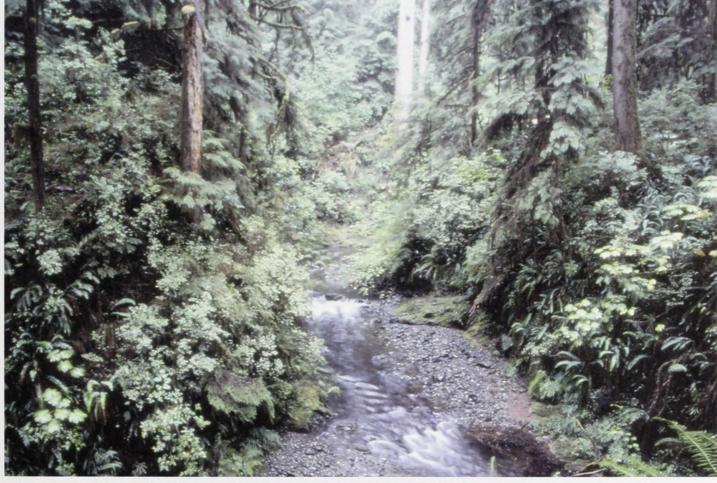# General Forest Ecological Processes
Chapter 10 from *Trees and Forests, a Color Guide*

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INTRODUCTION

Wooded land currently covers between 30 and 35% of the world's land surface (depending on what is counted as forest), or around 39 to 45 million k² [15 to 17 million square miles] (FAO 2003). Ecologists often distinguish between woodland and forest. Woodland is a small area of trees with an open canopy (usually defined as the canopy giving less than 40% cover, that is 60% or more of the sky is visible) so that plenty of light reaches the ground, encouraging other vegetation beneath the trees. By contrast, a forest is usually considered to be a relatively large area of trees forming a closed, dense canopy. For simplicity's sake, and because the underlying ecological processes at work are the same, in this chapter the term forest will be used to mean any wooded land.

A dense temperate rain forest in the Olympic Peninsula, Washington State, USA. It is composed mostly of *Psuedotsuga menziesii* (Douglas fir), *Tsuga heterophylla* (western hemlock), and *Thuja plicata* (western red cedar).

Open woodland at Needwood Forest, England. The sparse canopy of *Fraxinus excelsior* (European ash) and *Tilia* spp. (lime [linden]) standards allows abundant light to reach the shrub layer of coppiced *Corylus avellana* (hazel) and, on the ground, a mixed field layer dominated by *Hyacinthoides non-scripta* (bluebell). A sparse ground layer of mosses is also present.

SIZE AND GROWTH

The most obvious factor that separates forests from other types of habitat is the large weight or mass of organic material present, referred to as the biomass (or sometimes the standing crop). In most forests, more than 85% of the biomass is contained in the above-ground portion of the woody plants. Biomass above ground increases from the northern boreal forest southwards towards the tropics, starting from very low levels at the Arctic tree line, and reaching in excess of 940 t ha^{-1} [838,480 pounds per acre] in the Amazon basin. However, there are exceptionally large forests outside the tropics, notably the temperate forests of the Pacific Northwest of North America. These include stands of huge *Psuedotsuga menziesii* (Douglas fir), reaching 1,600 t ha^{-1} [1,427,200 pounds per acre], and *Sequoia sempervirens* (coastal redwoods), the tallest trees in the world, which have a biomass of up to 3,450 t ha^{-1} [3,077,400 pounds per acre] just in the trunks. Below-ground biomass in roots is significantly less (Jackson et al. 1996), averaging 29 t ha^{-1} [25,868 pounds per acre] in boreal forests, 40 to 42 t ha^{-1} [35,680 to 37,464 pounds per acre] in temperate and tropical deciduous forests, and 49 t ha^{-1} [43,708 pounds per acre] in tropical evergreen forests.

