at a cross-continental Mediterranean scale must be combined with public awareness strategies and international policy-making, not only to understand but also to protect Mediterranean ecosystems effectively and use them efficiently, now and in the future.

See also: **Biodiversity**: Biodiversity in Forests; Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Forest Management for Conservation; Population, Conservation and Ecological Genetics. **Landscape and Planning**: Landscape Ecology, the Concepts. **Silviculture**: Forest Dynamics. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Temperate and Mediterranean Forests**: Southern Coniferous Forests. **Temperate Ecosystems**: Fagaceae; Pines; Spruces, Firs and Larches. **Tropical Ecosystems**: Acacias; Eucalypts.

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TEMPERATE ECOSYSTEMS

Contents

Alders, Birches and Willows

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Early botanists considered the alders (*Alnus*), birches (*Betula*), and willows (*Salix*) part of a large, closely related group of catkin-producing, woody species, known as the Amentiferae. This group was presumed to have a single origin, and also included the walnuts, oaks, figs, and elms. We now know, based on detailed morphological and molecular analyses, that many of these families are not closely related and that superficial resemblance based on catkins is due to convergence. In addition to sharing catkins, alders, birches, and willows are ecologically similar since they are important pioneer species of the northern temperate region. Furthermore, they have a diverse array of similar uses, especially gunpowder production.

Alnus and *Betula* comprise the monophyletic subfamily Betuloideae of the family Betulaceae, whilst the other four members (*Carpinus*, *Corylus*, *Ostrya*, and *Ostryopsis*) comprise subfamily Coryloideae. Traditionally, *Salix* and the genus *Populus* have comprised the family Salicaceae. However, using molecular data it has been proposed that the family Salicaceae should also encompass other genera, most notably the acyanogenic genera of the Flacourtiaceae.

The biology and ecology of alders, birches, and willows are briefly described and then the

diverse uses of these important trees and shrubs are presented.

Alnus

The genus *Alnus* comprises approximately 25 species of small to large trees or shrubs of the temperate and boreal zones of the northern hemisphere and Central America to the high elevations of South America, although the genus is poorly understood in Central America and China. Members of the genus are often associated with wet sites, swamps, and stream margins, and their ability to fix nitrogen means *Alnus* species are important early successional species. For example, *A. viridis* is an important pioneer, whilst others are important components of mature forest (e.g., *A. rubra* in the floodplain forests of the North American Pacific North-west). Alders, as with other Betulaceae, have male and female flowers separated into different catkins. Alders are wind-pollinated, producing large amounts of pollen. Pollen release occurs before (subgenus *Alnus*) or at the same time (subgenus *Alnobetula*) as the new leaves unfold or in late summer (subgenus *Clethropsis*), just after the new catkins mature. The woody alder infructesences produce small, abundant, winged fruits that are carried primarily by wind but also by water. In some species (e.g., *A. serrulata*), the wings are reduced to ridges, and the fruits are dispersed primarily by water. *Alnus* species form a polyploid group ($2n = 14-56$; $2x-8x$). Fossil material attributable to the genera *Alnus* and *Betula* appears earlier in the fossil record than other Betulaceae, whilst *Alnus* fossils are known from as early as the Miocene. Furthermore, analyses of chloroplast DNA and pollen data have enabled the postglacial history of *A. glutinosa* to be reconstructed and glacial refugia to be identified.

The genus is divided into four subgenera: *Alnus*, *Alnobetula*, *Clethropsis*, and *Cremastogyne* (**Table 1**), although these have also been recognized as separate genera. *Alnus* nomenclature is complicated by morphological variation and hybridization. For example, in subgenus *Alnobetula*, numerous subspecies are described in the circumpolar species *A. viridis*. Alder hybrids form readily when species grow together; for example, in North America, *A. incana* subsp. *rugosa* hybridizes with *A. serrulata*, leading to extensive hybrid swarms that complicate the differentiation of the taxa. However, most species are either geographically or ecologically differentiated.

