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Populus: A Premier Pioneer System for Plant Genomics

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ABSTRACT

The genus *Populus* has emerged as one of the premier systems for studying multiple aspects of tree biology, combining diverse ecological characteristics, a suite of hybridization complexes in natural systems, an extensive toolbox of genetic and genomic tools, and biological characteristics that facilitate experimental manipulation. Here we review some of the salient biological characteristics that have made this genus such a popular object of study. We begin with the taxonomic status of *Populus*, which is now a subject of ongoing debate, though it is becoming increasingly clear that molecular phylogenies are accumulating. We also cover some of the life history traits that characterize the genus, including the pioneer habit, long-distance pollen and seed dispersal, and extensive vegetative propagation. In keeping with the focus of this book, we highlight the genetic diversity of the genus, including patterns of differentiation among populations, inbreeding, nucleotide diversity, and linkage disequilibrium for species from the major commercially-important sections of the genus. We conclude with an overview of the extent and rapid spread of global *Populus* culture, which is a testimony to the growing economic importance of this fascinating genus.

Keywords: *Populus*, SNP, population structure, linkage disequilibrium, taxonomy, hybridization

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1.1 Introduction

The genus *Populus* is full of contrasts and surprises, which combine to make it one of the most interesting and widely-studied model organisms. *Populus* seeds are among the smallest produced by North American trees (Hewitt 1998), yet these tiny propagules ultimately yield some of the fastest-growing and largest angiosperm trees in the temperate regions (Dickmann 2001), and some genotypes reach astounding sizes by spreading vegetatively across the landscape (Mock et al. 2008). These tiny seeds carry very little endosperm and therefore require nearly optimal conditions for establishment, yet this tree occurs in some of the harshest environments in the world, including nutrient-poor sand bars that are subject to frequent flooding and scouring, boreal landscapes with severe winters and short growing seasons, and even harsh desert climates with xeric, saline, and alkaline soils.

Populus is also renowned (and reviled) for being almost completely intolerant of competition from other species, and for being highly susceptible to numerous pathogens and herbivores, thereby acquiring a reputation among land managers as a "*prima donna*" (Dickmann et al. 1987). Consequently, *Populus* is often confined to early successional stages, and is therefore an ephemeral presence in some systems. However, *Populus* is also eminently adapted for a pioneer life history, and it thrives on the cycles of cataclysmic disturbance that are typical of riparian ecosystems, continuously forming nearly monotypic stands on freshly deposited substrates. Furthermore, some species can attain dominance on a landscape scale, and individual clones can persist for hundreds or even thousands of years in the same locales (Kemperman and Barnes 1976; Mock et al. 2008).

The genus appears to have relatively low species diversity compared to some other tree genera, with only 30 to 40 species recognized by most taxonomists (Eckenwalder 1996). However, this relative simplicity is deceptive, because hybridization is rampant across the genus, and many species form intergrading hybrid swarms, often involving multiple species mixing in all possible combinations (Eckenwalder 1984a; Floate 2004). Closely-related sympatric species, therefore, have variable levels of introgression, which creates challenges and opportunities for systematists and evolutionary biologists interested in mechanisms of species isolation and persistence. These hybrid swarms are also zones of tremendous genetic diversity layered upon substantial environmental heterogeneity. This has created a setting in which remarkably strong genetic effects are exerted by the host tree onto the complex communities of associated organisms, which has helped to spur the development of the new field of community genetics (Whitham et al. 2006). All of this and more has grown from the humble beginnings of a tiny, wind-blown seed. In this chapter we will provide a broad overview of the biological characteristics of this genus, with a particular focus on those features that make *Populus* a pioneer model organism in comparative, functional, and ecological genomics research.

1.2 Systematics and Evolution

1.2.1 *Taxonomic Position of the Genus* Populus

Populus and *Salix* (willows) have traditionally been considered the only two genera in the Salicaceae family (Eckenwalder 1996). However, a number of genera formerly included in the Flacourtiaceae are now assigned to Salicaceae *sensu lato*, within the Malpighiales order of the "Eurosid I" clade (Chase et al. 2002; Angiosperm Phylogeny Group 2003). The closest genera to *Populus* and *Salix* within the Salicaceae *sensu lato* are mostly woody tropical species, including the genera *Chosenia*, *Idesia*, *Itoa*, *Carrierea*, *Bennettiodendrion*, and *Poliothyrsis*, all native to the Asian subcontinent (Cronk 2005), which is apparently the center of diversity for the Salicaceae.

Recent molecular phylogenetic studies in the Salicaceae (Leskinen and Alstrm-Rapaport 1999; Cervera et al. 2005; Hamzeh et al. 2006) have shown that *Populus* and *Salix* clearly form two separate groups. Interestingly, in one of these studies the presumably most ancient species of *Populus* (*P. mexicana*; Eckenwalder 1996) showed higher similarity to *Salix* than to any other species of *Populus* (Cervera et al. 2005). It still remains an open question whether *Populus* and *Salix* are truly monophyletic.

1.2.2 Classification at the Species Level

There is broad disagreement about the number of species in the genus *Populus*, with some taxonomists recognizing as few as 22 species and others enumerating as many as 85 species, including 53 in China alone (Eckenwalder 1996; Dickmann 2001). The difficulties in taxonomy arise because of the extensive phenotypic variation observed within broadly-distributed *Populus* species, as well as the existence of many hybrids, which blur the lines between some species, and which themselves are sometimes misclassified as separate species (Eckenwalder 1996). The classification scheme most commonly used today is that of Eckenwalder (1996), who recognized 29 species subdivided into six sections based on relative morphological similarity and crossability (Table 1-1). A consensus cladogram from the 840 most parsimonious trees built based on 76 morphological characters (Fig. 6 in Eckenwalder 1996) provided evidence that all sections except for *Tacamahaca* are monophyletic. Section *Tacamahaca* was split into two monophyletic groups, one comprised of "typical balsam poplars" (e.g., *P. balsamifera* and *P. trichocarpa*) and the other comprised of "narrow-leaved, thin-twigged" species (e.g., *P. angustifolia* and *P. simonii*).

Table 1-1 Eckenwalder's (1996) classification of the genus *Populus*.