Biomass is a static measure of how much mass there is at any one time, with no indication of how quickly new growth is being added or lost, and so gives little insight into how the forest is functioning. More useful are estimates of the productivity of the forest, i.e. how much new material is being added per year, described as net primary productivity (NPP). This can vary from as little as 1 t ha^{-1} y^{-1} [892 pounds per acre per year] in cold boreal forests, to over 30 t ha^{-1} y^{-1} [26,760 pounds per acre per year] in tropical rainforests, with an average of 7 to12 t ha^{-1} y^{-1} [6,244 to 10,704 pounds per acre per year] in temperate forests. However, a maximum of 36.2 t ha^{-1} y^{-1} [32,290 pounds per acre per year] has been recorded in the Pacific Northwest from a 26-year-old forest of *Tsuga heterophylla* (western hemlock). These figures have sometimes been used to calculate how much additional forest needs to be planted to soak up (sequester) the huge amount of extra carbon that is being pumped into the atmosphere—usually approximately 25% extra forest globally. However, such an estimate is blatantly wrong. When a forest is mature it reaches an approximately steady state of mass, where NPP is balanced by an equal loss in biomass through decomposition. At this point, the productivity of the whole forest (the net ecosystem productivity - NEP) drops to near zero. Thus, it is only young forests that are carbon

sinks; once forests are mature they become carbon neutral. In reality, temperate and northern forests globally are a net sink of carbon, but this is primarily due to expansion of the amount of forest due to reforestation (Beedlow et al. 2004).

LIGHT

Trees have evolved as a life form to outcompete their neighbors for light by growing tall, so producing dense forests that inside are darker, more humid, and less prone to extremes of temperature variation than outside. In temperate forests at least, it is usually possible to recognize four reasonably distinct layers. At the top is the tree canopy, normally 5+ m [16.4 feet or greater] above ground. Below are the shrub layer (<5 m) [less than 16.4 feet], the field or herb layer of herbaceous plants and short woody plants such as brambles, and the ground or moss layer of mosses and liverworts, lichens, and algae. Each layer blocks sunlight so that a dense layer may preclude any layers below, and the forest floor may be very dark indeed. In temperate regions, the amount of light reaching the forest floor may be as high as 20 to 50% of full sunlight in an open birch wood, down to just 2 to 5% beneath *Fagus sylvatica* (European beech). In these deciduous forests, light levels are higher once the leaves have fallen, but the trunks and branches still block some light such that light levels are likely to be below 70 to 80% of full sun. Evergreen forests tend to cast similar shade all year round; in Europe, light levels below natural *Pinus sylvestris* (Scots pine) forests are usually around 11 to 13%, while below *Picea abies* (Norway spruce) they can be as low as 2 to 3%. In tropical rain forests, light levels at the forest floor may be even lower, just 0.2 to 2% of full sunlight.

Primula vulgaris (primrose), a wintergreen plant that keeps some leaves alive throughout the year.

As a rule of thumb, plants require 20% of full sunlight for maximum photosynthesis and at least 2 to 3% sunlight for photosynthesis to exceed background respiratory costs (the compensation point). This inevitably means that the floor of densest forests is at, or beneath, the limits of plant growth. Some forest floor plant specialists have overcome this problem with a number of physiological solutions.

- Using shade leaves that are thinner and more efficient at low light levels than sun leaves.

- Reducing the compensation point. Bates and Roeser (1928) found that coastal redwood in deep shade requires just 0.62% sunlight.

- Making use of sunflecks—patches of sunlight passing through gaps in the canopy—which can briefly give up to 50% of full sunlight and make up 70 to 80% of the total solar energy reaching the ground in a dense forest (Evans 1956). These flecks are especially important to shade plants that are capable of responding quickly to the brief flurries of light.

