



9Wt`c[m'cZ`K ccX`UbX`<YfVg`]b`HYa dYfUhY`8YV]Xi ci g': cfYghg
5i h\cf fjt`8Ybb]g': ""K \][\La
Gci fW. 5bbi U`F Yj]Yk `cZ`9Wt`c[mž`9j c`i h]cbž`UbX`GmghYa Uh]Vgž`J c`"") `f&\$\$ (tž`dd""), ' ! * &%
Di V`]g\ YX`Vm`[Annual Reviews](#)
GhU`Y`I F @` <http://www.jstor.org/stable/30034128>
5 VVggYX. : &) # \$, # & \$ % % %) . \$ *

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Annual Reviews is collaborating with JSTOR to digitize, preserve and extend access to Annual Review of Ecology, Evolution, and Systematics.

<http://www.jstor.org>

ECOLOGY OF WOODLAND HERBS IN TEMPERATE DECIDUOUS FORESTS*

Dennis F. Whigham

*Smithsonian Environmental Research Center, Edgewater, Maryland 21037
Harvard Forest, Petersham, Massachusetts 01366; email: whighamd@si.edu*

Key Words life history, reproduction, herbivory, mycorrhiza, conservation

■ **Abstract** The diversity of woodland herbs is one of the most striking features of deciduous forests in the temperate zone. Here I review the literature on the ecology of woodland herbs. The review is timely because, since Paulette Bierzychudek's seminal review of the subject in 1982, a number of species have become rare or threatened owing to the conversion of forests to other land uses, competition by alien plant species, and increased abundance of native wildlife that negatively impact woodland herbs (e.g., white-tailed deer). Although the basic biology of woodland herbs is mostly known, few species have been studied in detail, and we are only able to make broad generalities about their ecology. We are especially lacking in information needed to conserve and restore species in altered and threatened habitats.

INTRODUCTION

Woodland herbs account for most of the vascular plant species diversity in deciduous forests in eastern North America (e.g., Ramsey et al. 1993, McCarthy & Bailey 1996, McCarthy 2003), Europe (e.g., Hermy et al. 1999), and Japan (e.g., Kawano 1985). This diverse group of species has long attracted the interest of naturalists, and herbalists have used them since ancient times because many species (e.g., American Ginseng) contain medicinally active and therapeutic chemicals (Lewis & Zenger 1982, Smith et al. 1996). Ecologists have also long been interested in woodland herbs because of the wide array of life history attributes that make them ideal research subjects. In recent years, woodland herbs have attracted attention because landscape alteration and habitat destruction caused many species to become rare or threatened.

Species declines and losses are primarily due to the conversion of forests into nonforest land uses and to competition from invasive species (Jolls 2003, Meekins & McCarthy 2000), leading investigators to discuss conservation and restoration

*The U.S. Government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

of woodland herbs in deciduous forests (e.g., Drayton & Primack 1996, Robinson et al. 1994, Jolls 2003). Three issues related to the population ecology of woodland herbs have received the most attention in eastern North America: (a) Logging (Kochenderfer & Wendel 1983, Meier et al. 1995) and (b) deer browsing (Rooney & Dress 1997b, Waller & Alverson 1997, Rooney 2001, Bellemare et al. 2002; Rooney & Gross 2003) both negatively impact herb diversity, and (c) clear-cut areas abandoned to secondary succession will slow the recovery of herb diversity (Vellend 2003).

Most studies of the ecology of woodland herbs cite the 1982 review paper by Bierzychudek (1982a). During the intervening 20 years, additional information has been published on a range of topics related to the biology and ecology of woodland herbs (e.g., Gilliam & Roberts 2003). The objective of this contribution is to update and extend the analysis provided by Bierzychudek. My hope is that this synthesis will be useful to individuals who study woodland herbs as well as support efforts to develop more effective research, conservation, and restoration strategies.

