# Temperate Broadleaved Deciduous Forest

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## Introduction

Deciduous temperate forests (sometimes called summer-green forests) are dominated by broadleaved trees which lose their leaves during winter. They constitute the main potential natural vegetation over much of temperate Europe, eastern Asia, and north-eastern North America, and also appear in some climatically comparable, but much smaller, regions in the southern hemisphere. Owing to the deciduous habit of the main dominants and the characteristic dying-down of many of the associated plants as the trees come into leaf, these forests look entirely different in spring, summer, autumn, and winter. The deciduous habit is a strategy to deal with the lack of sunlight and cold temperatures in winter.

The regions potentially occupied by temperate broadleaved deciduous forest are among the most densely populated on earth and much of the original forest has been cleared. Only patches remain, few of which approach a truly natural condition, but many retain a seminatural character. Most of the earliest civilizations emerged in places with Mediterranean climates, and this led to early large-scale destruction of their forests. By the Middle Ages, the most important forest left in Europe was the broadleaved deciduous one. However, clearance of this was already widespread and more was lost or altered over the ensuing centuries. The fertile former forest ground was ideal for agricultural use as arable or pasture land. In some cases, the depredations of domestic animals were sufficient to prevent trees from regenerating and transformed these forests to grasslands.

## Distribution

Temperate broadleaved deciduous forests occur in three major zones. In western and central Europe they extend across Poland and central Russia, down the mountain chains of southern Europe and into Asia minor; eastern Asia, including eastern China, Korea and Japan; and eastern North America. There is a smaller zone in South America (**Figure 1**).

1. In western and central Europe the temperate deciduous forests occur from the Atlantic coast, northwards to almost 60° N, eastwards to the Ural mountains of central Russia and down into the Caucasus and Elburz mountains of northern Iran, and southwards at higher altitudes in central Spain, southern Italy, and Greece. The tree and shrub composition is relatively poor to the north, with many species having failed to return after past glaciations. In many parts of Europe (e.g., the

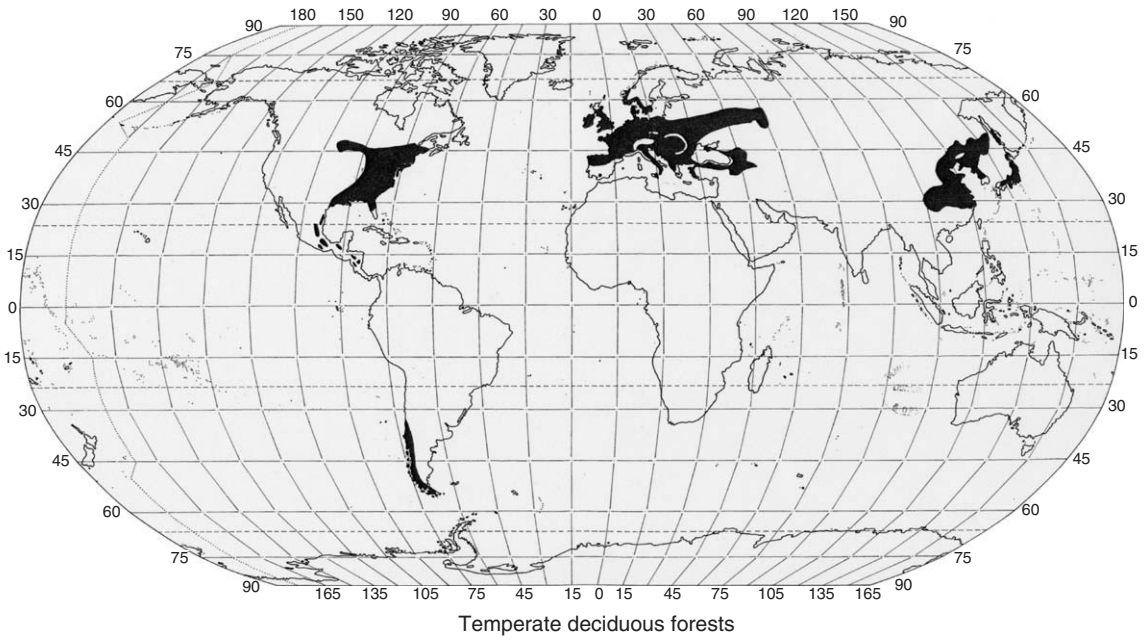


**Figure 1** Distribution of temperate deciduous forests. Reproduced with permission from Röhrig E and Ulrich B (eds) (1991) *Ecosystems of the World*, vol. 7, *Temperate Deciduous Forests*. London: Elsevier.

