

1 Introduction

The Herbaceous Layer—The Forest between the Trees

Frank S. Gilliam

Forest ecosystems have always been an integral part of human existence, whether as a source of food, fiber, and habitat, as an essential component in maintaining the atmospheric balance of O₂ and CO₂, or as a source of musical, artistic, or poetic inspiration. Yet, our image of forests often comes from the broad brush of a landscape perspective, whereby we see only the grandeur of the predominant vegetation—the trees. Such a distortion figuratively and literally masks the vegetation that, though of lesser prominence, contains the most spatially and temporally dynamic assemblage of forest plants. Often called the *herbaceous layer* (other synonyms are discussed later in this chapter), this stratum of forest vegetation carries with it an ecological significance to the structure and function of forest ecosystems that belies its diminutive stature.

Indeed, it has often been generalized—correctly, to be sure—that the herbaceous layer is the stratum of highest plant biodiversity in forests. To quantify this assertion, I surveyed the literature for studies in North America that quantified both overstory and herb layer richness on the same vegetation sample units, varying from plots to watersheds to an entire basin (the Coweeta Hydrologic Laboratory in Georgia) (Gilliam 2007). The ratio of herb layer species to woody overstory species generally ranged from ~ 3 to 10 (representing a range of relative richness in the herb layer of 75 to 91 percent), with the exception of a fire-maintained longleaf pine stand with its species-rich ground cover and overstory monoculture of *Pinus palustris* Mill., which had a ratio of ~ 250 (Platt et al. 2006; Gilliam et al. 2006). Indeed, conifer stands tend to have higher ratios, likely the result of lower overstory richness (Gilliam 2007). In addition, there was a significant positive relationship between herb layer richness and overstory richness, suggesting that site factors, such as soil fertility, may play an important role (fig. 1.1). The mean across all studies and sites (~ 30 in number), excluding the *P. palustris* study, was 5.6 ± 0.9 (95 percent confidence interval), suggesting that the herb layer generally represents 82–87 percent of plant diversity in forests (Gilliam

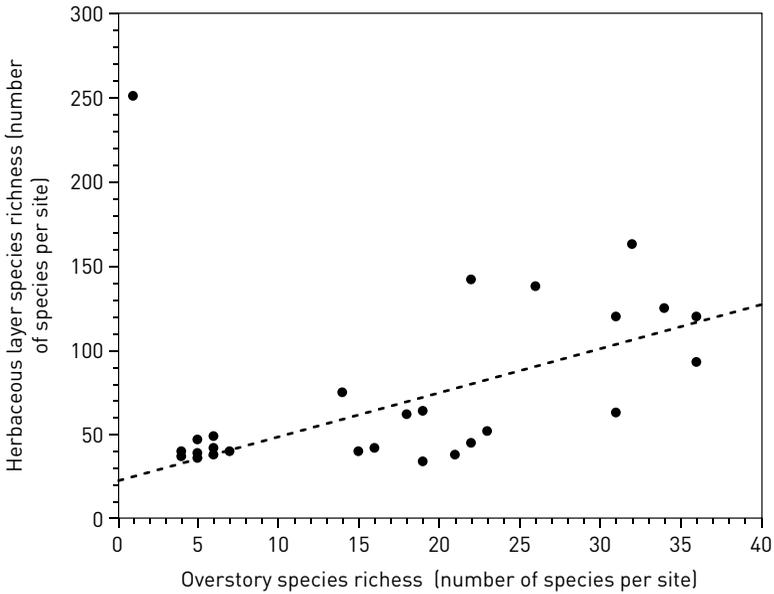


FIGURE 1.1 Herbaceous layer species richness versus overstory species richness across forest sites in North America.

2007), an impressive range considering that relative biomass of the herb layer is far less than 0.5 percent of aboveground biomass (Welch et al. 2007; chapter 2, this volume).

The purpose of this chapter is to introduce this second edition by documenting patterns of change in research interest in the herb layer, and by summarizing our general knowledge and understanding of the ecology and dynamics of forest herb layers. Because the literature contains numerous terms used synonymously with *herbaceous layer*, I begin with a discussion of the terminology and definitions that have been commonly applied to the herbaceous layer. Next, I document the increasing number of papers in the literature over the past several decades. I then develop a simple conceptual framework for understanding the spatial and temporal dynamics of the herbaceous layer. Finally, I describe the organization of the book.

