with superb characteristics could also affect non targeting insect species within the same habitat, which might be achieved by altering the food chain or breaking the equilibrium in competition (Frankenhuyzen & Beardmore, 2004). Thus, possible consequences on pest competitive suppression and trophic interactions (Schuler et al. 2001) that might shift arboreal organism com-

munity dynamic and local biodiversity should be precautiously examined before the release of anti-insect transgenics.

There are still some unknown mechanism, involvements and routes in biogeochemical process. Significant interactions between engineered traits and the environment might come within our sight anytime. Further studies and observations are necessary before stepping forward (Lu, 2008).

3.3.3 FOOD AND FEED SAFETY

Directly affecting ourselves are the food and feed safety issues caused by GM plants. The main concerns are about toxicity, allergy and long term effect on human and other living creatures' health caused by products from or under the impacts of GM plants.

Plenty of genes used in genetic modification are of the ability to cause toxicity, for example antibiotic marker gene, anti-insect genes that encoding for insecticidal protein or neurotoxins and genes coding for antibacterial chemicals all have a potential toxicity towards livestock that depends on poplar leaves and young tissues, and then humans (Liu et al., 2001; Anon, 2008; Séralini et al., 2011). Allergy is usually caused by pollens from GM plants. It may affect not only humans and animals within the forest stand, but also have the influence delivered with the distance travel pollens and seeds, and the anaphylaxis could be caused by direct contact with plant tissue or pollen, feeding on GM contaminated food and applying personal care products derived from GM plants or plant materials contaminated by GMOs (Madsen & Sandøe, 2008; Antignac et al., 2010; Domingo & Bordonaba, 2011). Although, the concerns about subchronic and chronic health effects has been raised for GMOs, especially those containing pesticides, either produced from their engineered insect tolerance mechanism or gained from the external application of chemicals based on their pesticide tolerance, and some statistically significant findings on the toxicity of GMOs on rodent have been revealed (Séralini et al., 2009; 2012), most relevant studies indicate no obvious deleterious effect. However, the no-obvious-effect situation is believed to be a consequence of insufficient studies limited by time and methods (Séralini et al., 2012).

3.4 STATUS QUO OF GM POPLARS IN CHINA

Leple et al. reviewed all genetically engineered *Populus* species and hybrids by the year of 2000 worldwide (Table 3-3). Eight herbicides resistant lines, 5 insect resistant lines and 10 growth alternated lines, as well as 6 lines developed for wood quality modification. There are two cultivars of transgenic poplars commercialised in China by 2003: one is Poplar Hybrid 741 with *Bt*, *CryI* and *API* genes inserted, the other is *Populus nigra* with single *Bt* inserted, and they are both engineered to resistant leaf-eating insects (Sigaud, FAO). By 2010, nineteen insect-resistant GM poplar lines was created in China (Hu et al., 2010) possessing genes or combination of genes encoding the production of proteinase inhibitors, insecticidal proteins, lectin or neurotoxin, all efficient in fighting against insects (Ewald et al., 2006).

While the research and application of genetic modification are developing rapidly, the relative policies in China remained brief and deficient. Table 4 reviewed major policy measures related to biotechnology carried out in China from early 1980s (Huang & Wang, 2002), from which we see the refining process of the national policies, however, it is still way too loose comparing with that of the EU (Jaffe, 2004). Also, based on my observation, the public awareness and participation are relatively low. There is barely no local NGO or community advocacy for genetic safety issues. This unbalanced situation might enlarge the nation's chance in confronting with genetic contamination and related negative ecological changes.

4. A proposal of “What we can do before it's too late”

4.1 TRANSPARENCY

First of all, I advocate for transparency in policy making procedures, which should not only be known within the high-level authority, as well as the data and information facilitating the decision making, which should not be kept within the authority group. The consumers have the right to informations that may benefit their choice and the farmers and foresters have the right to the

genetic resources on their land. It is not fair for the policy makers to keep them from knowing what they should know.

Also, I advocate for marketing transparency. Labelling products containing GM materials and products harvested or processed in and near GM poplar forests and nurseries, for example economic agriculture products harvested from undergrowth layer of forest stands constructed with GM poplars. What's more important, the labels should be obvious and easy to find. Based on my observation, GMO products in the market in China are either labeled ambiguous or the label is extremely small and hard to find. People who is not conscious about GMO related issues, or seniors and kids without sensitive observational ability may never notice the information, which is supposed to be carried out to each consumer. Every purchase and consume on GMO related products should be conducted by people who is fully aware of it, or it is no difference than market fraud. The government should standardise the labelling in the market with uniform marks. Not only should GM poplar products be labelled, GM poplar surrounding products should also be labelled. If a carton of mushroom is non-GMO itself but is harvested from GM poplar logs, the information should be clearly conducted to the customers. With such board scale of GM plants released and commercialised in China, no blind buying and trading of GM related products is still tolerable.

If the people cannot choose whether they want GMOs to be released and commercialised in their country, they should at least be ensured their access to information about what is going on exactly and their right of choosing whether to buy and used such product should be respected.

4.2 DEVELOP WELL ESTABLISHED RISK ASSESSMENT AND REGULATION SYSTEM

With all the concerns reviewed previously, insufficient risk assessing mechanism and the lack of efficient regulatory methods for the consequences of potential genetic contamination, the release and commercialisation of GM poplars were still carried out in China, which brought up the ur-

gent demand for a sensitive monitoring system as well as complementarity risk assessing and regulating mechanism.

To assess the risk and find regulatory methods, the foresters need to understand the condition first, and to really know what is going on with plantations containing GM poplars and the nature forests near the plantations, GIS monitoring is a great tool for risk assessment, record keeping, forest management and geographical genetics conservation (Fan, 2001).

However, it is very hard and costly to genotyping all the major poplar forest stand routinely and mark every genetic information on different layers in GIS to monitor the stability of target genes, the potential gene flow and both the long and short terms of ecological pressures. To lower the cost and increase the feasibility I suggest using asymmetry data as an indicator. Asymmetry data of plants is often fluctuating through its life history reflecting the living condition of the plant and could indicate their fitness, developmental stability and the stress level (ecotoxicity, competition, inbreeding, etc.) they are under (Clark et al., 1986; Jones, 1987; Graham et al., 1993; Kozlov et al., 1996; Rettig et al., 1997). Also, fluctuating asymmetry (FA) is more sensitive than life historical parameters, and is able to quantify the impact of GM poplars, especially the ecological pressure (Zhai, 2001), which made it suitable for combination with GIS. As the mensuration and analysis of FA data are relatively easy to conduct and there is no need for high-priced instruments, the data collecting could be done with hearing co-op students, which on one hand, will lower the labour costs, on the other hand will provide students with a hand-on experience in forest management and research, as well as better understanding in the forest ecosystem.

Many other risk assessment mechanisms are proposed by multiple authors. Most of them are laboratory operations, micro mimic nature system models (usually for microbes) and mathematical models that predict or determine the impacts and development trends of GM poplars (Domingo & Bordonaba, 2011). A combination of both field and laboratory assessment gives foresters better information and chance to regulate potential consequences of GM poplar releasing.

4.3 DO NOT BECOME TOO RELIED ON GENETIC ENGINEERING

Even though biotic disturbances resistant GM poplars are currently performing well in tolerating the attacks from insects and weedy, Chinese forestry should not rely entirely on transgenes to solve the issues. In some small scaled plantation and plantation close to nature forests, bio-pesticide and bio-herbicide, which are not as toxic to the surrounding ecosystems as chemical compounds could be used in case of insect attack or weed overgrowth.

Also, planting prescriptions could help with increasing the insect resistance of traditional cultivars and natural species of poplars. A common approach is mix planting. Pointed out by Ewald et al. (2006) Asian longhorn beetle (*Anoplophora glabripennis*) is the major damage causing pest for poplars in China. However, mix-plant non-GM poplars with *Ailanthus altissima* helps the stand resist against *Anoplophora spp.* (Jin, 2008), which tend to be a good solution for stands not planted for maximum biomass production.

Meanwhile, both commercial and researching organic farming and foresting should be encouraged, as a preservation of genetic resources, a life style choice for people and a research potential.

4.4 APPROACHING THE PROBLEMS THROUGH “TRADITIONAL BREEDING” OF POPLARS

Since Chinese forestry is confronted with several dilemmas mentioned in section 3.2, to become less relied on genetic engineering, Chinese foresters should try to breed certain non-transgenic poplar cultivars that is capable of solving part of the problems.

The first step of a breeding plan is to select for the suitable germplasm. In the breeding plan I am going to propose, the key species is *Populus euphratica*. It is a broadly distributed tree species in central Asia, of whom the natural habitats in China are located in the deserted area in Gansu, Qinghai, Xinjiang, Ningxia and Inner Mongolia (Peng et al., 2009; Zhang, 2009). *P. euphratica*

evolved from the harsh deserted habitat process great quality of salinity tolerance, waterlog tolerance, drought tolerance and sandstorm resistance. Also, it is no leaf feeding *lepisoptera* species hosting on *Populus euphratica* distributed in China (Table 5, Robinson et al., 2010).

Populus euphratica is the only species under the section *Turanga*, so the hybrid between it and any other *Populus* species will be characterised under distant hybridisation, which is highly affected by its interspecific incompatibility. To overcome the barrier, breeders employed artificial pollination on stigmas previously treated with female parental pollen extracts, in vitro ovule culture, and hybrid seedlings in vitro propagation techniques to force hybridisation. Based on the result achieved by multiple combinations tries through different breeding methods, when using *P. euphratica* as the pollen source, the hybrid progenies tend to possess more desired traits in *P. euphratica* (Peng et al., 2009). Also, the survival rate of seed germinated seedlings are much higher than that of the clones developed from sprout tillers, thus some asexual propagation might not be suitable for establishing hybrid *P. euphratica* stands (Shen et al., 2009). With the germplasm selected, the breeding methods developed and relative mechanism studied, the preferable cultivars will not remain hard to create for very long.

4.5 A P R O S P E C T

In my perspective, a desirable future condition of GM poplar forestry in China is constructed with three elements: well established risk assessing and regulating mechanism, elaborative record keeping and monitoring system and carefully restricted plantation area gradually replaced by mix-planting or traditional hybrids with no less biomass production making the utmost of the nature biodiversity. From scopes other than forestry, I am looking forward to see the government could hold on to its own word of valuing the principle of freedom of science, but advances in science must serve, not harm humankind, and will actually “mull over new rules and regulations to guide, promote, regulate, and guarantee a healthy development of science”, promoting the technology while showing appropriate precaution for biosafety, environmental health, food safety, and the commercialisation of biotechnology (Huang & Wang, 2002).

Conclusion

Genetic modification is a double-edged sword, from which we knew exactly what we would be benefiting, but what damage would it do were never thoroughly understood. The extensive cultivation of GM poplars in China has generated great benefits and helped solving a variety of issues both ecologically and economically. However, even while we are in the biotech era, the current information and data are not sufficient in showing the exact long-term influence of GM poplars on both bio-safety and human health. Great issues have been raised concerning GMO deployment at large. The fact that GM trees are already widely planted in China and the present risk assessment system is not adequate in addressing these concerns, then the establishing of a sophisticated risk assessment system is urgently needed. The plethora of available knowledge did not only provide us a way to deal with the present, but also should assist us to use biotechnology in a sustainable manner to save the future for all the living creatures. While benefiting from genetic engineering, an integrated standing system of research, monitoring, evaluating and readjusting should be established.

Appendix I

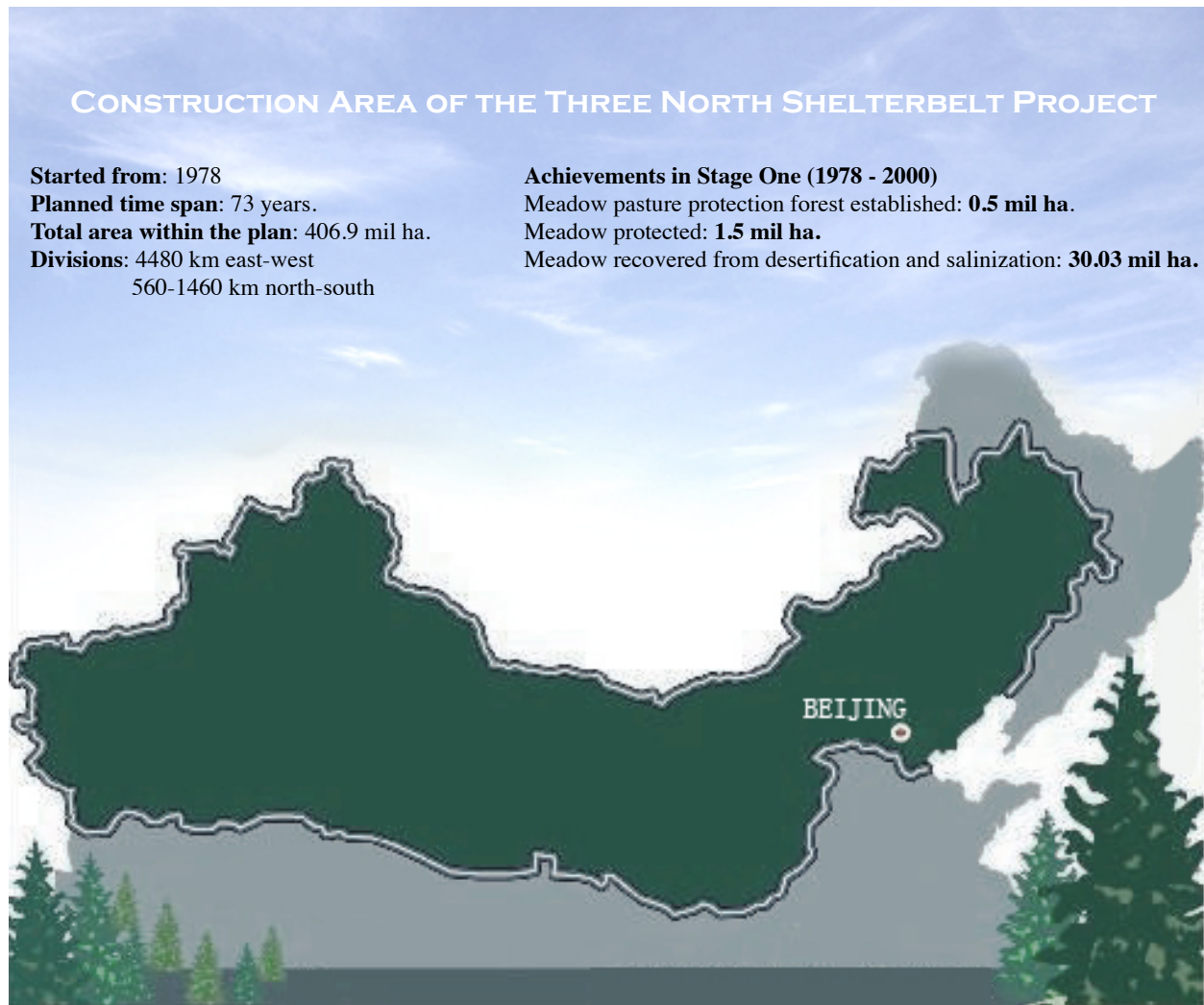


Figure 1-1. Construction area of the Three North Shelterbelt Project. (Edited from the original illustration by Ding, M. & Zhang, Y. Publish by Xinhua News Agency)