Section [synonym]	Species	Distribution
Abaso Eckenwalder	*Populus mexicana* Wesmael	Mexico
Turanga Bunge	*P. euphratica* Olivier	Africa, Asia
	P. ilicifolia (Engler) Rouleau	Africa
	P. pruinosa Schrenk	Asia
Leucoides Spach	*P. glauca* Haines *sl*[b]	China
	P. heterophylla L.	N America
	P. lasiocarpa Olivier	China
Aigeiros Duby	*P. deltoides* Marshall *sl*[c]	N America
	P. fremontii S. Watson	N America
	P. nigra L.	Eurasia, N Africa
Tacamahaca Spach	*P. angustifolia* James	N America
	P. balsamifera L.	N America
	P. ciliata Royle	Himalayas
	P. laurifolia Ledebour	Eurasia
	P. simonii Carrière	E Asia
	P. suaveolens Fischer *sl*[d]	China, Japan
	P. szechuanica Schneider	Eurasia
	P. trichocarpa Torrey & A. Gray	N America
	P. yunnanensis Dode	Eurasia
Populus[a]	*P. adenopoda* Maximowicz	China
	P. alba L.	Eurasia, Africa
	P. gamblei Haines	Eurasia
	P. grandidentata Michaux	N America
	P. guzmanantlensis Vazques & Cuevas	Mexico
	P. monticola Brandegee	Mexico
	P. sieboldii Miquel	Japan
	P. simaroa Rzedowski	Mexico
	P. tremula L.	Eurasia, Africa
	P. tremuloides Michaux	N America

[a] Synonymous with *Leuce* Duby.
[b] *Sensu lato.* Synonymous with *P. wilsonii* Schneider.
[c] Synonymous with *P. sargentii* Dode and *P. wislizenii* Sargent.
[d] Synonymous with *P. cathayana* Rehder, *P. koreana* Rehder, and *P. maximowiczii* A. Henry.

1.2.3 Origin and Evolution of **Populus**

Populus appears in the fossil record after the Eocene (40 million years ago (MYA)), and probably as early as the late Paleocene (58 MYA; Eckenwalder 1996; Dickmann and Kuzovkina 2008). A representative of the *Abaso* section related to modern *P. mexicana* is the oldest clearly identifiable *Populus* fossil specimen. The swamp poplars of the section *Leucoides* appeared in the late Eocene period (40 MYA) in temperate regions of North America and Asia. Fossils from the Oligocene period (30 MYA) representing ancestors of the sections *Tacamahaca* and *Aigeiros* have been found in both the new and old worlds. Representatives of section *Populus*, however, did not appear in fossil records until the early Miocene (20 MYA; Eckenwalder 1996; Cronk 2005).

Combining fossil records with information from phylogenetic analyses, Eckenwalder (1996) speculated that the genus originated in North America or tropical Asia during the Paleocene, and that the three "advanced" sections of the genus, *Populus*, *Aigeiros*, and *Tacamahaca*, evolved rapidly in their distinctive habitats during the Miocene. Recent studies based on molecular markers mostly support the delineations of sections and their evolutionary relationships (Cervera et al. 2005; Hamzeh et al. 2006). However, numerous questions remain to be resolved. For example, analyses based on chloroplast DNA clearly group *P. nigra* with section *Populus* (Smith and Sytsma 1990; Hamzeh and Dayanandan 2004), yet analyses based on nuclear DNA and morphology clearly place *P. nigra* in section *Aigeiros* (Eckenwalder 1996; Hamzeh and Dayanandan 2004; Cervera et al. 2005). There is also some ambiguity about the position of section *Populus* (also called *Leuce*), and the taxonomic status of *P. mexicana*, which may be divergent enough to be removed from the genus (Cervera et al. 2005). Also, *P. angustifolia* groups more closely with Asian species from section *Tacamahaca* rather than with the sympatric *P. trichocarpa* and *P. balsamifera* in some molecular phylogenies (Cervera et al. 2005), raising the possibility that the current sympatry with those two species is due to secondary contact following intercontinental migration. Many of these questions are likely to be resolved as molecular data accumulate throughout this genus.

1.2.4 Natural Hybridization

Many problems in the taxonomy of *Populus* may prove intractable due to the extensive occurrence of hybridization and the possibility that reticulate evolution has played a role in the evolution of the modern taxa (Eckenwalder 1996; Hamzeh and Dayanandan 2004; Cervera et al. 2005; Hamzeh et al. 2006). For example, based on variation in leaf morphology across the extensive range of *P. tremuloides* and similarity to fossil aspen taxa, Barnes (1967) and Eckenwalder (1996) hypothesized that the modern species is actually a "compilospecies" derived from hybridization among multiple ancestral species. Hybridization occurs freely within sections and also between closely-related sections of the genus (Fig. 1-1), and natural hybrids have been observed in most locations where compatible species co-occur (Eckenwalder 1984a, b, c; Rood et al. 1986; Campbell et al. 1993; Martinsen et al. 2001; Floate 2004; Lexer et al. 2005; Hamzeh et al. 2007). For example, most of the five North American species from sections *Aigeiros* and *Tacamahaca* overlap in their ranges (Fig. 1-2), and most hybrid combinations are found in the wild (Eckenwalder 1984a), including some complex hybrids involving three species (Floate 2004). Interestingly, many *Populus* hybrid zones show nonrandom patterns of introgression, with crossing often occurring preferentially in the direction of one of the parental species (Keim et al. 1989; Floate 2004; Lexer et al. 2005). Furthermore, not all portions of the genome introgress equally: some genome segments introgress more than expected based on overall rates of hybridization, and some portions seem to be inhibited in their introgression (Martinsen et al. 2001; Lexer and van Loo 2006).