UK and Ireland), no truly natural woodland at all has survived. As elsewhere, prehistoric people cleared the majority of the original natural forests.

2. In northern Japan and adjacent parts of eastern continental Asia, the forests lie mostly between 30° and 50° N, extending to 125° E in the northwest, and 115° E in the southwest. In China intensive agriculture has caused this region to be largely cleared of natural vegetation for at least 4000 years.
3. In eastern North America, the forests lie in a belt from the coast, northwards to between around 35–48° N, and to the Great Lakes, and west to beyond the Mississippi. Almost all the forests of eastern North America are second growth, the original forest having been cleared by early settlers, but they contain a great diversity of flora and fauna. This is especially true of the Appalachian plateau of eastern Kentucky and Tennessee which was never glaciated, and western North Carolina and Virginia. The Great Smoky mountains have been designated a world biosphere reserve to help protect the rich assortment of species.
4. In the southern hemisphere, there is a small area of temperate deciduous forest in Chile and southwestern Argentina between 35° and 55° S, and in Tasmania. The majority of southern deciduous forests are located in Chile where they extend from higher altitudes on the Coastal and Andean mountain ranges of central–southern Chile to temperate cold-humid climates in Patagonia and Tierra del Fuego. Since colonial times the forests of central–southern Chile have been under intense pressure for transformation to agricultural and pasture uses and, more recently, for the establishment of fast-growing exotic forest plantations.

## Climate and Seasonal Changes in the Forest

Most temperate deciduous forests have mild, damp climates, with average temperatures in the coldest months of between 18° and −30°C. Monthly average temperatures in the warmest months are greater than 10°C, but seldom exceed 22°C. Precipitation is reasonably well distributed throughout the year, totaling 750–1500 mm or more. The growing season is about 6 months or a little longer, and never less than 4 months.

No other ecosystem is characterized by such marked seasonal changes as the temperate deciduous forest. It has four distinct seasons, spring, summer, autumn, and winter (**Figures 2–5**). In the autumn (late August to early October) the leaves change

**Figure 2** Beech (*Fagus crenata*) in Ishikawa Prefecture, Japan, in autumn. The dark-green evergreen trees are *Cryptomeria japonica* and *Pinus parvifiora*. Courtesy of Koso Saito.

**Figure 3** Beech (*Fagus sylvatica*) woodland in winter in Belgium. The trees are leafless, and no green ground vegetation can be seen. Even in summer it is sparse in this type of woodland where the trees cast a very heavy shade.

**Figure 4** Walnut (*Juglans regia*) forest in summer in Kyrgyzstan. All the canopy trees in this picture are walnuts. The lower shrub/small tree stratum consists of fruit trees, including apples (the ancestors of many cultivated apples), plums and *Crataegus* species. Courtesy of Gabriel Hemery.

**Figure 5** Spring in oak (*Quercus robur*) woodland in southern England. Spectacular displays of bluebells (*Hyacinthoides non-scripta*) are characteristic of many of these woods.

color and fall off the trees. During the winter months nearly all the trees are leafless; only a few species (e.g., holly – *Ilex aquifolium*) retain their foliage.