The review is organized into topics that contain relevant literature citations and an overview of the current state of knowledge. I consider the topics covered by Bierzychudek (phenology, longevity, modes of reproduction, reproductive effort, seed dispersal and germination, patterns of mortality, population structure and stability) and additional topics (clonality, herbivory, genetic variability, mycorrhizae, nutrient storage and nutrient cycling, responses to disturbance) not included or only briefly considered in the 1982 review. Jolls (2003) has also reviewed topics considered by Bierzychudek and I have attempted to augment that material.

PHENOLOGY

Although most woodland herbs are deciduous, the range of phenological patterns has been more fully examined, and Givnish (1983, 1987) described the diversity of leaf phenology patterns in ecological and evolutionary contexts. Studies in Japan (Kawano 1985, Uemura 1993) provide a detailed comparative analysis of phenological patterns among woodland herbs. Uemura (1993) identified two groups of evergreen and three groups of deciduous species, as well as wintergreen and achlorophyllous species. Uemura's wintergreen groups were based on leaf longevity (one or two years). The deciduous groups, which accounted for most species, were based on whether the species had heteroptic (i.e., plants with both summer green and overwintering leaves), summer green, or spring green leaves. Four wintergreen species had no leaves in the summer, and three achlorophyllous species were in two families (Orobanchaceae and Orchidaceae). Kawano (1985) also recognized a similar range of phenological patterns in Japan and attributed the diversity of phenological patterns to having "differentiated as a result of adaptive response to woodland habitats where conspicuous periodicity in various physical and biotic regimes predominates."

Givnish (1983, 1987) provided rigorous analyses that supported Kawano's comments, and Neufeld & Young (2003) summarized the literature on the ecophysiology of woodland herbs. Excluding winter annuals, Givnish (1987) recognized six guilds on the basis of leaf phenology: spring ephemerals, early summer, late summer, wintergreen, evergreen, and dimorphic. Givnish found clear differences in leaf thickness and width between the spring ephemeral, early summer, and late summer guilds and clear evolutionary patterns within guilds and growth forms. Spring ephemerals had determinate growth and displayed foliage between 5–15 cm above the ground on basal leaves or short umbrellas. Leaves close to the ground have more efficient temperature regulation, permitting efficient use of light during the short period between emergence and development of the tree canopy. Early summer species had determinate growth with leaves from 10–160 cm above the ground, displayed in a variety of umbrella-like structures that minimize shading and maximize light capture with the lowest possible structural costs. Late summer species had indeterminate growth and displayed leaves at a greater height (40–160 cm). Evergreen and wintergreen species and the winter phases of dimorphic species displayed leaves close to the ground, resulting in enhanced winter photosynthesis (Minoletti & Boerner 1993, Tissue et al. 1995).

More recent studies support the earlier conclusions about flowering and fruiting, especially Bierzychudek's comment that caution needs to be applied to information on breeding systems because the degree of compatibility or incompatibility may vary from one location to another and geographic variability in breeding systems should be expected. *Trillium kamtschaticum* in Japan (Ohara et al. 1996) and *Podophyllum peltatum* in North America (Policansky 1983) are two species that have more than one breeding system over their ranges of distribution. Northern populations of *T. kamtschaticum* in Hokkaido, for example, are self-compatible and have a high degree of genetic diversity compared with mostly self-incompatible southern populations.

Several studies (Ashmun et al. 1982, Pitelka et al. 1985a, Collins & Pickett 1988, Givnish 1987) have shown that autumn flowering species respond positively to light gaps and have indeterminate growth and thin, broad leaves displayed along vertically elongating shoots. Most autumn flowering species do not develop preformed buds, whereas most spring flowering species do (Randall 1952, as described in Gerber et al. 1997b). Not described in the 1982 review were species that flower in midsummer, such as *Goodyera pubescens*, an evergreen orchid, and *Tipularia discolor* a wintergreen orchid that is leafless when it flowers (Snow & Whigham 1989, Whigham 1990).