TERMINOLOGY

A survey of the ecological literature reveals numerous synonyms for the term *herbaceous layer* used by ecologists, presenting a challenge to both experienced and beginning researchers. Whereas the term *herbaceous layer* has been adopted for the title of this book (and I will use it interchangeably with the more abbreviated *herb layer*), other authors use such terms as *herbaceous* (or *herb*) *stratum*, *herbaceous understory*, *ground layer*, *ground vegetation*, and *ground flora*. In addition, foresters and others interested in forest management sometimes refer to it as the *regeneration layer* (e.g., Waterman et al. 1995; Baker and van Lear 1998). This latter term arises from both an interest in patterns of regeneration of overstory dominant species and awareness that successful regeneration of such species can be determined largely by interactions among plant species in this stratum (chapter 14, this volume). Some terms even have a pejorative connotation. When I was a graduate student at Duke University, I once asked

the professor of the summer dendrology course about a particular forest herb while walking through the Duke Forest, to which he replied, “Oh, that’s just a *step-over*.” Such a dismissive term emphasizes the lack of importance given to the herb layer by some foresters, at least in the late 1970s, as comprising plants unworthy of study and thus to be “stepped over” while focusing on trees. There are likely other synonyms to be encountered in the literature, so this is not intended to be an exhaustive list. Rather, the goal is to provide some idea of the diversity of terms one should expect to find in the literature.

Gilliam (2007) summarized the results of a search of Ecological Abstracts initially reported in the first edition of this book for citations from the 20-year period of 1980 to 1999 that have the herb layer synonyms mentioned either in the title, as key words, or in the abstract. The search represented articles from some 3,000 journals and 2,000 other publications, including books and monographs, and thus provided an indication of the frequency with which one might expect to encounter the various terms in the literature. The number of occurrences was not necessarily mutually exclusive among terms. That is, it is possible that one article may have used, for example, *herbaceous layer* in the title, and *ground layer* as a key word; this would result in one occurrence in each of the two synonym categories.

Clearly, *herbaceous/herb layer* and *ground vegetation* have been the more commonly used terms in the ecological literature, receiving 34.0 and 31.1 percent frequency of use between 1980 and 1999, respectively. For reasons that are not immediately apparent, North American studies have tended to use *herbaceous/herb layer*, whereas non-North American (particularly European) studies tend to use *ground vegetation*. Given these observations, I am not suggesting that a single consensus term be used. In fact, as editor of this volume, I have avoided requiring that all authors use identical terminology. The main point is that, particularly for researchers just beginning in this field, there are several terms that one must expect to encounter in the ecological literature. Accordingly, from a practical standpoint, those performing searches for herb layer studies (e.g., using Web search engines—see below) would be strongly advised to either use several terms (but especially *herbaceous/herb layer* and *ground vegetation*) or focus the appropriate term toward the geographical area of interest.

TEMPORAL CHANGE IN RESEARCH INTEREST IN HERB LAYER ECOLOGY

One of the better metrics of research interest in a particular scientific discipline or topic can arise from documenting patterns of change over time in the number of citations in the pertinent literature. Of the many Internet search engines, Google Scholar® (hereafter GS) provides one of the more effective means of reaching a wide variety of publications, including peer-reviewed journals, doctoral dissertations, master’s theses, government white papers, and other scholarly documents. A further advantage of GS over the previous analysis used in the first edition is that GS searches text, in addition to simply searching titles, key words, and abstracts. Accordingly, I have performed GS searches on the two more common terms encountered in the literature: *herbaceous layer* and *ground vegetation*. As GS allows Internet searches to be broken down into set time periods, I have performed these by decade, beginning with the 1950s and extending to the present. In addition, GS allows searches on these terms exclusively, so that the results can be displayed for each term separately, as well as together.