In spring, the ground vegetation becomes active first, including many herbs with perennial bulbs, tubers, or corms. They exhibit a distinct seasonality, taking advantage of the brief period of maximum light to flower very early in spring, before the leaves of the trees expand and cut most of it off. They flower and fruit rapidly and die down soon afterwards, as in the case of the lesser celandine (*Ranunculus ficaria*), and bluebell (*Hyacinthoides non-scripta*). Other species such as yellow archangel (*Lamiastrum galeobdolon*) appear somewhat later while the trees' leaves are expanding. Activity in the ground vegetation is followed by the shrubs, and then the trees. Buds burst and the leaves expand quickly, as soon as temperatures become suitable. In Europe and North America, bud burst progresses from the south to the north and from the more maritime to the more continental regions. The foliage is fully developed early in the season, so little photosynthetic time is lost. Flowering of trees also tends to be completed early, giving ample time for the development and ripening of the fruit. In a few species, the flowers open before the leaves expand (e.g., *Corylus* and *Populus*), allowing freer access for the wind and insects for pollination. Most trees flower at the time the leaves begin to expand in spring; very few (like *Tilia*) flower in summer. Spring also sees many insects, and in America a few mammals emerge from hibernation; many birds breed in deciduous woodlands, and later various summer-migrant birds arrive.

During summer the leaves of the trees are fully grown and form a dense canopy that keeps the forest interior shady but cooler and more humid than in the open. Various shade-bearing lower plants are adapted to tolerate the low level of light, and make use of occasional sun flecks (e.g., wood sorrel (*Oxalis acetosella*)). Insect life is abundant, with plant leaves, nectar, and sap providing rich supplies of food – in turn, these provide food for resident and migrant birds and mammals.

Autumn can be the most visually striking season of all in some regions, offering brilliant displays of leaves: reds of maples, yellows of birches, and oranges of various other species. The change in color, triggered by shortening day length, is caused by the cessation of chlorophyll synthesis (the green pigment in leaves), and breakdown of existing chlorophyll. This unmasks the other colored pigments in the leaves which are phenolic compounds that are present all the time. They have two functions: (1) being unpalatable and relatively indigestible, they provide leaves with a partial means of resistance to attacks by damaging fungi and leaf-eating insects; and (2) they act as filters to ultraviolet light and prevent damage to the leaves from it. The main pigments are anthocyanin, which gives the glowing reddish colors (bluish purple to scarlet), depending on the acidity of the cell sap, and carotene and xanthophyll, which give the orange and yellow colors.

The actual colors particular trees assume depend upon the mixture of the particular pigments in the leaves. The variety of colors both between and within species is due to the slightly varying strategies trees adopt to provide protection from potential predators and fungi. Some species are dependable in producing good colors almost every year; others are spectacular quite irregularly. Some species change to only one color (e.g., birches and some maples turn yellow; *Acer palmatum* red). Others show every tint from purple to yellow (e.g., cherry).

Autumn is also the time when most trees and shrubs produce fruit. Some species, especially oaks, have 'mast' years. These occur periodically in, say, one year in 4 or 5 when vast numbers of acorns are produced. This glut of food is conserved by squirrels, woodpeckers, and jays by burial in the soil or in holes in trees.

Winter is a period of dormancy for many species of trees and also ground vegetation, insects, and some mammals. Some species of birds migrate instead.

## Why be Deciduous?

In comparison with the evergreen leaves of conifers, deciduous leaves are very efficient users of solar energy. They have higher photosynthetic rates per unit dry weight of leaf than the perennial evergreen leaves found on many conifers (about 10–14 mg $CO_2\,g^{-1}\,h^{-1}$ compared to 4–6 mg $CO_2\,g^{-1}\,h^{-1}$ in

conifers). They are also much less expensively constructed in terms of content of assimilated carbon so that a proportionally larger part of the carbon gain by the tree, due to photosynthesis, is available for the growth of the nonphotosynthetic stems, roots, and fruits. A deciduous habit is very effective at making trees competitive if the growing season is at least 4 months in duration, where the climate is relatively humid, and where soil water and nutrients are readily available. In such environments the trees can produce sufficient photosynthate for at least the year's maintenance, growth, and reproduction, and they are competitive with evergreens. Shedding thin deciduous leaves in winter and the protection of meristems from water loss represents a considerable energy saving compared to maintaining a mass of thick evergreen leaves over winter. However, when the growing season becomes unduly restricted by winter cold or a long dry season, and on soils with low mineral resources, evergreen leaves can be an advantage.

