

Another factor affecting low seed set is cone and embryo abortion. *Pinus* species are most sensitive to pollen supply where a substantial percentage of first-year conelets can abort due to inadequate pollen. However, in mature seed orchards, pollen supply is seldom limiting and cone retention is high. However, under field conditions where drought, high temperatures, and low humidity occur, poor uptake of pollen in *Pinus* species may result in increased cone abortion. It is also possible that drought, high temperatures, and low humidity could restrict fertilization and early embryo development in all species.

### Environmental Effects on Reproduction

Orchard environment can affect progeny performance. Progeny from parent trees growing in warmer southern seed orchard environments can display delayed flushing in the spring and extended growing periods and delayed growth cessation in the summer. They also developed frost-hardiness later compared to like genotypes derived from northern sources. This phenomenon has been termed seed orchard aftereffects and the effects can endure for several years, if not the lifetime of the tree. Similar effects have been demonstrated with progeny derived from like parents growing under greenhouse conditions compared to open orchard conditions. Further, progeny derived from seed reared under the warmer environment of greenhouses can also show lower spring and fall frost resistance.

We do not know the mechanism of this phenomenon, nor do we know at which stage of reproductive development the effect occurs. However, several hypotheses have been postulated. Since many of the genes expressed in the sporophyte are also expressed in the gametes, it is possible that gametophytic selection occurs. It is argued that pollination selection does not occur in conifers because the pollination mechanism allows too few pollen grains to enter the micropyle to provide sufficient selection pressure. However, three or four pollen grains in each of 100 ovules per cone and hundreds of cones per tree may provide a population sufficiently large to consider a directional selection of pollen under different temperature regimes. Furthermore, conifers have multiple archegonia (many egg cells) per ovule, which permits the possibility of temperature affecting the selection of many fertilized egg cells. Finally, the effect could also be non-Mendelian and represent a maternal effect that remains to be described.

**See also:** **Ecology:** Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Tree Physiology:** Physiology of Vegetative Reproduction;

Shoot Growth and Canopy Development; Tropical Tree Seed Physiology.

### Further Reading

- Bonnet-Masimbert M and Webber JE (1995) From flower induction to seed production in forest tree orchards. *Tree Physiology* 15: 419–426.
- Chalupka W (ed.) (1985) Flowering and seed-bearing in forest seed orchards. *Proceedings of the Symposium of Working Parties S2.01.00 and S2.0501*. Kornik, Poland.
- Day ME, Greenwood MS, and Diaz-Sala C (2002) Age- and size-related trends in woody plant shoot development: regulatory pathways and evidence for genetic control. *Tree Physiology* 22: 507–513.
- FAO (2001). *Global Forest Resources Assessment 2000. Part 1 Global issues*, pp. 23–38. FAO forestry paper 140 (FRA 2000 main report). Rome: FAO.
- Gelbart G and von Aderkas P (2002) Ovular secretions as part of pollination mechanisms in conifers. *Annals of Forestry Science* 59: 345–357.
- Henrik S, Cannell MGR, Johnsen Ø, Ryan MG, and Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist* 149: 369–400.
- Krugman SL and Katsuta M (eds) (1981) *Proceedings of the Symposium on Flowering Physiology*. 17<sup>th</sup> IUFRO World Congress Meeting, Kyoto, Japan.
- Pharis RP, Webber JE, and Ross SD (1987) The promotion of flowering in forest trees by gibberellin A<sub>4/7</sub> and cultural treatments: a review of the possible mechanisms. *Forestry Ecology Management* 19: 65–84.
- Sedgley M and Griffin AR (1989) *Sexual Reproduction of Crop Trees*. London: Academic Press.
- Webber JE, Owens JN, and Stoehr MU (eds) (1995) Biology and control of reproductive processes in forest trees. *Selected papers from Symposium Working Party S2.01.05*, Victoria, BC, Canada.

## Forests, Tree Physiology and Climate

**M Rebetez and Michael Reinhard**, WSL Swiss Federal Institute for Forest Snow and Landscape Research, Lausanne, Switzerland  
**Alexander Buttler**, University of Franche-Comté, Besançon, France

© 2004, Elsevier Ltd. All Rights Reserved.

### Introduction

Climate can be defined as the long-term integration of atmospheric parameters such as temperature, precipitation, wind, insulation, air humidity, or snow cover. It is one of the key factors conditioning the growth of vegetation and it is impossible to dissociate

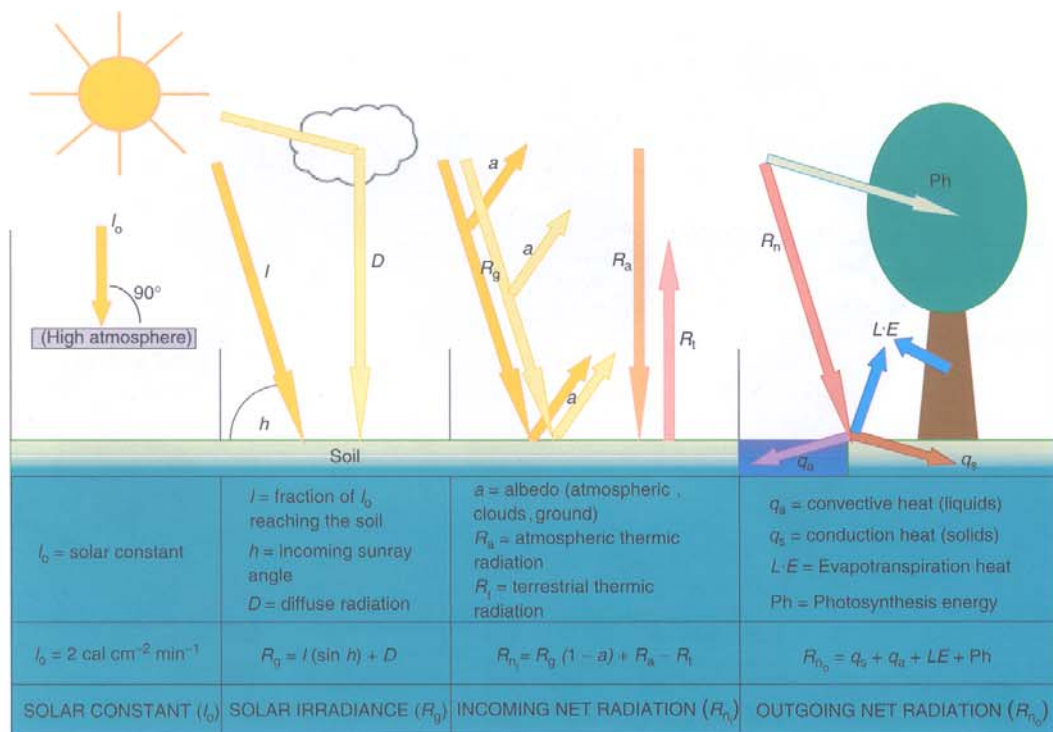
the history of forests, and all flora and fauna, from the history of the earth's climate. Climate controls vegetation patterns and dynamics and, conversely, vegetation also influences the climate. These relationships occur over different spatial and temporal scales.

