The Nature of Forests

To see a World in a Grain of Sand,
And a Heaven in a Wild Flower,
Hold Infinity in the palm of your hand,
And Eternity in an hour. . . .

William Blake (1757–1827)

William Blake's poetic approach of seeing the general in the specific is a useful approach, two centuries later, for launching into the ecology of forests. The biology of a single tree in a single hour connects outward in time to the course of the tree's development from a seed, back through evolutionary time for the genes comprising the tree's genome. The environmental influences on the tree also connect outward in space, with strong similarities to the forces shaping trees around the world. The value of this literary approach to describing and understanding forests has limits: trees comprise the greatest part of the living matter within a forest, but the vast majority of organisms and species in forests are not trees at all. The biodiversity of forests resides primarily in understory plants, animals, and especially very small organisms such as arthropods, fungi, and bacteria.

The ecology of forests can be explored using Blake's approach of starting very small to begin to understand very large and complex systems. The hourly, daily, and annual story for a single tree can be expanded outward to encompass the other trees in a forest, a landscape, and the forest biome, just as an hour can be expanded to a day, a year, a millennium, and evolutionary timescales.

Forest Ecology Deals with Individual Trees Across Time

A tulip poplar in the Coweeta Basin of eastern North America will be the launching point for developing insights about forests. This particular tree (Figure 1.1) would be over half a meter in diameter (at a height of 1.4 m above the ground, a common point for measuring) and over 30 m tall. Eighty years of biological processes have led to an accumulation of more than 1000 kg of wood, bark, leaves, and roots. The actual living weight of the living tree would be about twice this mass of the biomass, because trees typically contain as much water as dry matter.

The crown carries about 75 000 leaves, with a total mass of about 25 kg (not counting the water). This is enough leaves to provide more than four distinct layers of leaves above the ground area below by the tree crown. The multiple layers of leaves are displayed to capture 90% of the incoming sunlight. A sunny afternoon might have 1000 W of sunlight reaching each m^2 of ground area.

Many Processes Occur in a Tree Every Hour

Over the course of an hour, the tree leaves would intercept about 140 MJ of sunlight, and about half of the light arrives at wavelengths that can be used in photosynthesis. Perhaps 10–15% of the light reaching leaves reflects back into the environment, with no effect on the leaves. About one-third to one-half is converted to heat, warming the leaves, which then lose heat to the surrounding air (especially if the wind is blowing). Most of the rest of the intercepted energy is consumed as water evaporates from moist leaf interiors into the dry air, also cooling the leaves.

Forest Ecology: An Evidence-Based Approach, First Edition. Dan Binkley.

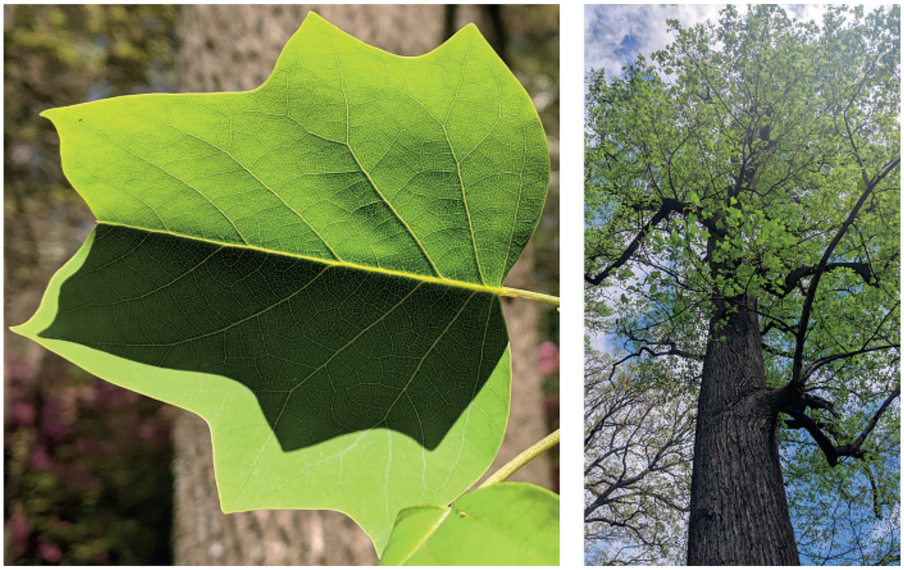

FIGURE 1.1 The Tree. This tulip poplar is a typical tree for temperate forests. The tree may live for a few centuries, integrating daily, seasonal, and yearly fluctuations in environmental conditions to turn carbon dioxide and water into wood (and thousands of types of chemicals).

A few percent of the radiant energy hitting leaves is harnessed to drive photosynthesis, producing about 30 g of sugar in this tulip poplar in an hour. The carbon contained in the newly formed sugar enters the leaves as carbon dioxide (CO_2) during the same hour as the light interception. Small, adjustable openings (stomata) in the underside of the leaves allow CO_2 to diffuse into the interior of the leaves as photosynthesis depletes the concentration of CO_2 inside leaf cells. The rate of diffusion from the air into the leaf depends on the difference in concentration between CO_2 in the atmosphere and inside the leaf. The air has about six times the concentration of CO_2 that would be found inside photosynthesizing leaves, providing a steep gradient for the movement into the leaves. The remarkable biochemical processes in the leaves depend on the presence of more than a dozen elements in the tree, including 500 g of nitrogen (N) and 50 g of phosphorus (P). The bulk of these nutrients were taken up from the soil earlier in the season, but a sizable portion came from reserves that were recycled from last year's leaves and stored over winter in the wood.