This is because they are retained for several years. The evergreen habit enables leaves that are already on the tree to contribute to photosynthetic gain as soon as environmental conditions are suitable, even if the new leaves flush relatively late. They can also store nutrients in excess of current requirements for later use. The disadvantage of being evergreen is that the carbon input, or cost of constructing the leaves, is much higher than for deciduous leaves. It takes several years for a substantial leaf biomass to accumulate. The high structural cost provides protection against heat, cold, desiccation, and possibly predation and can be justified if the leaves serve for long periods but the trees have to accumulate leaf biomass over several years before fast rates of growth are achieved. Some evergreen trees are more competitive than deciduous ones in temperate deciduous climates where soils have few mineral resources and are drought-prone. Thus pines are often found on sandy soils in these regions. For example, *Pinus rigida* is the dominant pine in the New Jersey Pine Barrens, and Scots pine (*P. sylvestris*) is found on the heathlands in much of western Europe. Evergreens also predominate in boreal climates and can be very productive in climates with prolonged droughts such as in tropical monsoon and Mediterranean regions.

Because of leaf retention, there is often a much greater leaf biomass, or leaf area index (LAI), in evergreen forests. (LAI indicates the area of leaves per unit area of ground, and is indicated in units of square meters of leaf per square meter of ground.) For example, the LAIs in deciduous forests are typically between 4 and 7 whereas among evergreen conifers they can range up to 20.

## Soil

Brown forest soils (alfisols, in the American soil taxonomy) develop under temperate broadleaved deciduous forests. These are among the most fertile, most easily worked, and most easily cleared of the temperate zone soils. Many have been under continuous cultivation since Neolithic times. Some of the world's major agricultural regions are found in the temperate deciduous forest zone, which is why there are so few of the original deciduous forests left. Part of the reason for their fertility is that most soils in the temperate deciduous forest zones are relatively young, having started to develop (in North America and Europe) after the last glaciation, about 12 000 years ago. They are therefore relatively rich in nutrient elements compared with, for example, most tropical rainforest soils, which are much older.

The leaves of deciduous broadleaved trees retain the major nutrient bases when they drop in the autumn. Thus the litter under this forest is not as acidic as under evergreen trees and aluminum and iron are not mobilized from the A horizon. The autumn leaf fall provides an abundant and rich organic matter which begins to decay rapidly in spring just as the growing season begins. The organic content gives both the A and B horizons a brown color.

Ultisols replace alfisols in the southeastern USA, where the older soils of unglaciated regions have been weathered to a much greater degree and are more completely leached than the younger soils to the north. Distinctive red or yellow subsoils have developed under the warmer climate. Ultisols are generally less fertile than alfisols.

## Productivity

The productivity of temperate deciduous forests tends to be higher in the southern part of its range (in the northern hemisphere), and generally at lower elevations. However, since climate and light levels are broadly similar, net productivity is controlled primarily by local variations in nutrient and moisture regimes, as well as the inherent capacities of the various species to grow.

Productivity of the trees in stable temperate deciduous forests is usually quoted as around 10–12 dry t $ha^{-1}$ $year^{-1}$. Young stands on productive sites can achieve as much as 25 t $ha^{-1}$ $year^{-1}$. The average usable production of wood is usually considered to be about 40% of net primary production, giving levels of 4–5 dry t $ha^{-1}$ $year^{-1}$. Total above-ground biomass in mature forests is 150–400 t $ha^{-1}$. In addition, in unmanaged forests, there may be about 20% of this volume lying as dead wood on the forest floor.

## Strata

Most temperate deciduous forests have closed canopies, but open stands occur as well, particularly where the climate is dry and/or large grazing animals are abundant. Trees usually form only a single main stratum, story, or layer, though there may be an understory of shrubs, medium-sized trees, and saplings below.