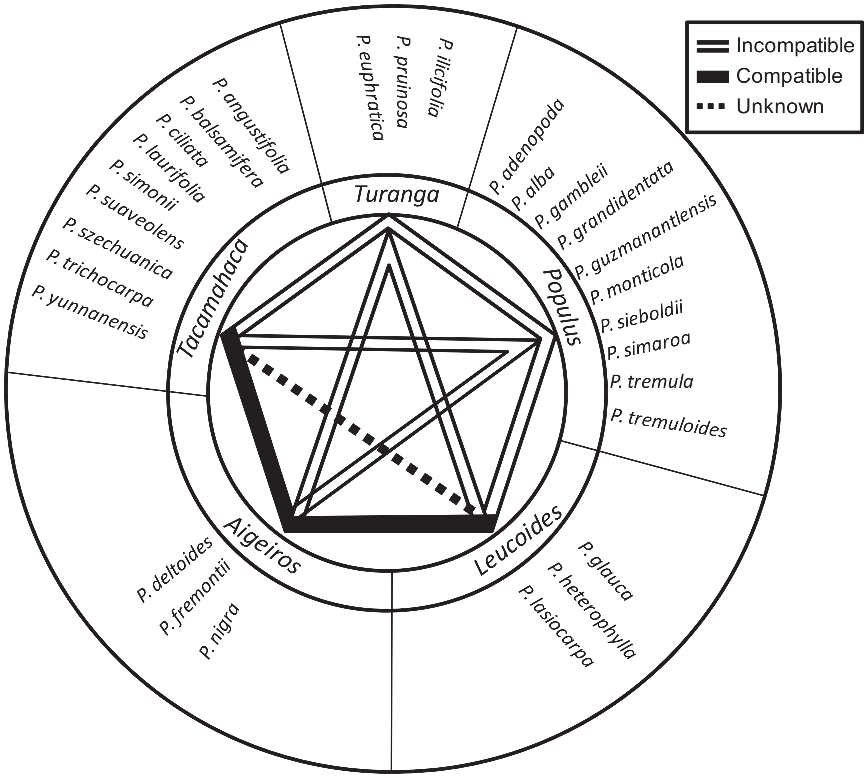

Figure 1-1 Crossing relationships for *Populus* species. Solid lines connecting sections indicate that species from these sections intercross freely. Open lines indicate that crosses do not normally occur spontaneously, and can only be accomplished using specialized procedures. The dashed line indicates that insufficient data exist to definitively characterize compatibility of species from sections *Leucoides* and *Tacamahaca*. After Willing and Pryor (1976).

Populus hybrids zones have proven to be fertile areas for ecological research because of their high levels of genetic variation and a diverse and sometimes unique assemblage of dependent organisms, including arthropods (Wimp et al. 2005), microbes (Schweitzer et al. 2005), and fungi (Bailey et al. 2005). Furthermore, the biotic community is apparently determined in part by the genotypic composition of the *Populus* hybrids, which has led to the development of concepts like community heritability and even community evolution (Whitham et al. 2006). *Populus* hybrids

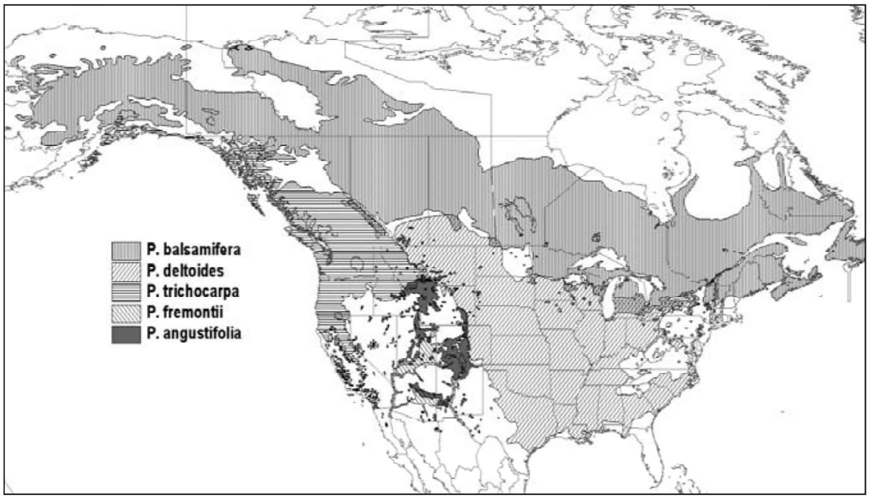

Figure 1-2 Ranges of the North American species from sections *Aigeiros* and *Tacamahaca*. Overlap occurs among most pairs of species in some portion of their range, and hybridization zones exist in many of these zones of overlap. Range maps were created from GIS layers obtained from the USGS Earth Surface Processes web site (*http://esp.cr.usgs.gov/data/atlas/little/*).

seem to have unique characteristics that set them apart from either of the parental species. For example, relict stands of hybrids often occur far away from the current distribution of one or both of the presumed species, suggesting that hybrids are adapted in locations where the parental species are not (Woolbright et al. submitted). Hybrid zones have therefore yielded numerous insights about the nature of species boundaries and the structure and functioning of communities and ecosystems, and the application of genomic tools in these natural laboratories is likely to accelerate the pace of discovery in many fields (Whitham et al. 2008).

1.3 Life History

1.3.1 Habitat

The supreme adaptability of *Populus* is revealed by its extensive and varied range. Although *Populus* species are mostly confined to the Northern Hemisphere, individual species span entire continents across a startling range of environments. For example, *P. tremuloides* is the most widely distributed tree in North America, spanning 111° of longitude and 48° of latitude, stretching from the west to east coasts and from northern Alaska to central Mexico (Perala 1990). *Populus* species also span a remarkable range of habitats. The cottonwoods, species from sections *Aigeiros* and *Tacamahaca*, are typically riparian (Fig. 1-3), thriving on the fresh sediments deposited by flooding (Fig. 1-4) and capitalizing on establishment opportunities created by ice scouring and even fire (Braatne et al. 1996; Rood et al. 2007). However, even within these sections there is substantial variation in habitats, with cottonwoods occurring on upland sites in northern regions

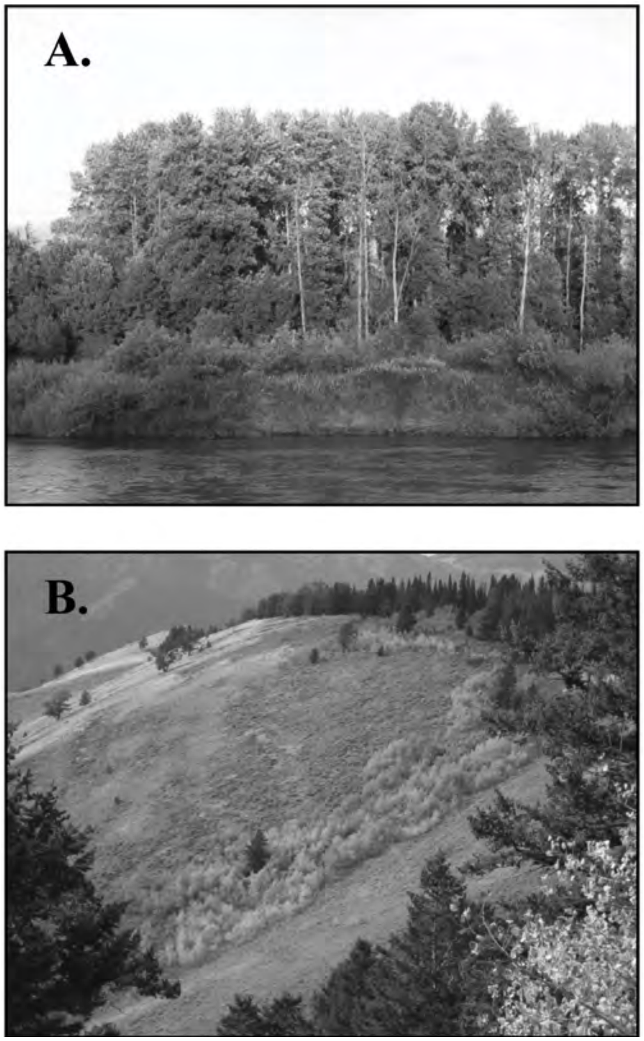

Figure 1-3 Photos of *Populus* habitats and reproductive structures. (A) A typical *P. trichocarpa* stand on the Willamette River near Salem, Oregon. (B) Stands of *P. tremuloides* in Grand Teton National Park, Wyoming. Different genets can be distinguished based on variation in fall leaf colors. All photos by S. DiFazio.