Plants can also cope with dark conditions by avoidance. Temperate deciduous forests are well-known for their colorful carpets of prevernal plants, which grow and flower early in spring. In the UK these include *Hyacinthoides non-scripta* (bluebell), *Ranunculus ficaria* (lesser celandine), and *Anemone nemorosa* (wood anemone). These plants make use of the light reaching the ground before the trees develop their canopy of leaves, and die back once the shade is too deep. Summergreen plants, such as *Mercurialis perennis* (dog's mercury) and *Galium odoratum* (woodruff), are similar but keep their leaves through the summer using what little light is available. As an extension of this strategy, wintergreen plants (which keep at least a few green leaves all year round) and true evergreen plants can start growth as soon as spring conditions allow, and continue growth into a warm late autumn after leaf fall. Such plants include wintergreen *Oxalis acetosella* (wood sorrel) and *Primula vulgaris* (primrose), and evergreens such as *Hedera helix* (ivy) and *Ilex aquifolium* (holly). Being evergreen is an efficient strategy for coping with seasonally abundant light, but it does carry costs. In winter, holly is a sitting target for herbivores such as deer, and so has evolved prickly spines to the leaves. These spines are absent above deer-browsing height, around 3 m [9.8 feet] above ground.

Tree seedlings face similar problems of shade, having to grow up through dark layers of vegetation before reaching the canopy. Different tree species vary tremendously in how much shade they can bear as seedlings and saplings. *Fagus sylvatica* (European beech) and *Acer saccharum* (sugar maple, from North America) are very tolerant of deep shade, while *Betula* spp. (birches) and *Populus* spp. (poplars) grow best under high light intensities. However, it is now apparent that the ability to tolerate shade can change through the lifespan of a tree (Poorter et al. 2005), so it is possible that many trees are more shade tolerant as seedlings than as adults.

Nevertheless, comparatively few trees can tolerate the full shade cast by their mature relatives. Consequently, they depend upon gaps appearing in the forest, by one or more trees dying or falling, for successful establishment

Seedlings of *Fagus sylvatica* (European beech) are very shade-tolerant and capable of growing under the dense canopy of their parents. Each seedling shows two distinctively shaped cotyledons below the young shoot.

of seedlings. Gaps are sufficiently important that while large-scale regional vegetation (e.g., oak forest) is determined by climate, soil, and topography, it is the dynamics of gaps that largely controls the proportions in which the various species grow in any one area. For example, in small gaps created by one tree falling, shade tolerant trees such as *Fagus* spp. (beech) or *Abies* spp. (fir) are more likely to do best and dominate. In larger gaps, species such as *Betula* (birch) and *Salix* (willow),

which invade quickly from light, wind-borne seeds and grow rapidly, are more likely to dominate initially but later give way to shade-tolerant trees. It is not just what goes on above ground that is important; in larger gaps there will also be less below-ground competition from the root systems of the large trees at the gap edge. The importance of such competition has been demonstrated experimentally by cutting roots (trenching) around the edges of a plot: seedlings inside the plot usually grow faster (e.g., Barberis and Tanner 2005). Competition may also happen below ground from the field layer vegetation by allelopathy, i.e., secretion of chemicals, which inhibit other root growth, into the soil (e.g., Orr et al. 2005). Further variability in seedling establishment is produced by small-scale heterogeneity of the forest floor. Pits and mounds of bare mineral soil created by falling trees offer less competition and a more constant water supply than the surrounding humus-rich forest floor. In a *Pinus sylvestris* (Scots pine) forest in Finland, Kuuluvainen and Juntunen (1998) found that although these bare sites covered just 8.4% of the forest, they held 60% of pine and 91% of birch seedlings and saplings. Dense field and ground layers can cause problems for tree regeneration, swamping small seedlings. This is one reason why, in temperate rainforests, seedlings are often most common on "nurse logs," which are continuously damp enough to provide moisture and lift the seedlings above the dense field layer.

As tree seedlings grow upwards into a gap, there can be intense competition to reach and keep the light; whichever seedlings grow quickest will dominate the gap, at least in the short term. A common strategy to get a head start, found in trees as diverse as *Fraxinus excelsior* (European ash), and shade-tolerant firs (Narukawa and Yamamoto 2001), is to have a seedling bank. Here, young plants survive in light conditions below their compensation point (i.e. they are sustaining a net loss of energy) and grow very slowly while their energy reserves last. These seedlings are then able to take rapid advantage of an opening in the canopy in the race for dominance.