The 30 g of sugar produced during an hour would be associated with a release of about 30 g of oxygen (O_2), as oxygen is released when water is split as part of photosynthesis. It may seem that this oxygen could be an important source of oxygen for the atmosphere, but it isn't. As with all accounting in ecology, half a picture might lead to the wrong conclusion. The sugar produced by the tree may be "respired" fairly soon to support the growth of new cells or to maintain old cells, and oxygen is consumed (reforming water) in this reaction. Some of the sugar ends up in longer-lived cells, but even these tend to be oxidized back to CO_2 over years or centuries. Unless the carbon content of a forest increases across generations of trees, the generation of oxygen in photosynthesis is matched by consumption during respiration and decomposition, leaving no extra oxygen in the atmosphere.

Some of the sugar produced by photosynthesis is consumed within the leaf to produce and support the metabolic needs of cells in the leaf. More than three-quarters of the sugar is loaded into the phloem and sent to flowers, twigs, branches, stems, roots and symbiotic root fungi (mycorrhizae).

Exposing the moist interiors of leaves to the dry air allows for uptake of CO_2, but also allows water to be pulled into the dry air. The production of one molecule of sugar entails an unavoidable loss of hundreds of molecules of water. The production of 30 g of sugar in an hour would be accompanied by a far greater loss of water, perhaps 10 liters (10 kg) of water. The water transpired by the leaves during an hour of photosynthesis would have been found lurking in the soil a day earlier, and may have been in the atmosphere a day or a week before.

The tree has tremendous surface area developed within the soil to facilitate uptake of water and nutrients. The surface area of fine roots may be in the order of 100 times the surface area of leaves in the crown, and the surface area of mycorrhizal fungi that colonize roots contribute more than 10 times the surface area of roots. This vast surface area of absorbing roots and fungal mycelia collects water (and nutrients) that move up through the sapwood of the tree. The sapwood is comprised of xylem vessels, each measuring about 0.1 mm in diameter by 1 mm in length. The water passes through more than 1000 vessels for every meter of tree height, taking half a day or a day to move from all the way from roots to leaves.

Lifting water from the soil to the crown requires energy to overcome gravity, about 300 J for 10 liters. This is a tiny amount of energy compared to energy consumed as liquid water in leaves becomes water vapor in the atmosphere (about 2400 kJ for each liter, or 24 MJ for 10 liters). All the energy consumption and dissipation by the tree crown result in a deep shade beneath the tree. The air temperature in the shade may be a degree or two cooler than the air above the crown, but the shade will feel much cooler to a person sitting under the tree because of the greatly reduced energy load from the incoming sunlight.

Tree Physiology Follows Daily Cycles

Over the course of a day, the tulip poplar responds to the changing environment through a daily cycle just as strongly as an animal would. The uptake of CO_2 (and loss of water) begins as the sky brightens across the hillside in the morning, increasing as the intensity of sunlight increases (Figure 1.2). Rates may be highest near noon, decreasing if clouds develop, or if the air becomes so dry that the tree tightens the stomata to avoid losing too much water. Increasing temperatures in the afternoon drive up the capacity of air to hold water, resulting in a climb in the vapor pressure deficit. This deficit is a key force driving the water use by the tree. The tulip poplar would produce about 250 g of sugar on a sunny summer day (more than the average mentioned above for all days of the growing season), when the soil was moist, and transpiration could total 70 liters of water.

Not all processes in the tree shut down when the sun sets. Chemical reactions inside cells continue to renew thousands of biochemicals, generating and expanding new cells, and actively absorbing nutrient ions (such as nitrate and phosphate) from the soil. All of these processes require energy, most of which is supplied directly or indirectly from the sugars formed by photosynthesis. The oxidation of the sugar leads to substantial release of CO_2 from the tree; this "respiration" in all the tissues of a tree may equal half of the total photosynthesis that occurs on a sunny day.