Table 1. Distribution of poplar species in North China. (Derived by Sigaud, FAO., based on Xu, 1988)

SPECIES	North East			Central North			North West					ALTITUDE (m)
	Heil	Jil	Liao	Mon	Heb	Shan	Shaa	Gan	Nin	Qing	Xin	
<i>P. afghanica</i>											√	1400 - 2800
<i>P. alba</i>											√	450 - 750
<i>P. amuyensis</i>	√			√								600 - 800
<i>P. canescens</i>											√	600 - 700
<i>P. cathayana</i>			√	√	√	√	√	√		√	√	800 - 3200
<i>P. charbinensis</i>	√											300 - 500
<i>P. davidiana</i>	√	√	√	√	√	√	√	√	√	√	√	200 - 3800
<i>P. euphratica</i>				√				√	√	√	√	2500 - 2900
<i>P. gansuensis</i>								√				1800 - 2000
<i>P. girinensis</i>	√	√										300 - 400
<i>P. hopeiensis</i>					√	√	√	√	√	√		700 - 1600
<i>P. hsinganica</i>	√			√	√							300 - 700
<i>P. iliensis</i>											√	600 - 750
<i>P. jrtyschensis</i>											√	200 - 2000
<i>P. koreana</i>	√	√	√									400 - 1100
<i>P. lasiocarpa</i>							√					1300 - 3500
<i>P. laurifolia</i>											√	1200 - 1700
<i>P. maximowiczii</i>	√	√	√	√	√		√	√				400 - 2000
<i>P. nakaii</i>	√	√	√	√	√							600 - 900
<i>P. nigra</i>											√	400 - 800
<i>P. ningshanica</i>						√	√					600 - 1000
<i>P. pamirica</i>											√	1800 - 2000
<i>P. pilosa</i>											√	1600 - 2300
<i>P. pruinosa</i>											√	300 - 1500
<i>P. przewalskii</i>				√			√		√			500 - 1500
<i>P. pseudomaximowiczii</i>					√		√					1000 - 1600
<i>P. pseudosimonii</i>	√	√	√	√	√	√	√	√		√		300 - 2300
<i>P. pseudotomentosa</i>						√						300 - 1400
<i>P. purdomii</i>					√		√	√				700 - 3300
<i>P. simonii</i>	√	√	√	√	√	√	√	√	√	√	√	600 - 2300
<i>P. suaveollens</i>	√			√								200 - 400
<i>P. szechuanica</i>							√	√				1100 - 4000
<i>P. talassica</i>											√	500 - 1800
<i>P. tomentosa</i>					√	√	√	√				200 - 1800
<i>P. tremula</i>											√	700 - 2300
<i>P. ussuriensis</i>	√	√	√									300 - 1400
<i>P. wilsonii</i>							√	√				1300 - 3300
NUMBER BY PROVINCE	12	8	8	11	11	8	14	12	5	6	16	37

***Heil** - Heilongjiang Province; **Jil** - Jilin Province; **Liao** - Liaoning;
Mon - Inner Mongolia Municipality; **Heb** - Hebei Province; **Shan** - Shanxi Province;
Shaa - Shaanxi Province; **Gan** - Gansu Province; **Nin** - Ningxia Municipality;
Qing - Qinghai Province; **Xin** - Xinjiang Municipality

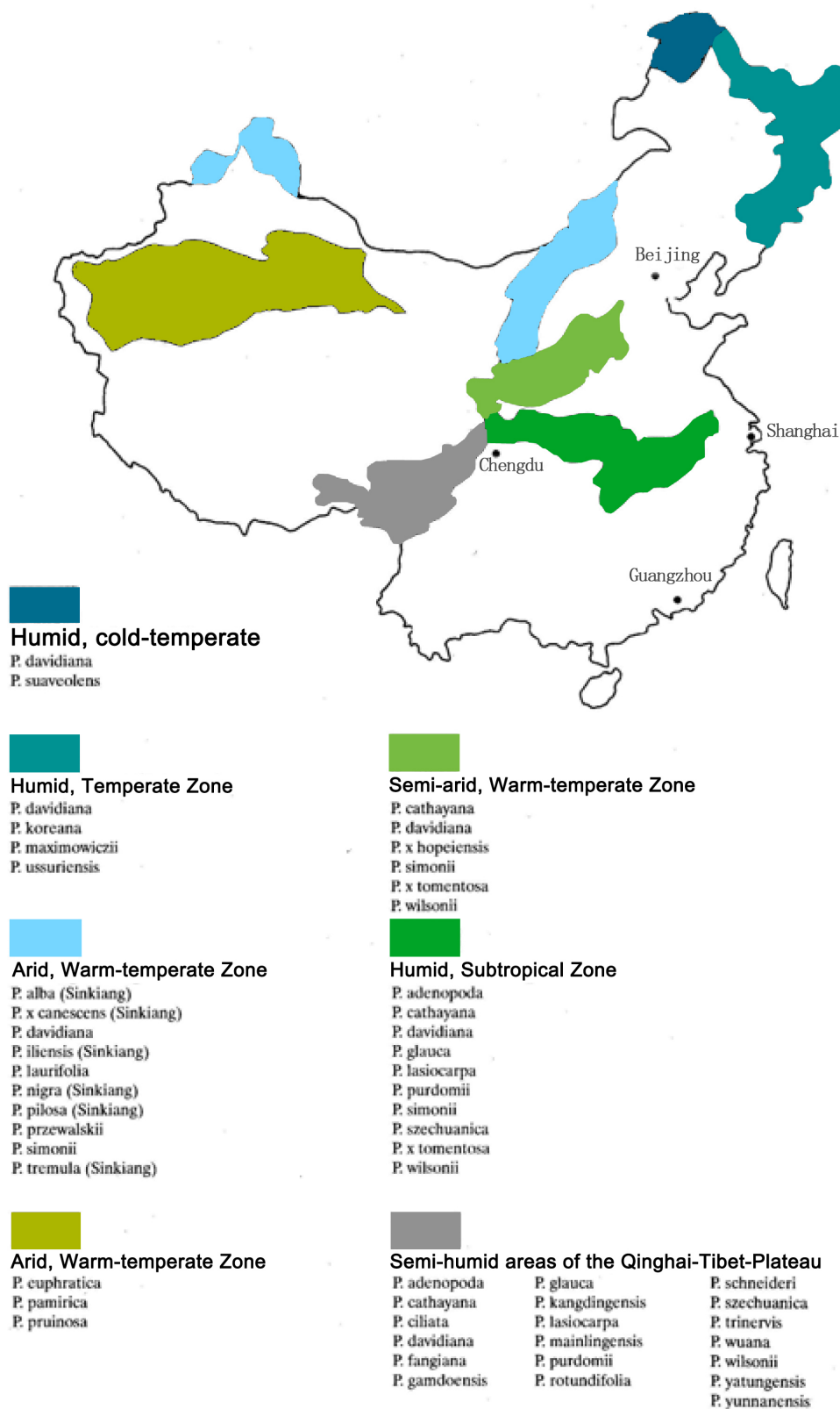


Figure 1-2. Classification and distribution of indigenous poplar species of China according the climatic zones (Weisgerber & Zhou, 1997. Translated from German to English and edited by the author)

Appendix II

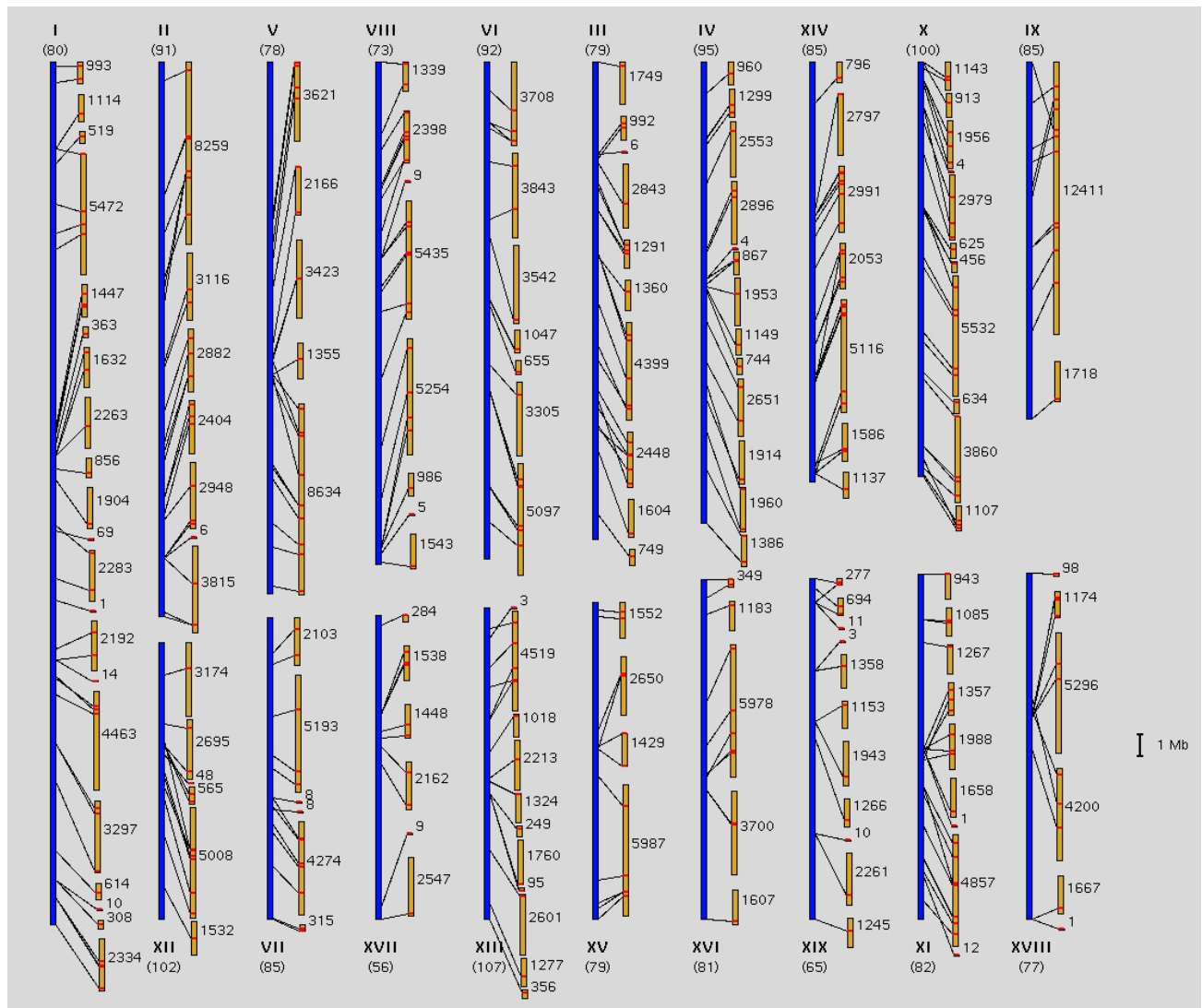


Figure 2-1. Representation of the 335 Mb of *Populus* genomic sequence contained in 155 Scaffolds aligned and oriented to a genetic map of the 19 *Populus* linkage groups (indicated by Roman numerals I - XIX) (Tuskan et al., 2006)

* Each scaffold (yellow bars) was mapped to a chromosome (blue bars) using micro-satellite markers with unique sequence locations (red lines). Numbers in parentheses are estimates of the percentage of the linkage group covered by assembled sequence (assuming uniform physical: genetic distance across the genome). Approximate size (in kb) is indicated to the right of each Scaffold. Gaps between scaffolds are known size.