WATER

Given that a single, large deciduous tree can use 400,000 liters [105,670 gallons] of water in transpiration in a summer (Thomas 2000), it is obvious that whole forests move immense amounts of water from the soil to the atmosphere. Nevertheless, water is rarely limiting for tree growth in temperate regions until rainfall decreases to such an extent that scrub and grasslands take over. Almost all roots tend to be quite shallow, so potential problems exist if the surface layers of the soil are drained of available water between rain events. This is obviated, however, by the process of hydraulic lifting present in a number of trees and a few grasses. Here, water is raised at night from moist areas lower in the soil (flowing along a hydraulic gradient through the roots) to nearer the surface. Hydraulic lifting is most common in savannas and other xeric (dry) woodlands, especially among older trees (Domec et al. 2004), but is found elsewhere. The amounts moved can be significant: a mature *Acer saccharum* (sugar maple) 19 m [62.3 feet] high can raise around 100 liters [26.4 gallons] of water each night compared to a water loss via transpiration of 400 to 475 liters [106 to 125 gallons] the following day (Emerman and Dawson 1996). This raised water also benefits other surrounding plants (Penuelas and Filella 2003; Filella and Penuelas 2003–2004).

Forests also play a significant role in the redistribution of water on a regional scale. Rainfall intercepted by the canopy is evaporated before it reaches the ground. When this and the transpiration of water are combined (evapotranspiration), the overall losses are in the order of 30 to 60% of precipitation in deciduous forests, 50 to 60% in tropical evergreen forests, and 60 to 70% in coniferous forests, compared to around 20% in grasslands. Not surprisingly, forested areas have water yields (measured as stream flow) 25 to 80% lower than pastures. Moreover, computer modeling by Calder et al. (2003) suggests that planting oak woodland in central England would eventually reduce recharge of aquifers and runoff to streams by almost one half. So, should forest be removed to improve water yield? Most data show that regardless of forest type, removal of up to 20% of the trees has an insignificant effect on water yield, presumably because of increased soil evaporation replacing evapotranspiration (Brown et al. 2005). Further clearance does improve water yield (Bosch and Hewlett 1982), but by comparatively small amounts until clearance is significant.

Many people have held the view that forests increase rainfall in a watershed through evaporating water, thus helping build clouds. However, in temperate areas, at least, the contribution of a forest to rainfall is likely to be insignificant and certainly less than 5% (Golding 1970). On a continental scale, forests help to increase rainfall in the sense that they repeatedly recycle the atmospheric moisture passing from the oceans to the land. For example, in the Amazon Basin, much of the daily rainfall is immediately evaporated to generate clouds for rainfall downwind. It is highly likely that continual clearance of the forest will reduce rainfall elsewhere in the region since much of the water will enter rivers and be lost to the system. Moreover, the effects of such tropical deforestation have far wider repercussions in mid- and high latitudes through large-scale links in the water cycle and weather. Avissar and Werth (2005) have shown, for example, that deforestation of Amazonia and Central Africa severely reduces rainfall in the Midwest of the United States.

NUTRIENTS

Nitrogen is usually the nutrient most limiting growth in temperate forests, while in other forests, especially on soils of great age, phosphorus may well be the limiting nutrient. Nutrients within a forest ecosystem are highly recycled and key to this recycling are the decomposer organisms that release nutrients from dead material. Larger soil fauna, such as earthworms and beetles, chew debris into fine particles suitable for the soil fungi and bacteria. A square meter of soil in temperate woodland may contain more than 1,000 species of animal, from protozoa to earthworms, and a gram of soil can contain more than 1,000 species and more than 200 million bacterial cells (Fitter, 2005).