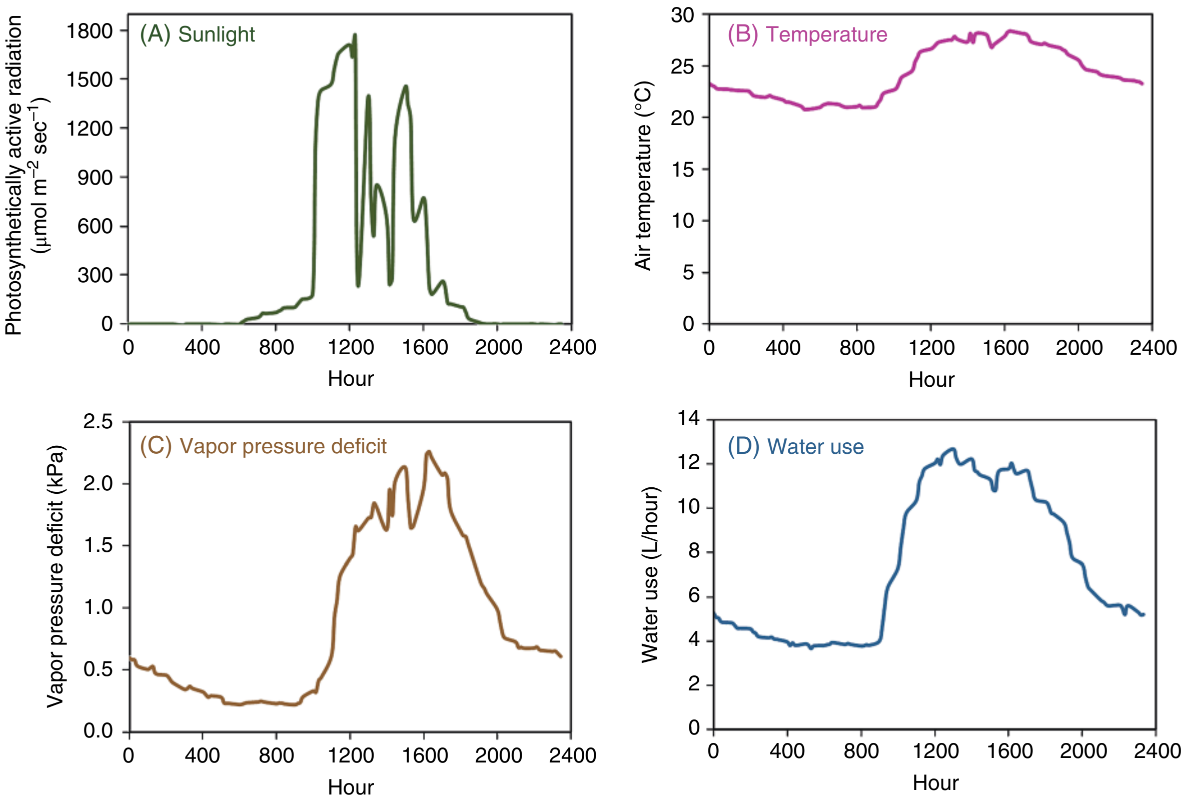

FIGURE 1.2 The daily pattern of incoming sunlight (A) reflects the geometry of the Earth's tilt, the aspect and slope of a hillside, and the passing of clouds through the day. Temperature patterns (B) are driven in part by incoming sunlight, moderated by winds and evaporation of water (which cools the air). The combination of temperature patterns determines the capacity of air to hold water, and the vapor pressure deficit (C) tracks the difference between the current humidity of the air and the saturation point of the air. All these factors influence the rate of water use by the tulip poplar (D), though the connection to vapor pressure deficit is the most direct. **Source:** Data from Chelcy Miniat.

Trees Must Cope with Seasonal Cycles Through Each Year

The environment surrounding the tulip poplar changes through the course of a year. The daily cycles of temperature swing between 5 and 10 °C, while the coldest and warmest day of the year may differ by 25 °C or more (Figure 1.3). Incoming sunlight in winter averages about half the level experienced in summer, as a result of shorter days, lower sun angles, and fewer clouds. These environmental changes lead to regular, predictable patterns in the phenology of the tree.

The tulip poplar begins an annual cycle of flowering and growth with the initiation of root growth late in the winter, followed by flowering in April and May. The tulip-shaped flowers are pollinated by bees and other insects, with 10 000 seeds raining from the crown in autumn. The leaves of the crown also expand in April and May, from expanding buds that were set the previous year. The initial burst of leaf growth depends on stored sugar, but the leaves rapidly provide new sugar for their own growth, and for the growth of all parts of the tree. The growth of a new leaf requires only about one-week's production of sugar; the rest of the span of the leaf's existence contributes to the growth and maintenance of other tissues.

Over the course of the growing season, the tulip poplar may produce 50 kg of sugar. Respiration would consume half, and the growth of short-lived roots and leaves might consume another quarter. Less than 25% of the annual production from the tree's leaves would be found in new stem wood, increasing the diameter and height of the tree. The annual growth of the tree might use more than 8000 liters of water.

Dry periods during the summer lower the rate of photosynthesis in two ways. Low supplies of water in the soil lead to closure of leaf stomata, restricting both the gain of CO_2 and the loss of water. The tulip poplar might also respond directly to the dryness of the atmosphere, and days with very high vapor pressure deficits may have low rates of photosynthesis, even if the soil is moist.

Trees Grow and Reproduce at Times Scales of a Century

Tulip poplar trees originate from seeds that develop following pollination of a flower by a bee or other insect. The flower may have developed on a parent tree as young as one or two decades, or as old as one or two centuries. Seeds develop over a period of five or six months, and then fall to the ground within a radius equal to a few times the height of the parent tree. A single seed

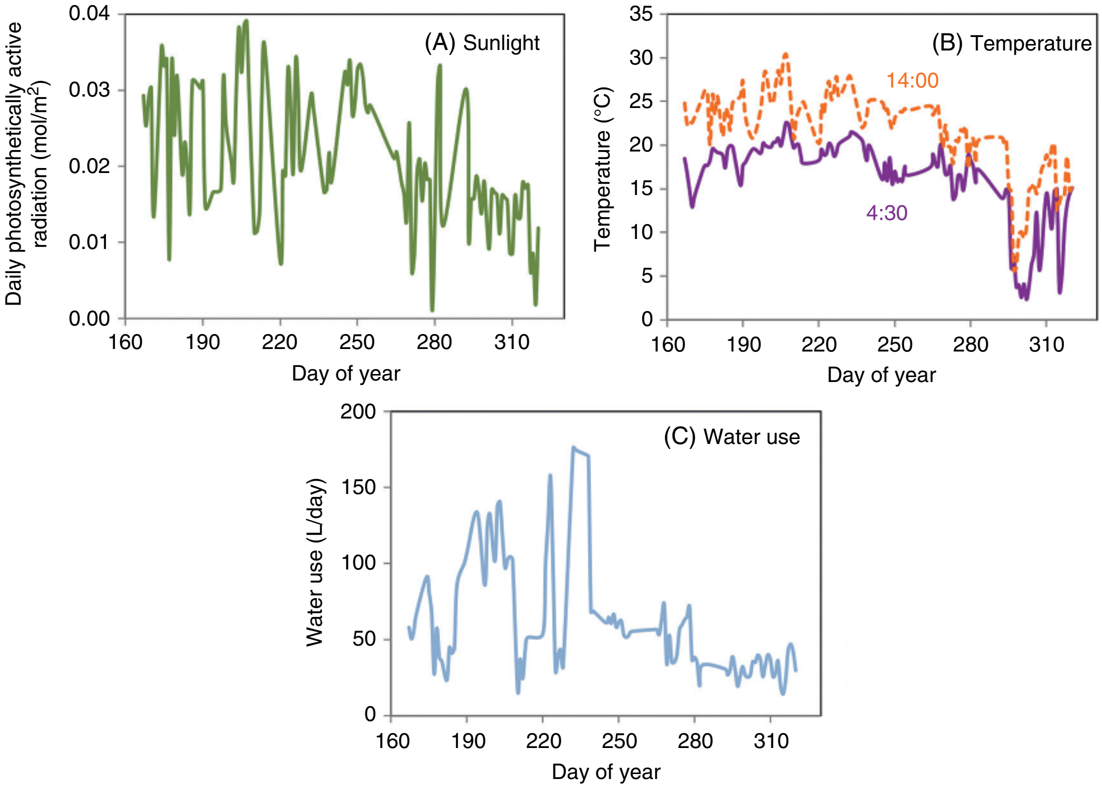

FIGURE 1.3 Seasonal trends in incoming sunlight (A) lead to almost twofold differences between summer and winter. The difference might be larger if not for the frequent cloud cover in summer. Patterns in incoming light lead to both daily and seasonal patterns in air temperatures (B). These environmental driving forces combine with the biology of the tulip poplar to determine the seasonal course of water use by the tree (C). **Source:** Data from Chelcy Miniat.