This article reviews the main aspects of the relationship between climate parameters and forests while the impacts of climate change and environment on forests as well as tree physiology and stress are covered in other articles within this publication.

### The Energy Cycle and Vegetation Growth

The sun is the basic source of energy for the earth and the maintenance of its biological systems. This energy reaches the planet by means of electromagnetic radiation. The solar constant represents  $2 \text{ cal } (8.3 \text{ J}) \text{ cm}^{-2} \text{ min}^{-1}$ , but the solar irradiance at the earth's surface, which is the driving force for the functioning of ecosystems, represents less than half of the solar constant (Figure 1).

The earth re-emits part of this radiation towards space (mainly in the infrared spectrum). Another part of it is trapped by the greenhouse gases in the atmosphere. The balance between the incoming, outgoing, and absorbed energy keeps the earth's climate virtually constant, at a mean temperature of about  $15\text{--}16^\circ\text{C}$  (warmer now, due to global warming, than it was a few decades ago). Without any greenhouse effect, which is brought about by the humidity and greenhouse gases such as  $\text{CO}_2$  in the earth's atmosphere, the mean temperature on the planet would be  $-18^\circ\text{C}$ . Thus, the total energy absorbed by the earth depends on the amount of greenhouse gases and of aerosols in the atmosphere. These depend in turn on different factors, including volcanic emissions, human sources linked to the burning of fossil fuels, and methane emissions from warming permafrost and agriculture. Only a small part of the sun's energy is used for vegetation growth, the photosynthetic yield, representing the transformation of radiation into chemical energy, being estimated at 1–1.5% for forest ecosystems. Primary



**Figure 1** Incoming and outgoing net radiation at the earth's surface. The incoming and outgoing radiation depend on the thickness of the cloud cover, which can act as a shield for the sunrays. The total amount of intercepted radiation at the ground level depends also on the density and thickness of the vegetation canopy. About 98% of the intercepted radiation is reflected or used to heat the tissues and only about 2% is used for photosynthesis. Reproduced with permission from Ozenda P (1982) *Les Végétaux dans la Biosphère*. Paris: Doin.

production contributes to the carbon cycle, and sometimes this organic matter becomes trapped underground as peat, oil, or coal. Through its albedo, the vegetation cover also influences the amount of energy absorbed at the earth's surface.

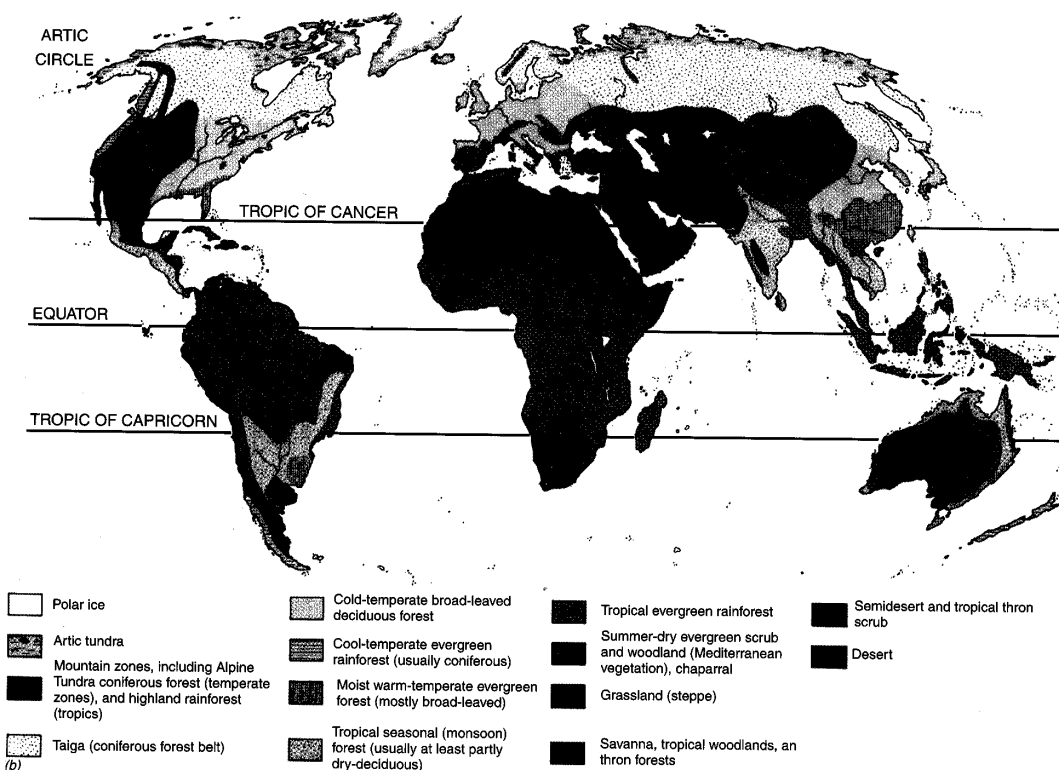
The energy emitted by the sun is not equally distributed over the earth's surface and this leads to compensating ocean currents and atmospheric circulation. The earth's spherical shape implies a spatially uneven incidence of the incoming solar irradiance, and its intensity changes with latitude. Throughout the year, the intertropical zone receives more energy than polar regions. As the tilt of the earth's axis is not perpendicular to the planet's orbit, the amount of energy received also changes throughout the year, thus determining the seasons. The total amount of energy received by the earth yearly also varies with the amount of energy released by the sun and also with the elliptical shape of the earth's orbit and its eccentricity. These orbital parameters determine climatic cycles on the order of 20 000 to 100 000 years. These differences are relatively small, but

important enough to explain major changes in the earth's ice, ocean, and vegetation cover in the past.