Soil organic matter (surface litter and humus incorporated into the soil) is thus the main bottleneck controlling nutrient availability to plants, and the slower decomposition is, the more of a limiting factor it is. This helps explain why slow plant growth occurs on cold northern soils that have large organic matter accumulations.

Fungi and bacteria are not altruistic in providing nutrients to plants. As dead material is decomposed, nutrients released by the microorganisms are immediately taken back up by other microorganisms, and so are effectively immobilized and unavailable to plants. However, as the carbon is progressively used up in their

respiration (and released as carbon dioxide), the conserved nutrients become more than the microbes can use, and the excess is released in inorganic form for plants to use. Consequently, when a fresh batch of litter arrives on the forest floor there is a variable time lag before its carbon has been reduced sufficiently to allow nutrients to be freed into the soil for plant growth, the process being regulated by the microbial community (Attiwill and Adams 1993; Agren et al. 2001). Plants can, however, circumvent this bottleneck in several ways. Firstly, more than 80% of the world's vascular plants have on their roots mycorrhizal fungi, which greatly assist in scavenging nutrients from the soil to the symbiotic benefit of both plants and fungi. Secondly, some plants are now known to be able to directly use organic nutrients, without the intervention of microorganisms first breaking them down into inorganic forms. For example, up to 50% of the total nitrogen in forest soils is usually in the form of dissolved organic nitrogen (DON), of which approximately 10 to 20% consists of amino acids. The degree to which plants can use DON is open to speculation, but it is becoming clear that many plants are capable of absorbing amino acids directly (Lipson and Nasholm 2001) and are thus able to short-circuit the microorganism bottleneck. The same may also be true for organic phosphorus.

Although nutrients are tightly recycled within a forest ecosystem, there are still (usually small) annual inputs and losses. Nutrients are added to forests

The effect of 14 years of nitrogen enrichment on *Pinus resinosa* (red pine) at Harvard Forest: (top) control plot with no extra nitrogen added above the background deposition of 7 to 8 kg N ha^{-1} y^{-1}; (middle) low N addition (50 kg N ha^{-1} y^{-1}); and (bottom) high N addition (150 kg N ha^{-1} y^{-1}).

through rain and dust, dissolved from rocks in the soil, and as biological input from nitrogen fixation by microbes. Losses of nutrients can be very rapid due to fire, wind, and erosion but the majority of losses, from temperate forests at least, are by leaching of nutrients as water percolates through the soil. However, since nutrients are vital to forest growth, plants and microbes are fairly efficient at reabsorbing and holding available nutrients and creating conditions of controlled decomposition. This has been admirably demonstrated by the Hubbard Brook Ecosystem Study in the White Mountain National Forest of New Hampshire, established in 1963 (Likens 2004). As part of this, a discrete watershed was clear-felled in 1965–1966 and treated with herbicides for three years to prevent any regrowth, while a similar watershed had the hardwood forest left intact. After clear-felling, stream flow went up (due to reduced evapotranspiration) and net losses of nitrate, calcium, and potassium in stream water generally peaked in the second year, each returning to pre-cutting levels at rates unique to each ion as the forest regrew. However, even decades after clear-felling, differences in stream water solutes can still be seen, especially in calcium (Likens et al. 1998).