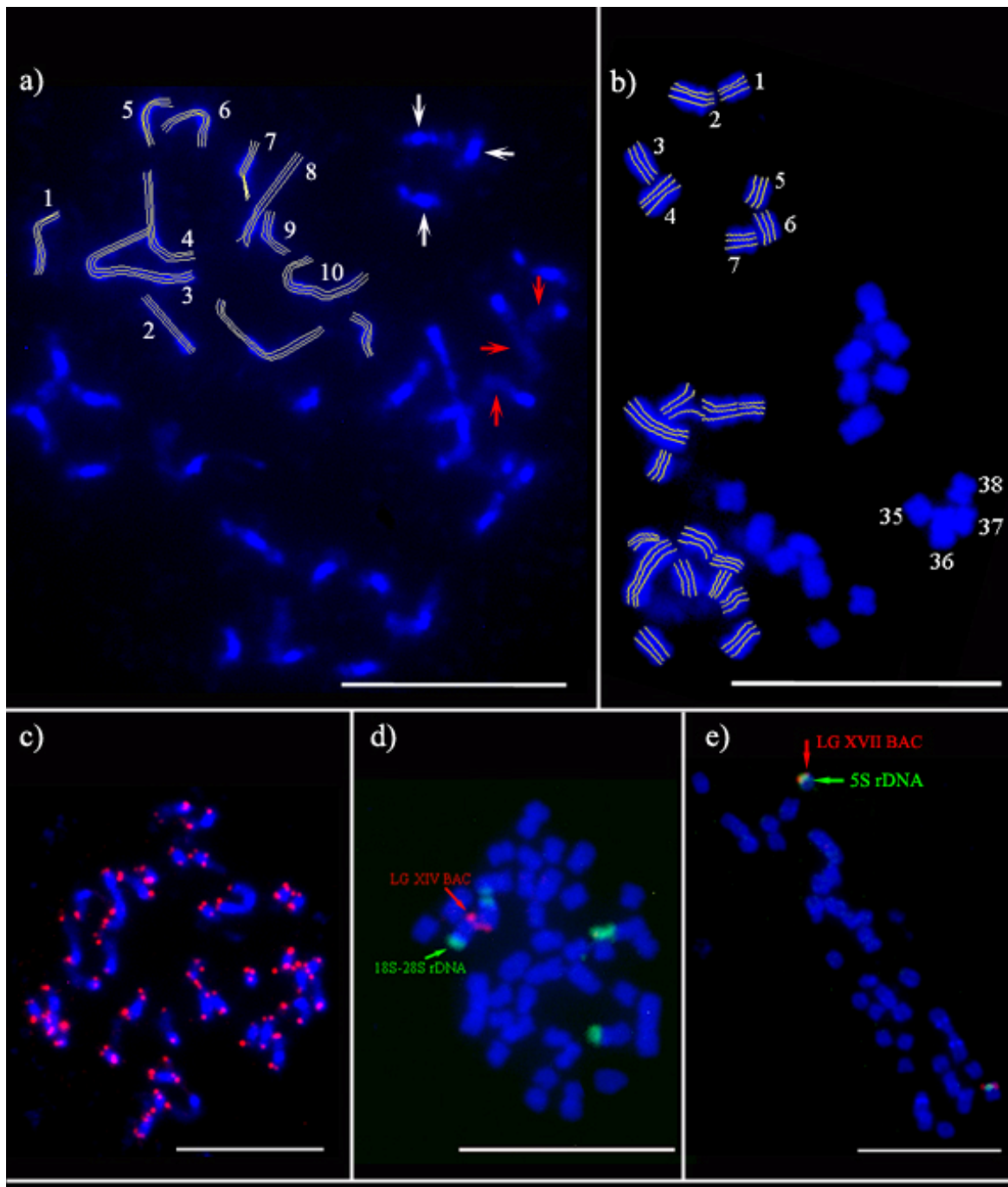


Figure 2-2. DAPI stained a) prophase and b) metaphase *Populus* somatic chromosomes and FISH using Arabidopsis-type telomere repeat sequence (A-type TRS), 18S-28S rDNA, 5S rDNA and linkage group (LG) specific *Populus* BAC clones as probes. (Tuskan et al., 2006)

* White and red arrows a) show heterochromatic (A-T rich, brightly stained) and euchromatic regions, respectively. For data collection, chromosomes were numbered arbitrarily from 1 to 38 in each cell and chromosome length was measured three times per chromosome (shown by white trace lines) using Optimas v6. c) A-type TRS FISH signals are observed at the end of all chromosome arms. d) BACs from

LGXIV are found to be co-localized with an 18S-28S rDNA site and (c) BACs from LGXVII are found to be co-localised with the 5S rDNA site. Bar is 10 μ m.

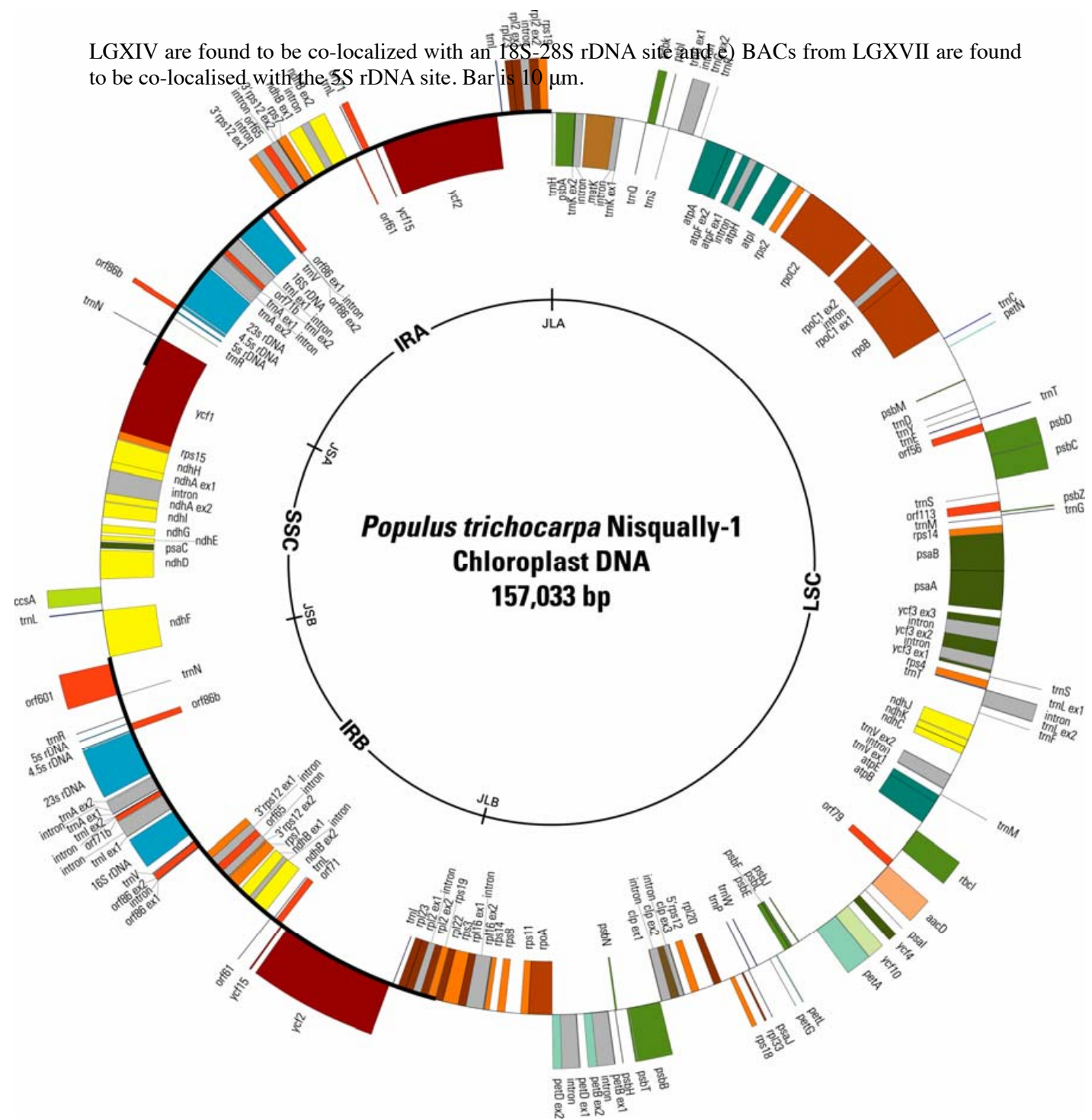


Figure 2-3. Graphic representation of the de novo whole-genome shotgun sequence assembly and annotation for the *Populus trichocarpa* chloroplast. (Tuskan et al., 2006)

* Each nucleotide is represented by an average of 410 sequence reads at a quality score of 40 or higher. Gene Models were predicted based on the Glimmer program at Oak Ridge National Laboratory

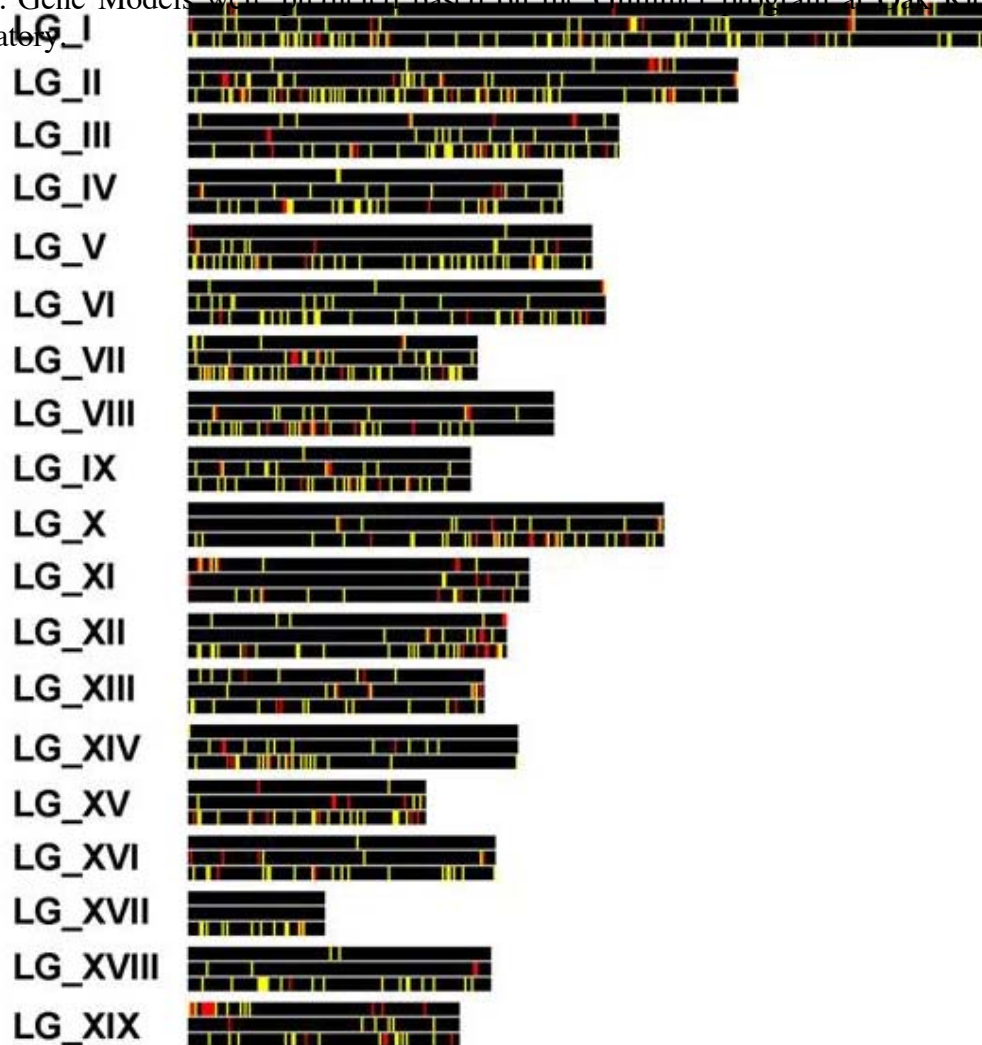


Figure 2-4. Chromosomal localization designated by linkage groups (LG), for disease resistance genes (top), genes coding for P450 enzymes (middle) and transcription factors (bottom). (Tuskan et al., 2006)

* Yellow denotes a single gene in a 100 kb window, red 2 or more genes in a 100 bp window.

Appendix III

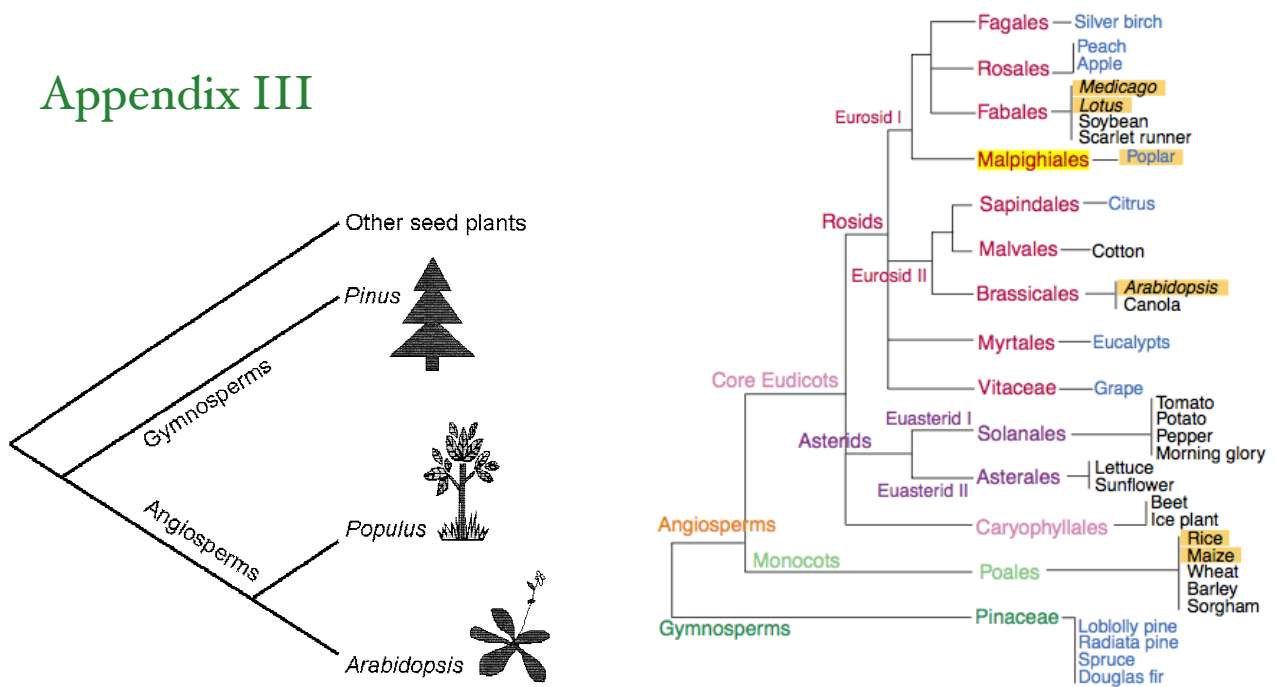


Figure 3-1-1. Phylogeny of *Populus*, which indicates poplars diverged relatively recently from other angiosperms, such as *Arabidopsis*. (Bradshaw et al., 2000; Brunner et al., 2004)

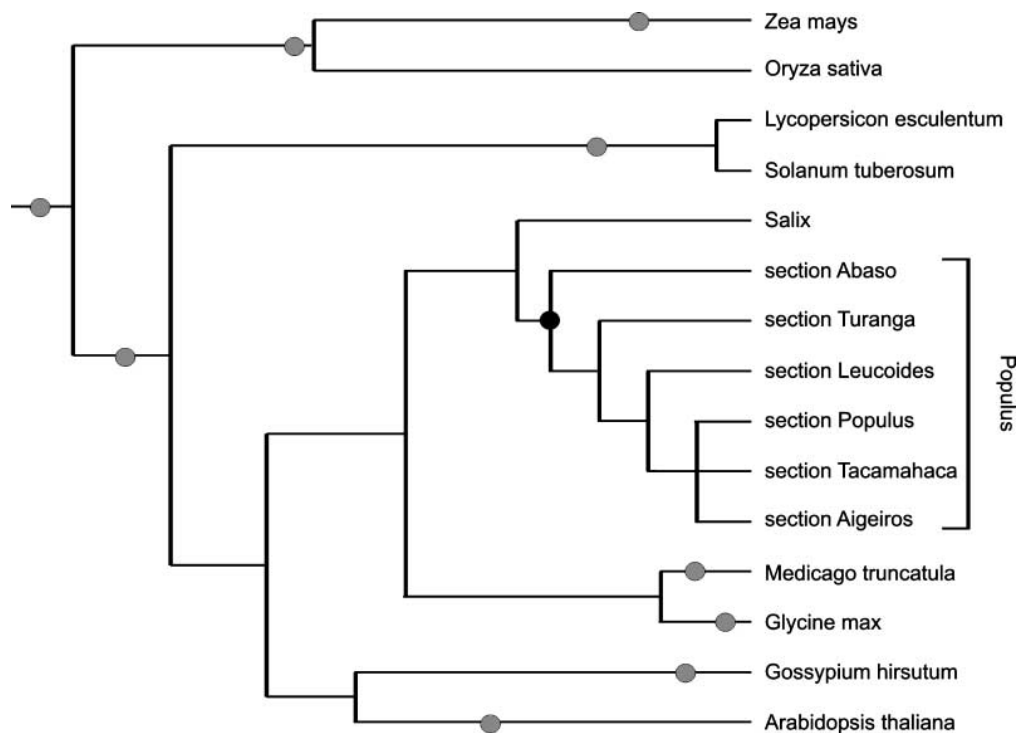


Figure 3-1-2. Intersectional phylogenetic relationship of the genus *Populus*. Schematic representation of the phylogeny of the genus *Populus* and some relevant plant species (Sterck et al., 2005).