Color image of this figure appears in the color plate section at the end of the book.

where desiccation is not excessive (Dickmann 2001), and even as isolated patches of trees associated with warm springs in vast stretches of arctic tundra (Zasada and Phipps 1990).

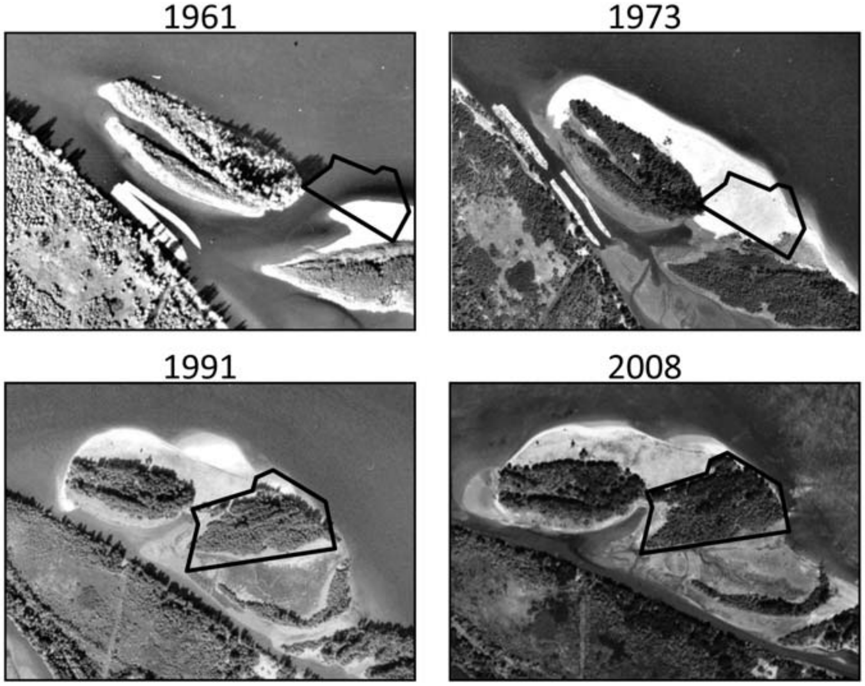

Figure 1-4 Chronosequence of air photos depicting establishment of *P. trichocarpa* populations on Gull Island on the Columbia River near Clatskanie, Oregon. A sand bar was deposited between 1961 and 1973, and a *P. trichocarpa* stand became established between 1973 and 1983 (indicated by a black outline in each photograph). Photos courtesy of U.S. Army Corps of Engineers, except 2008 photo, which is from Google Earth.

Poplars from section *Populus* show much broader ranges of habitats. For example, *P. tremuloides* and the closely-related *P. tremula* occur in mountainous or upland habitats and mixed conifer forests as well as in nearly pure stands in riparian areas (Perala 1990; Lexer et al. 2005). Other species of this section have more restricted habitats. For example, *P. alba* is almost exclusively riparian in some parts of its range in Europe (Lexer et al. 2005), whereas it is found on a much broader range of sites in other parts of its extensive range (Dickmann 2001). *P. grandidentata*, the North American big-toothed aspen, has a more restricted range than *P. tremuloides*, and tends to occur on sites with better drainage than *P. tremuloides* in their zones of overlap (Laidly 1990; Dickmann 2001). This ecological differentiation is perhaps one of the factors that maintains the various members of section *Populus* as separate species in Europe and North America despite extensive potential for hybridization (Lexer et al. 2005).

The genus also includes several species with distinctive habitats and distributions. Section *Leucoides* presents an interesting case because this was the first section to appear in the North American fossil record after *Abaso* (Eckenwalder 1996; Cronk 2005), perhaps indicating that it is ancestral to sections *Populus*, *Aigeiros*, and *Tacamahaca*. However, this section is now represented by only a single species in North America, *P. heterophylla*, which has a very limited distribution, restricted to permanent swamps of the eastern US (Johnson 1990). Perhaps the most ecologically idiosyncratic section of the genus is *Turanga*, which includes *P. euphratica*, a species that grows in extremely hot and dry environments with water tables as deep as 10–13 m (Ma et al. 1997; Hukin et al. 2005). This species shows high tolerance of salinity, surviving doses approaching sea water (300 mM; Chen et al. 2002).

1.3.2 Sexual Reproduction

Populus species are mostly dioecious, with separate male and female sexes, although the occurrence of cosexual trees has been reported in multiple species (Stettler 1971; Rottenberg et al. 2000; Rowland et al. 2002; Cronk 2005; Slavov et al. 2008). *Populus* flowers occur in pendent catkins with strongly reduced perianths (Boes and Strauss 1994; Eckenwalder 1996). *Populus* trees reach reproductive maturity within 4–8 years in intensively managed plantations and within 10–15 years under favorable conditions in natural populations (Stanton and Villar 1996). Flowering usually occurs before leaf emergence in early spring (Braatne et al. 1996; Eckenwalder 1996). Individual trees flower for 1–2 weeks (Stanton and Villar 1996), but the pollination period in a population can exceed one or even two months (Braatne et al. 1996). The timing of flowering depends in part on temperature, with populations at higher elevations, more northern latitudes, and more continental climates flowering later (DeBell 1990; Perala 1990; Zasada and Phipps 1990; Braatne et al. 1996). Pollen is dispersed by wind, and effective pollination distances can be extensive (Tabbener and Cottrell 2003; Lexer et al. 2005; Pospíšková and Šálková 2006; Vanden Broeck et al. 2006; Slavov et al. 2009). Fertilization occurs within 24 hours after a viable pollen grain has landed on a receptive stigma (Braatne et al. 1996). Capsules typically dehisce 4–6 weeks after fertilization, but seed development can occur in as little as 2–3 weeks or as long as 3–5 months in some species and locations.