may germinate the following summer, or several summers later. The vast majority of seeds may never germinate, or if they germinate may not lead to a successfully established seedling. New seedlings require a great deal of luck to establish, including obtaining enough water and nutrients from the soil to support the development of leaves, and enough sunlight (perhaps 10% of full sun) to drive photosynthesis. The full intensity of sunlight may dry out a seedling, or overwhelm the photochemistry of new leaves.

A tulip poplar stem may not be the "first generation" of the "tree." A tree stem may die (from a wind storm breaking the stem, or a saw harvesting the tree), and a new stem may develop from dormant buds in the stump. The early growth and development of sprouted stems is faster and more assured than the tenuous development of a new seedling.

Weather differs a lot from one year to the next, and the growth of the tree during favorable periods may be double the growth rate for droughtier times (Figure 1.4). This response of an individual tree is the outcome of several factors, including the direct effects of the environment on this tree's physiology, and the indirect effects of how fluctuations in the environment change the competition between trees in the forest.

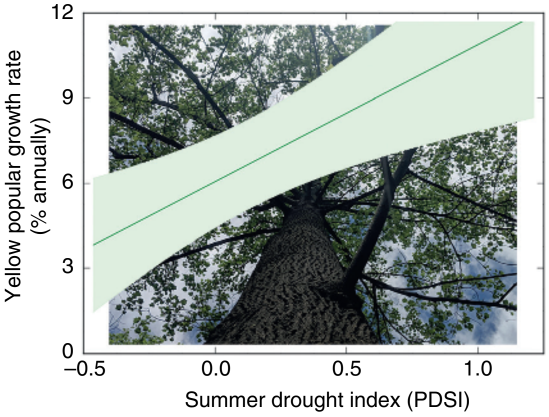

FIGURE 1.4 Growth of yellow poplar trees is low in drier summers (a negative value for the Palmer Drought Severity index), and increases with increasing summer moisture. **Source:** Data from Kardol et al. 2010.

The tree is larger than its local neighbors, and this "dominance" provides a twofold advantage. The tree obtains a higher supply of light, water, and nutrients than its neighbors, driving faster growth. Faster growth then leads to a positive feedback that increases the tree's capture of resources, allowing its growth to increase at the expense of neighbors.

The Story of Forests Is More than the Sum of the Individual Trees, Because Interactions Are So Strong

The tulip poplar tree is enmeshed in a complex ecological system (Figure 1.5). The tree provides habitat for an intricate community of insects and other arthropods. Each kilogram of leaves supports a total arthropod community of about 1 g (Schowalter and Crossley 1988), so the total leaf mass of the crown of 25 kg would support about 25 g of arthropods. Some of these invertebrates feed on the tree, eating leaves (or the insides of leaves), sucking sap, and boring into the wood of branches and the stem. Occasionally the populations of tree-feeding insects might increase to the point where much of the forest canopy is eaten; in most cases trees survive defoliation by native insect herbivores and form new canopies in the same season. Forests have other arthropods that feed on the species that feed on trees, forming complex food webs that include small mammals, a dozen or more species of birds, and even fish in streams and ponds that feed on arthropods from within the forests.

Does the tree benefit from neighbors, or is competition for resources the major effect of neighbors? Competition between trees is very important in all forests, but some possibilities exist for interactions between trees that actually benefit neighbors. One example is having a nitrogen-fixing black locust tree as a neighbor. The tulip poplar would compete with the locust for light, water, and other nutrients, but it might benefit from the enrichment of the soil N supply by the locust. Dozens of species of plants in the understory also compete with overstory trees for soil water and nutrients.

The diversity of plant species may be impressive, but this diversity is overshadowed by the diversity of invertebrates. Each square meter of soil contains about 60 large invertebrates with a total mass of about 1 g (Seastedt and

FIGURE 1.5 The dominant tulip poplar tree in the center of this springtime photo is part of a complex ecological system that includes other tulip poplars, other trees from more than a dozen species, several dozen species of understory plants, hundreds of species of arthropods and other invertebrates, and a soil that is itself a complex system with a level of biodiversity that dwarfs the diversity of the rest of the forest.

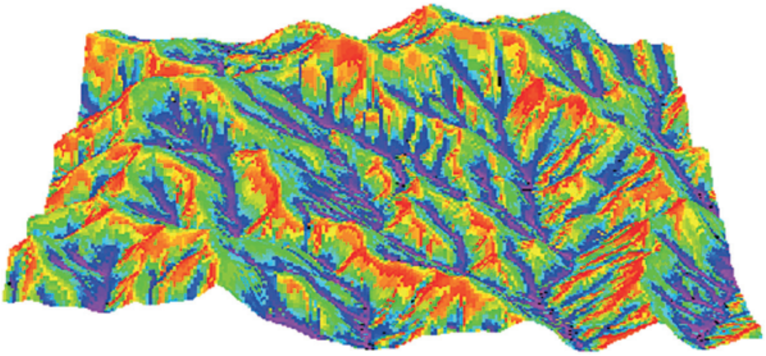

FIGURE 1.6 Although this looks like a topographic map of the Coweeta Basin, the colors actually represent the amount of water available for use by trees (hot colors are droughty sites, cool colors are wetter sites), and for draining into streams. Higher elevations receive more rainfall (and snow) than lower elevations, but water also flows downslope through soils, enriching lower parts of landscapes. **Source:** Map provided by D.L. Urban.