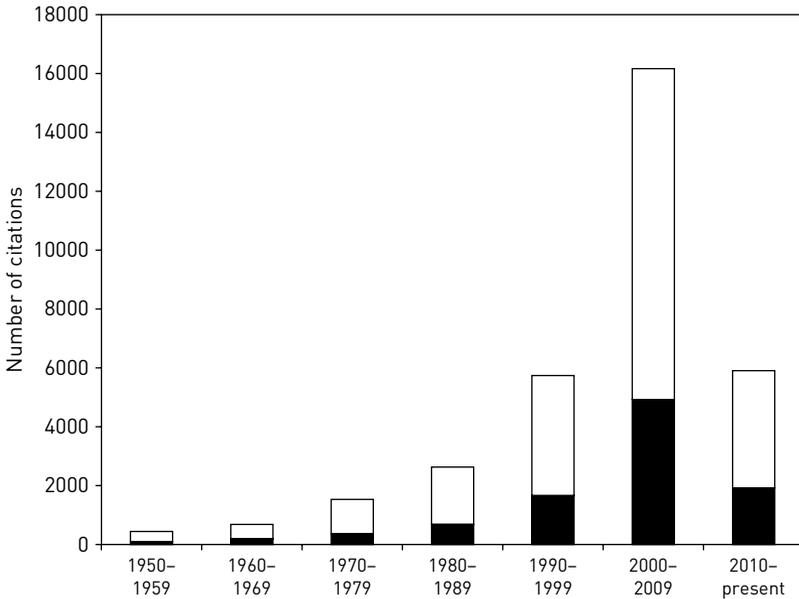


FIGURE 1.2 Number of papers with the terms *herbaceous layer* (closed bar) or *ground vegetation* (open bar) by decade, as searched by Google Scholar™.

In contrast to what was reported in the first edition of this book, *ground vegetation* is used more commonly than *herbaceous layer*, likely the result of the geographic distinction already discussed and the history of herb layer studies (i.e., because *ground vegetation* is used more among European studies and because such studies began earlier in Europe than in North America). More important than this distinction in use of terms, it is clear from such analyses that research interest in the ecology of forest herb layers has increased exponentially (fig. 1.2). Indeed, citation frequency has grown from < 400 in the 1950s to > 16,000 in the first decade of the new millennium. Furthermore, the number of citations in the current, incomplete decade (2010 to present) already exceeds that of the 1990s (fig. 1.2).

DEFINITIONS

The more commonly used definitions of the herbaceous layer emphasize its physical aspects as an assemblage of forest vegetation, with the focus on height, rather than on growth form. Commonly, the herb layer is defined as *the forest stratum composed of all vascular species that are ≤ 1 m in height*. The maximum height limit, however, varies among studies, as do the exclusion and inclusion of non-vascular plant species. In one of the earlier quantitative studies of the herb layer, Siccama et al. (1970) used 0.5 m as an upper limit for the Hubbard Brook Experimental Forest. Yorks and Dabydeen (1999) used 1.37 m to delimit the herb layer in clearcut hardwood stands of western Maryland. Using the terms *understory* and *inferior layer* interchangeably, Rogers (1981) defined this stratum as comprising vascular plants < 2 m in height for mature mixed mesophytic stands from Minnesota, Wisconsin, and Michigan.

Although it is rarely immediately evident why different studies use different height limits, the variation likely results from a combination of research inertia (i.e., “Well,

that's the way we've always done it in this lab") along with true variation among forest types in the structure of vegetation. For example, mature second-growth hardwood stands, such as those found in Watershed 6 of Hubbard Brook, often lack a prominent shrub component, so the use of 0.5 m as the upper height limit by Siccama et al. (1970) was certainly justified. Yorks and Dabydeen (1999) used the term *vascular understory* along with a height limit of 1.37 m. Although they provide no reason for such a distinct height limit, it corresponds to the "breast height" often used in conjunction with DBH (diameter at breast height). Other studies include non-vascular plants in their definition (e.g., Bisbee et al. 2001). Although such studies are relatively uncommon, they generally occur in forests where bryophyte cover can be prevalent (e.g., boreal forests; chapter 12, this volume). Still other studies fail to specify a maximum height to distinguish the herb layer from other forest vegetation strata.