The timing of seed dispersal tends to coincide with annual flooding, which creates favorable sites for seed establishment for many species (Braatne et al. 1996; Stella et al. 2006). Seeds are produced in great numbers (> 25 million per tree per year; Braatne et al. 1996), and their small size and cotton-like appendages facilitate dispersal over large distances by wind and water (Johnson 1994; Braatne et al. 1996; Karrenberg et al. 2002).

Seeds normally retain viability for only 1–2 weeks in natural systems, and germination occurs within 24 hours under warm, moist conditions (Braatne et al. 1996; Karrenberg et al. 2002). Seedlings can establish in great numbers on bare, moist mineral substrates (e.g., up to 4,000 m^{-2}), but mortality in the first year can be quite high due to the severe conditions found in most establishment sites (Braatne et al. 1996; Karrenberg et al. 2002; Dixon 2003; Dixon and Turner 2006).

1.3.3 Vegetative Propagation

The extensive occurrence of vegetative propagation (also called asexual reproduction) sets *Populus* apart from most other dominant temperate trees (Dickmann 2001). Vegetative propagation is one of the traits that enable *Populus* to occupy tumultuous habitats along river banks and to persist long-term in landscapes that are frequently reset by large-scale fires. Vegetative propagation is also one of the traits that make *Populus* such an attractive model organism and one of the features that allows rapid deployment of genetically improved materials due to an almost unlimited capacity for replicating high-performing genotypes, thus capturing both additive and nonadditive genetic variation.

The extent and modes of reproduction vary tremendously among the different sections of the genus. Some species from section *Populus* have extensive vegetative propagation, as typified by the North American quaking aspen (*P. tremuloides*; Fig. 1-3). This species spreads vegetatively through the production of vegetative sprouts from adventitious buds on shallow lateral roots, a process known as “suckering” (Perala 1990). Suckering is believed to have been the predominant means of reproduction of *P. tremuloides* in the western part of its range in the recent past, with sexual reproduction from seeds occurring only rarely (Romme et al. 1997, 2005). Some aspen clones have reached a remarkable size, and have even been described as the largest organisms known (Kemperman and Barnes 1976; DeWoody et al. 2008; Mock et al. 2008). These large clone sizes and putative rarity of sexual reproduction have led to speculation that aspen clones could be thousands of years old (Barnes 1975; Mitton and Grant 1996). However, relatively high genotypic diversities have been observed in most genetic studies of aspen clones (Hyun et al. 1987; Jelinski and Cheliak 1992; Lund et al. 1992; Liu and Furnier 1993; Yeh et al. 1995; Namroud et al. 2005), suggesting that sexual reproduction may be more frequent and/or its impact on the genetic structure of aspen populations may be more persistent than previously assumed. Observations of large numbers of somatic mutations in vegetative tissues of extensive aspen clones suggests that advanced ages are possible for individual genets, but accurate estimation of clone age remains a substantial technical challenge (Ally et al. 2008; Mock et al. 2008).

Trees from section *Tacamahaca*, including the North American cottonwoods *P. balsamifera*, *P trichocarpa*, and *P. angustifolia*, commonly spread vegetatively through rooting of shoots from broken branches or entire tree trunks that have been toppled during storms and floods and then buried in sediment (Braatne et al. 1996; Rood et al. 2003; Barsoum et al. 2004; Rood et al. 2007; Smulders et al. 2008). One unusual mode of vegetative propagation in this section is cladoptosis, the continuous self-pruning of live short-shoots, which then act as propagules that can be dispersed by wind or water and become established (Galloway and Worrall 1979; Dewit and Reid 1992). However, in some settings, the breakage and subsequent transport of large branches by flood waters is the most important mode of vegetative propagation in this section, and cladoptosis contributes little to vegetative spread (Rood et al. 2003). Stem coppicing and root sprouting also occur in *Tacamahaca* cottonwoods, but these are usually not as important as branch and stem sprouting for vegetative spread (Rood et al. 1994; Rood et al. 2003) except when shallow roots are disturbed or the main stem is destroyed by fire or breakage (Rood et al. 1994; Gom and Rood 1999a, b).

Trees from section *Aigeiros* typically have less extensive vegetative propagation than species from *Populus* or *Tacamahaca* (Braatne et al. 1996; Bradshaw and Strauss 2001; Rood et al. 2007). For example, the North-American plains cottonwood (*P. deltoides*) and Fremont cottonwood (*P. fremontii*) have relatively rare vegetative propagation, which occurs primarily via coppicing of broken or killed shoots (Braatne et al. 1996; Gom and Rood 1999b; Schweitzer et al. 2002; Rood et al. 2003), although there are reports of extensive root sprouting in *P. fremontii* in some settings (Howe and Knopf 1991). *P. nigra* shows higher levels of vegetative propagation than North American cottonwoods from this section, sprouting extensively from branches, roots, and broken stems (Legionnet et al. 1997; Arens et al. 1998; Barsoum et al. 2004).

1.3.4 Sex Ratios

Sex ratios in natural *Populus* populations are highly variable, with many studies revealing male-biased ratios, some studies showing no deviation from the 1:1 expectation, and a few studies showing a female bias (reviewed by Braatne et al. 1996; Farmer 1996; Stanton and Villar 1996; see also Gom and Rood 1999b; Rottenberg et al. 2000; Rowland et al. 2001; Hultine et al. 2007). Although no consistent pattern has emerged, several of these studies suggest that biases in sex ratio may be driven by differential responses of the sexes to environmental conditions. For example, several studies have shown that males are more common and have superior growth at high elevations, as well as in warmer, drier, and more extreme environments, while females predominate where moisture is higher and resources are more abundant (Grant and Mitton 1979; Sakai and Burris 1985; Rottenberg et al. 2000). Controlled physiological studies have recently supported the contention that male and female *P. cathayana* (*P. suaveolens sensu lato*) have differential drought responses, with males showing smaller growth reductions than females (Xu et al. 2008b), and greater photosynthetic adjustment under drought treatments (Xu et al. 2008a). Similarly, male clones of *P. tremuloides* showed higher basal photosynthetic rates and greater responsiveness to elevated CO_2 compared to male clones (Wang and Curtis 2001). There are therefore intriguing possibilities for sexual selection in dioecious species like *Populus*, especially given the possible existence of a sex chromosome with reduced recombination (Yin et al. 2008). However, future studies on natural populations will need to take into account developmental differences between the two genders (e.g., male trees may reach reproductive maturity before female trees, thus possibly skewing sex ratios; Stanton and Villar 1996) and the effects of clonality, which can greatly reduce genotypic sampling and therefore yield apparently skewed sex ratios due to sampling error.