There is still a good deal to learn about mechanisms of nutrient retention in forests. For example, Muller and Bormann put forward the vernal dam hypothesis in 1976. This proposes that prevernal plants, which grow early in spring before canopy closure, take up nitrogen and other nutrients before they can be leached; these are subsequently made available to other plants as the prevernal plants die back from lack of light. At Hubbard Brook, plants of *Erythronium americanum* (yellow trout lily) saved almost half of the important nutrients from being washed away. In the spring they used 43 and 48% of the released potassium and nitrogen, respectively, with the rest being lost in stream water. Some subsequent experiments (e.g., Tessier and Raynal 2003) have supported the theory. However, other contradictory studies have shown that the microbe population itself is better at soaking up the spring burst of nutrients (e.g., Zak et al. 1990). Also, while the dying back of vernal plants can produce a burst of nutrients (e.g., Anderson and Eickmeier 2000), the plants may not be very efficient at taking up nutrients in the first place (e.g., Anderson and Eickmeier 1998; Rothstein 2000). Undoubtedly, some of the experimental differences come from investigating different plant species in several forests. The tight recycling of nutrients within the forest ecosystem can cause problems if too much arrives as pollution. Nitrogen enrichment, particularly in northern temperate areas, is just such a case (Nosengo 2003). Since the 1980s, normal background nitrogen deposition of <1 kg ha^{-1} y^{-1} [less than .892 pounds per acre per year] has increased by 10 to 40 times or even higher. The effect of too much nitrogen is clearly seen in long-term experiments running at Harvard Forest, Massachusetts since 1988 (Magill et al. 2004). In one of these, a plantation of *Pinus resinosa* (red pine) was subjected to three levels of nitrogen: a control, low N addition, and high N addition. After 14 years, annual wood production had decreased by 31% and 54% relative to the control in the low N and high N plots, respectively, and the canopies had thinned due to dieback under higher nitrogen levels. Mortality also increased (control 12%; low N 23%; high N 56%) and the whole high N stand was expected to die in the near future.

COARSE WOODY DEBRIS

The vital importance of dead wood in forest carbon budgets, and also as an invaluable wildlife resource, has been increasingly appreciated over the last decade (Kirby and Drake 1993). Dead wood appears in many forms, sizes, and positions including standing dead trees (snags), dead branches in the canopy, and trunks and branches on the ground. A useful term for this motley collection is coarse woody debris (CWD). Typically, CWD in a forest forms up to a quarter of all the above-ground biomass and is normally in the range of 11 to 38 t ha^{-1} [9,812 to 33,896 pounds per acre] in deciduous forests, with the largest amounts in cooler regions where decomposition is slower. Conifer forests generally hold more CWD than deciduous forests, typically around 100 t ha^{-1}, [89,200 pounds per acre] but up to 500 t ha^{-1} [446,000 pounds per acre] in the coastal redwood forests of California and the rain forests of the Pacific Northwest. Tropical forests, with more rapid decomposition, usually have lower amounts of woody accumulation, but levels up to 100 t ha^{-1} [89,200 pounds per acre] are possible in more water-logged areas of the Amazonian forest. If 100 t ha^{-1} [89,200 pounds per acre] of wood was spread evenly over the forest floor it would amount to 10 kg [22 pounds] in each square meter. However, because the bulk of the wood is in large pieces, typically less than 5% of the ground will be covered by CWD, although this can rise to around a third cover in very dense coniferous forests. Snags are of particular wildlife interest. In the Białowieża forest of Poland, one of the most pristine forests in Europe, Bobiec (2002) found that standing dead wood varied from 3 to 21% of total CWD, and figures of 25% are typical in many of the world's forests.

Wood is difficult to decompose. It is composed of 40 to 55% cellulose, 25 to 40% hemicelluloses, and 18 to 35% lignin (conifers having a greater proportion of lignin than hardwoods). Wood is thus high in structural carbohydrates (which require specialized enzymes to break them up) but also poor in nutrients such as nitrogen: 0.03 to 0.1% N (by mass) compared to 1 to 5% in foliage.

In most forests, wood (CWD) will be colonized by fungi within a year and completely colonized within 5 to 10 years. However, decay rates of wood vary tremendously depending upon the climate, decaying organisms available, and the size and type of wood. In general terms, pioneer trees such as birches and willows invest less energy in protecting their wood from rot (going for

Temperate rain forests, such as the one here on western Vancouver Island, Canada, can contain large quantities of dead wood, in part because of the size of some of the fallen logs. The one shown here is of *Picea sitchensis* (Sitka spruce).

speed of growth rather than defense) and logs on the ground rot away within a few decades. Wood from longer-lived trees such as oaks may persist for a century or much longer, while in cool climates such as the Pacific Northwest wood may persist for up to 600 years (Franklin et al. 1981). Even in tropical rain forests, wood above 3 cm [1.2 inches] diameter takes at least 15 years to decompose (Anderson and Swift 1983). Again, however, environmental conditions play an important role in determining decay rates; logs of *Populus balsamifera* (balsam poplar) in North America, which would decay away within 40 to 60 years on land, last for over 250 years when waterlogged in a beaver pond.