LONGEVITY

Not much was known about the longevity of woodland herbs in 1982, and little has changed since then (Jolls 2003). Most woodland herbs are perennial and clonal. Annuals (Baskin & Baskin 1998) and pseudoannuals (Baskin & Baskin 1988,

Cook 1988) that produce ramets at the ends of short-lived spacers typically live for one year (Wijesinghe & Whigham 1997). Some species (e.g., *Viola* spp.) have individuals that live between 1 and 10 years (Bender et al. 2000, 2002), and others live for as long as 30–50 years. *Clintonia borealis* is an example of a clonal species with long-lived individuals (Pitelka et al. 1985b), and *Panax quinquefolia* (Lewis & Zenger 1982) and species of *Trillium* (Davis 1981) are examples of long-lived nonclonal species.

For some woodland herbs, longevity cannot be easily interpreted. For example, individuals of the nonclonal orchid *Galearis spectabilis* failed to produce seeds in or near permanent plots for more than 10 years, and fewer than 5% of the individuals originally marked are still alive (D. Whigham, unpublished data). Most individuals appear aboveground for 1–2 years, and new plants appear each year. I suspect that the new plants are seedlings or individuals that have persisted underground as heterotrophic plants supported by mycorrhiza (e.g., Gill 1996, Shefferson et al. 2001), and thus establishing ages of individuals is difficult.

PATTERNS OF MORTALITY

Recent studies have provided more information on mortality. Seedling mortality can be negatively (Syrjänen & Lehtilä 1993) or positively (Smith 1983a) related to density. Groups of *Floerkea proserpinacoides* seedlings, for example, have a greater chance of pushing through leaf litter and surviving. Some species have low mortality at all life history stages or mortality may be independent of age (e.g., Solbrig 1981). Mortality rates of most species are, however, higher for juveniles (Meagher & Antonovics 1982b, Inge & Tamm 1985, Matlack 1987) and smaller plants (Pitelka et al. 1985b, Scheiner 1988, Bloom et al. 2001). In dioecious species, mortality may (Meagher & Antonovics 1982a) or may not (Bawa et al. 1982) be higher for females.

One would expect diseased plants to have higher mortality. Ramets of *Actaea spicata* had higher mortality when infected with the smut *Urocystis carcinodes*, and voles consumed infected plants at a higher rate (Wennström & Ericson 1994). Larger infected plants, however, produced more fruits because large plants may have enough resources to allow the fungus to remain in a latent condition even though mortality would be higher if the smut became virulent.

MODES OF REPRODUCTION

As described in the phenology section, most woodland herbs are perennials, and the majority are clonal. Clonality has arisen separately in many groups of plants, and many of the 21 clonal growth forms identified in the European flora (Klimés et al. 1997) have also been described for North American (Table 1) and Japanese floras (Kawano 1975). However, a complete analysis of the distribution of clonal

TABLE 1 Asexual reproduction (+ or - in Column 2) for woodland herbs. Shown here are ferns and fern allies. For a more complete list, follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>

Species (Family)	Vegetative propagation	Structure	Growth (cm/yr)	Frequency of branching ^a	Physiological integration	Duration of connection ^b	Number of ramets produced ^b	Source
<i>Ainsliaea apiculata</i> (Asteraceae)	+	Rhizome	NA ^c	NA	NA	NA	NA	Hori & Yokoi 1999
<i>Athyrium filix-femina</i> (Aspidiaceae)	+	Rhizome	<1.0	NA	NA	NA	NA	Sobey & Barkhouse 1977
<i>Dryopteris phegopteris</i> (Aspidiaceae)	+	Rhizome	1.5-3.0	Irregular	NA	NA	NA	Sobey & Barkhouse 1977
<i>D. spinulosa</i>	+	Rhizome	<1-4	NA	NA	NA	NA	Sobey & Barkhouse 1977
<i>Lycopodium lucidulum</i> (Lycopodiaceae)	+	Rhizome	1-3	Irregular	NA	NA	NA	Sobey & Barkhouse 1977
<i>L. annotinum</i>	+	Rhizome	0.1-8	Frequent	Fully integrated	NA	1	Sobey & Barkhouse 1977, Jónsdóttir & Watson 1997
<i>L. clavatum</i>	+	Rhizome	8-74	Frequent	NA	NA	1-4	Sobey & Barkhouse 1977
<i>L. obscurum</i>	+	Rhizome	13-20	Frequent	NA	NA	1	Sobey & Barkhouse 1977