These forests are among the most intensively managed in the world, so often they comprise only a single layer of developing overstory trees. Although natural temperate deciduous forests are more structured, they still tend to be far less luxuriant than moist tropical forests. Typically they consist of:

1. An overstory tree stratum, 20–35 m high, dominated regionally by various combinations of a rather limited number of genera.
2. A moderately developed subcanopy, mixed with but below the overstory and containing dying light-demanding trees and suppressed shade-tolerant trees; the latter can include younger specimens of the tall trees, but also medium-sized species such as (in Virginia, northeast USA) the Allegheny serviceberry (*Amelanchier arborea* var. *laevis*) and (in western Europe) the wild service tree (*Sorbus torminalis*) or field maple (*Acer campestre*).
3. An understory or shrub layer, including shrubs, smaller species of trees, and/or saplings of the taller trees. Species usually limited to this layer include (in Europe) hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), and holly (*Ilex aquifolium*). This stratum is most noticeable when the tree stratum is not well developed; when it is, the development of shrubs and regeneration beneath it is scanty and may be missing altogether.
4. A low-growing herb layer of perennial forbs that flower in early spring; and sometimes, a ground layer mainly of mosses; lichens and mosses also grow on the trunks of trees.

The tree stratum occasionally consists of pure or nearly pure stands, with only slight differences in age (e.g., *Fagus sylvatica* in Europe). Mixed-species stands that are more or less even-aged and composed predominantly of late successional species (e.g., *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia* and *Tilia americana*) are common in northeastern North America. More mixed-age forests occur, for example, in the oak-dominated forests of Europe, with hornbeam (*Carpinus betulus*) and other species as an understory. Truly all-aged forests are found where a strongly continental climate or very moist or very dry soils prevent the dominance of any species with a high degree of shade tolerance.

Climbers such as ivy (*Hedera helix*), honeysuckle (*Lonicera periclymenum*) in Europe, and wild grape (*Vitis* spp.), poison ivy (*Rhus* spp.), and Virginia creeper (*Parthenocissus quinquefolia*) in North America climb the trees to flower and fruit high in the forest canopy. However, they are relatively few in number.

## Tree Flora

Many tree genera are common to all three of the northern hemisphere temperate deciduous forest zones. Included among them are *Acer* (maple), *Castanea* (chestnut), *Fagus* (beech), *Juglans* (walnut), *Quercus* (oak), *Tilia* (basswood or lime), and *Ulmus* (elm). Different species of the genera occur on each continent. In South America, *Nothofagus* is a common genus (**Figure 6**).

In other respects, the climatic changes and successive glaciations during the Pleistocene, which gave rise to repeated migrations of the flora, have

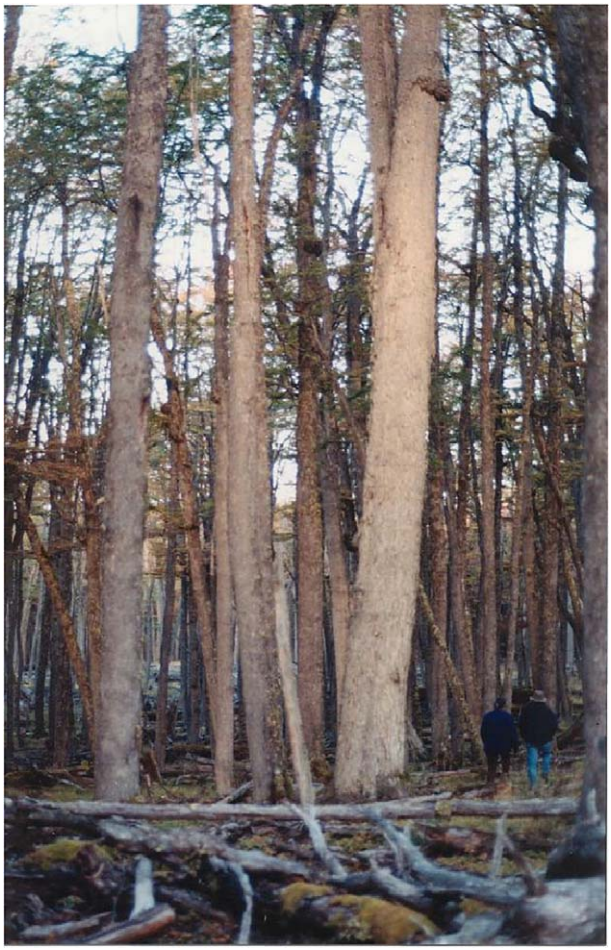

**Figure 6** Dense and apparently undisturbed *Nothofagus pumilio* forest in autumn, Tierra del Fuego, Chile. Courtesy of Franz-E Arnold.