Crossley 1988). The number of small invertebrates would be on the order of 10 000 individuals (from hundreds of species) in each square meter; most of these feed on soil fungi.

Each kg of the upper mineral soil contains about 1 or 2 g of fungi, bacteria, and Archaea (Wright and Coleman 2000). The microorganisms are responsible for the majority of the processing of dead plant materials, returning carbon dioxide to the atmosphere, releasing inorganic nutrients into the soil, and altering soil structure and aggregation in ways that protect some organic matter from decomposition for decades, centuries, and even millennia. The small size of the soil microorganisms is matched by an almost unimaginable diversity of "species" or taxonomic units (as the concept of species does not apply well to many microbes). A 10 m by 10 m patch of soil likely contains more than 1000 species (or taxonomic units) of Archaea, another 1000 species of fungi, more than 10 000 species of bacteria, and 10 000 varieties of viruses (Fierer et al. 2007). This biocomplexity remains a largely unexplored frontier in the ecology of forests.

No two locations in the Coweeta Basin have exactly the same forest structure and composition, because local details (such as small variations in soils, or legacy of historical events) always shape local forests. Some broad forest patterns do repeat across the landscapes, as a result of patterns in topography. Precipitation increases by about 5% with each 100 m increase in elevation, rising from about 1500 mm yr^{-1} at 700 m elevation to more than 2200 mm yr^{-1} at 1500 m. Local topography modifies this elevational pattern, as wind flow near ridges can lead to 30% less precipitation falling below the ridgelines than would be expected based on elevation alone (Swift et al. 1988). The water available for use by trees (and flow into streams) depends heavily on local topography. Forests on ridgelines receive water from precipitation, and lose water through evaporation, transpiration by plants, and seepage downhill. Forests lower on the landscape receive water not only as precipitation, but also as water draining from higher slopes. Although more rain falls at higher elevations at Coweeta, some forests at lower elevations have access to more water because of this downhill flow (Figure 1.6).

Temperature also changes with elevation, falling by about 0.5 °C for every 100 m gain in elevation; moist air shows less temperature change with elevation than dry air. The landscape pattern in temperature is also strongly influenced by slope and aspect; the amount of incoming sunlight can vary by more than a factor of two from south-facing slopes to north-facing slopes, generating temperature differences of several degrees. Steep slopes receive more light than flat areas if the aspect points toward the sun, or less light if the aspect faces away from the sun.

These patterns in soil water, sunlight, and temperature lead to predictable patterns in forest structure and composition. Concave slopes (coves) have abundant supplies of water and deep soils, with large forests dominated by tulip poplar, black birch, and eastern hemlock. Dry ridges and convex slopes have smaller forests of oaks and pitch pine. Uniform slopes at lower elevations have mixed-deciduous forests dominated by white and red oaks, hickories, and nitrogen-fixing black locust. Uniform slopes at higher elevations are typically dominated by northern hardwood forests, with sugar maple, red oak, and beech.

Differences in species with elevation and topography also lead to differences in forest diversity and size. Lower elevation forests in the Coweeta Basin average about 18 tree species in a hectare, with diversity declining to about 14 tree species ha^{-1} at upper elevations (Figure 1.7). Diversity shows no trend with topography, as concave locations (coves) have about the same number of species ha^{-1} as convex (ridge) locations. The largest forests occur at middle elevations, and in concave locations.