(Continued)

TABLE 1 (Continued)

Species (Family)	Vegetative propagation	Structure	Growth (cm/yr)	Frequency of branching ^a	Physiological integration	Duration of connection ^b	Number of ramets produced ^b	Source
<i>L. flabelliforme</i>	+	Rhizome	17-31	Frequent	Highly integrated-intermediate	NA	1	Sobey & Barkhouse 1977, Lau & Young 1988, Jónsdóttir & Watson 1997
<i>L. tristriachyum</i>	+	Rhizome	ca. 15	NA	NA	NA	NA	Sobey & Barkhouse 1977
<i>Osmunda claytoniana</i> (Osmundaceae)	+	Rhizome	<0.5	Very infrequent	NA	NA	1-75	Sobey & Barkhouse 1977
<i>Polystichum acrostichoides</i> (Aspidiaceae)	+	Rhizome	<1.0	Infrequent	NA	NA	NA	Sobey & Barkhouse 1977
<i>Pteridium aquilinum</i> (Pteridiaceae)	+	Rhizome	15-30	Frequent	Fully integrated	NA	1	Sobey & Barkhouse 1977, Jónsdóttir & Watson 1997

^aSobey & Barkhouse 1977.

^bper year or as otherwise provided.

^cNA = Information not provided in reference.

growth forms among herbs in temperate forests of North America, Japan, and other parts of Asia has not yet been done.

Further studies support Bierzychudek's finding that although many woodland herbs reproduce clonally, sexual reproduction is important. Kudoh et al. (1999), for example, found that some patches of *Uvularia perfoliata* contained only one genotype, indicating establishment from a single seed. A patch in a gap habitat, in contrast, had a very high level of genetic diversity, indicating establishment of individuals from many seeds.

In 1982, most woodland herbs were considered hermaphroditic (table 3 in Bierzychudek 1982a). About half were self-compatible and the other half partially or completely self-incompatible. Studies cited in Table 2 indicate that there is an almost equal distribution between the three categories, suggesting that some level of self-incompatibility may be more common than previously thought.

CLONALITY

Many woodland herbs are clonal and have a wide range of growth patterns (Klimés et al. 1997). I now consider aspects of clonality that influence current and future growth and reproduction.

Physiological Integration

Jónsdóttir & Watson (1997) divided clonal species into four categories on the basis of clone size and the degree of physiological integration. Using the same categories to characterize woodland herbs, Table 3 shows that physiological integration has been studied in few woodland herbs and most species examined form large and highly integrated clones (Pitelka & Ashmun 1985). Patterns of physiological integration range from species such as *Aster acuminatus*, which form large patches with short-lived connections and little physiological integration, to species such as *Clintonia borealis*, which form large patches with long-lived connections that are highly integrated (Ashmun et al. 1982). *Clintonia borealis* may be typical of many species of spring flowering herbs, as similar patterns have been shown for *Podophyllum peltatum* (Landa et al. 1992) and *Aralia nudicaulis* (Flanagan & Moser 1985b). Patterns of resource sharing are complex in herbaceous species that have a high degree of physiological integration (e.g., Hutchings & Mogie 1990, Price & Hutchings 1992). Tables 1 and 3 demonstrate, however, that too few woodland herbs have been examined in detail to draw broad generalities regarding physiological integration in woodland herbs.