EVERGREEN AND DECIDUOUS LEAVES

At first sight, the occurrence of evergreen and deciduous trees in different forests can appear haphazard, but in reality it demonstrates the interactions of many of the ecological processes described above (Thomas 2000). Deciduous trees lose their leaves during an unfavorable season (winter in temperate areas), while evergreen trees always have some leaves on the tree and individual leaves may live from six months to over 30 years. If growing conditions are favorable all year round, as in tropical rain forests, then there is no selective advantage in being deciduous and so evergreen angiosperms dominate. In climates with a dry summer or cold winter, it is cheaper to grow thin disposable leaves than to grow more robust leaves capable of surviving the off-season, so in most moist temperate areas deciduous trees dominate. However, if environmental conditions become worse, it may once again be more beneficial to grow evergreen leaves. This includes areas with a very short growing season, where evergreen leaves are able to start growing as soon as conditions allow and so none of the growing season is wasted.

Evergreen conifers, such as *Abies lasiocarpa* (subalpine fir) shown here in the Canadian Rocky Mountains, are typical of areas with short growing seasons where deciduous trees are disadvantaged by wasting part of the season producing new leaves.

Deciduous forest in Harvard Forest, Massachusetts, USA. In a seasonal temperate climate it is more economical for trees to grow a set of disposable leaves each spring rather than build leaves capable of surviving the winter.

This accounts for evergreen leaves in northern and alpine areas, and also among woodland understory shrubs such as holly and ivy, which benefit from an early spring start and late autumn finish when the canopy has no leaves. Evergreen leaves are also found in Mediterranean climates where the winter growing season is dry; leaves that are protected enough to cope with the droughty conditions will also survive the hot dry summer, and so effectively

In the very short growing season of the tundra overlying permafrost, evergreen shrubs give way to deciduous *Salix* spp. (willows). (The graves are those of 19th century whalers who overwintered and died here on Herschel Island in the Arctic Ocean.)

become evergreen and need to be kept for several years to repay the high investment cost. In areas where the climate becomes even more severe, such as at the Arctic tree line or in alpine areas, deciduous leaves re-appear. Despite the problems of a very short growing season and acute shortage of nutrients, the winter is so severe that it is cheaper to build new leaves every year rather than attempting to keep leaves alive. Thus, the northernmost trees in the Arctic and uppermost trees in alpine areas are deciduous trees such as species of *Betula* (birch), *Larix* (larch), and *Salix* (willow).

CONCLUDING REMARKS

Forest ecosystems work in much the same way as any other ecosystem, but size and complexity create ecological situations that are unique to forests. The large amounts of biomass that can be grown in a year appear useful for carbon sequestration in relation to global warming, but must be weighed against the decompositional losses in mature forests, and possibly the extra methane—a potent greenhouse gas—that these will generate (Keppler et al. 2006). To maintain sequestration rates, new forests are constantly needed. Light availability presents problems for those plants living below the dense forest canopy, but these problems are solved by making do with less light or growing when light is available in the spring or during brief sunflecks. The role of forests in the water cycle still needs to be fully clarified, but it is of great importance due to the likely pressure on forests as human water needs increase. Nutrient dynamics in forests are crucial to their long-term well-being and it is important that we improve our understanding of the effects of climate change and pollution on decomposition and nutrient cycling. Of necessity, this chapter gives only a resume of a very large subject. A more detailed account of forest ecology is provided by Thomas and Packham (2007).

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