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Introduction
Conceptual Framework for Studies of the Herbaceous Layer

Frank S. Gilliam
Mark R. Roberts

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 O_2 and CO_2, 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 stature, contains the most diverse and 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 the forest ecosystem that belies its physical stature.

In a synthesis of species richness among several general plant and animal taxa of North America, Ricketts et al. (1999) found that species richness of non-tree vascular plants (a taxon representing a high percentage of herbaceous layer species) correlated much better with richness of several animal taxa (including birds, butterflies, and mammals) than did richness of tree species. They also found that richness of non-tree vascular plant species in eastern North America was higher than that in any other region of North America and was more than 13 times that of tree species richness in the region (Ricketts et al. 1999). However, of the plant species currently listed by The Nature Conservancy/Association for Biodiversity Information as either "extinct," "missing and possibly extinct," or "extinct/missing in the wild, but still extant in cultivation," virtually none are tree species (Stein et al. 2000). Indeed, herbaceous plant species have extinction rates that are more than

twice those of woody species (Levin and Wilson 1976; Levin and Levin 2001). Thus, this diverse assemblage of forest vegetation also contains some of the more sensitive, threatened, and endangered plant species.

We introduce this edited volume by summarizing our general knowledge and understanding of the ecology and dynamics of forest herbaceous layers. Because the literature contains numerous terms used synonymously with the term *herbaceous layer*, we begin with a discussion of the terminology and definitions that have been commonly applied to the herbaceous layer. Next, we develop a simple conceptual framework for understanding the spatial and temporal dynamics of the herbaceous layer. Finally, we describe the organization of the book.

Terminology

Our survey of the ecological literature revealed numerous synonyms for the term *herbaceous layer* used by ecologists, presenting a challenge to experienced and beginning researchers alike. Whereas we have adopted the term *herbaceous layer* for the title of this book (and 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 an awareness that successful regeneration of such species can be determined largely by interactions among plant species in this stratum (chapter 11, this volume). When we were graduate students at Duke University, the professor of the summer dendrology course referred to plants of the herb layer as *step-overs* while walking through the Duke Forest. Such a hyperbolic 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 were to be stepped over while learning about trees. There are likely still other synonyms we have not encountered, so this is not intended to be an exhaustive list. Rather, our goal is to provide some idea of the diversity of terms one should expect to find in the literature.

We have summarized the results of a search of *Ecological Abstracts* for citations from the past 20 years that have the herb layer synonyms mentioned either in the title, as key words, or in the abstract (table 1.1). The search represents articles from some 3000 journals and 2000 other publications, including books and monographs, and thus provides an indication of the frequency with which one might expect to encounter the various terms in the literature. It should be noted that the number of occurrences are 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*

Table 1.1. *Synonyms for herbaceous layer and number of occurrences in the ecological literature in the last 20 years.*

Synonym	Occurrences		
	1980–1989	1990–1999	Total
Herbaceous/herb layer	73	164	237
Herbaceous/herb stratum	10	11	21
Herbaceous understory	4	20	24
Ground layer	40	64	104
Ground vegetation	56	161	217
Ground flora	27	68	95
Step-overs	0	0	0
Total	210	488	698

Information taken from *Ecological Abstracts* (Elsevier Science Ltd.), representing approximately 3000 primary journals and 2000 other publications, including books, monographs, reports, and theses.

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* are the more commonly used terms, together representing about 65% of the nearly 700 occurrences since 1980. For reasons that are not immediately apparent, North American studies tend to use *herbaceous/herb layer*, whereas non-North American (particularly European) studies tend to use *ground vegetation*.

We are not suggesting that a single, consensus term be used. In fact, as editors of this volume, we have not required that all authors use identical terminology. Rather, we would like to point out, particularly to researchers just beginning in this field, that there are several terms that one must expect to encounter in the ecological literature. Accordingly, from a practical standpoint, one performing searches for herb layer studies (e.g., using web search engines) would be strongly advised to use either several terms (but especially *herbaceous/herb layer* and *ground vegetation*) or focus the appropriate term toward the geographical area of interest.

It is also notable that the number of occurrences more than doubled during 1990–1999 compared to 1980–1989. In other words, nearly 70% of the occurrences from the past 20 years came in the past decade. This substantial increase is indicative of greatly increased interest in the herb layer of forest ecosystems among plant ecologists, forest ecologists, conservation biologists, and resource managers.

Definitions

It is not surprising that there are almost as many definitions of the herb layer of forests as there are investigators who study it. 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. We have defined the herb layer, as have numerous studies, as the forest stratum composed of all vascular species that are ≤1 m in height. The maximum height limit, however, varies greatly among studies, as does exclusion/inclusion of nonvascular 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 Hubbard Brook Experimental Forest. More recently, 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 forests, such as that found in Watershed 6 of Hubbard Brook, often lack a prominent shrub component, so 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 their 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 nonvascular 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 10, this volume). Still other studies fail to specify a maximum height to distinguish the herb layer from other forest vegetation strata.

Just as we sought no consensus on a single term to be used for studies of the herb layer of forest ecosystems, it is similarly not our intention in this book to establish a uniform definition of the herb layer. For the very reasons brought out here (particularly the great intersite differences in the physical structure of forest vegetation), vegetation scientists should feel the freedom of adapting their definitions appropriately. However, we do suggest that researchers base their definition on a careful consideration of the biological and physical structure of the forest system and articulate specifically their working definition of the herb layer, along with a justification of their definition, especially if it departs greatly from the typical height range of 0.5–1.0 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 in the early twentieth 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, seeds). Still in use today, Raunkiaer's life forms represent one of the more successful endeavors to place 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 1999b). 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 (Körner 1994).