Foraging for Resources

Foraging has been demonstrated in clonal herbs (Hutchings & de Kroon 1994), but few species have been studied (e.g., de Kroon & Hutchings 1995, Cain et al. 1996, Wijesinghe & Whigham 2001). Wijesinghe & Hutchings (1997) suggested

TABLE 2 Flowering characteristics of woodland herbs

Species	Flowering period	Compatibility	Breeding system	Pollinator limited seed set	Insect visitors	Source
<i>Aralia nudicaulis</i> (Araliaceae)	June	Self-incompatible	Dioecious	Yes/No	Bumblebees, solitary bees, syrphids	Barrett & Helenurm 1987, Flanagan & Moser 1985a
<i>Anemone nemorosa</i> (Ranunculaceae)	NA ^a	Mainly self-compatible	Hermaphrodite	NA	NA	Müller et al. 2000
<i>Carex pedunculata</i> (Cyperaceae)	April	Self-compatible	Monococious	NA	NA	Handel 1976
<i>Caulophyllum thalictroides</i> (Berberidaceae)	Late April–mid-May	Self-compatible	Hermaphrodite	Yes	Diptera, hemiptera, hymenoptera	Hannan & Prucher 1996
<i>Chamaelirium luteum</i> (Liliaceae)	Mid-May	NA	Dioecious	NA	NA	Meagher & Antonovics 1982a,b
<i>Chimaphila umbellata</i> (Pyrolaceae)	Late July	Partially self-incompatible	Hermaphrodite	Yes	Syrphids	Barrett & Helenurm 1987
<i>Claytonia virginica</i> (Portulacaceae)	Late March–early May	Self-compatible, Self-incompatible ^b	Hermaphrodite	Yes	24 sp. Andrenid was primary pollinator	Schemske 1977

<i>Clintonia borealis</i> (Liliaceae)	Early June	Partially self-incompatible	Hermaphrodite	Yes	Bumblebees, solitary bees	Barrett & Helenurm 1987, Galen et al. 1985
<i>Cornus canadensis</i> (Cornaceae)	Mid-June	Self-incompatible	Hermaphrodite	Yes	Bumblebees, solitary bees, bee flies, syrphids	Barrett & Helenurm 1987
<i>Corydalis ambigua</i> (Papaveraceae)	Late April-early May	Self-incompatible	Hermaphrodite	Yes	Honeybees, bumblebees	Ohara & Higashi 1994
<i>Cypripedium acule</i> (Orchidaceae)	Mid-June	Self-incompatible	Hermaphrodite	Yes	Bumblebees	Barrett & Helenurm 1987, Davis 1986
<i>Erythronium albidum</i> (Liliaceae)	Late April	Self-compatible	Hermaphrodite	NA	Bees	Harder et al. 1993
<i>E. americanum</i>	Late April	Self-incompatible	Hermaphrodite	NA	Bees	Harder et al. 1993
<i>Geranium maculatum</i> (Geraniaceae)	May	Partially self-incompatible	Hermaphrodite	No	Halictid bees, flies, bumblebees, beetles, ants	McCall & Primack 1987
<i>Hepatica americana</i> (Ranunculaceae)	March-April	Self-compatible	Hermaphrodite	No	Mostly solitary bees, bee flies, halictid bees	Monten 1982
<i>Jeffersonia diphylla</i> (Berberidaceae)	April	Self-compatible (facultative autogamy)	Hermaphrodite	No	Halictids, honeybees	Smith et al. 1986
<i>Linnaea borealis</i> (Caprifoliaceae)	Early July	Partially self-incompatible	Hermaphrodite	No	Solitary bees, syrphids	Barrett & Helenurm 1987

(Continued)

TABLE 2 (Continued)