1.4 Genetic Variation

1.4.1 Neutral Diversity and Differentiation

Numerous studies have characterized patterns of variation in *Populus* using putatively neutral molecular markers like allozymes, Restriction Fragment Length Polymorphisms (RFLP), and microsatellites (Simple Sequence Repeat, SSR). Although there is substantial variation among species and marker types, the overall conclusion is that *Populus* species show high levels of variation within populations and low levels of differentiation among populations (Table 1-2), as is expected for obligately outcrossing organisms with large effective population sizes and long-distance dispersal of pollen and seeds (Hamrick et al. 1992). Levels of polymorphism and expected heterozygosity are higher for *Populus* than for plants in general ($A = 1.5$, $H_e = 0.11$), but close to the mean values for long-lived woody species ($A = 1.8$, $H_e = 0.15$; Hamrick et al. 1992), with SSR markers showing substantially higher allelic diversity and heterozygosity than allozymes and RFLP, as expected. Multiple studies show a deficiency of heterozygotes compared to Hardy-Weinberg expectations, which is probably due in part to undetected substructure in population samples (Hedrick 2005), and/or null alleles (Ewen et al. 2000). Population differentiation as measured by F_{ST} (Wright 1965) is quite low in most studies, with differences among populations accounting for only 1 to 12% of the total genetic variation (Table 1-2). In comparison, the mean F_{ST} for long-lived woody species is 0.084, and that for plants in general is 0.228 (Hamrick et al. 1992). The relatively

Table 1-2 Molecular diversity and differentiation in *Populus* based on allozymes (Allo.), RFLP, and SSR markers.

Section	Species	Marker	N_{loci}	N_{pop}	N	A	H_o	H_e	F_{IS}	F_{ST}	Reference
Aigeiros	*P. deltoides*	Allo.	33	9	84	1.7	0.06	-	-	-	Rajora et al. 1991
		Allo.	22	21	-	1.5	-	0.08	-	0.064	Marty 1984
	P. fremontii	RFLP	36	4	47	1.5	0.18	0.15	-0.175	0.074	Martinsen et al. 2001
	P. nigra	Allo.	8	3	146	-	-	0.16	0.113	0.063	Legionnet and Lefvre 1996
		SSR	6	22	574	-	0.78	0.73	-0.077	0.047	Imbert and Lefevre 2003
		SSR	7	17	921	-	0.74	0.76	0.027	0.081	Smulders et al. 2008
Tacamahaca	*P. angustifolia*	RFLP	36	10	281	1.4	0.10	0.08	-0.236	0.022	Martinsen et al. 2001
	P. balsamifera	Allo.	17	5	248	-	-	0.04	0.061	0.014	Farmer et al. 1988
	P. trichocarpa	Allo.	18	10	456	1.2	-	0.09	-	0.063	Weber and Stettler 1981
		SSR	10	2	282	17.5	0.71	0.77	0.058	-	Slavov et al. 2008
		SSR	9	47	372	6.1	0.60	0.80	0.293	0.078	M. Ismail, unpublished data
Populus	*P. alba*	SSR	19	1	169	6.4	0.37	0.38	0.027	-	van Loo et al. 2008
	P. grandidentata	Allo.	14	-	96	1.4	0.07	0.08	0.125	-	Liu and Furnier 1993
		RFLP	37	-	75	1.8	0.12	0.13	0.077	-	Liu and Furnier 1993
	P. tremula	SSR	9	3	113	-	0.35	0.41	0.120	0.117	Suvanto and Latva-Karjanmaa 2005
		SSR	25	12	116	-	0.50	0.62	0.197	0.015	Hall et al. 2007
	P. tremuloides	Allo.	13	-	118	2.8	0.19	0.25	0.240	-	Liu and Furnier 1993
		Allo.	17	6	156	2.4	0.32	0.29	-0.102	0.030	Jelinski and Cheliak 1992
		Allo.	15	8	200	2.7	0.13	0.24	0.462	0.068	Hyun et al. 1987
		Allo.	26	7	222	2.3	0.52	0.42	-0.238	-	Cheliak and Dancik 1982
		Allo.	10	9	347	2.6	0.22	0.22	0.017	0.003	Lund et al. 1992
		RFLP	41	-	91	2.7	0.21	0.25	0.160	-	Liu and Furnier 1993
		SSR	16	11	189	4.9	0.41	0.45	0.093	0.045	Cole 2005
		SSR	4	-	266	8.8	0.47	0.67	0.300	-	Namroud et al. 2005
Turanga	*P. euphratica*	Allo.	20	3	85	1.8	0.10	0.24	0.592	-	Rottenberg et al. 2000
	Median	Allo.	17	7.5	156	2.1	0.16	0.22	0.113	0.063	
		RFLP	36.5	7.0	83	1.7	0.15	0.14	-0.049	0.048	
		SSR	9.0	11.5	266	6.4	0.50	0.67	0.093	0.063	

N_{loci} is the number of loci used; N_{pop} is the number of populations sampled; N is the number of genets (or trees) analyzed; A is the average number of alleles per locus detected in each population; H_e is the expected heterozygosity (Nei 1973); F_{IS} is the fixation index as reported in the study or calculated as $F_{IS} = (H_e\text{-}H_o)/H_e$; F_{ST} is the among-population differentiation (Wright 1965).

weak differentiation among *Populus* populations is probably a reflection of extensive gene flow by pollen, which is corroborated by numerous direct studies based on paternity analysis (Tabbener and Cottrell 2003; Pospíšková and Šálková 2006; Vanden Broeck et al. 2006; Slavov et al. 2009).

It is intriguing that trembling aspen species (*P. tremula* and *P. tremuloides*) have consistently higher numbers of alleles per locus and expected heterozygosity for allozyme and RFLP markers compared to other *Populus* species (Table 1-2). The median gene diversity from six studies of *P. tremuloides* ($H_e = 0.25$) is comparable to that from two studies of its "sister" species *P. tremula* in Europe ($H_e = 0.20$), and is more than two times higher than that for other species of *Populus* ($H_e = 0.09$). This is in agreement with the general trend in woody plants (mean $H_e = 0.25$ for species with both asexual and sexual reproduction versus $H_e = 0.14$ for species that only reproduce sexually; Hamrick et al. 1992). One possible explanation lies in the extensive occurrence of vegetative propagation in aspens, as described above. Highly clonal organisms typically show higher allelic diversity and heterozygosity compared to organisms with similar life histories due to the accumulation of mutations (Balloux et al. 2003; Halkett et al. 2005; de Meeûs et al.2007). Another possible explanation is that some of the sampled trees were polyploids, an occurrence that seems to be relatively common in section *Populus* (Mock et al. 2008; Zhu et al. 1998; DiFazio et al., unpublished). Polyploidy could cause an apparent excess in allelic diversity and heterozygosity due to sampling of extra chromosomes (Krieger and Keller 1998; Ridout 2000). A final possibility is that this increased allelic diversity is a result of the hypothesized hybrid origin of these species, as described above (Barnes 1967). It will be interesting to see if this phenomenon is upheld by rangewide studies of genetic variation in microsatellite and SNP markers, and if further insights are gained into the mechanisms of elevated genetic diversity in aspen.