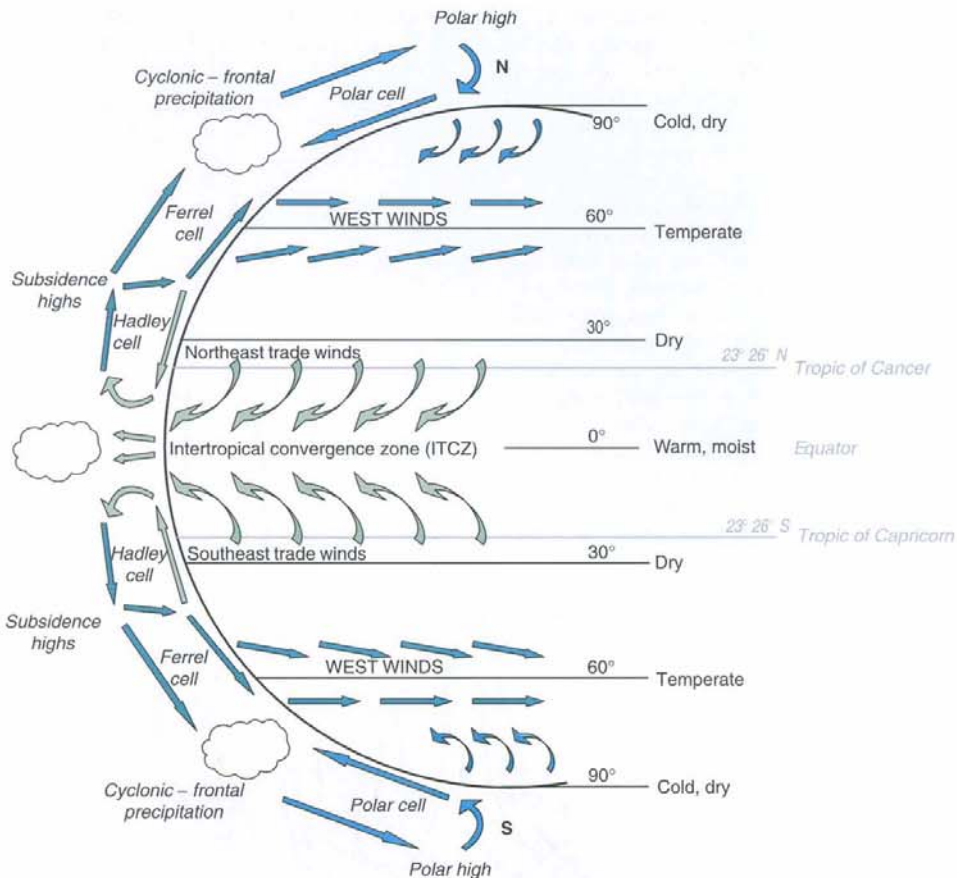
### The Impact of Climate on Vegetation

Climate and the resulting distribution of vegetation over the earth's surface is primarily determined by the available energy. At a large geographical scale, climatic zones follow one another in parallel from the equator to the poles and determine zonal macroecosystem belts called biomes (Figure 2).

The strong warming of the earth's surface in equatorial regions causes air to rise. As the warm, moist air rises, it cools, resulting in frequent precipitation and allowing the development of rainforests. This air circulation pattern is linked to a belt of low atmospheric pressure upon which winds converge (Figure 3). The warm air masses circulate back the earth's surface north and south of the equatorial region, in a subsidence movement that is linked to high air pressures. During this process, the air temperature remains relatively high but the



**Figure 2** Distribution of the major vegetation types across the globe. Reproduced with permission from Aber JD and Melillo JM (2001) *Terrestrial Ecosystems*, 2nd edn. London, UK: Academic Press.

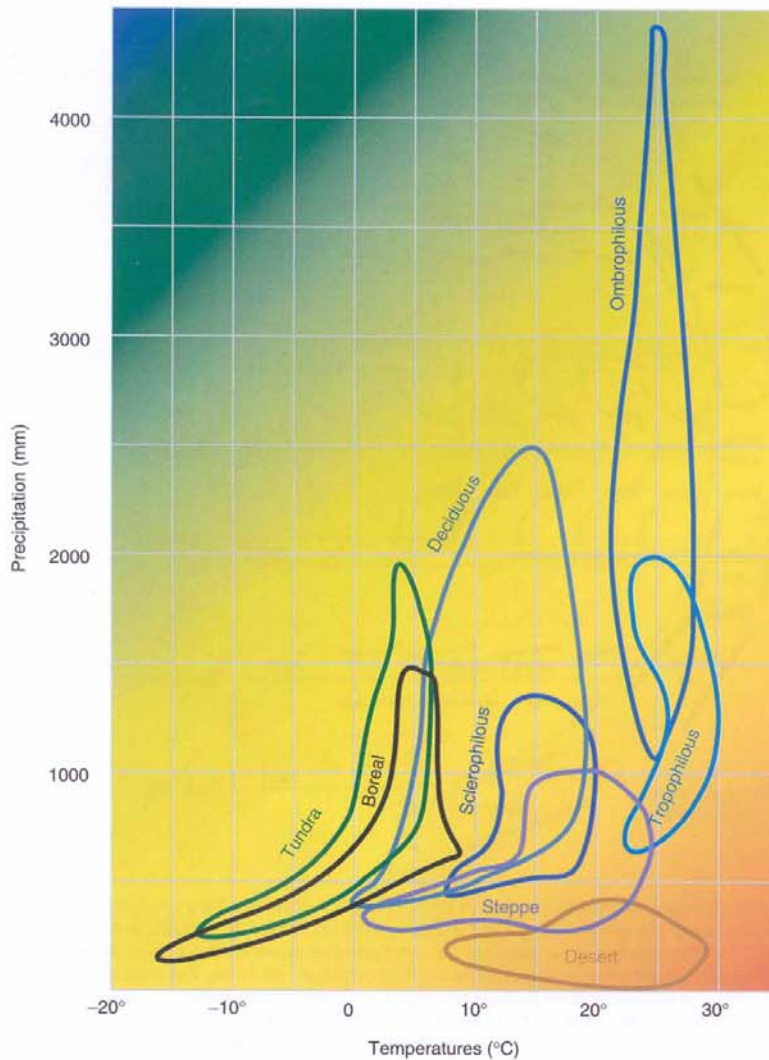


**Figure 3** Global earth atmospheric circulation and main winds. The planet's surface receives decreasing solar radiation from the equator to the poles because of the spherical shape of the earth and its tilt. Heated air expands and loses density. There is thus a relation between the temperature gradient of the earth and the atmospheric pressure system. Hence, we would expect the air masses to move from the cold poles (dense air, high pressure) to the warm equators (dilute air, low pressure) to cancel out the pressure gradient. In reality, we observe various cyclonic (lows) and anticyclonic (highs) pressure systems leading to three main components (Hadley, Ferrel, and polar cells) in both hemispheres. Adapted from Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan and Dincauze DF (2001) *Environmental Archaeology*. Cambridge, UK: Cambridge University Press.

moisture and precipitation decrease progressively, leading to drier climatic zones with more pronounced seasonality. A precipitation gradient of approximately  $1 \text{ mm year}^{-1} \text{ km}^{-1}$  occurs from approximately  $10^\circ \text{ N}$  to  $18^\circ \text{ N}$ . Below a threshold of approximately  $400 \text{ mm year}^{-1}$ , the lack of precipitation shapes the steppe and desert vegetation. The Sahara Desert, the Sahel zone, and their transition zone have been defined as having the following rainfall values: Sahara Desert,  $0\text{--}100 \text{ mm year}^{-1}$ ; Saharan-Sahelian transition zone,  $100\text{--}200 \text{ mm year}^{-1}$ ; and the Sahel proper,  $200\text{--}400 \text{ mm year}^{-1}$ .

