UNDERSTORY PLANTS IN TEMPERATE FORESTS

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Summary

Much of the vascular plant diversity in temperate forests occurs in the understory, and the species present there represent a wide variety of growth forms and functional groups. Understory plants comprise the habitat for many kinds of animals, influence ecosystem functions such as nutrient cycling, and can have important effects on the canopy. Many canopy trees established as post-disturbance cohorts, but many others started in the understory, especially in old forests, and understory species can have a major influence on which tree species are successful. Thus the understory is an important structural and functional component of temperate forests.

Although many species grow in the forest understory, this environment is not

necessarily a favorable one for plant growth. Light levels are often very low, and nutrients can also be limiting, partly because of competition with canopy trees. Species typical of such habitats can perhaps best be described as stress tolerant. As in some other high-stress environments, however, growth-form diversity can be high, indicating that there are multiple ways to deal with low resource levels. Seedling establishment is often difficult because of low light levels, thick litter layers, and burial by debris falling from the canopy. Understory species have numerous ways of dealing with the adversities of this environment, such as large seeds, storage organs, a long lifespan, and the ability to tolerate very low light levels. In particular, many forest understory species have clonal growth, which decreases dependence on the difficult seedling establishment stage. Seedlings are rare, and almost all individuals (ramets) result from clonal growth in some species. Herbs and shrubs that spread via rhizomes are especially common in many forest understories, and can form large patches. Much of the patchy nature of forest understories relates to clonal growth, although variation in the canopy is also of fundamental importance in inducing spatial structure.

The forest understory is a heterogeneous and dynamic habitat. Even in very old forests, microsite conditions are continuously changing, as are populations of understory species. As canopy trees die, gaps are formed that often have increased resources, which frequently results in greatly increased total abundance, and altered species composition of understory plants. In addition to within-stand patch dynamics, most temperate forests are prone to intense disturbances that can kill most or all canopy trees. Many forest understory species are well adapted to surviving disturbance, even when canopy trees are destroyed. Their ability to sprout from rhizomes, roots, and various kinds of storage organs, allow them to grow new shoots after disturbances, including fires. Furthermore, some species typical of closed forest understories rarely flower in that habitat, but do flower abundantly after disturbance, which can offer a window of opportunity for seed production and seedling establishment. However, within a few years following disturbance, competition from early successional species and dense stands of young trees can become intense, and very adverse for many species typical of forest understories. Thus survival through disturbance is no guarantee of long-term survival. Some individuals, however, generally do survive through both disturbance and early seral stages, and these are critical to subsequent redevelopment of the forest understory vegetation.

Because the understory contains the bulk of the species diversity of vascular plants in temperate forests, is important to ecosystem functioning, and has important influences on the canopy, understanding of understory plants is critical to forest management. Clearly, efforts to preserve biodiversity and promote long-term sustainability in temperate forests cannot ignore the understory species.

1. Introduction

Most of the interest in forests has traditionally been focused on trees because they both define a forest and are of major economic importance. However, most of the vascular plant diversity in temperate forests occurs in the understory. Species representing various types of herbs and shrubs are abundant in the understory of most temperate forests. Although these species contribute much less to total ecosystem biomass and

productivity than do the canopy trees, they represent important structural and functional components of the forest. Understory plants provide food and habitat for many animals, especially ground-based species. Some understory species can survive disturbances that destroy canopy trees, providing a degree of continuity during cycles of disturbance and subsequent succession. Understory plants can have an important influence on nutrient cycling, and interact with larger plants of the forest in a variety of ways. Although many trees establish following a major disturbance that removes the canopy, many others establish from seed in the forest understory—and seedling establishment is usually the most critical stage in the life cycle. Thus, characteristics of the understory can have a major impact on the future species composition of the canopy, in a sense acting as a sieve through which trees must pass on their way to the canopy. Understory plants are clearly an important component of temperate forests, and managers of these forests need to be cognizant of the multiple roles they play.

2. The Understory Environment

The forest understory is not necessarily a favorable environment for plant growth, and is in several respects a high-stress environment where the vital resources that plants need are often in short supply. In particular, light levels can be very low, providing little energy for plant growth. The primary advantage of being tall is better access to light; the well lit, high resource world of the canopy bears little resemblance to the forest understory, which only receives the leftovers. When light levels under the canopy increase, plant growth in the understory often increases dramatically. Water and nutrients can also be limiting for understory plants. Canopy trees use large amounts of water and nutrients, and they have access to the energy to support prolific root growth and build large root systems, allowing them to obtain belowground resources effectively. In contrast, understory species have limited energy to use for acquisition of water and nutrients. Trenching studies have repeatedly demonstrated that growth of understory plants increases, often markedly, when root competition from trees is removed, even when light is unaffected. The forest understory is an environment with multiple resource limitations, and these limitations can interact to make the forest understory very inhospitable to plant growth. In the densest temperate forests, understory plants can be almost non-existent, whereas forests with more open canopies can have a luxuriant and diverse understory.

Some aspects of the understory environment are quite favorable to plant growth and survival. Temperature extremes are moderated over those in the open, reducing damage from frost and desiccation related to high temperatures. Humidity is higher in the forest understory than in the open. Competition for soil water may be intense, but shading, high humidity, and the greatly decreased amount of wind under the canopy reduces evaporation from the surface soil, the demand for water by understory plants, and the possibility of desiccation damage. Although trees remove large amounts of water from the soil, they can also redistribute water in the soil via hydraulic lift, which is beneficial to shallow rooted understory species if water is moved from deep soil layers to surface soil. Thus the surface of the soil is generally damper than in the open, and the microclimate more moderate. However, these positive aspects for plant growth are no substitute for limited light.