resulted in substantial differences in the floras of deciduous forests. In North America and eastern Asia migrations were relatively unaffected by the large north–south mountain ranges (e.g., the Rocky Mountains and Appalachians), whereas the east–west ranges in Europe reduced the opportunities for plants to retreat to warmer regions and recolonize during interglacial periods. As a result, there are far fewer genera and species in Europe compared with eastern Asia and North America and, because of this, the relatively few European species tend to be more dominant due to the lack of competitors.

Although they naturally intergrade, as well as vary in detail, a number of main types of deciduous temperate forests are usually recognized:

- Western and central European oakwoods tend to be relatively open and light. The dominant species are the pedunculate and sessile oaks (*Quercus robur* and *Q. petraea*). Associated trees that are more or less common according to the nature of the soil include ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), birch (*Betula pendula* and *B. pubescens*), elm (*Ulmus glabra, U. procera, U. carpinifolia*), lime (*Tilia cordata, T. platyphyllos*), cherry (*Prunus avium*), alder (*Alnus glutinosa*), and aspen (*Populus tremula*). Small trees and large shrubs include hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*), crab apple (*Malus sylvestris*), and three species of *Sorbus* (rowan, wild service tree, and whitebeam). There are also two evergreens, yew (*Taxus baccata*) and holly (*Ilex aquifolium*).
- The more luxuriant forests of eastern North America, eastern Asia, and southeastern Europe/Asia minor differ in species composition but are similar in appearance. The principal species usually include various oaks (*Quercus* spp.), beeches (*Fagus* spp.), birches (*Betula* spp.), hickories (*Carya* spp.), walnuts (*Juglans* spp.), maples (*Acer* spp.), limes (*Tilia* spp.), elms (*Ulmus* spp.), ash (*Fraxinus* spp.), tulip trees (*Liriodendron* spp.), sweet chestnuts (*Castanea* spp.), and hornbeams (*Carpinus* spp.). The lower stories are normally more luxuriant and varied than in the western and central European forests. In the colder eastern and more northern parts of North America, conifers such as *Pinus strobus* begin to appear with the deciduous trees.
- Beech forests which, especially in Europe, with the very shade-tolerant *Fagus sylvatica* form almost uniform, closed canopies and cast such dense shade that few shrubs or herbs can grow. Similar types, though on a smaller scale, are found with *F. orientalis* in Turkey and other parts of its range, and with *F. crenata* in Japan. In the higher mountains of central and southern Europe, the conifers *Abies alba* and *Picea abies* become admixed.
- Southern beech, especially *Nothofagus nervosa* (syn. *N. procera*) and *N. obliqua*, usually with associated evergreens such as *Laureliopsis philippiana, Laurelia sempervirens*, and *Persea lingua*. Numerous ferns and bryophytes are features of these forests.
- The damper deciduous woodlands, especially those on marshy ground, are dominated by alders (*Alnus* spp.), willows (*Salix* spp.), poplars (*Populus* spp.) and birches (*Betula* spp.). The understories may be dense, and climbers and epiphytes numerous.

*See also*: **Forest Ecosystems**: Fagaceae (Oaks, Beeches, Hickories and Nothofagus); Juglandaceae (The Walnut Family: Walnuts, Hickories, Pecans). **Plant Diversity in Forests**. **Genetics of Oaks**.

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# Mediterranean Forest Ecosystems

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## Introduction

Occupying only 2% of the world's surface area, the Mediterranean biome contains nearly 20% of the