At higher latitudes, beyond these anticyclonic zones, the climate is dominated by westerly winds. The Mediterranean climate is characterized by dry

and hot summers with wet and mild to cold winters. The temperate climate experiences air masses from the north or south at all seasons: warm air masses from the tropics alternate with cold air from the polar regions. Temperatures can consequently vary from one day to the next and vegetation must be adapted not only to cold winters and hot summers but also to rapid changes, including for instance a return to below-freezing temperatures during a mild spring. At the highest latitudes, temperature and light remain very low throughout the year. The vegetation is limited by the cold and partly by snow or ice cover, resulting in cold deserts. The broad pattern of world biome types can be represented in relation to humidity and temperature (Figure 4). The concept



**Figure 4** Distribution of vegetation types according to mean annual temperature and precipitation. The planet's vegetation cover is largely linked to temperature and precipitation gradients. This figure gives an insight into the coarse ombrothermic distribution of the major biomes. At finer scale, the species composition determines many other plant communities. Furthermore, the natural distribution and extension of the biomes is altered by human activities. Adapted from Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan.

of the ecocline can be used to relate communities to climate on a worldwide scale.

The distribution of vegetation on the earth's surface is also influenced by other factors. Because of the uneven distribution of land and water over the globe, the biomes are distributed unequally between the northern and southern hemispheres (Figure 2). Regionally, they also depend on proximity to oceans, on the degree of continentality, or on topography. Temperate areas located near oceans are often

referred to as 'oceanic,' as the oceans bring moisture and reduce the variation in temperature between summer and winter as well as between day and night. As air masses from the west move over the continent, losing moisture, the 'continentality' increases, which means longer drought periods and greater temperature fluctuations, and consequently the development of dry vegetation types such as steppes and deserts.

At intermediate scales, the regional climate setting can modify the general pattern of vegetation. Greater

elevations can be considered as equivalent to higher latitudes. On Mount Kilimanjaro, Mount Everest, and Mont Blanc, the climate is comparable to that of the poles (cold deserts) although these mountains are in tropical and temperate regions. On the sides of these mountains, the climate follows a gradient determined by altitude. The temperature, in particular, decreases with altitude at a mean rate of approximately  $0.7^{\circ}\text{C}$  per 100 meters (depending mainly on the air humidity and pressure), and the vegetation communities reflect these changes (Figure 5). The vegetation changes that occur with altitude are similar to those occurring with latitude. For example, 100 meters change in elevation is equivalent to an increase of  $1^{\circ}$  of latitude. The degree of sun exposure and more generally the topography of the landscape can change the altitudinal distribution of vegetation communities (Figure 6). Features such as valleys where temperature inversions occur can host specialized communities and even reverse the altitudinal distribution of vegetation (Figure 7).

## Light

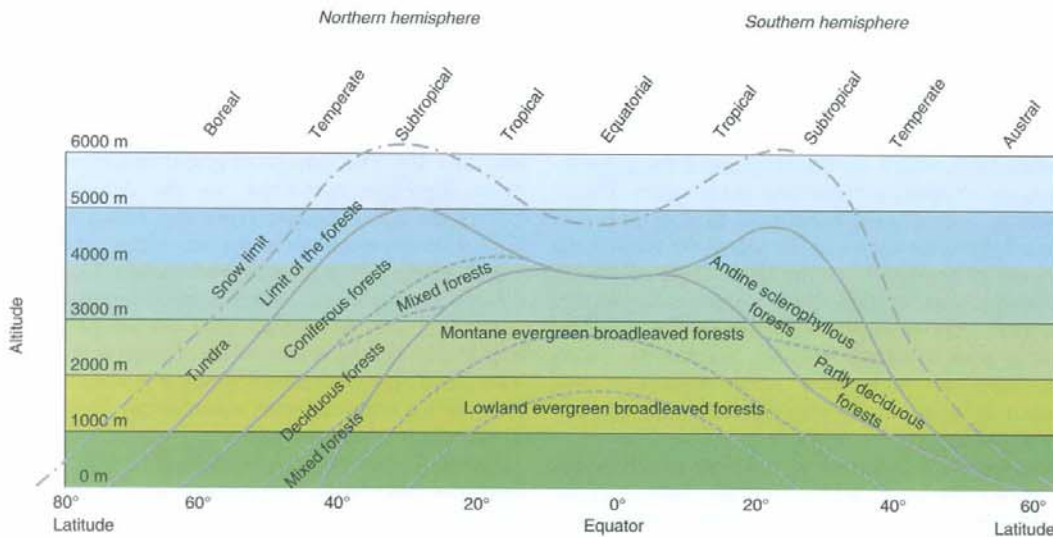
Light is a fundamental climatic parameter providing the energy for photosynthesis and controlling the availability and production of vegetation. The amount of light and energy that penetrates the forest or is reflected depends on the species composition, which determines the canopy structure, and on other

properties such as the color of leaves, their position and density, the age of the stand, and the season (Figure 8). The loss of light with increasing distance from the top of the canopy is termed light attenuation, and can be expressed by:

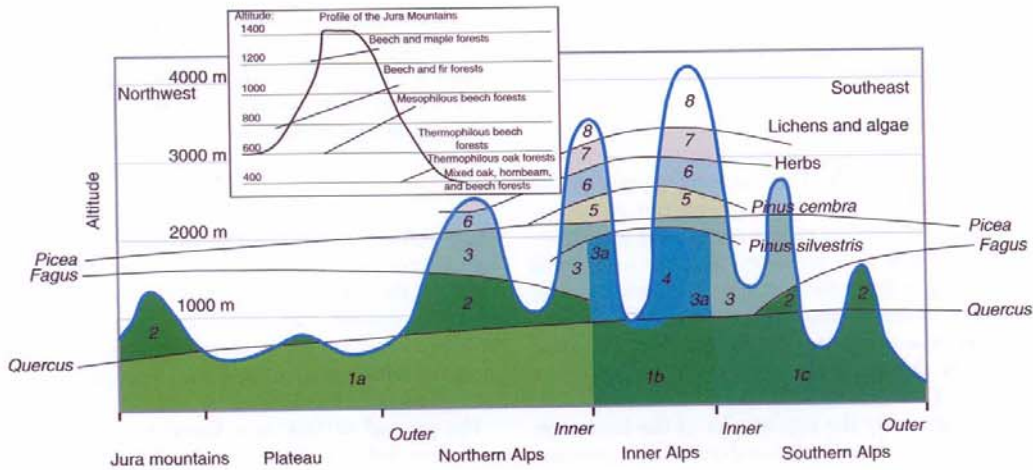
$$IL/IO = e^{-kLAI(L)}$$

where  $IL/IO$  is the percentage of light at the top of the canopy ( $IO$ ) reaching depth  $L$  in the canopy,  $LAI(L)$  is the cumulative leaf area (in  $\text{m}^2$  of leaf area per  $\text{m}^2$  of ground area, called leaf area index) from the top of the canopy to depth  $L$ ,  $k$  is a stand- or species-specific constant, and  $e$  is the base of natural logarithms (2.718).