Resident versus Transient Species

We propose a simple conceptual framework for the forest herbaceous layer, composed of two functional groups: resident species and transient species. *Resident species* are those with life-history characteristics that confine them to above-ground heights of 1–1.5 m (or perhaps others, depending the height distinction used in one's definition of the herb layer). These species would include, for example, annuals, herbaceous perennials, and low-growing shrubs. *Transient species* comprise plants whose existence in the herb layer is temporary 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). 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), we view the herb layer as a dynamic assemblage of these two groups.

We should emphasize that our use of 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 compete 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 7, this volume). Thus, it is important to understand the interactions between the herbaceous layer and other forest strata (chapter 8, this volume). Although Parker and Brown (2000) called into question the usefulness of applying the term *stratification* to forest canopies, we find 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 thallophyte (nonvascular 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. codominance in the overstory was nearly twice that in stands with little or no *F. grandifolia* (0.78 vs 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% vs 54%, 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 likelihood of reaching suitable habitat, but positively correlated with probability of successful germination. Furthermore, a disproportionate number of resident species are cryptophytes and hemicryptophytes (chapter 5, 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 7 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 after 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 Pakeman considered, white-tailed deer (*Odocoileus virginianus* Zimmermann) and moose (*Alces alces* L.), have particular relevance for the herb layer of eastern North American forests (chapter 13, 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 leads 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.

When seed dispersal mechanisms are compared between resident and transient species, seeds are dispersed much greater distances for transient species.
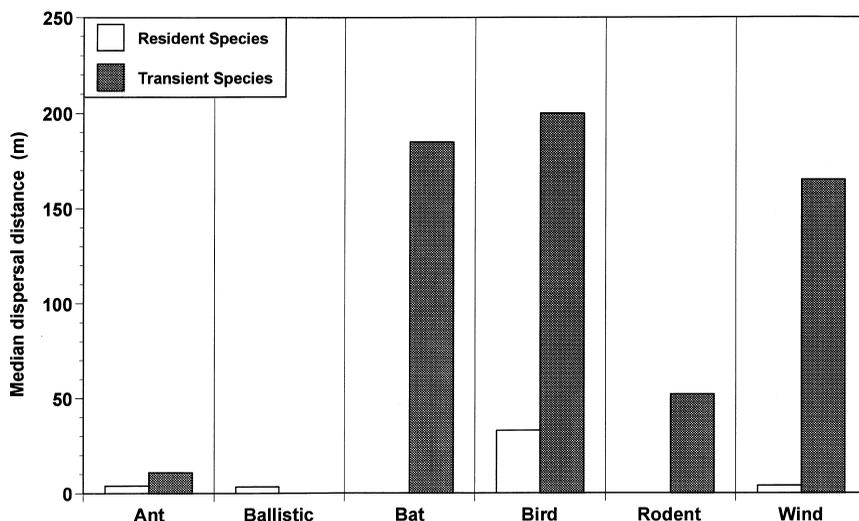
Figure 1.1. Distances of dispersal by biotic and abiotic vectors for resident versus transient species of the herbaceous layer. Based on data from Cain et al. (1998).

This is not a surprising result, considering the respective sizes of seed-bearing individuals of the two groups. Figure 1.1 summarizes a subset of data from Cain et al. (1998) to make direct comparisons between transient species (trees and shrubs in the original article) and resident species (woodland herbs in the article) for both the mechanism and the distance of seed dispersal. Ballistic dispersal was the only mechanism unique to resident species, whereas bat and rodent dispersal were unique to transient species. For mechanisms common to both, median seed dispersal distances were consistently far greater for transient species, by factors of 2.5, 6.0, and nearly 40 for ant, bird, and wind dispersal, respectively (fig. 1.1).

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 table 1.1 likely has 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 response of herb communities, to disturbances to the forest canopy. We have taken a cue from this hierarchy of organization as a general approach to organizing this book.

Organization of the Book

Our own research on the herbaceous layer of eastern North American forests has generally been on the level of the ecological community, as has that of many of our colleagues and collaborators. The 1998 symposium that led to this book (see the Preface to this volume) even 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, the herb layer has several important roles in maintaining structure and function of forest ecosystems. Accordingly, we wanted 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. We have sought ecologists with noted expertise in each of these fields to be contributors to this book.

The book is divided into five major sections. Part I addresses aspects of the environment in which plants of the herbaceous layer grow, including nutrient relations and light in chapters 2 and 4 (Robert Muller and Wendy Anderson), and ecophysiological adaptations of herbaceous species to environment in chapter 3 (Howard Neufeld and Donald Young). In part II, Claudia Jolls discusses population dynamics, with a particular focus on conservation ecology and rare species. Community dynamics of the herbaceous layer is the subject of part III. Chapters 6–8 of part III deal with mechanisms of herbaceous layer dynamics, with emphasis on old-growth forests (Brian Mc-Carthy), habitat heterogeneity (Susan Beatty), and linkages between the herbaceous layer and overstory (Frank Gilliam and Mark Roberts). Chapters 9 and 10 are syntheses of studies of community dynamics in two widely contrasting forest types, oak-hickory forests of the North Carolina Piedmont (Norm Christensen and Frank Gilliam) and the boreal forest of Québec (De Grandpré and others). The focus of part IV is community dynamics of the herbaceous layer and the role of disturbance, including competitive interactions between the herbaceous layer and tree seedlings (chapter 11, Lisa George and Fakhri Bazzaz), impacts of invasive species (chapter 12, James Luken), and an overview of the interactions of the herbaceous layer with disturbance (chapter 13, Mark Roberts and Frank Gilliam). Finally, in part V we attempt to assess our state of knowledge with respect to the herbaceous layer in eastern forests, summarize and synthesize some of the key ideas presented in previous chapters, and suggest areas for further research (chapter 14, Frank Gilliam and Mark Roberts).