1.4.2 Nucleotide Diversity

The whole-genome sequence of *P. trichocarpa* provides an excellent resource for enhancing our understanding of the population genetics and genomics of the genus. Levels of nucleotide diversity in *Populus* are highly variable (Table 1-3), but generally comparable to those in other tree species (González-Martínez et al. 2006b; Savolainen and Pyhäjärvi 2007). Interestingly, nucleotide diversity in trees does not seem to be substantially higher than in other plants, including the nearly completely selfing annual *Arabidopsis thaliana* (Savolainen and Pyhäjärvi 2007). Presumably, this is due to the long generation times of trees, and the possible existence of genetic bottlenecks in the evolutionary history of many trees (Savolainen and Pyhäjärvi 2007; Ingvarsson 2008). Although data on among-population differentiation for

Table 1-3 Nucleotide diversity, linkage disequilibrium, and differentiation in *Populus*.

Species	N_{genes}	N_{pop}	N_{hap}	S_{kb}	π	π_S	π_N	$LD_{0.2}$	F_{ST}	Reference
P. nigra	9	-	48	38.7	0.0070	0.0107	0.0046	300	-	Chu et al. 2009
P. trichocarpa	9	-	78	7.7	0.0018	0.0029	-	-	-	Gilchrist et al. 2006
P. balsamifera	11	7	185	18.7	0.0020	0.0030	0.0008	-	0.053	Keller et al. 2010
P. balsamifera	460	15	30	10.5	0.0026	0.0045	0.0012	-	-	Olson et al. 2010
P. angustifolia	3	8	64	17.5	0.0024	-	-	120	0.086	Slavov et al., unpublished data
P. tremula	5	4	48	-	0.0111	0.0220	0.0059	<100	0.117	Ingvarsson 2005b
	6	4	44	68.0	0.0144	0.0207	0.0117	-	0.107	Ingvarsson 2005a
	1	4	48	39.3	0.0061	0.0085	0.0030	-	0.045	Ingvarsson et al. 2006
	76	-	24–38	19	0.0042	0.0120	0.0017	<100	-	Ingvarsson 2008

N_{genes} is the number of genes sequenced; N_{pop} is the number of populations analyzed; N_{hap} is the number of haplotypes sequenced; S_{kb} is the number of Single Nucleotide Polymorphisms (SNP) per 1 kb of sequence; π is the overall nucleotide diversity; π_S is the nucleotide diversity for synonymous sites; π_N is the nucleotide diversity for nonsynonymous sites; $LD_{0.2}$ is the distance (bp) at which mean linkage disequilibrium between pairs of loci (r^2) decays to 0.2; F_{ST} is the average among-population differentiation based on SNP.

SNP markers are still extremely limited in *Populus*, the few available values of F_{ST} appear slightly higher but generally comparable with those based on other types of codominant markers (Tables 1-2 and 1-3).

In contrast to nucleotide diversity, the rate of decay of linkage disequilibrium (LD) with distance among sites appears to be extraordinarily high in some *Populus* populations. For example, average LD (as measured by the r^2 statistic) has been observed to decay below 0.2 within several hundred bp in *P. nigra*, *P. tremula*, and *P. angustifolia*, but other studies in *P. trichocarpa* and *P. balsamifera* have found that decay occurs over much greater distances (Table 1-3). In contrast, LD declines to background levels within 0.5 to 1.5 kb in conifers (Neale and Savolainen 2004; Krutovsky and Neale 2005; Heuertz et al. 2006; González-Martinez et al. 2006a), and within 10 kb in Arabidopsis thaliana. The reasons for this discrepancy among Populus species is far from clear, but it appears to be driven in part by population structure and population history (Invarsson 2008; Olsen et al. 2010) as well as substantial variation in recombination rates across the genome (Slavov et al. in preparation).

The levels of LD have major implications for gene discovery and characterization using association genetics in natural populations of *Populus*. On the one hand, low LD makes candidate gene association studies very accurate because polymorphisms underlying an association are expected to be within <1 kb of the SNP used to detect it. On the other hand, however, low LD renders whole-genome approaches unfeasible in the near future because millions of markers would be needed to scan a tree genome. The creative combination of plant materials characterized by high LD (e.g., sib families or hybrids) with natural populations characterized by very low LD, as well as the development of appropriate study designs and analytical approaches is a major short-term priority for population and quantitative geneticists working with *Populus* and other forest trees (Lexer and van Loo 2006; Lexer et al. 2007).

1.4.3 Adaptive Traits

Populus trees typically have high levels of adaptive genetic variation both within and among populations (Farmer 1996; Dunlap and Stettler 1996; Howe et al. 2003). Furthermore, differentiation among populations is generally much higher for adaptive traits than for neutral genetic markers (Merila and Crnokrak 2001; McKay and Latta 2002; Howe et al. 2003; Savolainen et al. 2007), which suggests that divergent selection has played a dominant role in shaping adaptive genetic variation. Finally, and most importantly, genecological studies have revealed strong and repeatable correspondence between clinal genetic variation for adaptive traits, and climatic and geographic factors are believed to be important agents of natural selection (Morgenstern 1996; St Clair et al. 2005; Aitken et al. 2008). For example, genetic variation for phenological traits occurs along latitudinal gradients in multiple *Populus* species (Farmer 1996; Böhlenius et al. 2006; Hall et al. 2007; Friedman et al. 2008), suggesting that tradeoffs between length of growing season and risk of frost damage have driven patterns of adaptive differentiation in *Populus* populations. All of this suggests that *Populus* populations are likely to be locally adapted (i.e., genotypes originating from a given habitat tend to have higher fitness in that habitat than genotypes originating from other habitats; Kawecki and Ebert 2004). This has serious implications for potential responses of *Populus* species to rapid anthropogenic climate change (Savolainen et al. 2007; Aitken et al. 2008), although the situation for *Populus* is arguably better than that for other, less vagile forest trees.