The ground surface in a forest receives progressively less light as the forest grows; at the time of canopy closure, the ground in a pine stand will only be receiving approximately 7–8% of the ambient light. However, as a stand ages beyond this stage, the light penetration gradually increases, reaching approximately 30% of ambient by maturity. In the deciduous forests of temperate zones, the amount of light reaching the ground is highest in spring, being 5–10 times higher than that experienced in summer, when only 1–5% of the ambient light reaches the soil. Combined with the increase of temperature over the growing season, this change in light condition allows phenological shifts of the vegetation that are particularly obvious in the herbaceous strata.



**Figure 5** The relationship between altitude, latitude, and main forest types. The snow limit is lower at the equator because of the high precipitation and the related snow amount in comparison to the tropics. In general, coniferous forests mark the limit of the forests in the northern hemisphere, whereas deciduous forests do so in the southern. Adapted from Otto HJ (1998) *Ecologie Forestière*. Paris: Institut pour le Développement Forestier.



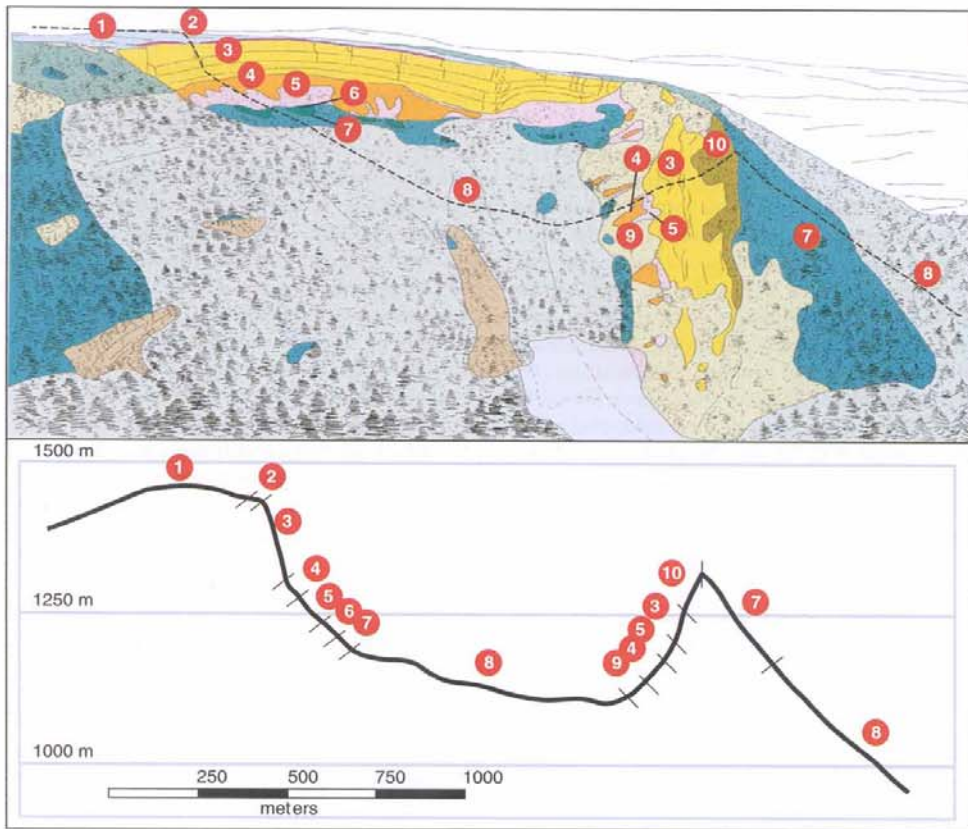
**Figure 6** Influence of geomorphology and sun exposure on the altitudinal distribution of trees and vegetation strata and communities: an example from Switzerland with a transect from the Jura Mountains to the Alps. 1, Hilly strata (*Quercus*); 1a, Northern variation, mostly *Quercus robur*, *Q. petraea*, *Carpinus betulus*, and *Fagus sylvatica*; 1b, Inner alpine variation, mostly *Q. pubescens*; 1c, Southern variation, mostly *Q. pubescens*, other *Quercus* spp., and *Castanea sativa*; 2, Montane strata (*Fagus sylvatica*–*Abies alba*, together with *Picea abies*); 3, Subalpine strata (mostly *Picea abies*); 3a, Continental variation, *Pinus sylvestris* mixed with *Picea abies*; 4, Continental montane strata (*Pinus sylvestris*); 5, Suprasubalpine strata (*Pinus cembra* and *Larix decidua*); 6, Alpine strata, mostly alpine lawns; 7, Sub snow strata, mostly low-statured plants in patchy communities; 8, Snow strata, isolated plants, mostly lichens and algae. Modified from Gallandat JM and Landolt E (1994) *Compte Rendu de la 2<sup>ème</sup> Excursion Internationale de Phytosociologie en Suisse (14–21 Juillet 1991)*. Veröffentlichung de Geobotanischen Institutes der Eidg. Tech. Hochschule, 119. Heft. Zurich: Stiftung Rübel.

Within the vertical strata of a forest stand, both the quantity and quality of light follow a gradient, which determines the ecological niches for species and contributes to the biodiversity of the stand. Hence, only a small amount of the direct light reaches the lowest forest strata and a distinction must be made between direct and diffuse radiation (Figure 1). Radiation within the forest canopy is characterized by the high transmission and reflection of green and infrared light, whereas blue and red-orange light, which are the most useful for assimilation, are depleted towards the lower strata. Photosynthetic assimilation in response to solar radiation has a hyperbolic shape. At the top of the curve is the saturation point (SP), or the light saturated rate of photosynthesis, beyond which plants cannot further increase light absorption. Some authors consider that if solar radiation increases beyond this point, photosynthesis diminishes in a process termed photoinhibition, and at very high levels of radiation photodamage occurs in the form of destruction of photosynthetic pigments and thylakoid structures. However, generally, leaves are well adapted to the local light conditions and their pigmentation allows for the dissipation of excess energy or the capture of energy when it is limited. This means that species growing under full-sun conditions generally show higher rates of photosynthesis and have higher

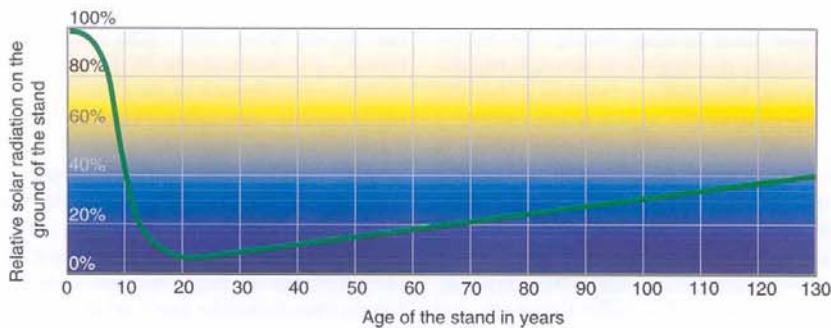
saturation points than those normally growing under partial shade.