Just as no consensus on a single term was sought for use in studies of the herb layer of forest ecosystems, it is similarly not the intention of this book to establish a uniform definition of the herb layer. For the very reasons discussed here (and particularly the great inter-site differences in the physical structures of forest vegetation), vegetation scientists should feel free to adapt their definitions appropriately. However, it is imperative that researchers (1) fashion their definitions around key biological and physical characteristic of the forest system, and (2) state clearly their working definitions of the herb layer, along with an appropriate justification, especially if it departs greatly from the typical height range of 0.5 to 1.0 m.

CONCEPTUAL FRAMEWORK FOR STUDIES OF THE HERBACEOUS LAYER

Because the plant kingdom comprises species of an impressive array of physical growth forms, life history characteristics, and patterns of resource use, botanists and plant ecologists have long endeavored to group plant species into categories based on shared characteristics. This serves the dual purpose of decreasing the complexity and increasing the understanding of the ecological significance of those characteristics. One of the earliest such attempts was made by the Danish botanist Christen Raunkiaer, whose pioneering work was published originally in Danish in the early 20th century and later translated into English in the classic book *The life forms of plants and statistical plant geography* (Raunkiaer 1934). As the title implies, he classified plants into life forms (also called *growth forms*), a classification he based on the location of the structure that allows a plant to exist from one growing season to the next (i.e., the perennating structure—buds, rhizomes, and seeds). Still in use today, Raunkiaer's life forms represent one of the more successful endeavors placing plant species into ecologically meaningful categories.

Categories such as these are essentially groups of plant species based on common ecological functions. Appropriately, then, in more recent literature, they are often referred to as *plant functional groups*, and their ecological relevance has been expanded to include such phenomena as maintenance of biodiversity and stability of ecosystems, and effects on nutrient cycling (Huston 1994; Hooper and Vitousek 1998; Díaz and Cabido 1997). Other terms in the literature synonymous with *functional groups* include *guilds* and *functional types* (Wilson 1999). Körner (1994) discussed criteria for determining levels of organization within functional groups, and suggested that such levels represent a gradient of integration from sub-cellular structures up to ecosystems,

and that ecological relevance increases along this spatially expanding gradient at the expense of precision.

Resident versus Transient Species

I have proposed a simple conceptual framework for the forest herbaceous layer, comprising two functional groups: *resident species* and *transient species* (Gilliam et al. 1994). *Resident species* are those with life history characteristics that confine them to aboveground heights of 1–1.5 m. These species would include, for example, annuals, herbaceous perennials, and low-growing shrubs. *Transient species* are plants whose existence in the herb layer is temporary (i.e., transient) because they have the potential to develop and emerge into higher strata (e.g., shrub, understory, and overstory layers). This group would include larger shrubs and trees. Juveniles (i.e., seedlings and sprouts) of regenerating overstory species must pass through this layer and compete as transient species with resident species (Morris et al. 1993; Wilson and Shure 1993; chapter 13, this volume). Because resident species play an important role in competition among themselves (Muller 1990) and with seedling and sprouting individuals of potential forest canopy dominants (Maguire and Forman 1983; Davis et al. 1998, 1999), the herb layer is a dynamic assemblage of these two groups.

Note that the term *transient* has a specific temporal and physical connotation that should not be confused with Grime's (1998) classification of plant species into dominant, subordinate, and transient species. His classification is based on the different roles species have in linking plant diversity to ecosystem function. Thus, his *transient* species are so called because they are transient in abundance and persistence, not in the strata of forest vegetation. In this sense, Grime's (1998) transient species are closely analogous to the *satellite* species of Hanski's (1982) core and satellite species hypothesis (see Gibson et al. 1999 for an excellent synthesis of both Grime's and Hanski's concepts).

As transient species emerge from the resident species, they become members of the other, overlying forest strata. These higher strata interact with the herbaceous layer through shading and utilization of moisture and nutrients (Maguire and Forman 1983). In addition, higher strata affect substrates for the herbaceous layer through inputs of litter and creation of tip-up mounds (chapter 8, this volume). Thus, it is important to understand the interactions between the herbaceous layer and other forest strata (chapter 9, this volume). Although Parker and Brown (2000) called into question the usefulness of applying the term *stratification* to forest canopies, there appears to be considerable ecological justification for it, considering the widely contrasting height-growth strategies seen among plant species of forest communities. Indeed, there may be a large number of forest strata, including several canopy layers, epiphytes and lianas within the tree canopy, shrubs, the herbaceous layer, and the thalphyte (non-vascular plant) layer (Harcombe and Marks 1977; Kimmins 1996; Oliver and Larson 1996).