* Grey dots indicate large-scale duplication events; the black dot denotes the large-scale duplication event in poplar proposed in the current study.

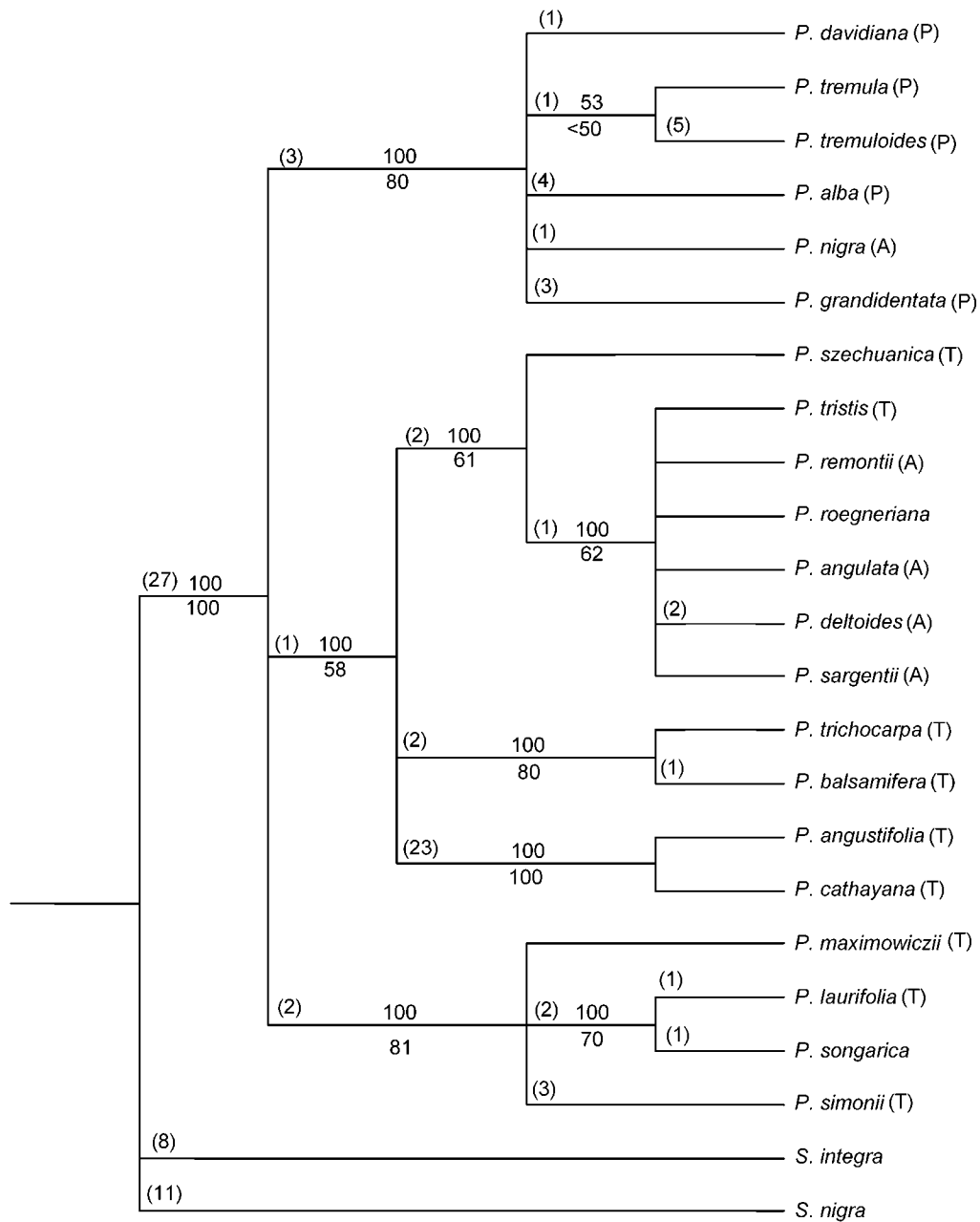


Figure 3-1-3-a. Interspecific phylogenetic relationship of the genus *Populus*. (Hamzeh & Dayanandan, 2004)

The majority rule consensus tree of 30,939 equally parsimonious trees (tree length 118; consistency index = 0.924) based on three noncoding regions of trnT-trnF of cpDNA sequences from *Populus* species.

* Numbers above branches show the frequency of occurrence in 50% majority rule consensus tree, and numbers below branches indicate bootstrap percentage values.

* Numbers in brackets show branch lengths (number of nucleotide substitution).

* A, *Aigeiros*; P, *Populus*; T, *Tacamahaca*.

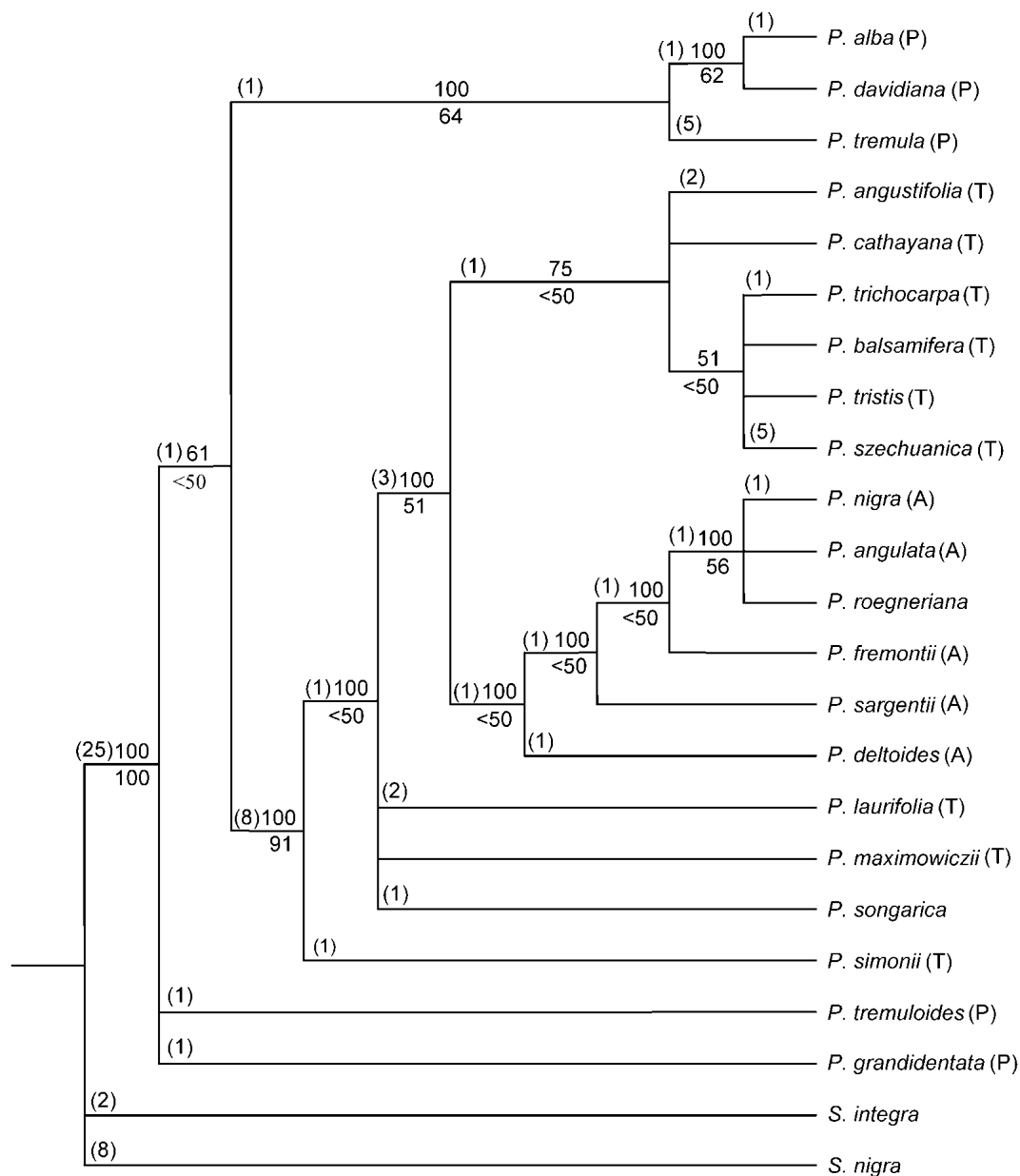


Figure 3-1-3-b. Interspecific phylogenetic relationship of the genus *Populus*. (Hamzeh & Dayanandan, 2004)

The majority rule consensus tree of 497 equally parsimonious trees (tree length 94; consistency index = 0.851) based on partial 5.8S RNA gene, ITS1 and ITS2 and part of 28S subunit sequences from *Populus* species.

* Numbers above branches show frequency of occurrence in 50% majority rule consensus tree, and numbers below branches indicate bootstrap percentage values.

* Numbers in brackets show branch lengths (number of nucleotide substitution).

* A, *Aigeiros*; P, *Populus*; T, *Tacamahaca*.

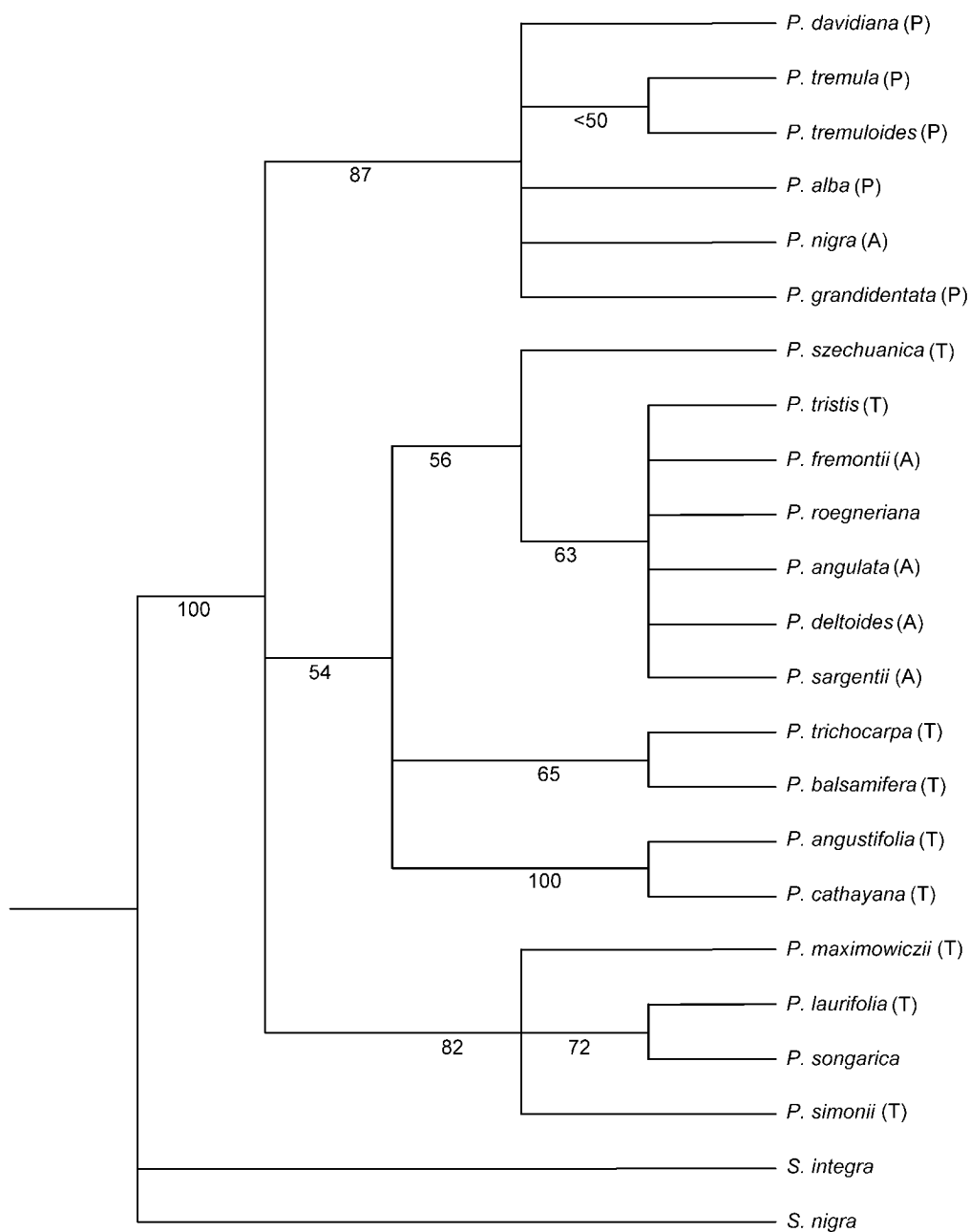


Figure 3-1-3-c. Interspecific phylogenetic relationship of the genus *Populus*. (Hamzeh & Dayanandan, 2004)

Maximum likelihood tree based on three noncoding regions of trnT-trnF of cpDNA sequences from *Populus* species.