These processes play a determinant role in the plant composition of forests as different species have different light requirements. There are heliophyte plants, requiring high quantities of sunlight, and sciophytes, which prefer shade and sometimes still have a positive carbon balance, and finally species that have a rather large ecological amplitude. For instance, mosses and herbs on the forest ground have very low SPs. The amount of global radiation is the most important parameter for the definition of heliophyte and sciophyte types and hence for the vegetation composition in forests. Light conditions are also very heterogeneous horizontally. Light can directly penetrate into forest stands, creating light patches at the soil surface that are of particular importance for the regeneration of vegetation. Such light flecks can cover 20–25% of the ground surface at noon in a tropical forest, contributing 70–80% of the energy reaching the soil.

Plants do not only physiologically adapt to the light, they also do so morphologically. For example, the shape of leaves is smaller and thicker where insulation is important, whereas the opposite occurs in less exposed locations. The same tree species may show very different stature depending on whether it is growing in a dense or open stand. For example,



**Figure 7** Distribution of the main vegetation types in the Creux-du-Van in the Swiss Jura Mountains. The site is shaped by a 200-m high cliff which encircles a semiclosed depression with a cold local climate. In the scree at the foot of the cliff, a permafrost has built up as a remnant of a local glacier. The figure shows that a spruce subalpine forest is developing in the cold depression and on north-facing slopes, whereas, on the contrary to normal vegetation distribution (see **Figure 6**) beech forests can be found at higher altitudes than the spruce forest. 1, Beech and maple forests, pastures; 2, Rock pioneer vegetation on the cliff; 3, Maple forests and pioneer vegetation on the scree; 4, Subalpine spruce forest on the scree, together with subalpine herbaceous species; 5, Beech and fir forests; 6, Thermophilous beech forest and pine forest. Modified with permission from Büttler A, Gallet F, and Gobat JM (2001) *Végétation et flore*. In: *Le Jura*, pp. 77–151. Paris: Collection Bibliothèque du naturaliste, Editions Delachaux et Niestlé.



**Figure 8** Relationship between the age of the stand and the relative amount of light received on the ground of the forest. On average, forests are thickest at about 20 years of age, which corresponds to the period when the smallest amount of light reaches the forest ground. Later, as the stand grows older, it loosens allowing for more light on the ground. Adapted from Flemming G (1995) *Wald, Wetter, Klima: Einführung in die Forstmeteorologie*. Berlin: Deutscher Landwirtschaftsverlag Berlin.

shaded leaves may have less chlorophyll per unit leaf surface area than sun-exposed leaves.

## Temperature

Temperature is very important to poikilotherm organisms such as trees. Poikilotherm organisms assume the temperature of their environment. The lower the temperature, the lower the metabolic activity of the plant and the less the photosynthetic activity. Tree species all have different temperature optima for photosynthesis: a boreal forest tree conducts photosynthesis at far lower temperatures than tropical trees. On average, temperatures are harmful to vegetation when they rise above 50–60°C, which is the protein alteration threshold, and when they drop below 0°C, at the threshold for cellular structural deterioration. At both thresholds, the cell wall stability is critical. However, trees may adapt physiologically where temperatures frequently pass beyond these values. For example, in Siberia, trees have to cope with temperatures as low as –68°C.

Cold is a limiting factor that can cause freeze stress to trees unless they are acclimated. If the temperatures are too low and the growing season too short, trees cannot grow. Freezing damage is more important during daytime, when photoinhibition is also induced, and when vegetation is active, for example at the beginning of the growing season. Ice crystals form inside the plant cell and break the cell walls, which kills the cells. Extracellular freezing may also induce cell dehydration. Freezing within the xylem vessels can be followed, during melting, by the development of occlusions that hamper hydraulic conductivity. Trees therefore need to adapt to temperature, and they do this using particular strategies. In temperate climates, deciduous forests are dormant during wintertime. Trees lose their leaves, which cannot withstand frost, leaving only the relatively resistant dormant buds. Coniferous trees do not lose their needles during the winter season and overcome freezing stress through physiological adaptations. Intracellular freezing is avoided by chemical alteration of the liquids inside the cell, a phenomenon called supercooling. Supercooling is enhanced by partial rejection of water outside the cells, dropping the freezing point of the solute content of the cell. Water can freeze outside the cell, whose walls are able to deform. However, despite the use of both supercooling and extracellular freezing, most coniferous trees need a time to adapt and become frost resistant for the winter, a process called frost hardening. If the temperature drops too quickly, then even coniferous trees suffer from freezing stress, resulting in the development of injury to the foliage.

Hence, winter temperatures set the broad geographic distribution of many tree species in both the northern and southern hemispheres. Under natural conditions, this ecological limitation can be recognized on mountains by the upper growing limit of the trees – the treeline.

High temperatures can also disturb or disrupt photosynthetic activity and harm the plant. The rate of photosynthetic activity depends on the species. Observations suggest that there is a relationship between latitude and the sensitivity of photosynthesis in a species to temperature. However, there is also evidence of considerable plasticity in this relationship. Several factors can lead to the decline of photosynthetic activity at high temperature, including the more rapid increase in respiration rate than photosynthesis that accompanies increasing temperature; the breakdown of temperature-intolerant enzymes thought to be critical for photosynthesis; the alteration of the cell structure, cell membrane thinning, and cell leakage; and stomatal closure and the inhibition of the carbon dioxide, water, and oxygen exchange essential for photosynthesis. Plants can adapt physiologically to high temperatures. For example, some leaves have a reflective coating. Other forms of adaptation concern the form or the orientation of the leaves, which may be vertical in order to reduce the exposure to the sun. For example, if a leaf orientated perpendicular to the sun absorbs 1.0 cal (4.19 J) of energy  $\text{cm}^{-2} \text{s}^{-1}$ , then one orientated at 60° to the sun will only absorb 0.5 cal (2.09 J)  $\text{cm}^{-2} \text{s}^{-1}$ . In cases when there is sufficient water available, another adaptive mechanism is to increase the transpiration rate, which then cools the leaves.