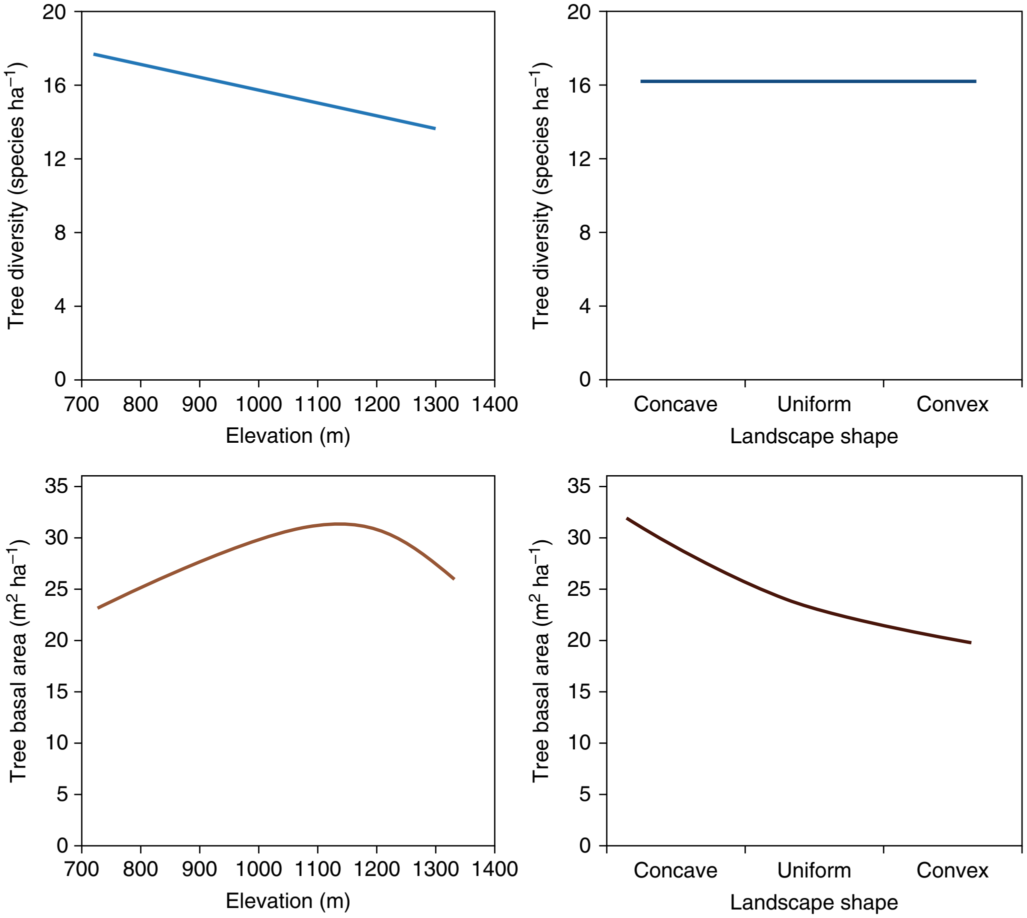

FIGURE 1.7 Forest patterns commonly vary with elevation and with local topography. The number of tree species occurring in a hectare at Coweeta declines slightly with increasing elevation (upper left), whereas tree diversity shows no pattern among concave (cove) locations through to convex (ridge) locations (upper right). The basal area of trees tends to be highest at middle elevations (lower left), and in concave slope locations. **Source:** Data from Elliott 2008.

The Coweeta Forests Aren't the Same as Two Centuries Ago

Forests with large, old trees may give an impression of an unchanging system that seem to be stable for decades and centuries. Some temperate forests may fit this image, but most are quite dynamic. If we could visit a forest before and after 50 years of changes occurred, we would likely find that many of the small trees had died (perhaps replaced by others), along with some of the medium- and large-size trees. The overall size of the forest, in terms of height or mass of wood in living trees, may have increased, but typically this increase in the size of larger trees comes in part at the expense of smaller trees that died.

Forests also change more rapidly, as a result of rapid events that alter the typical year-to-year progression of changes. The forests at Coweeta experienced massive changes in the past two centuries (Figure 1.8) as a result of direct human impacts and unintended, indirect impacts.

The most noticeable change in the forests in the Coweeta Basin is the loss of the formerly dominant tree species, American chestnut. Long-lived, large chestnut trees were the most notable part of the forest in 1900. About half the trees in the forest were chestnuts, and chestnuts comprised about half of the forest biomass. An exotic fungal disease from Asia, chestnut blight, killed almost all the mature chestnuts in forests of eastern North America within a few decades. Not all the mature trees were killed outright, as the fungus creates a canker on the stem that topples the tree. Surviving root systems continue to send up hopeful shoots, but these also form cankers when the stems are few meters tall.

What did the demise of chestnut mean for the forest? Given that competition is so important in the interactions among trees, the loss of chestnut led to a dramatic increase in the biomass of other species, particularly oaks, red maple, and tulip poplar. These species responded not by increasing the number of trees in the forest, but with accelerated growth of the already-present stems.

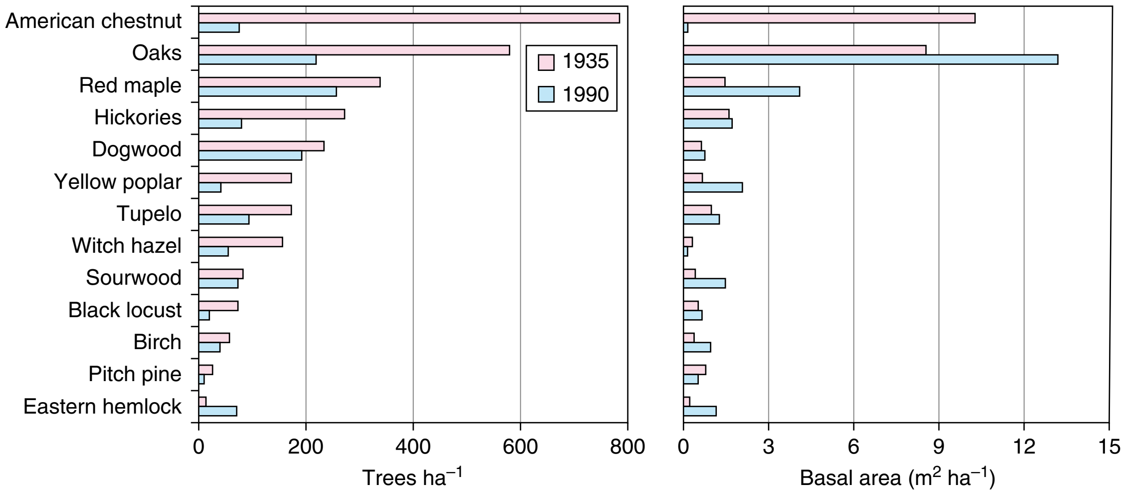

FIGURE 1.8 Forest composition in the Coweeta Basin in 1935 and in 1990. The total density of trees (left) declined from 3000 trees ha^{-1} to 1200 trees ha $^{-1}$, while basal area (right) increased slightly from 27 to 28 m^2 ha^{-1}. The decline in tree density is a common feature of growing forests; as dominant trees increase in size, many smaller trees die. However, the trend in this forest was largely influenced by the drastic decline of chestnut. This formerly dominant species was decimated by the exotic chestnut blight disease. **Source:** Data from Elliott 2008.

Another major event reshaped parts of the forests of Coweeta after the vegetation survey in 1990 summarized in Figure 1.8. Before this time, eastern hemlock was a major tree species in wetter locations, such as coves and valley bottoms. The hemlock woolly adelgid is an exotic, invasive insect that has killed most of the eastern hemlocks across much of eastern North America. About half the hemlocks died within the first 5 years of the adelgid's arrival (Ford et al. 2012), with 90% or more dead after 15 years (Ford et al. 2012; Abella 2018). The loss of large hemlocks led to drops in the number of trees in the forests by about half, and long-term changes may include expansion of both trees of other species and understory woody plants (such as rhododendrons).