Seed is an effective way of raising alder, although many species can be vegetatively propagated. Large areas of alder growth may give the impression of extensive clonal population growth. However, allozyme studies indicate that populations of *A. incana* subsp. *rugosa* and *A. viridis* subsp. *crispa* are the result of sexual reproduction. Furthermore, inbreeding is very low and gene flow is high. For best growth, alders (e.g., *A. glutinosa*, *A. rubra*, *A. cordata*) must be symbiotically associated with the nitrogen-fixing actinomycete *Frankia*, which leads to formation of root nodules. Few pests and diseases appear to affect alders, although scale insects can be a problem in *A. serrulata* in North America. However, in recent years in the UK, natural populations of *A. glutinosa* have been lethally affected by the fungal pathogen *Phytophthora cambivora*. In North America, *Fomes ignarius* is the most significant fungal pathogen of

Table 1 Characteristics of the main grouping within the genus *Alnus*

	Subgenus Alnus	*Subgenus* Alnobetula	*Subgenus* Clethropsis	*Subgenus* Cremastogyne
Distribution	Temperate and boreal northern hemisphere, Central and South America	Temperate and boreal northern hemisphere	Eastern North America, eastern Asia	South-central Asia
Habit	Small trees to medium-sized shrubs	Small trees to shrubs	Small trees	Small to medium-sized trees
Fruits	Wingless or narrow wings	Two large lateral membranaceous wings	Wingless	Broad hyaline wings
Infructesence	Short pedunculate	Long pedunculate	Short pedunculate	Long pedunculate
Catkins	Catkins racemose, develop during growing season before anthesis and exposed during winter	Catkins racemose, develop during growing season before anthesis and only male exposed during winter	Catkins solitary or racemose clusters	Catkins solitary
Flowering	Spring	Spring	Fall	Spring
Buds	Stipitate, two-scaled	Subsessile, several imbricate scales	Naked	Stipitate, two-scaled
Examples	*A. incana A. serrulata*	*A. viridis A. sieboldiana*	*A. maritima A. nepalensis*	*A. cremastogyne*

trees older than 40 years, whilst *Taphrina* species may affect female catkins.

Betula

The genus *Betula* comprises approximately 35 species of small to large trees or shrubs of the temperate and boreal zones of the northern hemisphere. The genus occupies a wide range of habitats, including peat lands, stream banks, lake shores, damp woods, ruderal habitats (including road and rail margins), and alpine and tundra sites. In addition, the genus reaches the northern limit of tree growth. Birches are wind-pollinated, producing large amounts of pollen, and the achenes are wind-dispersed. The female catkins appear with the new growth, whilst anthesis occurs as the leaves unfold. However, ovule fertilization occurs much later than pollination. *Betula* species form a polyploid group ($2n = 28$–112; $2x$–$8x$), whilst some hybrids are aneuploid. Fossil material attributable to the genus *Betula* has been found in deposits from the Upper Cretaceous and appears to have been highly diversified by the Middle Eocene.

The genus is divided into four series, Albae, Costatae, Acuminatae and Humiles (**Table 2**), although some species (e.g., *B. utilis*, *B. nigra*) are difficult to place in these series. *Betula* nomenclature is complex due to the patterns of morphological variation, the wide ecogeographic range of some species (e.g., *B. pubescens*) and the existence of hybridization and introgression within and between the series. In northern Europe, there has been considerable discussion as to whether *B. pendula* and *B. pubescens* are separate species or intraspecific variants. In many cases across their ranges, the two species are readily distinguished. However, morphological intermediates do occur, although these are rarely sterile, triploid hybrids, as might be expected (*B. pendula* ($2n = 2x = 28$), *B. pubescens* ($2n = (4x) = 56$)), which suggests that there is a complex interaction between the morphological and cytogenetic variation. Areas where introgression is important include Kamchatka (e.g., *B. platyphylla* introgresses with *B. ermanii*) and north-east North America (e.g., *B. populifera* introgresses with *B. cordifolia*), whilst in northern Europe *B. pubescens* hybridizes with *B. nana*.

Series Albae and Costatae contain the most important forestry species. Seed is an effective way of raising birch although, when seed is collected from natural or cultivated specimens, the possibility that it may be of hybrid origin must be considered. Birch seed is orthodox, and if dried and stored in cool conditions it will remain viable for many years. Many *Betula* species can be vegetatively propagated from soft or semiripe side shoots, whilst grafting is important if particular genotypes are to be maintained. In the case of grafting, the scion and rootstock should come from the same series of the genus, although in practice *B. pendula* is very commonly used.