At a local scale, temperatures are controlled within forest ecosystems by the strong moderating effect of the stand on radiation. In deciduous forests, daytime temperatures are highest within the crown during the growing season, and highest at the soil surface once the leaves have been shed. Temperatures inside forests, and particularly at the ground surface, are of major significance as they have such a bearing on physiological processes. The temperatures inside forest stands are regulated, whereas the temperatures outside wooded areas can vary greatly between day and night, and over the seasons. Forests reduce the diurnal temperature range: days are cooler and nights are warmer than they are outside the forest. However, on average, temperatures are cooler in forests than in nearby open areas. The differences are greatest at the ground level. For instance, the average difference between field and forests is about 1 K at ground level, 0.7 K at about 2 m above the ground, and 0.3 K at the crown level. This is the result of the

poor distribution of light and of the high rate of evaporation within the forests. Tree crowns retain cool air during the day, and at night, they capture the thermal radiation near the ground. In winter, snowless crowns have a lower albedo than the surrounding fields and, hence, temperatures are higher in the forests when there is snow on the ground. The spatial heterogeneity of the forest, and in particular the presence and distribution of larger gaps in the stands, can alter the thermal exchanges within the forest and its temperature gradients. This can be critical for the regeneration of trees.

### Precipitation and Water Availability

Water availability at a particular location and the hygrometric condition of the atmosphere are of the utmost importance for terrestrial organisms, as their survival depends on the desiccation rate in conjunction with temperature. For many species, precipitation is a more important determinant of survival than temperature per se. Precipitation is a primary determinant of vegetation structure, with trees occurring only where annual precipitation is in excess of 300 mm. Vegetation needs water to achieve photosynthesis as much as it needs optimal temperatures and light. Moreover, plants need water for physiological activities such as protein synthesis or cell growth, and to maintain the rigidity (turgor) of the cells. Eventually, water is necessary for nutrient transportation in plants. Water is transported in vascular plants by physical processes: water moves from the high vapor pressure at the roots to the low pressure at the stomata. Water leaves trees through the stomata, which are usually located under the leaves, and this loss creates an upward water flux from the soil to the plant. The loss of water is termed transpiration, and the rate at which it occurs depends on the air temperature, humidity, and wind conditions, and on the particular stomata shape and behavior. Evapotranspiration is the total amount of water transmitted into the atmosphere by vegetation transpiration added to the total amount of evaporation from the plant and ground surfaces at the same location. The total yearly transpiration of a temperate forest stand ranges from 200 to 600 l m<sup>-2</sup>. Thus, vegetation cover largely influences air humidity.

Observations indicate that there is a relationship between annual precipitation and the main vegetation types. This is particularly true for regions with extreme precipitation. However, this relation is blurred at regional and local scales. This is because of annual precipitation patterns, which regulate the available and usable water quantity for vegetation. Other parameters such as topography, soil, and the

vegetation itself can influence the hydrological budget at a site. The fate of the rainwater depends partly on the forest stand. In temperate deciduous forests, the canopy can intercept between 10% and 40% of the annual precipitation, which is subsequently lost from the stand through evaporation. Higher interception rates have been reported for coniferous forests.

Trees need to adapt to hydrological conditions as well as to light and to temperature. Hygrophyte plants grow in environments close to the water saturation point while xerophyte plants live in dry environments. In water-saturated environments, trees are adapted to the poor oxygen availability in the soils; these include poplar (*Populus* spp.), willow (*Salix* spp.), alder (*Alnus* spp.), *Taxodium distichum*, *Nyssa* spp., mangroves, and a few palms, such as *Nyssa fruticans*. The diffusion of oxygen in water-saturated soils is about 10 000 times slower than in dry soils. Consequently, plants need to adjust their roots to the conditions that they are growing in: aerial roots from stems, ventilating tissue (aerenchyma) along the stems, and longitudinal air spaces along roots are examples of observed adaptations.

Drought is also an important factor limiting vegetation. It influences the distribution of plants and occurs when a deficit develops between precipitation and evapotranspiration, leading to a reduction in the soil water content. Water stress occurs when, as a result of water deficit, the relative water content of the plant tissue decreases. Many plants cannot extract water from soils when the matric potential (a measure of the attraction between soil particles and water in the soil) falls below -1.5 Mega Pascals (MPa) - termed the permanent wilting point. Plants adapted to very dry conditions have permanent wilting points well below -1.5 MPa, such as the dryland vegetation described below. A lack of water will drastically disturb photosynthetic activity: the plant closes its stomata to avoid desiccation and to maintain the cell's rigidity and, hence, uptake of carbon dioxide for photosynthesis is halted. Trees that adjust to dry conditions are called water-stress avoiders because they develop particular resistance strategies. A general, long-term response to water stress is for the osmotic potential of leaf cells to be altered through an increase in the concentration of cations, sugars, and low-molecular-weight solutes in cells. This increases the differences in water potentials between leaf and soil and decreases the gradient between leaf and atmosphere, facilitating the movement of water from the soil to the leaf and reducing the rate of water movement from the leaf to the atmosphere. Other mechanisms also occur. For instance, the baobabs (*Adansonia*

*digitata*) use their thick trunks to store water, which is then used during dry periods. They can store up to 120 000 l of water and at maturity have a circumference of about 20 m. Some shrubs develop a particularly deep root system that can reach groundwater located at considerable depths. For example, mesquite shrubs (*Prosopis* spp.) develop roots penetrating as deep as 53 m. Families such as *Olea*, *Myrtus*, and *Phillyrea*, which are fairly tolerant of fluctuations in water content, are termed hydrolabile. Families such as *Laurus*, *Arbutus*, and the evergreen *Quercus* species cope with water stress by adjusting transpiration rates; this behavior is termed hydrostable. Dormancy is another adaptation. Some trees adapt by shedding leaves during the dry season. However, plants retaining their leaves during the dry season are often adapted to water stress by having hard and waxy leaves, termed sclerophyllous leaves.

Precipitation and moisture in their solid form, snow and ice, are also important ecological factors in the mountains and in cold climates. They act as water reservoirs during the summer. Snow can protect against desiccation and against cold temperatures. However, snow can also harm trees because of its weight. The length of the snow cover season influences the spatial distribution of plant communities, and topography has an influence on the length of snow cover. A snow depth of 20 cm will prevent between 85% and 99% of the ambient light reaching the ground, depriving plants of the light necessary for photosynthesis. Fog and dew are other factors that can play an important role in some circumstances, for example in providing a significant source of water in what would otherwise be relatively dry ecosystems (see Hydrology: Hydrological Cycle).

## Wind

Winds emerge from the atmospheric pressure system. Their strength depends on the difference between high- and low-pressure areas, modulated by topographical features of the earth's surface such as mountains and valleys. At ground level, air masses always move from high to low pressure at all the global, regional, and local scales, contributing to the precipitation distribution. As a result of the earth's rotation, winds in circular air movement patterns move to the left in the northern hemisphere and to the right in the southern hemisphere.