* Numbers below branches show bootstrap percentage values.

* **A**, *Aigeiros*; **P**, *Populus*; **T**, *Tacamahaca*.

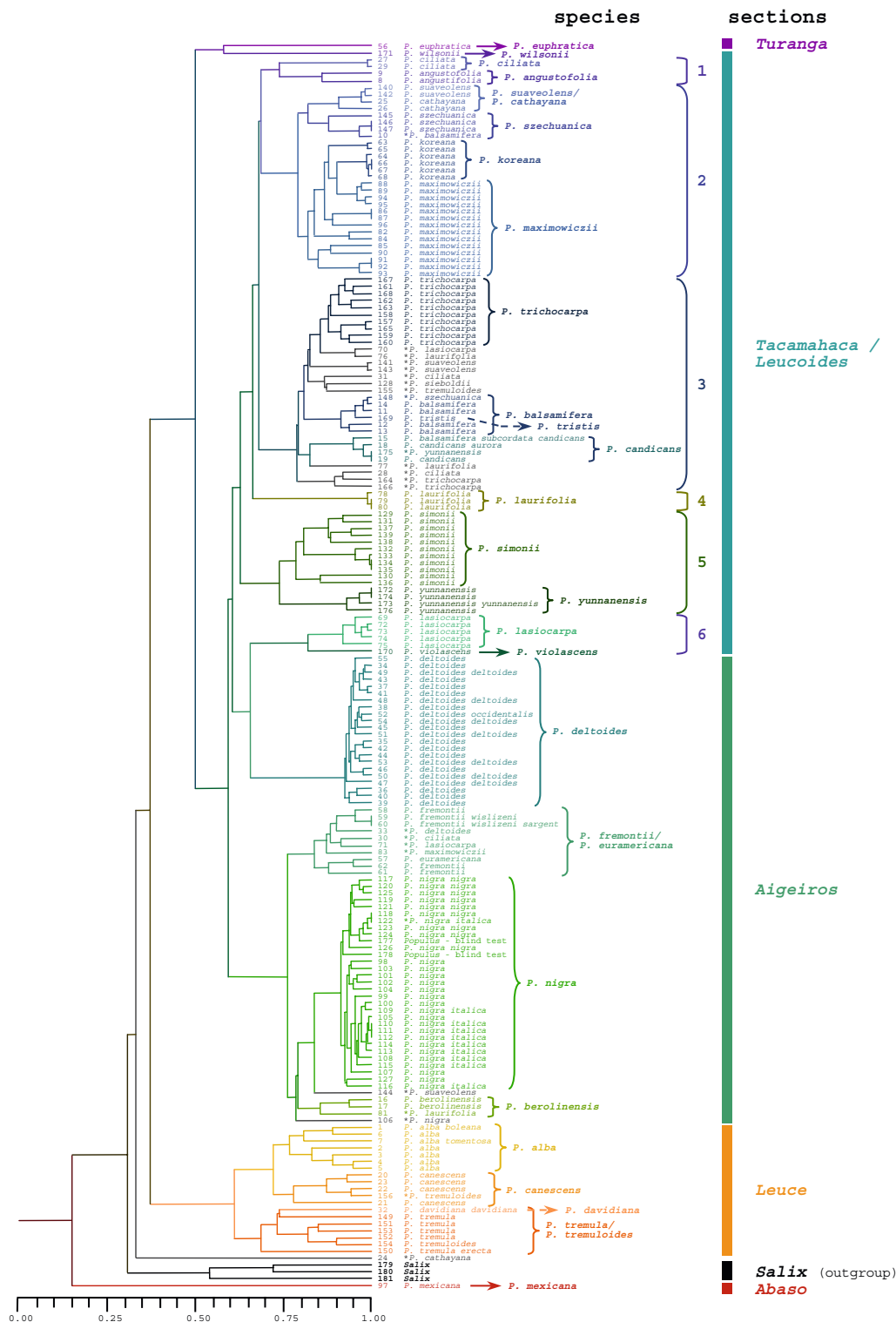


Figure 3-1-4. Dendrogram of *Populus* accessions with *Salix* as an outgroup, constructed from AFLP fragment similarities (Dice coefficient) with the UPGMA clustering method, and based on AFLP markers resolved by five primer combinations. (Cervera et al., 2005)

* Accessions marked with an asterisk are potentially mislabeled species or hybrids. Species are marked by brackets and arrows, whereas lines group sections.

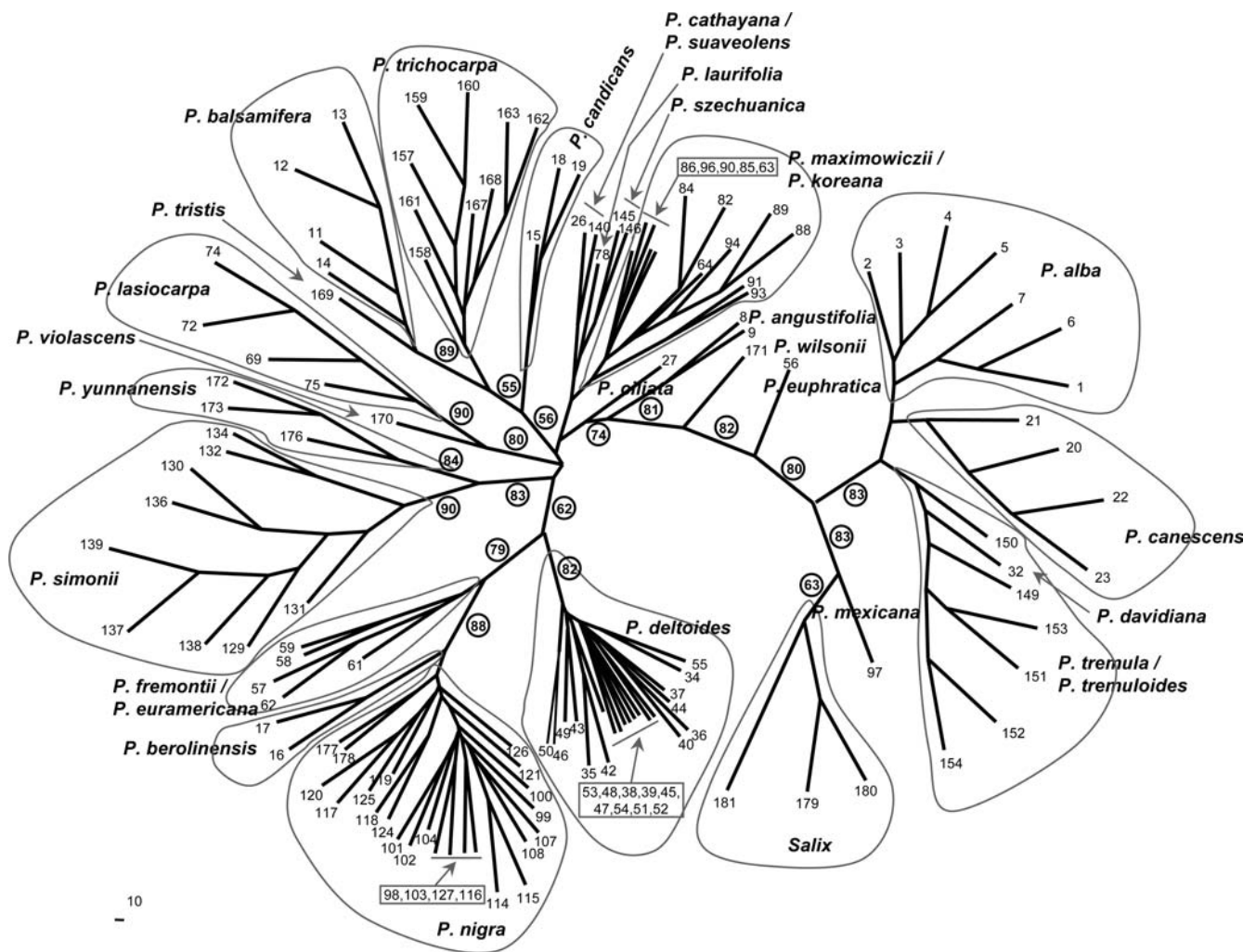


Figure 3-2. The single most parsimonious bifurcating unrooted tree, based on the Wagner method, representing the phylogeny of *Populus*. Plain and circled numbers correspond to accession codes (Table 3-1) and bootstrap values (only those above 50% are shown for main branches, grouping several species), respectively. (Cervera et al. 2005)

Table 3-1. Information on individual poplar accessions of 32 typical *Populus* species and hybrids within 5 main sections analysed in Fig. 3-1-4 & Figure 3-2. (Cervera, 2005)

Accession number	Species	Variety or cultivar	Clone name	Origin	Provider	New tentative assignation ^e
1	<i>P. alba</i>	<i>boleana</i>			CN	
2	<i>P. alba</i>		603.02		FR, INRA	
3	<i>P. alba</i>		A.L05.010	IT	IT, ISP	
4	<i>P. alba</i>		BO-1	IT	IT, ISP	
5	<i>P. alba</i>		Villafranca	IT	IT, ISP	
6	<i>P. alba</i>		B	BE	BE, VIB-UG	
7	<i>P. alba</i>	<i>tomentosa</i>			FR, INRA	
8	<i>P. angustifolia</i>		46/69		DE, HLFWW	
9	<i>P. angustifolia</i>		ANG		FR, INRA	
10	<i>P. balsamifera</i> ^c	<i>subcordata candicans</i>	1-5	US, MN	BE, IBW	<i>P. szechuanica</i>
11	<i>P. balsamifera</i>		8-6	US, MN	BE, IBW	
12	<i>P. balsamifera</i>		21-7	US, WI	BE, IBW	
13	<i>P. balsamifera</i>		15-5	US, MI	BE, IBW	
14	<i>P. balsamifera</i>		19-2	US, MI	BE, IBW	
15	<i>P. balsamifera</i>			BE, IBW	<i>P. candicans</i>	
16	<i>Populus</i> × <i>berolinensis</i>				BE, arboretum Kalmthout	
17	<i>Populus</i> × <i>berolinensis</i>		19870019	FR	BE, arboretum Meise	
18	<i>P. candicans</i>	<i>aurora</i>	19860364		BE, arboretum Meise	
19	<i>P. candicans</i>		19810762		BE, arboretum Meise	
20	<i>Populus</i> × <i>canescens</i>		90000054		BE, arboretum Meise	
21	<i>Populus</i> × <i>canescens</i>		limbrichterbos		BE, arboretum Kalmthout	
22	<i>Populus</i> × <i>canescens</i>		Grauwe abeel 1		BE, IBW	
23	<i>Populus</i> × <i>canescens</i>		Grauwe abeel 2		BE, IBW	
24	<i>P. cathayana</i> ^c		E6		IE, Teagasc	unclassified
25	<i>P. cathayana</i> ^b		306-52		DE, HLFWW	
26	<i>P. cathayana</i>				US, Washington University	
27	<i>P. ciliata</i>		72-085		IT, ISP	
28	<i>P. ciliata</i> ^c		65-017		IT, ISP	<i>P. trichocarpa</i> × <i>P. maximowiczii</i>
29	<i>P. ciliata</i> ^a		72-085		FR, INRA	
30	<i>P. ciliata</i> ^c		102L7		IE, Teagasc	<i>Populus</i> × <i>canadensis</i>
31	<i>P. ciliata</i> ^c		D1D4E3		IE, Teagasc	intrasectonal
32	<i>P. davidiana</i>	<i>davidiana</i>			FR, INRA	<i>Tacamahaca</i> hybrid
33	<i>P. deltoides</i> ^c		V12	US, IL	BE, IBW	<i>Populus</i> × <i>canadensis</i>
34	<i>P. deltoides</i>		V1	CA, ONT	BE, IBW	
35	<i>P. deltoides</i>		V2	CA, ONT	BE, IBW	
36	<i>P. deltoides</i>		V3	US, MN	BE, IBW	
37	<i>P. deltoides</i>		V7B	US, MO	BE, IBW	
38	<i>P. deltoides</i>		S174-1	US, ND	BE, IBW	
39	<i>P. deltoides</i>		S197-1	CA, ON	BE, IBW	
40	<i>P. deltoides</i>		S329-31	US, OH	BE, IBW	
41	<i>P. deltoides</i> ^b		S333-53	US, MI	BE, IBW	
42	<i>P. deltoides</i>		S235-3	US, IL	BE, IBW	
43	<i>P. deltoides</i>		S193-1	US, ND	BE, IBW	
44	<i>P. deltoides</i>		DO-006	US, TX	IT, ISP	
45	<i>P. deltoides</i>		DI-180A	US, OH	IT, ISP	
46	<i>P. deltoides</i>		S336-4	US, CT	BE, IBW	
47	<i>P. deltoides</i>	<i>deltoides</i>	D37	CA, ON ^g	CA, O.P. Rajora	
48	<i>P. deltoides</i>	<i>deltoides</i>	D43	CA, ON ^g	CA, O.P. Rajora	
49	<i>P. deltoides</i>	<i>deltoides</i>	D68	US, IN ^g	CA, O.P. Rajora	
50	<i>P. deltoides</i>	<i>deltoides</i>	D70	US, IL ^g	CA, O.P. Rajora	
51	<i>P. deltoides</i>	<i>deltoides</i>	D56	CA, ON ^g	CA, O.P. Rajora	
52	<i>P. deltoides</i>	<i>occidentalis</i>	D87	US, KS ^g	CA, O.P. Rajora	
53	<i>P. deltoides</i>	<i>deltoides</i>	D109	US, MS ^g	CA, O.P. Rajora	
54	<i>P. deltoides</i>	<i>deltoides</i>	D121	US, IL ^g	CA, O.P. Rajora	
55	<i>P. deltoides</i>		S9-2	US	BE, IBW	
56	<i>P. euphratica</i>			CN	VIB-UG	

Table 3-1. (Continued).