1.5 Domestication and Silviculture

Populus cultivation began in Europe, Asia, and the Middle East over 300 years ago (Evelyn 1670). Breeding programs have focused on the production of interspecific hybrids since the early days of tree improvement in this genus, capitalizing on the hybrid vigor of the F_1 generation. These first-generation genetic gains can be readily captured for silvicultural purposes because of the ease with which many *Populus* hybrids can be vegetatively propagated (Stanton and Villar 1996; Stettler et al. 1996b). In Europe, spontaneous hybrids of the imported *P. deltoides* and the European native black poplar, *P. nigra*, were discovered around 1775. Initially named black Italian poplars, they were later renamed *P.* x *canadensis* by Mönch in 1795 (McNabb 1997). Although naturally-occurring poplar hybrids were common in 18th and 19th century Europe, systematic poplar breeding began only in the early 20th century at the Kew Botanical Gardens, England. The first recorded attempt of crossing poplars was made on flowers of *P. deltoides* with pollen of *P. trichocarpa*, with the resultant hybrid named as *P.* x *generosa*. Subsequent poplar breeding programs began around 1920 in Canada, USA, Denmark, and France (McNabb 1997).

A major consolidation of global poplar research was initiated through the establishment of the International Poplar Commission (IPC) in 1947, which is one of the technical statutory bodies of the Food and Agriculture Organization (FAO) of the United Nations. Their mandate is to promote cultivation, conservation and utilization of poplars and willows (*www.fao.org/forestry/site/ipc/en*). The IPC assists researchers in the direction and coordination of scientific efforts and promotes conservation and exchange of poplar germplasm among the member nations. The IPC also supports research and management activities that explore issues of concern to its 37 member countries through six working parties: harvesting and utilization;

diseases; insect pests; genetics, conservation and improvement; production systems; and environmental applications. The IPC also promotes the economic and ecological benefits of poplars and willows in developed and developing countries.

Although poplar cultivation has been traditionally integrated into many temperate and sub-tropical agricultural systems, the use of poplars and willows as biomass for renewable energy is a novel application (Dinus et al. 2001; Perlack et al. 2005). Research specific to Short Rotation Woody Crops (SRWCs), such as hybrid poplar, has been taking place around the US for the last 25 years, with particularly active programs in the northwest and the upper midwest. SRWCs are seen as a way to grow more wood fiber on less land in order to reduce potential conflicts between increasing demand for wood fiber and other forest land uses. Researchers felt that optimum tree growth could be realized by borrowing the intensive cultivation techniques common in other forms of agriculture, including the use of hybrids. Most genetic and silvicultural research in SRWCs involved hardwoods, particularly poplars, because of their rapid growth. Interest in SRWCs intensified in 1977 when the oil embargo provided an impetus for additional funding from the US Department of Energy (DOE) to consider wood as an alternative to fossil fuels. There has been a recent resurgence in interest since the spike in oil prices during 2007 and 2008, with a concomitant increase in federal funding for improvement of short rotation biomass crops, including *Populus* (Rubin 2008).

High intensity cultivation of woody biomass crops has great economic potential, and *Populus* is one of the premiere candidates for implementation of intensive, biotechnology-driven forestry (Balatinecz and Kretschmann 2001; Sedjo 2001; Strauss 2003). Over 70 million ha combined of natural poplar stands existed in 2004 in the 21 countries belonging to the IUFRO poplar commission (*http://www.fao.org/forestry/ipc2004*). The three countries with the largest areas of poplar forest were Canada (28.3 million ha), the Russian Federation (21.9 million ha) and the US (17.7 million ha). The next six countries containing significant areas of natural poplar forests are China (2.1 million ha), Germany (100,000 ha), Finland (67,000 ha), France (39,800 ha), India (10,000 ha) and Italy (7,200 ha). The global area of poplar plantations in 2004 was 6.7 million ha, of which 3.8 million ha (57%) was planted primarily for wood production and 2.9 million ha (43%) for environmental purposes. China reported the most planted poplar overall (4.9 million ha, or 73% of the global total), followed by India with 1.0 million ha. The other countries with significant areas of planted poplar included France with 236,000 ha, Turkey with 130,000 ha, Italy with 118,800 ha, Argentina with 63,500 ha and Chile with 15,000 ha. Only two countries reported significant annual removals of wood from natural stands of poplars: the Russian Federation (100 million m^3) and Canada (16 million m^3). Other countries that reported annual removals of more than 1 million m^3 of poplar wood from planted forests were Turkey (3.8 million m^3), China (1.85 million m^3), France (1.8 million m^3), Italy (1.4 million m^3), and India (1.2 million m^3) (*http://www.fao.org/forestry/ipc2004*).

Poplars provide a wide range of wood products, including industrial roundwood and poles, pulp and paper, reconstituted boards, plywood, veneer, sawn timber, packing crates, pallets, and furniture. Non-wood products from poplar include fodder, fuelwood, and bioenergy. Finally, poplar provides valuable services such as shelter, shade, conservation and protection of soil, water, crops, livestock and dwellings (Balatinecz and Kretschmann 2001; Stanton et al. 2002). Pulp, paper and cardboard have traditionally been one of the most favored end uses in Europe, North America, China and Argentina, but recent drops in global pulp prices have driven these countries toward using *Populus* for solid wood products, including plywood, oriented strand board, and laminated veneer (Stanton et al. 2002). Packaging (pallets, boxes and crates) is another favored end use in Europe, the Republic of Korea, the Russian Federation, Canada, China and India. Poplar is also used for matches in Chile, the Russian Federation, India, the Republic of Korea and Sweden. The use of poplar as an energy feedstock is most advanced in Sweden, the United Kingdom and Turkey, but this use is expected to grow in coming years (Stanton et al. 2002; Perlack et al. 2005). Finally the principal use of poplar and willow resources in China, the Republic of Korea, Serbia, Montenegro and Sweden is for environmental conservation, thus providing valuable services rather than forest products.

1.6 Concluding Remarks

Members of the genus *Populus* form an exceptional group of plants that has attracted the interest of researchers, funding agencies, and land managers for many years. In the genomics era *Populus* has now been catapulted into the forefront of basic and applied research in tree biology and tree improvement (Wullschleger et al. 2002; Bhalerao et al. 2003; Brunner et al. 2004; Jansson and Douglas 2007). We have summarized some of the salient biological characteristics that have driven this interest. Other, extensive reviews are available for those who would like more details about this fascinating genus (Stettler et al. 1996a; Dickmann et al. 2001; Dickmann and Kuzovkina 2008).

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