The leaves of birches are often rich in resins, whilst the barks, particularly of white-barked birches, are rich in phenolics. Furthermore, the bark of series Albae species contains granules of the triterpenoid betulin, which makes the bark waterproof. These compounds are thought to be important antifeedants, especially effective against browsing mammals, in the winter months. Many insect species feed

Table 2 Characteristics of the main grouping within the genus *Betula*

	Series Albae	*Series Costatae*	*Series Acuminatae*	*Series Humiles*
Distribution	Circumpolar	North America, Transcaucasia, temperate Far East	Japan, Sino-Himalayas	Circumpolar
Habit	Small to medium-sized trees	Large trees	Medium-sized trees	Shrubs
Leaves	Thin, weakly veined with long petiole	Strongly and deeply veined, most with single-toothed margin	Strongly and deeply veined, double-toothed margin	Small, rounded, with few veins
Stem	Bark white (due to betulin), peeling in sheets	Bark dark, most lack betulin	Bark dark, most lack betulin	Bark dark, lack betulin
Catkins	Pendulous, long, fragile, and break up readily in the fall	Upright, short (even globose), persistent, often until early spring	Pendulous, long	Upright, male catkins borne laterally
Ecology	Pioneer species. Fast-growing, relatively short-lived, requiring high light intensity. Not adversely affected by wind exposure	Mixed mesophytic forests. Shade-tolerant, wind-shy	Mesophytic forests	Montane and alpine regions. Peat lands, bogs, tundra
Examples	*B. papyrifera B. populifolia*	*B. alleghaniensis B. lenta*	*B. maximowicziana*	*B. nana B. glandulosa*

on birch, of which one of the most economically important in North America is the bronze birch borer (*Agrilus anxius*), although others include the gypsy moth (*Lymantria dispar*), tent caterpillars, leaf miners, and scale insects. Fungal diseases may also be significant, especially the heartwood rots, caused by *Fomes* and *Poria* species, e.g., *F. ignarius*, and nectria canker (*Nectria galligena*).

Salix

The genus *Salix* comprises approximately 400 species of dwarf or procumbent shrubs to large trees and is found in most parts of the world, particularly the temperate and boreal regions, although there are tropical and subtropical species (e.g., *S. humboldtiana*). One species *S. mucronata*, crosses the equator in Kenya. The genus is very diverse, but poorly known, in western China. Willows occupy a wide range of habitats and climatic zones; the majority of species are pioneers and shade-intolerant (e.g., *S. repens*). Most willows are scrub, marginal, or riverine species, although some are forest-dominants; the association of willows with water is reflected in the origin of the generic name (derived from Celtic, meaning 'near water'). Willows become increasingly important on upland and northward from the boreal forest into the arctic, where they are the most important woody species (e.g., vegetation succession on glacial moraines). In such habitats, willows tend to have underground branches and act as herbaceous perennials. *Salix* species are almost all dioecious, having separate male and female plants, and produce catkins in the spring. Willows, except subgenus *Chosenia*, are usually insect-pollinated (Hymenoptera and Lepidoptera), and the seeds have tufts of hair that aid in wind dispersal. *Salix* species form a polyploid group ($2n = 38$–224; base numbers 11, 12, 19), although aneuploidy appears to be common in some species and hybrids. Fossil material attributable to the genus *Salix* has been found in deposits from as early as the Miocene.

The genus is conveniently divided into four subgenera: *Salix*, *Caprisalix*, *Chamaetia*, and *Chosenia* (**Table 3**); subgenus *Chosenia* is sometimes regarded as a distinct genus. However, the intrageneric division of *Salix* is controversial and numerous alternative schemes have been published. Subgenus *Salix* species are commonly called the true willows, whilst the members of subgenus *Caprisalix* are the sallows and osiers. The accurate identification of *Salix* species is difficult since it is often necessary to have mature flowers and leaves, structures that are usually not available at the same time. *Salix* nomenclature is complex due to the patterns of morphological variation and hybridization, although most species of subgenus *Salix* do not hybridize with those of the other two sections. Most hybrids are fertile, hence it is possible for individual plants to have complex hybrid parentages, e.g., artificial hybrids have been created involving up to 14 *Salix* species, whilst hybrids of three or more species are frequently found in the UK. This means that in areas where there are numerous interfertile species it may be difficult to establish accurately the identity of individual trees. Furthermore, many hybrids are clones of a single sex, e.g., *S.* × *calodendron* is known only from female plants. Furthermore, natural hybridization is complicated by the separation of the sexes and interspecific differences in flowering periods.