The dynamic balance of resident and transient species in forest herbaceous layers, in terms of both numbers of species (i.e., richness) and cover, is mediated by (1) competitive interactions, (2) responses to disturbances, such as windthrow of canopy trees, herbivory, and harvesting, and (3) responses to environmental gradients, such as soil moisture and fertility, and other factors that vary spatially and temporally. Working in

mature mesophytic stands from Minnesota to Michigan, Rogers (1981) found that the ratio of transient species cover to resident species cover in stands with high *Fagus grandifolia* Ehrh. Co-dominance in the overstory was nearly twice that in stands with little or no *F. grandifolia* (0.78 versus 0.40, respectively). Gilliam et al. (1995) found that relative cover of resident species was significantly higher in early successional stands than in mature stands of central Appalachian hardwood forests (71 percent versus 54 percent, respectively).

Resident versus Transient Species: Reproduction and Dispersal

Among the unique aspects of the herbaceous layer, then, is the intimate spatial and temporal coincidence of resident and transient species, which are two otherwise-disparate plant groups. The distinction between them is manifested not only in the more obvious differences in growth form, but also in the factors that determine their distribution and patterns of reproduction. Transient (in particular, tree) species are generally limited in their distribution by various combinations of disturbance patterns (Loehle 2000), and indeed have the potential for rapid migration (Clark 1998). In contrast, the distribution of resident species (predominantly woodland, or forest, herbs) is determined more by availability of suitable habitats, the likelihood of seeds to be dispersed to those habitats, and the successful germination (and subsequent growth) of seeds that reach them (Ehrlén and Eriksson 2000; Verheyen and Hermy 2001). Seed size can be an important variable in these latter two factors. Ehrlén and Eriksson (2000) found that seed size was negatively correlated with the likelihood of reaching suitable habitat, but positively correlated with the probability of successful germination. Furthermore, a disproportionate number of resident species are cryptophytes and hemicryptophytes (chapters 5 and 6, this volume) with the capability of asexual (clonal) reproduction (especially in the absence of disturbance), whereas far fewer transient species use this reproductive mode in the absence of disturbance. Singleton et al. (2001) found that only seven of 50 forest herb taxa from central New York lacked clonal expansion. McLachlan and Bazely (2001) suggested that knowledge of dispersal mechanisms of understory herbs could be applied to their use as indicators of recovery of deciduous forests following disturbance.

There are also sharp contrasts between transient versus resident species in their respective mechanisms of seed dispersal. For transient species (again, tree species in particular), the predominant mechanisms are wind and vertebrate herbivores (e.g., birds and rodents) (Cain et al. 1998; Clark et al. 2001). In contrast, the predominant dispersal vectors for resident species are invertebrates, particularly the phenomenon of myrmecochory, or seed dispersal by ants (Handel et al. 1981; Kalisz et al. 1999). Pakeman (2001) examined an additional dispersal vector for woodland herbs—large mammalian herbivores—and distinguished between endozoochory (seeds consumed and passed through the gut) and ectozoochory (seeds carried externally) as mechanisms for dispersal. He concluded that endozoochory could be an important mechanism for long-distance dispersal of herb species. Two mammalian herbivore species he considered, white-tailed deer (*Odocoileus virginianus* Zimmermann) and moose (*Alces alces* L.), have particular relevance for the herb layer of eastern North American forests (chapters 13, 16, and 17, this volume).

Based on a recent survey of literature, Cain et al. (1998) concluded that most woodland herbaceous species are substantially limited in their seed-dispersal capabilities (chapter 5, this volume). Whitney and Foster (1988) cited poor colonizing ability (based largely on limited dispersal) as one of several factors that lead to the uniqueness of regional herb layer floras. Matlack (1994b) also demonstrated both slow clonal growth (asexual reproduction, e.g., via rhizomes) and low rates of plant migration via seed dispersal for forest herbs in hardwood forests of the Delaware/Pennsylvania Piedmont.

