

1 *Populus* Trees

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1.1 Introduction

The genus *Populus*, which includes poplars, cottonwoods and aspens, is widely distributed over the northern hemisphere. Their rapid growth lends to their use as a source of fuel, fiber, lumber, wind-breaks and protective stands to prevent soil erosion. Their ease of vegetative propagation means that they have been closely associated with agriculture since before the Middle Ages in the Near and Middle East. In recent years, poplars have received increasing attention as a renewable source of biomass for energy and short-fiber furnish for papermaking.

The genus also has an important role in the natural populations of their native habitat, particularly riparian ecosystems. Poplars are dioecious and wind-pollinated and produce large amounts of pollen and small, cotton-tufted seed that is dispersed by wind and water in early summer. Capable of rapidly invading disturbed sites, many species occupy habitats in the dynamic environment of riverside floodplains where they form a key component of riparian forests (Braatne et al. 1996). Others, such as the aspens, commonly colonize upland areas after intense, stand-replacing fires (Burns and Honkala 1990). All poplars also have the capacity to reproduce asexually, mostly by sprouting from the root collar of killed trees or from abscised or broken branches that become embedded in the soil.

Traditionally, *Populus* and *Salix* have been regarded as the only two members of the family Salicaceae. However, recent views include many of the genera previously assigned to Flacourtiaceae, giving more than 50, largely tropical, genera. Poplars, cottonwoods, or aspens are the common names

for species of the genus *Populus*, recognized as the most abundant woody plant genus in temperate forests around the world. Some estimates put the number of species as high as 70 or more, and there are a number of naturally occurring hybrids. Many species are found in cultivation as well as numerous hybrids and cultivars (Hillier and Coombes 2002).

Populus spp. are fast-growing deciduous trees with alternate leaves. The flowers are extremely reduced and borne in catkins and trees are usually dioecious. For this reason *Populus* spp. have a tendency to hybridize in their natural habitat and especially in cultivation (US Environmental Protection Agency 1999; Wyckoff and Zasada 2003). The extensive interspecific hybridization and high morphological diversity in this group pose difficulties in identifying taxonomic units for comparative evolutionary studies and systematics (Hamzeh and Dayananadan 2004). *P. lasiocarpa* is one of the species that breeds true as it can be monoecious. Because of the extent of hybridization, and the fact that seeds are generally viable for only a short time, most *Populus* trees are propagated vegetatively by cuttings. Good rootability is a property of the members of two sections: Aigeiros and especially Tacamahaca.

The morphology and physiology in *Populus* species vary between geographically distinct populations and are strongly linked with the environment. It follows that any responses to stress will depend not only on the species but also on the particular genotype (Weber et al. 1985; Rogers et al. 1989; Braatne et al. 1992; Dunlap and Stettler 2001; Rowland et al. 2001). Dunlap et al. (1993), for example, looked at poplars growing in different river valleys and found that there was variation of physiological processes like photosynthesis both within and between locations.

1.1.1

Taxonomic Classification

Kingdom Plantae
 Subkingdom Tracheobionta (Vascular plants)
 Superdivision Spermatophyta (Seed plants)
 Division Magnoliophyta (Flowering plants)
 Class Magnoliopsida (Dicotyledons)
 Subclass Dileniidae
 Order Salicales
 Family Salicaceae (Willow family)
 Genus *Populus* L. (cottonwood)

Bean (1976) describes five sections in the genus *Populus*, from which section Turanga, represented by *P. euphratica*, is the least cultivated as it is a species that is difficult to grow, native to North Africa through southwest and central Asia to China. The rest are mentioned briefly as follows, as they include distinctive features:

Section Populus (Leuce) includes the white and grey poplars characterized by a woolly leaf abaxial surface. It includes *P. alba*, *P. x canescens*, and *P. tomentosa*, all native to the Old World, and the Aspens, with glabrous leaves, noted for their restless movement. This subsection includes *P. grandidentata*, *P. tremula*, and *P. tremuloides*. All of these have poor rootability.

Section Leucoides includes a combination of American species such as *P. heterophylla* and Asiatic species such as *P. lasiocarpa* and *P. wilsonii*. The main characteristic of these species is the large and leathery leaves.

Section Tacamahaca, known as the balsam poplars, is a very distinctive group with fragrant buds and scented leaves for which it is named. The leaves are usually whitish and waxy on the underside. This section includes *P. angustifolia*, *P. balsamifera*, *P. koreana*, *P. laurifolia*, *P. maximowiczii*, *P. simonii*, and *P. trichocarpa*. A distinctive characteristic is that all the members of this section are easily propagated by hardwood cuttings or by suckers.

Section Aigeiros, known as Black poplars, includes plants with green leaves on both sides and a large petiole, nearly always in movement. This section is distributed in North America, Europe, and Western Asia. Of all the species in this group, *P. deltoides* is the only one that cannot be propagated easily by hardwood cuttings.

Although *Populus* trees share several floral features with *Salix*, molecular data show a clear separation between the two genera; the most consistent and

evolutionarily significant being their mode of pollination. Wind pollination in poplars, combined with their dioecy, has led to natural hybridization, allowing interspecies gene exchange. The outbreeding habit in combination with effective seed dispersal effects the genetic variation within *Populus* species. Patterns of isozyme variation across several species in over 30 enzyme systems show a recent theme of little differentiation among populations, with over 90% of the variation being within populations. Polymorphisms within populations are also common in morphological and phenological traits.