Subgenera *Salix* and *Caprisalix* contain the most important forestry species, although subgenus *Chamaetia* contains some of the most important high-latitude species. In natural populations, *Salix* produces large amounts of easily germinated, very short-lived seed, whilst some species form extensive clonal stands (e.g., *S. repens*, *S. herbacea*). In

Table 3 Characteristics of the main grouping within the genus *Salix*

	Subgenus Salix	*Subgenus* Caprisalix	*Subgenus* Chamaetia	*Subgenus* Chosenia
Distribution	Temperate and boreal, plus few tropical and subtropical Old and New World	Temperate and boreal, plus few tropical and subtropical Old and New World	Temperate and boreal	North-East Asia
Habit	Medium-sized trees, large shrubs	Small trees, shrubs	Dwarf, creeping shrubs	Large trees
Floral nectaries	2 + nectaries in male flowers, 1–2 nectaries in female flowers	1 nectary	Nectaries fused	Absent
Male flowers	3–10(12) stamens	2 stamens	(1–)2 stamens	Five stamens
Catkins	Erect; stalked on leafy shoots	Erect; sessile or subsessile, precocious	Erect; on leafy shoots	Pendulous
Pollination	Insect	Insect	Insect	Wind
Examples	*S. alba S. babylonica*	*S. caprea S. viminalis*	*S. herbacea S. polaris*	*S. arbutifolia*

cultivation, *Salix* species are readily propagated from seed, although more generally they are vegetatively propagated from hardwood cuttings; some species, e.g., *S. caprea*, are difficult to root from cuttings. Vegetative reproduction has the advantage that particular cultivars can be maintained, and it is essential for the propagation of male clones. The economic importance of the genus has led to the selection of many local *Salix* genotypes, all of which are maintained through clonal propagation. For established lowland species, coppicing and pollarding are effective forms of management for wood products, although large amounts of organic material must be available in the soil.

Willows are the hosts of many insect species. Willows are prone to fungal diseases (e.g., *Melampsora* leaf rusts and *Armillaria*), and the planting of single areas with single clones may make disease control difficult. The bacterium *Erwinia salicis* is an important threat to the production of high-quality cricket bats from *S. alba*.

Utilization

Timber

Betula species (e.g., *B. alleghaniensis*, *B. lenta*, *B. pubescens*) are important hardwoods for the production of veneers and plywoods. *Alnus* species produce soft, fine-grained woods used for pilings, beams, and shipbuilding (e.g., *A. acuminata*, *A. jorullensis*). The wood of larger *Salix* species is used for building purposes, whilst female clones of *S. alba* var. *caerulea* are the sole source of wood for cricket bats. *Alnus*, *Betula* and *Salix* species are important pulpwood sources.

Wood Products

Salix is an important raw material of rural crafts (e.g., hurdles, coracles, baskets) in both the New and Old Worlds. Basketry is an example where particular species produce different qualities of products, e.g., *S. triandra* (rods), *S. purpurea* (thin withies for fine basketry), and *S. viminalis* (withies for basketry). Furthermore, male and female clones produce different qualities of rods and withies. Birch bark (e.g., *B. papyrifera*) is used for canoe and roof construction. Furthermore, birch bark has been used as writing material, e.g., the oldest (*c.* 1800 years old) known Buddhist manuscripts. Birch branches have also been used for brush construction and administering corporal punishment (the name *Betula* is derived from the Latin 'to beat'). *Betula* and *Salix* species are used as short-rotation biomass crops.

Fuelwood

Alnus, *Betula*, and *Salix* species are important fuelwood sources, e.g., *Salix* woodchips in Sweden. All three genera have been widely used for charcoal production and are important in gunpowder manufacture.