Accession number	Species	Variety or cultivar	Clone name	Origin	Provider	New tentative assignation ^c
114	<i>P. nigra</i>	'Italica'	PI88-058	TR	IT, ISP	
115	<i>P. nigra</i>	'Italica'	PI88-063	BG	IT, ISP	
116	<i>P. nigra</i>	'Italica'	Zaragoza	ES	ES, SIA	
117	<i>P. nigra</i>	<i>nigra</i>	N13	CZ ^h	CA, O.P. Rajora	
118	<i>P. nigra</i>	<i>nigra</i>	N19	NL ^h	CA, O.P. Rajora	
119	<i>P. nigra</i>	<i>nigra</i>	N20	FR ^h	CA, O.P. Rajora	
120	<i>P. nigra</i>	<i>nigra</i>	N29	NL ^h	CA, O.P. Rajora	
121	<i>P. nigra</i>	<i>nigra</i>	N40	NL ^h	CA, O.P. Rajora	
122	<i>P. nigra</i> ^b	<i>nigra</i>	N84	DE ^h	CA, O.P. Rajora	
123	<i>P. nigra</i> ^b	<i>nigra</i>	N85	DE ^h	CA, O.P. Rajora	
124	<i>P. nigra</i>	<i>nigra</i>	N96	CZ ^h	CA, O.P. Rajora	
125	<i>P. nigra</i>	<i>nigra</i>	N100	CZ ^h	CA, O.P. Rajora	
126	<i>P. nigra</i>	<i>nigra</i>	N102	CZ ^h	CA, O.P. Rajora	
127	<i>P. nigra</i>		Ghoy	BE	BE, IBW	
128	<i>P. sieboldii</i> ^c		Sie	GB	IE, Teagasc	<i>P. trichocarpa</i> × <i>P. balsamifera</i>
129	<i>P. simonii</i>		1/9		BE, IBW	
130	<i>P. simonii</i>		81-001-003	CN	IT, ISP	
131	<i>P. simonii</i>		81-002-003	CN	IT, ISP	
132	<i>P. simonii</i>		108/49		DE, HLFWW	
133	<i>P. simonii</i> ^b		57/65		DE, HLFWW	
134	<i>P. simonii</i>		147/65		DE, HLFWW	
135	<i>P. simonii</i> ^b		141/66		DE, HLFWW	
136	<i>P. simonii</i>		58/90		DE, HLFWW	
137	<i>P. simonii</i>		59/90		DE, HLFWW	
138	<i>P. simonii</i>		60/90		DE, HLFWW	
139	<i>P. simonii</i>	<i>fastigiata</i>			BE, VIB-UG	
140	<i>P. suaveolens</i>		21/65		DE, HLFWW	
141	<i>P. suaveolens</i> ^c		15/74		DE, HLFWW	<i>P. trichocarpa</i> × <i>P. balsamifera</i>
142	<i>P. suaveolens</i> ^a		21/65		DE, HLFWW	
143	<i>P. suaveolens</i> ^{a,c}		15/74		DE, HLFWW	<i>P. trichocarpa</i> × <i>P. balsamifera</i>
144	<i>P. suaveolens</i> ^c		20/65		DE, HLFWW	<i>P. × canadensis</i> × <i>P. nigra</i>
145	<i>P. szechuanica</i>		SZC		FR, INRA	
146	<i>P. szechuanica</i>		275/49		DE, HLFWW	
147	<i>P. szechuanica</i> ^b		67/65		DE, HLFWW	
148	<i>P. szechuanica</i> ^c		144/65		DE, HLFWW	<i>P. balsamifera</i>
149	<i>P. tremula</i>		130-19		FR, INRA	
150	<i>P. tremula</i>	<i>erecta</i>			BE, arboretum Beveren	
151	<i>P. tremula</i>		1H		BE, IBW	
152	<i>P. tremula</i>		2H		BE, IBW	
153	<i>P. tremula</i>		3H		BE, IBW	
154	<i>P. tremuloides</i>		210-22		FR, INRA	
155	<i>P. tremuloides</i> ^c		HI-10		IE, Teagasc	intrasectional <i>Tacamahaca</i> hybrid
156	<i>P. tremuloides</i> ^c				BE, arboretum Kalmthout	<i>Populus</i> × <i>canescens</i>
157	<i>P. trichocarpa</i>		FPL		FR, INRA	
158	<i>P. trichocarpa</i>		19-73		FR, INRA	
159	<i>P. trichocarpa</i>		36-77		FR, INRA	
160	<i>P. trichocarpa</i>		101-74		FR, INRA	
161	<i>P. trichocarpa</i>		S3-31		BE, IBW	
162	<i>P. trichocarpa</i>		V509		BE, IBW	
163	<i>P. trichocarpa</i>		V510		BE, IBW	
164	<i>P. trichocarpa</i> ^c	'Fritzi Pauley'	V235	US, WA	BE, IBW	<i>P. trichocarpa</i> × <i>P. maximowiczii</i>
165	<i>P. trichocarpa</i> ^b		212-161		FR, INRA	
166	<i>P. trichocarpa</i> ^{a,c}	'Fritzi Pauley'			BE, arboretum Kalmthout	<i>P. trichocarpa</i> × <i>P. maximowiczii</i>
167	<i>P. trichocarpa</i>	'Trichobel'			BE, IBW	
168	<i>P. trichocarpa</i>	'Columbia river'	V24	US, OR	BE, IBW	
169	<i>P. tristis</i>		24/65		DE, HLFWW	

Table 3-1. (Continued).

Accession number	Species	Variety or cultivar	Clone name	Origin	Provider	New tentative assignation ^c
170	<i>P. violascens</i>		19860054	UK	BE, arboretum Meise	
171	<i>P. wilsonii</i>		19820416	DE	BE, arboretum Meise	
172	<i>P. yunnanensis</i>		82001		FR, INRA	
173	<i>P. yunnanensis</i>	<i>yunnanensis</i>			FR, INRA	
174	<i>P. yunnanensis</i> ^b		V535		BE, IBW	
175	<i>P. yunnanensis</i> ^c				BE, arboretum Beveren	<i>P. candicans</i>
176	<i>P. yunnanensis</i>				BE, arboretum Beveren	
177	<i>Populus-unknown</i> ^d		22616		BE, arboretum Kalmthout	<i>P. nigra</i>
178	<i>Populus-unknown</i> ^d		22031		BE, arboretum Kalmthout	<i>P. nigra</i>
179	<i>Salix</i>				BE, VIB-UG	
180	<i>Salix</i>				BE, VIB-UG	
181	<i>Salix</i>		22010		BE, arboretum Kalmthout	

* Countries are abbreviated according to ISO 3166-1-Alpha-2 code

(**BE** Belgium, **BG** Bulgaria, **CA** Canada [ON Ontario], **CN** China, **CZ** Czech Republic, **DE** Germany, **DK** Denmark, **ES** Spain, **FR** France, **IE** Ireland, **IT** Italy, **JP** Japan, **MX** Mexico, **NL** The Netherlands, **TR** Turkey, **GB** United Kingdom, **US** United States [IL Illinois, IN Indiana, KS Kansas, MN Minnesota, MO Missouri, MS Mississippi, ND North Dakota, OH Ohio, OR Oregon, TX Texas, WA Washington State, WI Wisconsin], **YU** Yugoslavia).

* **HLFWW** Hessian Forest Center for Management, Planning, Research and Ecology (Munden, Germany),

IBW Instituut voor Bosbouw en Wildbeheer (Geraardsbergen, Belgium),

INRA Institut National de la Recherche Agronomique (Orleans, France),

ISP Istituto di Sperimentazione per la Pioppicoltura (Casale Monferrato, Italy),

SIA Servicio de Investigacion Agroalimentaria Diputacion General de Aragon (Zaragoza, Spain), Teagasc Irish Agriculture and Food development Authority (Dublin, Ireland),

VIB-UG Vlaams Interuniversitair Instituut voor Biotechnologie-Universiteit Gent (Gent, Belgium).

* Accessions in bold were used to perform the phylogenetic analysis

a. Samples known to be duplicates before the start of the analysis and confirmed by AFLP

b. Accessions showing GS of ≥ 0.98 based on AFLP fragment similarities

c. Possibly mislabeled and/or misclassified accessions based on AFLP analysis

d. Based on morphological descriptors (blind test). These clones showed AFLP patterns typical of *P. nigra*

e. Tentative assignation of misclassified accessions based on AFLP patterns, GS values and the dendrogram in Fig. 3-1-3

Table 3-2. Interspecific and intraspecific GS among pairs of *Populus* and *Salix*, with average similarities between parentheses. (Cervera, 2005)