Within forest stands, wind influences temperature and moisture gradients. Where winds blow strongly and constantly, trees develop specific features reflecting the dominant wind direction. This phenomenon is called anemomorphism and is particularly frequent in coastal zones and some mountain regions. Where

winds are too strong, arborescent species cannot grow and give way to shrubs and grass fields. Trees often grow up to a limit of 2300 m above sea level in the European Alps, for example, whereas because of wind they barely reach 1450 m in the French Auvergne, located only a few hundreds of kilometers away.

Locally, forests can act as windbreaks. Next to the forest boundary, turbulence is produced, altering the effect of the wind. For deciduous forests, this effect is most effective during the growing season. In many regions of the world, trees are used to shelter crops, buildings, and other features from wind.

**See also:** Environment: Environmental Impacts; Impacts of Elevated CO<sub>2</sub> and Climate Change. Hydrology: Hydrological Cycle. Tree Physiology: Canopy Processes; Stress.

## Further Reading

- Aber JD and Melillo JM (2001) *Terrestrial Ecosystems*, 2nd edn. London, UK: Academic Press.
- Barry RG and Chorley RJ (1995) *Atmosphere, Weather and Climate*, 6th edn. London: Routledge.
- Berger A (1992) *Le Climat de la Terre: Un Passé pour Quel Avenir?*. Brussels: De Boek Université.
- Büttler A, Gallet F, and Gobat JM (2001) Végétation et flore. In: *Le Jura*, pp. 77–151. Paris: Collection Bibliothèque du naturaliste, Editions Delachaux et Niestlé.
- Dincauze DF (2001) *Environmental Archaeology*. Cambridge, UK: Cambridge University Press.
- Flemming G (1995) *Wald, Wetter, Klima: Einführung in die Forstmeteorologie*. Berlin: Deutscher Landwirtschaftsverlag Berlin.
- Gobat JM, Avagno M and Matthey W (1998) *Le sol vivant. Bases de Pédologie et biologie des sols*. Collection géner l'environnement. Lausanne, Switzerland: Presses Polytechniques et Universitaires Romandes.
- Gordon M (1984) *Ecologie de la Végétation Terrestre*. Paris: Masson.
- Kimmins JP (1987) *Forest Ecology*. New York: Macmillan.
- Lacoste A and Salanon R (1999) *Éléments de Biogéographie et d'Ecologie Végétale*, 2nd edn. Paris: Nathan.
- Larcher W (2003) *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, 4th edn. Berlin: Springer-Verlag.
- Lawford RG, Alaback PB, and Fuentes E (1996) *High-Latitude Rainforests and Ecosystems of the West Coast of the Americas*. New York: Springer-Verlag.
- Lüttge U (1997) *Physiological Ecology of Tropical Plants*. Berlin: Springer-Verlag.
- MacDonald GM (2003) *Biogeography: Introduction to Space, Time and Life*. New York: John Wiley.
- Mitscherlich G (1982) *Wald, Wachstum und Umwelt: Eine Einführung in die Ökologischen Grundlagen des Waldwachstums*, 2nd edn. Frankfurt am Main, Germany: D. Sauerländer's Verlag.
- Otto HJ (1998) *Ecologie Forestière*. Paris: Institut pour le Développement Forestier.

- Ozenda P (1982) *Les Végétaux dans la Biosphère*. Paris: Doin.
- Tucker CJ, Dregne HE, and Newcomb WW (1991) Expansion and contraction of the Sahara Desert between 1980 and 1990. *Science* 253: 299–301.
- Tyree MT and Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* 40: 19–38.
- Walter H (1977) *Vegetationszonen und Klima*. Stuttgart, Germany: Ulmer.
- Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan.

## Physiology of Vegetative Reproduction

R R B Leakey, James Cook University, Cairns, Queensland, Australia

© 2004, Elsevier Ltd. All Rights Reserved.

### Introduction

Vegetative regeneration is both a natural process and an artificial process. The artificial process is used by agriculturalists, horticulturalists, and foresters to capture and multiply individual genotypes, and so to produce cultivars and clones. Clonal approaches to forestry and horticulture have a history going back more than 800 and 3000 years respectively, originating in China. Typically the process is used to develop superior planting stock, although there are also many applications in research where clonal uniformity is a powerful tool in the separation of genetic effects from physiological and environmental impacts on growth processes in plants.

The level of understanding about vegetative regeneration using stem cuttings has progressed enormously since the 1970s, the period when clonal forestry was becoming a reality in Europe, USA, tropical Africa, and Latin America. Although the focus of this review is primarily on the physiology of rooting cuttings, some mention is also made of related issues in air-layering/marcotting, grafting/budding, and different *in vitro* propagation methods.

This contribution draws heavily on studies done with *Triplochiton scleroxylon*, a tropical hardwood of West Africa, because of the large number of relatively comparable experiments done using a similar type of material (single-node leafy cuttings) under similar environmental conditions, to seek some physiological principles of wider relevance. In addition, the review offers some suggestions on how future research should be implemented to enhance

the identification of underlying physiological principles determining successful rooting of stem cuttings. The problem that needs to be overcome is the high level of interaction between the large number of factors pre-severance, post-severance, and in the propagation environment.

### Rooting Stem Cuttings

Stem cuttings can come in many forms but the two major groups are leafy softwood cuttings from relatively un-lignified, young shoots (Figure 1), and leafless hardwood cuttings from older and more lignified shoots which typically have already shed their leaves due to the onset of winter or a dry season. It is important to understand that the factors determining the rooting of these two types of cuttings are very different: leafy cuttings depend on current photosynthates produced in the propagation bed, while hardwood cuttings depend on the hydrolysis and availability of carbohydrates stored within the stem tissues.

When trying to root leafy stem cuttings, there are four stages when a good physiological understanding of the factors influencing rooting ability is necessary: (1) in the propagation environment; (2) post-severance; (3) in cutting origin and environment; and (4) in the pre-severance stockplant environment.

### The Propagation Environment

The most important aspect of the propagation environment is that it encourages physiological activity (photosynthesis and transpiration) in the leaf to minimize the physiological stresses experienced by the tissues, from transpiration and respiration, and encourages meristematic activity (mitosis and cell differentiation) in the stem. The transport of assimilates and nutrients from the leaf to the base of the stem, and of water from the base of the stem to the leaf, are also important. Recent physiological measurements confirm general experience that the duration of physiological shock arising from severing a cutting from its stockplant and inserting it in a propagator can be minimized by controlling the propagation environment. Minimizing this shock enhances rooting.

There are many different types of propagation systems for stem cuttings, but the most common are: (1) fogging systems; (2) intermittent mist (Figure 2), controlled by a range of different sensors; and (3) airtight, watertight, high-humidity, nonmist propagators (Figure 3). These are all very effective, but vary in their cost and sophistication. The nonmist