Medicines, Food, Chemicals

Alder, birch, and willow have limited food value, although *Salix* species are important pollen and nectar sources for bees early in the year. In the northern Appalachians, *B. lenta* sap is tapped in spring and fermented to produce birch beer, tea is made by infusing birch bark and twigs, and birch bark (rich in oil and starch) is a famine food. Medicinally, salicin has been extracted for centuries from willow bark and used as a febrifuge and analgesic, although this has been superseded by salicylic acid (aspirin), and wintergreen (methyl salicylate) is extracted from *B. lenta* and *B. alleghaniensis*. The astringent properties of alder bark are used for the treatment of burns and infections, whilst the triterpenes betulin and lupeol, extracted from bark and wood of *A. rubra*, have some *in vitro* antitumor activity. Birch and alder pollens are important sources of hayfever allergens, whilst birch sap may cause contact dermatitis. Distillation of *B. pendula* bark and wood is used to produce pyroligneous oil for the preparation of leather, and *B. pubescens* and *B. pendula* leaves produce a green dye.

Habitat Amelioration

Salix species are often planted along riverbanks, subject to extensive flooding, to minimize soil erosion, whilst others (*S. purpurea*, *S. interior*) are used for estuarine land reclamation. *Salix* species are also important as windbreaks and for the treatment of wastewater. *Betula* species are used as heavy-metal bioindicators (e.g., *B. populifolia* for lead in Wisconsin, USA), whilst alder leaves accumulate gold.

Ornamentals

Alnus and white-barked *Betula* species have wide-ranging horticultural uses. Many *Salix* species and selected cultivars (particularly males) are grown (e.g., for stem color), whilst weeping (e.g., *S. babylonica*) types are popular in riverine situations.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Genecology and Adaptation of Forest

Trees; Genetic Systems of Forest Trees; Population, Conservation and Ecological Genetics. **Temperate and Mediterranean Forests**: Subalpine and Boreal Forests; Temperate Broadleaved Deciduous Forest. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

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Fagaceae

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Introduction

The following sections characterize members of the beech family (Fagaceae) in relation to their taxonomy, distribution, ecology, and silviculture. Also included is information about their botanical importance as well as their significance in meeting human needs.

The beech family contains some of the world's most important trees to human culture. Uses are myriad and include such things as woven baskets, toys, storage containers, ship timbers, and food sources. However, members of the beech family are generally acknowledged as most important sources of hardwood timber (oak (*Quercus*), beech (*Fagus*), and chestnut (*Castanea*)), chestnut, and cork and tannins from the oaks (**Figure 1**).

Figure 1 Cork oak (*Quercus suber*) plantation in Portugal showing tree trunks whose bark has been stripped for cork. Photograph courtesy of Heinrich Speicker, Institut für Waldwachstum, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany.

Taxonomy

The beech family contains from six to nine genera (*Fagus*, *Nothofagus*, *Lithocarpus*, *Castanopsis*, *Colombobalanus*, *Castanea*, *Chrysolepis*, *Quercus*, and *Trigonobalanus*) and includes between 600 and 900 species, although numerous classification issues exist which accounts for the variation in the number of genera (**Table 1**). Perhaps the best-known members of the beech family are the oaks which are recognized by their distinctive fruit, the acorn (**Figure 2**). The genera of Fagaceae as we know them probably became established about 60 million years ago during the late Cretaceous period in geologic history following migration from areas centered in tropical mountains.

Characteristics that unite members of the family include leaves with a single blade that are either persistent or deciduous and which often remain on the tree after withering and dying. Leaflike appendages (stipules) are present at the base of a relatively short leaf stem (petiole). Leaves are arranged in an alternate pattern on the stem. Veins of the leaves are featherlike and have branches that are laterally connected to a central stem.

Male and female flowers are found within the same tree. Female flowers are wind pollinated. Male flowers are pendulous spikelike structures while female flowers are on short spikes with few flowers or may be grouped in clusters near the base of the male flowers. Although female flowers may contain one or two ovules, only one develops to maturity.

The fruit is distinctive and consists of a nut that is surrounded by an outer somewhat firm yet elastic coat that is partially or completely enclosed by a cluster of bracts (**Figure 3**). The nut contains only one seed which lacks food reserves associated with the embryo but which has large, fleshy primary