	<i>P. euphratica</i> (1)	<i>P. ciliata</i> (2)	<i>P. lasiocarpa</i> (5)	<i>P. alba</i> (7)	<i>P. davidiana</i> (1)	<i>P. sibirica</i> (1)	<i>P. tremula</i> (5)	<i>P. tremuloides</i> (1)	<i>P. angustifolia</i> (2)	<i>P. balsamifera</i> (5)	<i>P. canadensis</i> (4)	<i>P. cathayana</i> (2)	<i>P. laurifolia</i> (3)	<i>P. maximowiczii</i> (14)
<i>P. euphratica</i>	–													
<i>P. ciliata</i>	0.50–0.51 (0.51)	0.99												
<i>P. lasiocarpa</i>	0.46–0.47 (0.47 ± 0.01)	0.56–0.59 (0.58 ± 0.01)	0.90–0.99 (0.95 ± 0.03)											
<i>P. alba</i>	0.29–0.45 (0.36 ± 0.05)	0.29–0.4 (0.32 ± 0.04)	0.34–0.44 (0.40 ± 0.03)	0.70–0.95 (0.81 ± 0.06)										
<i>P. davidiana</i>	0.40	0.35	0.36–0.38 (0.38 ± 0.01)	0.57–0.65 (0.60 ± 0.03)	–									
<i>P. sibirica</i>	0.48	0.62	0.60–0.62 (0.61 ± 0.01)	0.39–0.47 (0.44 ± 0.03)	0.43									
<i>P. tremula</i>	0.34–0.47 (0.40 ± 0.04)	0.36–0.43 (0.39 ± 0.02)	0.35–0.49 (0.41 ± 0.04)	0.53–0.70 (0.59 ± 0.04)	0.71–0.78 (0.74 ± 0.03)	0.38–0.51 (0.46 ± 0.05)	0.67–0.86 (0.75 ± 0.07)							
<i>P. tremuloides</i>	0.39	0.37	0.37–0.43 (0.41 ± 0.02)	0.52–0.66 (0.59 ± 0.05)	0.71	0.47	0.63–0.90 (0.77 ± 0.11)	–						
<i>P. angustifolia</i>	0.54–0.60 (0.57)	0.72–0.76 (0.74 ± 0.02)	0.57–0.66 (0.62 ± 0.03)	0.34–0.55 (0.43 ± 0.06)	0.40–0.45 (0.43)	0.65–0.67 (0.66)	0.4–0.50 (0.45 ± 0.03)	0.42–0.43 (0.42)	0.86					
<i>P. balsamifera</i>	0.46–0.53 (0.50 ± 0.03)	0.58–0.67 (0.64 ± 0.03)	0.57–0.65 (0.62 ± 0.02)	0.33–0.47 (0.39 ± 0.03)	0.35–0.43 (0.40 ± 0.03)	0.80–0.88 (0.85 ± 0.03)	0.31–0.51 (0.43 ± 0.06)	0.40–0.47 (0.45 ± 0.03)	0.61–0.72 (0.67 ± 0.03)	0.89–0.99 (0.94 ± 0.03)				
<i>P. canadensis</i>	0.51–0.52 (0.51 ± 0.01)	0.67–0.72 (0.69 ± 0.02)	0.66–0.70 (0.68 ± 0.01)	0.37–0.52 (0.41 ± 0.05)	0.44–0.47 (0.45 ± 0.01)	0.80–0.85 (0.82 ± 0.02)	0.35–0.49 (0.45 ± 0.05)	0.44–0.45 (0.45 ± 0.01)	0.64–0.73 (0.68 ± 0.03)	0.75–0.87 (0.81 ± 0.03)	0.94–1.00 (0.97 ± 0.02)			
<i>P. cathayana</i>	0.44	0.67–0.73	0.54–0.63 (0.58 ± 0.03)	0.30–0.45 (0.34 ± 0.05)	0.38–0.41 (0.40 ± 0.04)	0.65–0.70 (0.68)	0.32–0.46 (0.40 ± 0.04)	0.40–0.43 (0.42)	0.59–0.69 (0.64 ± 0.04)	0.62–0.72 (0.68 ± 0.03)	0.65–0.73 (0.69 ± 0.03)	0.89		
<i>P. laurifolia</i>	0.39–0.40 (0.40 ± 0.01)	0.63–0.65 (0.64 ± 0.01)	0.47–0.54 (0.51 ± 0.02)	0.26–0.38 (0.31 ± 0.03)	0.33–0.35 (0.34 ± 0.01)	0.67–0.68 (0.68 ± 0.01)	0.31–0.41 (0.37 ± 0.03)	0.36–0.37 (0.37 ± 0.01)	0.56–0.61 (0.64 ± 0.02)	0.60–0.66 (0.68 ± 0.03)	0.61–0.67 (0.63 ± 0.02)	0.69–0.72 (0.70 ± 0.02)	0.99–1.00 (0.99 ± 0.01)	
<i>P. maximowiczii</i>	0.45–0.52 (0.47 ± 0.02)	0.69–0.74 (0.71 ± 0.02)	0.52–0.62 (0.58 ± 0.02)	0.27–0.49 (0.35 ± 0.05)	0.37–0.44 (0.42 ± 0.02)	0.60–0.69 (0.66 ± 0.03)	0.30–0.49 (0.41 ± 0.04)	0.40–0.44 (0.42 ± 0.02)	0.62–0.73 (0.68 ± 0.03)	0.59–0.73 (0.67 ± 0.03)	0.62–0.75 (0.68 ± 0.03)	0.73–0.86 (0.81 ± 0.03)	0.73–1.00 (0.85 ± 0.06)	
<i>P. koriana</i>	0.44–0.45 (0.45 ± 0.01)	0.67–0.69 (0.68 ± 0.01)	0.55–0.61 (0.58 ± 0.02)	0.31–0.47 (0.35 ± 0.05)	0.41–0.43 (0.42 ± 0.01)	0.63–0.67 (0.65 ± 0.01)	0.36–0.45 (0.41 ± 0.02)	0.41–0.45 (0.42 ± 0.02)	0.63–0.72 (0.68 ± 0.03)	0.60–0.71 (0.67 ± 0.03)	0.65–0.70 (0.67 ± 0.02)	0.78–0.84 (0.82 ± 0.02)	0.65–0.71 (0.68 ± 0.02)	
<i>P. simonii</i>	0.34–0.46 (0.39 ± 0.04)	0.48–0.62 (0.55 ± 0.05)	0.49–0.63 (0.56 ± 0.03)	0.27–0.45 (0.34 ± 0.04)	0.38–0.44 (0.41 ± 0.02)	0.53–0.62 (0.57 ± 0.02)	0.36–0.45 (0.45 ± 0.03)	0.33–0.41 (0.39 ± 0.02)	0.54–0.62 (0.59 ± 0.03)	0.50–0.69 (0.59 ± 0.03)	0.60–0.68 (0.63 ± 0.02)	0.56–0.73 (0.65 ± 0.06)	0.50–0.58 (0.55 ± 0.03)	
<i>P. suaveolens</i>	0.44	0.70–0.73	0.57–0.63 (0.60 ± 0.01)	0.30–0.46 (0.35 ± 0.05)	0.41	0.70	0.37–0.47 (0.41 ± 0.03)	0.43	0.60–0.67 (0.64 ± 0.04)	0.63–0.72 (0.69 ± 0.04)	0.69–0.73 (0.70 ± 0.01)	0.91–0.98 (0.94 ± 0.04)	0.67–0.70 (0.69 ± 0.01)	
<i>P. szechuanica</i>	0.45–0.49 (0.47 ± 0.02)	0.67–0.70 (0.68 ± 0.01)	0.57–0.61 (0.59 ± 0.01)	0.30–0.47 (0.34 ± 0.05)	0.37–0.39 (0.38 ± 0.01)	0.64–0.71 (0.66 ± 0.03)	0.32–0.48 (0.39 ± 0.04)	0.39–0.44 (0.40 ± 0.03)	0.63–0.71 (0.66 ± 0.03)	0.63–0.73 (0.69 ± 0.03)	0.66–0.72 (0.68 ± 0.02)	0.82–0.86 (0.84 ± 0.02)	0.69–0.76 (0.71 ± 0.02)	
<i>P. yunnanensis</i>	0.42–0.45 (0.44 ± 0.02)	0.62–0.65 (0.64 ± 0.02)	0.58–0.66 (0.62 ± 0.03)	0.32–0.49 (0.39 ± 0.04)	0.45–0.48 (0.46 ± 0.02)	0.63–0.67 (0.65 ± 0.02)	0.36–0.51 (0.45 ± 0.05)	0.46–0.49 (0.48 ± 0.02)	0.61–0.68 (0.65 ± 0.03)	0.56–0.69 (0.64 ± 0.03)	0.66–0.72 (0.68 ± 0.02)	0.68–0.76 (0.73 ± 0.03)	0.55–0.61 (0.59 ± 0.02)	
<i>P. trichocarpa</i>	0.40–0.50 (0.48 ± 0.03)	0.62–0.70 (0.67 ± 0.02)	0.58–0.75 (0.65 ± 0.03)	0.30–0.48 (0.40 ± 0.04)	0.38–0.47 (0.41 ± 0.02)	0.82–0.89 (0.86 ± 0.02)	0.32–0.55 (0.45 ± 0.05)	0.41–0.51 (0.46 ± 0.04)	0.62–0.76 (0.70 ± 0.04)	0.71–0.87 (0.81 ± 0.04)	0.74–0.87 (0.80 ± 0.03)	0.63–0.78 (0.69 ± 0.03)	0.63–0.68 (0.66 ± 0.01)	
<i>P. deltoides</i>	0.41–0.49 (0.44 ± 0.02)	0.52–0.61 (0.56 ± 0.02)	0.61–0.72 (0.66 ± 0.02)	0.30–0.44 (0.37 ± 0.03)	0.37–0.45 (0.40 ± 0.02)	0.57–0.64 (0.59 ± 0.02)	0.28–0.43 (0.37 ± 0.04)	0.39–0.42 (0.41 ± 0.01)	0.54–0.69 (0.61 ± 0.04)	0.53–0.66 (0.60 ± 0.03)	0.68–0.81 (0.75 ± 0.03)	0.54–0.71 (0.59 ± 0.03)	0.49–0.60 (0.53 ± 0.02)	
<i>P. × euramericana</i>	0.37–0.45 (0.43 ± 0.03)	0.53–0.64 (0.59 ± 0.03)	0.53–0.64 (0.59 ± 0.02)	0.26–0.42 (0.35 ± 0.04)	0.35–0.42 (0.39 ± 0.02)	0.58–0.65 (0.63 ± 0.02)	0.27–0.46 (0.38 ± 0.04)	0.36–0.40 (0.39 ± 0.02)	0.58–0.71 (0.65 ± 0.04)	0.51–0.67 (0.61 ± 0.04)	0.64–0.79 (0.74 ± 0.03)	0.50–0.66 (0.60 ± 0.04)	0.50–0.56 (0.53 ± 0.01)	
<i>P. nigra</i>	0.41–0.48 (0.45 ± 0.02)	0.53–0.61 (0.57 ± 0.02)	0.45–0.53 (0.49 ± 0.01)	0.22–0.38 (0.29 ± 0.03)	0.30–0.40 (0.34 ± 0.02)	0.59–0.65 (0.62 ± 0.02)	0.31–0.42 (0.35 ± 0.03)	0.29–0.39 (0.32 ± 0.02)	0.58–0.67 (0.61 ± 0.02)	0.51–0.66 (0.59 ± 0.03)	0.57–0.67 (0.62 ± 0.02)	0.49–0.61 (0.55 ± 0.03)	0.50–0.64 (0.52 ± 0.02)	
<i>P. violascens</i>	0.49	0.69	0.79–0.83 (0.82 ± 0.02)	0.36–0.46 (0.39 ± 0.04)	0.41	0.69	0.40–0.46 (0.42 ± 0.02)	0.43	0.67–0.70 (0.68)	0.61–0.69 (0.67 ± 0.03)	0.77 (± 0.01)	0.70 (0.58 ± 0.01)	0.58–0.59 (0.58 ± 0.01)	
<i>P. wilsonii</i>	0.58	0.61–0.62 (0.61)	0.58–0.61 (0.59 ± 0.01)	0.38–0.47 (0.42 ± 0.03)	0.41	0.66	0.39–0.48 (0.44 ± 0.03)	0.41	0.65 (0.65 ± 0.04)	0.59–0.68 (0.65 ± 0.04)	0.59–0.63 (0.61 ± 0.02)	0.56–0.59 (0.57)	0.46 (0.58 ± 0.03)	
<i>P. trisatis</i>	0.51	0.66–0.67 (0.66)	0.61–0.65 (0.63 ± 0.01)	0.37–0.45 (0.41 ± 0.03)	0.40	0.89	0.36–0.51 (0.45 ± 0.06)	0.50	0.71–0.72 (0.71)	0.88–0.96 (0.93 ± 0.03)	0.80–0.87 (0.83 ± 0.03)	0.67–0.72 (0.70)	0.63–0.64 (0.63 ± 0.01)	
<i>P. berolinensis</i>	0.41–0.43 (0.42 ± 0.01)	0.60–0.66 (0.63 ± 0.03)	0.49–0.54 (0.51 ± 0.02)	0.26–0.37 (0.33 ± 0.03)	0.31–0.37 (0.33 ± 0.02)	0.60–0.64 (0.62 ± 0.02)	0.33–0.40 (0.37 ± 0.02)	0.34–0.35 (0.35 ± 0.01)	0.60–0.64 (0.61 ± 0.02)	0.51–0.63 (0.59 ± 0.04)	0.62–0.67 (0.63 ± 0.02)	0.59–0.69 (0.66 ± 0.04)	0.64–0.68 (0.65 ± 0.01)	
<i>P. × canadensis</i>	0.35–0.39 (0.37 ± 0.02)	0.31–0.41 (0.38 ± 0.04)	0.37–0.43 (0.40 ± 0.02)	0.63–0.79 (0.72 ± 0.04)	0.61–0.66 (0.64 ± 0.02)	0.44–0.46 (0.45 ± 0.01)	0.57–0.72 (0.65 ± 0.05)	0.58–0.64 (0.61 ± 0.03)	0.42–0.5 (0.47 ± 0.03)	0.34–0.46 (0.41 ± 0.03)	0.36–0.46 (0.42 ± 0.04)	0.33–0.42 (0.38 ± 0.03)	0.31–0.36 (0.34 ± 0.02)	
<i>P. mexicana</i>	0.14	0.13	0.13–0.17 (0.14 ± 0.02)	0.05–0.14 (0.10 ± 0.04)	0.26 (0.26 ± 0.04)	0.16	0.12–0.20 (0.16 ± 0.03)	0.14	0.11–0.16 (0.13)	0.10–0.13 (0.12 ± 0.01)	0.14–0.16 (0.16 ± 0.01)	0.09–0.12 (0.25 ± 0.02)	0.23–0.26 (0.13 ± 0.02)	
<i>Salix</i>	0.31–0.38 (0.34 ± 0.04)	0.17–0.29 (0.25 ± 0.05)	0.25–0.35 (0.31 ± 0.03)	0.26–0.44 (0.33 ± 0.06)	0.29–0.36 (0.32 ± 0.04)	0.29–0.34 (0.31 ± 0.03)	0.22–0.32 (0.28 ± 0.03)	0.26–0.35 (0.30 ± 0.04)	0.27–0.35 (0.31 ± 0.03)	0.26–0.37 (0.32 ± 0.04)	0.30–0.37 (0.33 ± 0.02)	0.24–0.30 (0.28 ± 0.02)	0.28–0.33 (0.31 ± 0.02)	

Table 3-2. (Continued).

	<i>P. koreana</i> (6)	<i>P. simonii</i> (11)	<i>P. suaveolens</i> (2)	<i>P. szechuanica</i> (4)	<i>P. yunnanensis</i> (4)	<i>P. trichocarpa</i> (10)	<i>P. deltoidea</i> (22)	<i>Populus × canadensis</i> (10)	<i>P. nigra</i> (31)	<i>P. violascens</i> (1)	<i>P. wilsonii</i> (1)	<i>P. tristis</i> (1)	<i>P. × berolinensis</i> (3)	<i>P. × canescens</i> (5)	<i>P. mexicana</i> (1)
<i>P. euphratica</i>															
<i>P. ciliata</i>															
<i>P. lasiocarpa</i>															
<i>P. alba</i>															
<i>P. davidiana</i>															
<i>P. sieboldii</i>															
<i>P. tremula</i>															
<i>P. tremuloides</i>															
<i>P. angustifolia</i>															
<i>P. balsamifera</i>															
<i>P. canadensis</i>															
<i>P. cathayana</i>															
<i>P. laurifolia</i>															
<i>P. maximowiczii</i>															
<i>P. koreana</i>	0.85–1.00 (0.92±0.07)														
<i>P. simonii</i>	0.51–0.74 (0.63±0.06)	0.75–1.00 (0.83±0.07)													
<i>P. suaveolens</i>	0.80–0.84 (0.83±0.01)	0.57–0.73 (0.64±0.06)	0.98												
<i>P. szechuanica</i>	0.74–0.79 (0.76±0.01)	0.52–0.71 (0.61±0.07)	0.80–0.83 (0.81±0.01)	0.87–1.00 (0.93±0.05)											
<i>P. yunnanensis</i>	0.67–0.71 (0.69±0.01)	0.67–0.79 (0.74±0.04)	0.71–0.76 (0.74±0.02)	0.63–0.67 (0.66±0.02)	0.91–1.00 (0.95±0.03)										
<i>P. trichocarpa</i>	0.61–0.74 (0.68±0.03)	0.54–0.72 (0.63±0.04)	0.65–0.78 (0.70±0.03)	0.60–0.74 (0.66±0.03)	0.58–0.75 (0.69±0.04)	0.91–1.00 (0.95±0.03)									
<i>P. deltoidea</i>	0.57–0.65 (0.60±0.02)	0.51–0.66 (0.56±0.02)	0.56–0.72 (0.61±0.03)	0.57–0.72 (0.61±0.02)	0.57–0.71 (0.62±0.02)	0.54–0.68 (0.60±0.03)	0.89–0.99 (0.94±0.02)								
<i>P. × canadensis</i>	0.53–0.66 (0.61±0.03)	0.54–0.73 (0.61±0.04)	0.54–0.66 (0.62±0.03)	0.50–0.64 (0.58±0.03)	0.57–0.71 (0.65±0.02)	0.54–0.71 (0.63±0.03)	0.67–0.83 (0.75±0.03)	0.78–1.00 (0.87±0.02)							
<i>P. nigra</i>	0.53–0.64 (0.59±0.02)	0.48–0.78 (0.59±0.06)	0.52–0.61 (0.57±0.02)	0.53–0.62 (0.57±0.02)	0.53–0.63 (0.56±0.02)	0.54–0.68 (0.61±0.03)	0.45–0.60 (0.53±0.02)	0.68–0.87 (0.76±0.03)	0.84–1.00 (0.93±0.03)	0.52–0.58 (0.55±0.02)					
<i>P. violascens</i>	0.71–0.72 (0.72±0.01)	0.56–0.65 (0.61±0.03)	0.70–0.72 (0.71)	0.65–0.69 (0.68±0.02)	0.69–0.73 (0.72±0.02)	0.66–0.76 (0.71±0.03)	0.64–0.71 (0.67±0.03)	0.59–0.68 (0.65±0.03)	0.52–0.58 (0.55±0.02)	0.45–0.54 (0.49±0.02)	–				
<i>P. wilsonii</i>	0.54–0.59 (0.56±0.02)	0.43–0.55 (0.49±0.05)	0.56–0.59 (0.58)	0.59–0.62 (0.61±0.01)	0.50–0.54 (0.52±0.02)	0.59–0.68 (0.64±0.03)	0.46–0.55 (0.50±0.02)	0.43–0.52 (0.49±0.03)	0.45–0.54 (0.49±0.02)	0.58	–				
<i>P. tristis</i>	0.67–0.71 (0.69±0.01)	0.52–0.64 (0.58±0.04)	0.70–0.72 (0.71)	0.69–0.71 (0.70±0.01)	0.65–0.69 (0.67±0.02)	0.80–0.87 (0.84±0.03)	0.62–0.68 (0.64±0.02)	0.58–0.68 (0.65±0.03)	0.60–0.67 (0.63±0.02)	0.69	0.66	–			
<i>P. berolinensis</i>	0.57–0.73 (0.67±0.05)	0.55–0.74 (0.62±0.05)	0.63–0.68 (0.66±0.02)	0.55–0.63 (0.59±0.03)	0.60–0.68 (0.63±0.02)	0.57–0.69 (0.64±0.03)	0.48–0.55 (0.52±0.02)	0.67–0.78 (0.72±0.03)	0.73–0.85 (0.79±0.02)	0.61–0.65 (0.63±0.02)	0.45–0.51 (0.48±0.03)	0.59–0.64 (0.61±0.03)	0.84–0.94 (0.88±0.05)		
<i>P. canescens</i>	0.34–0.40 (0.37±0.02)	0.27–0.46 (0.38±0.04)	0.33–0.44 (0.40±0.04)	0.31–0.41 (0.36±0.03)	0.34–0.49 (0.42±0.04)	0.37–0.53 (0.44±0.04)	0.28–0.41 (0.34±0.03)	0.27–0.41 (0.35±0.03)	0.24–0.47 (0.34±0.04)	0.38–0.44 (0.42±0.02)	0.40–0.51 (0.46±0.04)	0.39–0.46 (0.43±0.03)	0.34–0.41 (0.37±0.02)	0.73–0.94 (0.85±0.07)	
<i>P. mexicana</i>	0.13–0.15 (0.14±0.01)	0.14–0.23 (0.18±0.03)	0.09	0.11–0.14 (0.11±0.02)	0.16–0.18 (0.16±0.01)	0.12–0.19 (0.17±0.02)	0.13–0.18 (0.15±0.01)	0.15–0.20 (0.17±0.02)	0.15–0.22 (0.18±0.02)	0.14	0.12	0.10	0.21–0.22 (0.22±0.01)	0.08–0.14 (0.10±0.03)	–
<i>Salix</i>	0.23–0.31 (0.26±0.03)	0.20–0.34 (0.29±0.05)	0.24–0.30 (0.27±0.03)	0.27–0.36 (0.32±0.03)	0.25–0.43 (0.35±0.06)	0.24–0.38 (0.30±0.03)	0.26–0.42 (0.34±0.04)	0.22–0.40 (0.32±0.06)	0.20–0.41 (0.30±0.05)	0.28–0.36 (0.32±0.04)	0.24–0.34 (0.30±0.05)	0.29–0.37 (0.32±0.04)	0.23–0.33 (0.28±0.04)	0.24–0.38 (0.30±0.05)	0.13–0.16 (0.15±0.02)