In addition to low resource levels there are other difficulties for life in the forest understory. Hazards such as burial, stem breakage, herbivory and disease may be especially damaging because plants have limited resources for repair. Understory plants are often small and easily buried by litter and falling debris from the canopy. Litter that accumulates on long-lasting snowpacks is especially effective at burying plants because it forms wet compact mats that descend onto plants already bent to the surface by snow. Litter is an important way in which canopy trees influence the understory; experimental studies have shown that different types and amounts of litter can have a major impact on the species composition of forest understory plants. Large leaves have a much greater ability to bury plants than do small needles. In forests with large, fairly persistent leaves, bryophytes and small vascular plants are often restricted to convex microsites from which litter is shed. Falling debris frequently breaks or bends woody plants, which may be of little consequence for trailing shrubs, but is a major setback for erect species, especially young trees.

The forest understory is a highly variable environment. The canopy largely imposes the distinctive features of the forest understory environment, and canopies can vary greatly within forests. Different species of trees intercept different amounts of light, and canopies are almost invariably broken by gaps that yield microsites in the understory with much elevated resource levels. Tree species also vary greatly in the chemical and physical characteristics of the litter they produce, which influences soil properties, and results in complex patterns of variation in soil within a forest. In addition, the forest floor is a variable substrate because of the presence of logs in various states of decay, and because there is often pronounced microtopography. In particular, decomposing logs can provide microsites that are very different from the rest of the forest floor; logs are critical habitat for some species. Some forests contain exposed rock, which provides unique habitat, often in small patches. Thus spatial variation in the microhabitat over very short distances is typical of forest understories.

3. Structure of Forest Understory Vegetation

The forest is a vertically complex community, with plants varying greatly in size from canopy trees to diminutive herbs and bryophytes. Any plants below the canopy could be considered to be in the understory. However, usage of the term “understory” is commonly restricted to species of shrub size and smaller. Trees are often not considered understory plants, although some tree species are small and occur below other trees. Such subcanopy trees are abundant in many tropical forests, but are a less important component of many (although not all) temperate forests. Of course, even canopy trees are initially small, in some cases spending a large part of their life cycle in the understory. Thus there is no clear division between understory and canopy species. Here the emphasis will be placed on the species that occur at lower levels in the forest (up to tall shrubs), with some consideration of small individuals of larger species.

Forests often have multiple layers of understory species (e.g., shrub layer, herb layer, bryophyte layer). Some analyses indicate that variation in plant size is fairly continuous, but often layers can be recognized, in part because of one or a few dominant species with a rather consistent height. Shrubs commonly form a prominent and fairly continuous layer 1–2 m high. Multiple shrub layers may occur, with taller shrubs

forming an intermittent layer over lower shrubs. In some forests, most shrubs are small and structurally part of a herb layer. A prominent layer of herbaceous vascular plants is characteristic of many temperate forests. Most herbs in temperate forests are small, within 1 m of the ground, but variation in size among species can result in considerable vertical structure near the ground surface. In parts of Asia and South America, temperate forests often have a dense layer of bamboos 2 m or more in height. Many temperate forests have a pronounced bryophyte layer on the surface of the soil.

Horizontal variation is also pronounced in the structure of most forests. Forests typically are patchy with layers of understory plants occurring intermittently and varying in height among microsites. Much of this variation relates to canopy conditions, such as gaps and different canopy species. Factors such as variation in the substrate, clonal growth, and the history of a given patch are also important.

4. Diversity and Composition of Forest Understory Plants

Temperate forests vary at many scales. Variation in climate, canopy characteristics, and soil microsites all contribute to variation in the diversity and composition of understory species. The amount of difference between sites may be only weakly related to their spatial separation. For example, evergreen conifer and deciduous hardwood forests on adjacent sites frequently have very different composition of understory species, whereas forests separated by large distances but with similar canopies and climates may have a fairly similar understory species composition.

Forest understory plants tend to form a distinct suite of species, with most species largely restricted to that type of habitat. These species are probably poor competitors in more open habitats and generally exhibit features typical of stress-tolerant species, such as innately slow growth rates, and conservative patterns of resource allocation. Adaptation to low light and other features of the forest understory environment probably requires tradeoffs with characteristics that would be beneficial in more open habitats. Thus there is usually limited overlap in species composition between the forest understory, and permanently open habitats such as grasslands, meadows, and many savannas. Only when the canopy becomes so discontinuous that its influence is much diminished, as in some woodlands, is there pronounced overlap with open habitats.

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Biographical Sketch

Dr. Joseph A. Antos was born in 1950. He has the degrees of B.S. (1972) in Biology from Northern Illinois University, M.A. (1977) in Botany and Plant Ecology from the University of Montana, and Ph.D. (1984) in Botany and Plant Ecology from Oregon State University. His professional experience is as follows: Graduate Teaching Assistant, University of Montana (1975–1977); Graduate Teaching Assistant, Oregon State University (1978–1981); Graduate Research Assistant, Oregon State University (1981–1983); Visiting Scientist, University of Victoria (1985–1987); Visiting Scientist, University of California, Davis (1987–1988); Adjunct Assistant Professor, University of Victoria (1988–1995); and Adjunct Associate Professor, University of Victoria (1995–).