In conclusion, these numerous differences in resident versus transient species in the herbaceous layer of forest ecosystems create a forest stratum with impressive spatial and temporal variability, the very dynamic nature of vegetation originally articulated by Cowles (1899). Some of the substantial increase in herb layer research documented in fig. 1.2 (see also fig. 14.1 in chapter 14 for similar data on literature focused on the response of the herb layer to disturbance) has likely arisen from an increasing awareness among plant ecologists of the excitement and challenge of understanding the complex ecology of this important vegetation stratum, and of the urgency of applying this knowledge toward the wise, sustainable use of forest resources that will conserve herb layer species. Such complexity can be seen at all levels of ecological organization, from species-specific differences in light and nutrient use to the response of herb communities to disturbances to the forest canopy, which is the hierarchy of organization generally used in this book.

ORGANIZATION OF THE SECOND EDITION

The 1998 symposium that led to the first edition of this book had the term *forest communities* in its title. It is not surprising, then, that this book has a decidedly community-level orientation in its approach to examining the ecology of the herb layer within this broad region. As already discussed, however, the herb layer comprises plant species with widely varying responses to environmental factors and with widely varying population dynamics. Although seemingly inconsequential in biomass relative to trees (Gilliam 2007; chapter 2, this volume), the herb layer has several important roles in maintaining the structure and function of forest ecosystems. Accordingly, it is important to address the herb layer on all levels of ecological organization, from ecophysiological and population levels to community and ecosystem levels, much as one would find in a college ecology course. Ecologists with noted expertise in each of these fields were sought to contribute to this second edition.

The book is divided into five major sections. Part One addresses aspects of the environment in which plants of the herbaceous layer grow, including nutrient relations and light in chapters 2 (Robert Muller) and 4 (Wendy Anderson), and ecophysiological adaptations of herbaceous species to the environment in chapter 3 (Howard Neufeld and Donald Young). Part Two focuses on population biology of herb species, with chapter 5 (Carol Goodwillie and Claudia Jolls) providing an extensive review of reproductive strategies. Chapter 6 (Claudia Jolls and Dennis Whigham) discusses population dynamics with a particular focus on conservation ecology and rare species. Community dynamics of the herbaceous layer is the subject of Part Three. Chapters 7–9 in this section deal with mechanisms of herbaceous layer dynamics, with emphasis on old-growth forests (Brian McCarthy), habitat heterogeneity (Susan Beatty), and linkages between the herbaceous layer and the overstory (Frank Gilliam and Mark

Roberts). Chapters 10–12 are syntheses of studies of community dynamics in widely contrasting forest types, forests and woodlands of the southeastern United States (Robert Peet et al.), oak-hickory forests of the North Carolina Piedmont (Robert Peet et al.), and the boreal forest of Québec (De Grandpré et al.). The focus of Part Four is community dynamics of the herbaceous layer and the role of disturbance, beginning with an overview of the interactions of the herbaceous layer with disturbance (chapter 13, Mark Roberts and Frank Gilliam), followed by more specific discussions of disturbance vectors/mechanisms of herb response to disturbance, including competitive interactions between the herbaceous layer and tree seedlings (chapter 14, Lisa George and Fakhri Bazzaz), impacts of invasive species (chapter 15, James Luken), effects of deer herbivory (chapter 16, Don Waller), interactive effects of catastrophic windthrow and deer browsing (chapter 17, Carson et al.), impacts of timber harvesting (chapter 18, Julie Wyatt and Miles Silman), long-lived (legacy) effects of agricultural practices (chapter 19, Kathryn Flinn), impacts of excess nitrogen (chapter 20, Frank Gilliam), and responses of the herb layer to climate change (chapter 21, Jesse Bellemare and David Moeller). Finally, in Part Five, chapter 22 (Frank Gilliam) assesses our state of knowledge with respect to the herbaceous layer in eastern forests, summarizing and synthesizing some of the key ideas presented in previous chapters.