The number of accessions analyzed per species is indicated between parentheses in the heading

Table 3-3. Overview of traits introduced into poplar *via* genetic engineering (Leple et al., 2000)

Species/hybrid	Methods	Transgenes ^a	Characteristics	Reference
Resistance to herbicides				
<i>P. alba</i> × <i>P. grandidentata</i>	Fillatti et al. (1987)	<i>aroA</i>	Glyphosate resistance	Fillatti et al. (1987)
<i>P. tremula</i> × <i>P. alba</i>	De Block (1990)	<i>bar</i>	Basta resistance	De Block (1990)
<i>P. trichocarpa</i> × <i>P. deltoides</i>	De Block (1990)	<i>bar</i>	Basta resistance	De Block (1990)
<i>P. tremula</i> × <i>P. alba</i>	Devillard (1992)	<i>bar</i>	Basta resistance	Devillard (1992)
<i>P. tremula</i> × <i>P. alba</i>	Brasileiro et al. (1991)	<i>crs1-1</i>	Chlorsulfuron resistance	Brasileiro et al. (1992)
	Leplé et al. (1992)			
<i>P. tremula</i> × <i>P. alba</i>	Chupeau et al. (1994)	<i>crs1-1</i>	Chlorsulfuron resistance	Chupeau et al. (1994)
<i>P. tremula</i> × <i>P. alba</i>	Chupeau et al. (1994)	<i>bar</i>	Basta resistance	Chupeau et al. (1994)
<i>P. alba</i> × <i>P. grandidentata</i>	Fillatti et al. (1987)	<i>aroA</i>	Glyphosate resistance	Donahue et al. (1994)
Resistance to insects				
<i>P. alba</i> × <i>P. grandidentata</i>	McCown et al. (1991)	<i>cryIA(a)</i>	<i>Malacosoma disstria</i> (L) ^b <i>Lymantria dispar</i> (L)	McCown et al. (1991)
<i>P. nigra</i>	Tian et al. (1993)	<i>cryIA(c)</i>	<i>Lymantria dispar</i> (L) <i>Apochemia cinerarius</i> (L)	Wang et al. (1996)
<i>P. tremula</i> × <i>P. tremuloides</i>	Leplé et al. (1992)	<i>cryIIIA</i>	<i>Chrysomela tremulae</i> (C)	Cornu et al. (1996)
<i>P. tremula</i> × <i>P. tremuloides</i>	Brasileiro et al. (1991)	<i>ocl</i>	<i>Chrysomela tremulae</i> (C)	Leplé et al. (1995)
	Leplé et al. (1992)			
<i>P. alba</i> × <i>P. grandidentata</i>	Klopfenstein et al. (1991)	<i>pinII</i>	<i>Lymantria dispar</i> (L)	Heuchelin et al. (1997)
Flower development				
<i>P. tremuloides</i>	Nilsson et al. (1992)	<i>leafy</i>	Precocious flowering	Weigel and Nilsson (1995)
Alteration of metabolism				
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>ipt</i>	Cytokinin content	Von Schwartzenberg et al. (1994)
<i>P. tremula</i> × <i>P. alba</i>	Nilsson et al. (1992)	<i>iaaM</i> , <i>iaaH</i>	Hormone metabolism	Tuominen et al. (1995)
<i>P. tremula</i> × <i>P. tremuloides</i>	Nilsson et al. (1992)	<i>rolC</i>	Hormone metabolism	Nilsson et al. (1996)
<i>P. tremula</i> × <i>P. tremuloides</i>	Fladung et al. (1996)	<i>rolC</i>	Hormone metabolism	Ahuja and Fladung (1996)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>gor</i>	Glutathione metabolism	Foyer et al. (1995)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>gshII</i>	Glutathione metabolism	Foyer et al. (1995); Strohm et al. (1995); Arisi et al. (1997)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>gshI</i>	Glutathione metabolism	Noctor et al. (1996) Arisi et al. (1997)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>AS comt</i>	Lignin composition	Van Doorselaere et al. (1995)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>AS cad</i>	Lignin extractability	Baucher et al. (1996a)
Promoter studies				
<i>P. tremula</i> × <i>P. grandidentata</i>	Klopfenstein et al. (1991)	<i>ppin2/cat</i>	Wound-induced expression	Klopfenstein et al. (1991)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>pcad/gus</i>	Xylem-specific expression	Feuillet et al. (1995)
<i>P. tremula</i> × <i>P. tremuloides</i>	Nilsson et al. (1992)	<i>prolC/gus</i>	Seasonal-specific expression	Nilsson et al. (1996)
<i>P. tremula</i> × <i>P. alba</i>	Leplé et al. (1992)	<i>p-SAM/gus</i>	Tissue-specific expression	Mijnsbrugge et al. (1996)
<i>P. tremula</i> × <i>P. tremuloides</i>	Nilsson et al. (1992)	<i>p35S/gus</i>	Constitutive expression	Nilsson et al. (1996)
Transposable elements				
<i>P. tremula</i> × <i>P. tremuloides</i>	Fladung et al. (1996)	<i>p35S/Ac/rolC</i> <i>prbcs/Ac/rolC</i>	Phenotype modification	Ahuja and Fladung (1996)

* **aroA**: mutant EPSP synthase (glyphosate resistance);
bar: phosphinotricin acetyl transferase (phosphinotricin resistance);
cad: cinn3myllilcohol dhydrogenllse;
cat: ehloramphenieal acetyl transferase; **comt**: caffeic acid *O*-methyl transferase; **crs1-1**: mutant acetolactate synthase (chlorsulfuron resistance);
cryIA(c), **cryIA(a)**, **cryIIIA**: *Bacillus thuringiensis* δ -endotoxins genes;
gshI: γ -glutamylcysteine synthetase;

gshII: glutathione synthetase; **gor**: glutathione reductase;
gus: β -glucuronidase;
ipt: isopentenyl transferase;
iaaH: indole-3-acetamide hydrolase;
iaaM: tryptophan-2-mono-oxygenase;
luxF2: luciferase; **ocl**: cysteine proteinase inhibitor from rice (oryzacystatin);
p: promoter;
pinII: potato protease inhibitor II.

* L: Lepidoptera; C: Coleoptera.

Appendix IV

Table 4. Major policy measures related to biotechnology in China since the early 1980s (Huang & Wang, 2002).

Key Breakthrough Science & Technology Projects	Started in 1982 by SDPC. Updated every five years. One of major components of these projects is biotechnology R&D.
Patent system	Patent law promulgated 1985. A total of 1,599 applications on genetic engineering for invention patents were filed between 1985 and 1999.
National Biotechnology Development Policy Outline	Prepared by scientists and officials led by MOST, SDPC, and others in 1985. Formally issued by the State Council in 1988. The Outline defined the research priorities, development plan and measures to achieve targets.
National Key Laboratories (NKLs) on Biotechnology	Started in 1985 under MOST. Thirty National Key Laboratories in biotechnology (15 on agriculture or agriculture related) have been established. NKLs are open laboratories, inviting both domestic and international visiting fellows.
The Climbing Program	A National Program for Key Basic Research Projects, including biotechnology program, initiated in the early 1980s.
High Technology Research and Development Plan (863 Plan)	Approved in March 1986 with 10 billion RMB for 15 years to promote high-technology R&D in China. Biotechnology is one of seven supporting areas, with a total budget of about 1.5 billion RMB from 1986-2000.
Natural Science Foundation of China	Established in 1986 to support basic science research. Life science and agronomy are two support areas related to agrobiotechnology.
Biosafety regulations	MOST issued the Biosafety Regulations on Genetic Engineering in July of 1993, which include the biosafety grading and safety assessment, application and approval procedure, safety control measures, and legal regulations.
Agricultural biosafety regulations	MOA issued the Safety Administration, Implementation, and Regulations on Agricultural Biological Genetic Engineering in July 1996.
973 Plan	Initiated in March 1997 to support basic science and technology research. Life science is one of the key supporting areas.
Agricultural GMO Biosafety Committee	Ministry-level Agri GMO Biosafety Committee was set up in MOA in 1997. The Committee was updated in 2002 to national level with its office in MOA.
Special Foundation for Transgenic Plant Research and Commercialization	A five-year program launched in 1999 by MOST to promote the research and commercialization of transgenic plants in China. The total budget of this program in the first five years is 500 million RMB.
Key Science Engineering Program	Started in the late 1990s under MOST and SDPC to promote basic research, including biotechnology program. The first project on biotech (crop germplasm and quality improvement) was funded in 2000 with 120 million RMB.
Foundation for high-tech commercialization	A special program supported by the SDPC to promote the application and commercialization of technologies, started from 1998.
Seed Regulation and Law	Regulation on the Protection of New Varieties of Plants was issued in 1999. The first Seed Law was issued in 2000.
Updated and amended agricultural biosafety regulations	1996 MOA's biosafety regulation was amended and issued by the State Council in May 2001. Three regulations on the biosafety management, trade, and labeling of GM farm products were issued by MOA to take effect after March 20, 2002.
Foreign investment in GMOs	In April 2002, the SDPC, State Economic and Trade Commission, and MOTEC jointly issued a Guideline List of Foreign Investment, which puts GMO as a prohibited area for foreign investment

Appendix V

Table 5. All *lepisoptera* species feeding on *Populus euphratica* and their distribution (Robinson et al., 2010).

Lepidoptera Family	Lepidoptera Name	Hostplant Family	Hostplant Name	Country
Gelechiidae	<i>Istrianis squamodorella</i>	Salicaceae	<i>Populus euphratica</i>	Iraq
Gelechiidae	<i>Istrianis squamodorella</i>	Salicaceae	<i>Populus euphratica</i>	Palaeartic
Gracillariidae	<i>Phyllonorycter pruinoseella</i>	Salicaceae	<i>Populus euphratica</i>	Palaeartic
Noctuidae	<i>Helicoverpa armigera</i>	Salicaceae	<i>Populus euphratica</i>	India
Noctuidae	<i>Helicoverpa armigera</i>	Salicaceae	<i>Populus euphratica</i>	India
Sesiidae	<i>Synanthedon ommatiaeformis</i>	Salicaceae	<i>Populus euphratica</i>	India
Sesiidae	<i>Synanthedon ommatiaeformis</i>	Salicaceae	<i>Populus euphratica</i>	Oriental
Tortricidae	<i>Eucosma hapalosarca</i>	Salicaceae	<i>Populus euphratica</i>	India
Tortricidae	<i>Eucosma hapalosarca</i>	Salicaceae	<i>Populus euphratica</i>	Iran
Tortricidae	<i>Eucosma hapalosarca</i>	Salicaceae	<i>Populus euphratica</i>	Iraq
Tortricidae	<i>Eucosma hapalosarca</i>	Salicaceae	<i>Populus euphratica</i>	Palaeartic
Tortricidae	<i>Eucosma xerophloea</i>	Salicaceae	<i>Populus euphratica</i>	India
Tortricidae	<i>Eucosma xerophloea</i>	Salicaceae	<i>Populus euphratica</i>	Oriental
Tortricidae	<i>Gypsonoma riparia</i>	Salicaceae	<i>Populus euphratica</i>	India
Tortricidae	<i>Gypsonoma riparia</i>	Salicaceae	<i>Populus euphratica</i>	Oriental
Tortricidae	<i>Gypsonoma riparia</i>	Salicaceae	<i>Populus euphratica</i>	Oriental
Tortricidae	<i>Gypsonoma riparia</i>	Salicaceae	<i>Populus euphratica</i>	Pakistan

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