Continuing back in time, the most notable event of the nineteenth century was the extinction of the passenger pigeon. This large (30 cm) bird was a major consumer of large tree nuts, including acorns, beechnuts, and chestnuts (Halliday 1980; Johnson et al. 2010). Huge flocks contained tens of thousands (perhaps even millions) of birds, with large impacts on dispersal of tree seeds and nutrient cycling (with concentrated feces beneath favored roost and nest trees). Passenger pigeons were the most dominant species of bird in eastern North America, and perhaps the most numerous bird species in the world. Over the course of a few decades, this species spiraled to extinction as a result of massive hunting, and perhaps the effects of changing forest cover and even exotic diseases. How did the forests change in the absence of passenger pigeons? This important question is easily asked, but probably cannot be answered without stronger historical records.

Two other human-related events marked the 1800s in the Coweeta Basin. The second half of the century saw Euroamerican settlers occupying the land. Their major impacts included some logging, agricultural cropping on a few hundred hectares, widespread grazing of pigs and cattle, and hunting of wildlife for food. The prior inhabitants were Cherokee Indians, forcibly removed in the 1830s. Cherokee influences on the forests included some agriculture (maize, squash, and beans), extensive hunting (primarily deer, turkeys, and bears); food collection (including tree nuts); and frequent use of fire to clear the forest understory (Van Derwarker and Detwiler 2000; Gragson and Bolstad 2006).

Across Dozens of Generations of Trees, Almost Everything Changed at Coweeta

The past 10 000 years have seen dozens of generations of trees and forests come and go in the Coweeta Basin, in response to fluctuations in climate, events such as hurricanes, and probably sizable fluctuations in populations of humans and other animal species that influence forest dynamics. The frequency of fires may have increased as people ignited forest fires (intentionally or unintentionally). Fires may have burned the tulip poplar/mixed broadleaf stands every 200 years or so over the millennium before European settlement (Fesenmeyer and Christensen 2010). Some notable events include a near-disappearance of eastern hemlock throughout its range, between about 5500 and 6500 years ago (Calcote 2003; Heard and Valente 2009), followed by recovery. The cause of the decline is unknown, and speculations include some sort of novel disease. This also happened to be one of the coolest times in the past 10 000 years, so multiple factors may have been involved.

Continuing back to 12 500 years ago, the continent (and much of the globe) was undergoing rapid warming as the most recent Ice Age ended. Temperatures in the Coweeta Basin would have risen by more than 5 °C from conditions that prevailed for 100 000 years. Under colder conditions, the forests in the Basin would have resembled forests that are currently found farther north, with pines and spruces dominating even the lower elevations. During some periods, the assemblages of trees species across the region included combinations that have no modern analog in local forests, or in forests now found farther north (Jackson and Williams 2004). Assemblages of tree species change in response to interactions among temperature, precipitation, and biotic factors. Unlike organisms, the genotypes of forests change routinely as species come and go.

The most notable difference in the forest at the end of the Ice Age would have been the presence of many large species of mammals in the region. The list of now-extinct species includes tree-browsing American mastodons; grass and tree-browsing Columbian mammoths; woody-plant browsing stag moose; tree-eating giant beavers more than 2 m in length; and large predators such as dire wolves, sabretooth cats, and massive short-faced bears. The now-extinct mammals would have been joined by at least one now-extinct tree species, Critchfield spruce (Jackson and Weng 1999).

The Futures of the Tree and the Forest Will Depend on Both Gradual, Predictable Changes and Contingent Events

The future is largely unpredictable for individual trees, but some predictions may have a high probability of coming true. The dominant situation enjoyed by the tulip poplar featured in this chapter would generally predict steady growth into the future. Growth might even increase as neighbors are suppressed. Dominant trees of this species may live for more than two centuries, and such a long lifespan provides opportunities for dispersing millions of seeds.

A long lifespan also increases the odds that the tree will experience rare weather events. For example, a severe drought with a probability of occurrence once in 100 years might severely challenge a tree's survival. A tree that lives only about five decades would have a 60% chance of never experiencing a 100-year-magnitude drought (if weather is random), whereas a tree that lived two centuries would have an 87% probability of experiencing at least one 100-year drought.

A host of other future factors are more difficult to assign probabilities. The death of a neighboring tree may suddenly increase the supplies of resources available to this tree, or the falling neighbor may collide and uproot this tree as well. Lightning tends to kill large trees more often than smaller trees. Outbreaks of insect populations and fungal diseases influence the long-term development of many forests. The climate experienced by this tree (and its ancestors) may not continue into the future. Novel pests may arrive in the forest, as a result of widespread transport associated with world-wide travel by people and materials. The future of the tree may also depend very heavily on choices made by people; a large tulip poplar tree can be transformed into thousands of dollars-worth of furniture and other products.

Some changes in a forest tend to be cyclic, with repeating patterns of species and growth rates following major events. The major recolonizing species will have predictably high tolerance for full sunlight and rapid early growth, whereas trees that remain after two centuries will likely grow slowly and the community will include trees that thrive under shady conditions. Other changes are clearly not cyclic, and lead us to expect that the future forests in the Coweeta Basin will not be simple analogs of past forests (Jackson and Williams 2004). The development of forests responds to changes in climate, and climatic patterns (and the responses of trees and species to these patterns) have long legacies (Kardol et al. 2010). Changes in future climates may have modest effects on the forests compared to novel insects and diseases. The chestnut blight removed the dominant tree species from the Coweeta forests, and the hemlock wooly adelgid decimated the population of eastern hemlock trees. What will be the legacies of the loss of almost all the chestnuts and hemlocks trees from Coweeta's forests? Might we be able to predict the response of surviving species to the disappearance of hemlock, based on the patterns from 6000 years ago when eastern hemlock experienced another decline, or will other factors (such as changing climate) limit the ability of the past to illuminate the future? We might speculate about how other species will take advantage of reduced competition from these species, but the actual impacts will include the ecological legacies of changes in soils and in animal communities. Forests often respond to more than one event; future forests develop from the combined legacies of historical events (such as losses and gains of species) in combination with current conditions. Warming climate, rising atmospheric concentrations of carbon dioxide, and other factors will influence future forests, shaping the legacies of the losses of chestnuts and hemlocks. Will new species of exotic insects arrive and remove other tree species from Coweeta's forests?