Fossil records show evidence that ancestral poplars were widespread across North America. Members of section Abaso were the sole poplars in North America until the late Eocene, when the precursors of other sections appeared and the first Eurasian poplar fossils are recorded (Collinson 1992).

1.1.2

Botany

Populus species are single-stemmed, deciduous (or semievergreen) trees mostly spread clonally by means of rootborne sucker shoots (sobiliferous). They are among the fastest growing temperate trees, a quality tied ecologically to their role as vegetational pioneers as well as functionally to their heterophyllous growth habit. Poplar shoots continue to grow after bud burst by initiating, expanding, and maturing leaves (neoformed or late leaves) throughout the growing season. Cessation of growth and bud formation is induced by photoperiod in some poplars (Pauley and Perry 1954). Preformed and neoformed leaves often differ considerably in texture, shape, and tothing, with preformed leaves often more taxonomically diagnostic than neoformed leaves. Neoformed leaves are relatively convergent among unrelated poplar species, with the exception of the unique lobed leaves of *P. alba* and its hybrids.

The separate male and female trees flower before leaf emergence in spring (except in some subtropical species) from specialized buds containing preformed inflorescences, enabling wind pollination before canopy closure. The capsules and their airborne seeds, which have a readily detached coma of cottony hairs, mature with or after the overwintered preformed leaves.

Poplars have been recognized as a group since very early times and have a unique combination of characteristics that distinguish them from all other genera of plants. The defining features are primarily in the reproductive structures. The flowers are borne in pendent racemes (catkins, aments) that vary in flower number and density among poplar species. Among temperate trees with female catkins, only poplar and willow have seeds with a coma of cottony hairs on parietal placentas in thin-walled capsules. Individual flowers of both catkin types are subtended by thin bracteoles that fall as the catkins elongate during flowering. The caduceus bracteoles distinguish the catkins of poplars from those of willows. There are no ordinary petals or sepals, but 5 to 60 stamens or solitary pistils are borne on a more or less expanded floral disk.

Overwintering vegetative and reproductive buds are covered by several bud scales. The buds are covered with exudates that are rich in a variety of hydrophobic organic chemicals (Greenaway and Whalley 1990) that are thought to be involved in winter hardiness.

The rapid, nearly continuous growth during the favorable season results in a light diffuse-porous wood structure. Poplar wood differs from that of willow in that it has homocellular rays as opposed to the heterocellular rays. The wood differs from many similar light-colored woods in that it lacks some more specialized features like the marginal parenchyma or the spiral thickening and multi-seriate rays. The bark remains thin for a longer period than in most trees.

The leaves are alternate, stipulate, and petiolate with the petiole often transversely flattened and simple with glandular teeth along the margin and often with glands at the junction of the blade and petiole. Poplars generally have a high soil moisture requirement explaining the growth of most species along floodplains of rivers or lake shores.

1.1.3

Poplars as Crops

Rapid growth is the hallmark of poplars. It derives from a growth system that starts with the elongation of a preformed shoot from its bud and then continues to initiate and expand shoot segments and leaves throughout the growing season. The wood is diffuse-porous, light in weight, and yet capable of building trees of 40 m height in less than 20 years.

Several of these features have made poplars attractive to humans since ancient times. Today, poplar is cultivated worldwide in plantations for pulp and paper, veneer, excelsior (packing material), engineered wood products (e.g., oriented strandboard), lumber, and energy. Grown at a commercial scale under intensive culture for 6- to 8-year rotations, production rates with hybrid poplar can be as high as 17 to 30 Mg/ha/year of dry woody biomass (Zsuffa et al. 1996), comparable to the biomass produced by row crops such as corn. Historically, poplar has been widely used in windbreaks and for erosion control. Most recently, poplars have proven to be effective in the phytoremediation of environmental toxins (Flathman and Lanza 1998) and as bioindicators for ozone pollution in the environment (Jepsen 1994).

Poplars have three main properties that make them excellent for short-rotation intensive-culture management: rapid juvenile growth, immediate response to cultural practices, and their coppicing property (Bradshaw et al. 2000). The hybrids of section *Tacamahaca* are considered to have particularly high water-use efficiency (Mazzoleni and Dickmann 1988). Hybrids are more drought tolerant than native cottonwoods (Hinckley et al. 1989; Wyckoff and Zasada 2003), and this characteristic makes them attractive as a crop to supplement the diminishing supply of natural hardwoods.

An important feature in poplar hybrids and species, linked to their high productivity, is their high rate of stomatal conductance (g_{max} are near 600 mmol m⁻² s⁻¹), which suggests the transpiration of large volumes of water (US Environmental Protection Agency 1999). Therefore, considerable attention has been given to the study of water regulation in several species, hybrids and cultivars that exhibit a wide range of variation (Reich 1984; Schulte and Hinckley 1987; Schulte et al. 1987; Ceulemans et al. 1988; Mazzoleni and Dickmann 1988; Tschaplinski and Blake 1989b; Bassman and Zwier 1991; Dickmann et al. 1992; Liu and Dickmann 1992, 1996; Dunlap et al. 1993; Tschaplinski et al. 1994; Ridolfi et al. 1996). Important work has been carried out on growth and biomass rates in large-scale poplar plantations (Tschaplinski et al. 1998b; Rae et al. 2004).

The commercial planting of poplars date from half a century ago, and it occurs mainly in America, Canada, Europe, and China. In the UK, the best region in which to grow poplars is the southern half of England, where the best conditions prevail for sustaining high growth rates. It has been shown that *Populus* does



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