The future development of a tree, and of a forest, derives from the gradual accumulation of routine changes, such as annual increases in height and mass of stems. Over limited periods, these gradual, expected trends are punctuated by contingent events that are largely unpredictable, such as hurricanes and invasions by exotic pathogens. Humans are another force for change in forests, through direct management (typically favoring some species over others, often limiting the opportunity for old trees to develop) and indirect activities (such as nutrient enrichment of rain, air pollution, and climate change).

Given all these forces of change, how can we predict future forests? The short answer is simply that we cannot predict future forests with much confidence. The longer (and more useful) answer is that we can indeed develop insights about the likely forests of the future, if we understand some of the basic features that have shaped forests in the past, and how ecological interactions will combine to shape future forest.

Ecological Afterthoughts: Is a Forest an Organism?

A variety of traits and processes characterize all organisms: they process high-energy sources from the environment (such as sunlight or organic compounds) into low-energy byproducts (such as heat), and they grow, reproduce, and die. Forests do these same things. So are forests like organisms? We have a strong tendency for using analogies to make sense of the world, and sometimes we go beyond analogies to use metaphors, where one is not simply like another, but is essentially the same. Ideas about forests have arisen commonly from analogies, and sometimes even from metaphors. For example, an influential ecologist asserted a forests-are-organisms metaphor a century ago:

> *The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures and dies. . . The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. . . Succession is the process of reproduction of a formation, and this reproductive process can no more fail to terminate in the adult form than it can in the case of the individual.*
>
> *(Clements 1916)*

Our ideas about forests can shape what we can see in forests, and the belief in the organism-nature of ecosystems led this ecologist to strong confidence in untested ideas, simply because he was seduced by the beauty of the organism metaphor:

> *It can still be confidently affirmed that stabilization is the universal tendency of all vegetation under the ruling climate, and that climaxes are characterized by a high degree of stability when reckoned in thousands or even millions of years.*
>
> *(Clements 1936)*

A metaphor that was true might be very useful, but a poor metaphor may be useless or even harmful. An untested metaphor could be a good starting point for science, but could not be a reliable conclusion. If forests were the same as organisms, the future composition, structure and function of forests would be largely predictable. Any deviations in that progression would risk the continued persistence of the forest. If forests are quite unlike organisms, such a belief would befuddle our ability to see the forest and the trees.

The "ecological afterthoughts" in later chapters are open-ended invitations to apply ideas from the chapters to specific situations. The afterthoughts are not intended to convey information or answers, but just to raise questions. This first chapter goes a bit further, highlighting how the afterthoughts might be used for insights.

A listing of similarities and differences would immediately show this metaphor of "Forests are Organisms" would be weak at best, and maybe harmful if taken too seriously. Forests clearly differ from organisms in fundamental ways (Figure 1.9). A tulip poplar seed can only lead to a tulip poplar tree, with growth rates and forms that are shaped by environmental factors and the genes of the tree. A tulip poplar that deviated from normal structure and function would soon be a dead tulip poplar, with no chance to send more of its genes into future generations.

A forest that contains tulip poplar trees is much less constrained in its future development. Unlike organisms, forests routinely gain and lose genes as members of species enter and leave the forest; there is no single way for a forest to be, and no single path that must be followed if a landscape will remain dominated by trees. If we believe forests are organisms, the loss of major components should be expected to endanger the whole. The death of an organism is an event that encompasses all its parts. The "death" of a forest is always a matter of perspective; major events kill some trees, plants and animals, leading to greater opportunities for the surviving trees, plants and animals. Forests persist through the gains and losses of individuals and species; organisms generally don't persist through the gains and losses of organs (aside from seasonal senescence of leaves and fine roots). A tree that lost its leaves and never regrew a new set of leaves would die; a forest that lost all members of a given tree species (with that species never returning), would remain quite viable.

Several of the dominant species formerly found in tulip poplar forests disappeared from the landscape in recent times, including chestnut trees, passenger pigeons, wolves and mountain lions, while the human influences shifted from Cherokee to European cultures. Nevertheless, forests that contain tulip poplar trees continue to exist and change, as individual organisms and species shift in response to changing stresses and opportunities. The forests of the future will not be the same as those in the past, and change over time is a normal aspect of forests.

FIGURE 1.9 As with the tulip poplar and tulip poplar forest examined in this chapter, all *trees* have very limited scope in their development from seed to mature tree, and all *forests* have very broad scope in their composition and structure over time. This ponderosa pine tree (left) developed from a seed that contained genetic material from two parent trees. The potential future states of this plant were determined and constrained by these genes. The actual development of the tree depended on climate, weather events, fires, and interactions with a huge variety of microorganisms, animals, and other plants. No two ponderosa pine trees are identical, yet the range of differences among ponderosa pine trees is miniscule compared to the range differences in the composition of forests that contain ponderosa pine trees. Unlike the tree, the forest where this tree grew did not have a particular beginning; major events such as fires killed many trees, but many survived (including the root system of aspens that sent up a new generation of stems from ancient root stocks), as did many of the understory plants. The dynamics of the forest were not determined or constrained by the genes of a single species, and the composition of the forest shifted over the decades in response to climate, rapid events, and management. The forest continues as the death and birth of individuals subtracts and adds genetic possibilities for the future.

This flexibility in the genetic composition of forests ensures that the organism metaphor confuses rather than enlightens. Complex, changeable forests have far greater capacity for change than organisms, ensuring that the future development of forests is anything but precisely predictable.