Species	Flowering period	Compatibility	Breeding system	Pollinator limited seed set	Insect visitors	Source
<i>Maianthemum canadense</i> (Liliaceae)	Early June	Self-incompatible	Hermaphrodite	No	Solitary bees, bee flies, syrphids	Barrett & Helenurm 1987, McCall & Primack 1987
<i>Medeola virginiana</i> (Liliaceae)	Late June	Self-incompatible	Hermaphrodite	Yes	Flies?	Barrett & Helenurm 1987, McCall & Primack 1987
<i>Oxalis montana</i> (Oxalidaceae)	Early July	Partially self-incompatible	Hermaphrodite (Chasmogamous, cleistogamous)	Yes	Solitary bees, syrphids, flies, thrips, beetles	Barrett & Helenurm 1987, Jasiniuk & Lechowicz 1987
<i>Orchis</i> (= <i>Galearis</i>) <i>spectabilis</i> (Orchidaceae)	Late April-early June	Partially self-incompatible	Hermaphrodite Polygamodioecious	Yes	Bumblebees	Dieringer 1982
<i>Panax quinquefolium</i> (Araliaceae)	June-August	NA	Hermaphrodite	Yes?	NA	Lewis & Zenger 1982
<i>Podophyllum peltatum</i> (Berberidaceae)	May	Partially self-incompatibility	Polygamodioecious	Yes	Bumblebees	Policansky 1983, Lavery & Plowright 1988
<i>Primula veris</i> (Primulaceae)	May	Self-incompatible	Hermaphrodite (distylous)	NA	NA	Leimu et al. 2002
<i>P. vulgaris</i>	May	Self-incompatible	Hermaphrodite (distylous)	Yes	Bee-flies, bumble bees, butterflies	Boyd et al. 1990

<i>Pyrola secunda</i> (Pyrolaceae)	Mid-July	Self-compatible	Hermaphrodite	Yes	Bumblebees, solitary bees	Barrett & Helenurm 1987
<i>Trientalis borealis</i> (Primulaceae)	Early June	Self-incompatible	Hermaphrodite	Yes	Syrphids	Barrett & Helenurm 1987
<i>Trillium kamischaticum</i> (Liliaceae)	May	Partially self-compatible	Hermaphrodite	No	Bumblebees, butterflies, flies	Ohara et al. 1996
<i>T. undulatum</i>	Late May	Highly autogamous Obligat apomictic	Hermaphrodite	Unclear	Solitary bees	Barrett & Helenurm 1987
<i>T. erectum</i>	May	Self-compatible Highly apomictic	Hermaphrodite	Yes	Dipterans, Hymenopterans, Coleopterans	Davis 1981, Irwin 2000
<i>T. grandiflorum</i>	May	Self-incompatible and self-compatible	Hermaphrodite	Yes	Dipterans, Hymenopterans, Coleopterans	Kalisz et al. 1999, Irwin 2000
<i>T. niveale</i>	March	Self-compatible	Hermaphrodite	Yes	Honeybees, beetles,	Nesom & LaDuke 1985
<i>Uvularia sessilifolia</i> (Liliaceae)	May	Self-incompatible	Hermaphrodite	No	Halictid bees, bumblebees	McCall & Primack 1987
<i>Viola mirabilis</i> (Violaceae)	Early May—end of growing season	Self-compatible	Hermaphrodite (Chasmogamous, cleistogamous)	NA	Bumblebees	Mattila & Salonen 1995

^aInformation not provided in original source material.

^bBold indicates information also in Bierzychudek (1982a).

TABLE 3 Four categories of ramet systems based on the number of ramets and the degree of physiological integration (Jónsdóttir & Watson 1997). The number of species found in each category is shown in the second column and the number of the species examined that are found in woodland habitats is shown in the third column

Type of integration	Number of species examined	Number of woodland herb species
Restrictive integration in small ramet systems	4	1
Restrictive integration in large ramet systems	25	2
Full integration in small ramet systems	6	0
Full integration in large ramet systems	17	7

that species that have the potential for rapid clonal expansion respond to resource variability differently than species with a limited potential for horizontal expansion. Woodland species that typically produce preformed bulbs, corms, and short rhizomes, for example, may be more responsive to small-scale variations in habitat conditions than species with the potential to spread rapidly by clonal propagation. Wijesinghe & Whigham (2001) found little evidence for nutrient foraging in two clonal species of *Uvularia*, and Cain & Damman (1997) also found that nutrient foraging might not be important in woodland herbs.

Competition

There is evidence for (e.g., Handel 1978, Hughes 1992) and against (Pitelka 1984, Kudoh et al. 1999) intra- and interspecific competition in clonal woodland herbs. Givnish (1982) concluded that the degree of competition depends on habitat characteristics, such as the level of productivity, and that clonal species in productive habitats can minimize interspecific competition through allelopathic interactions or by maintaining a dense leaf cover close to the ground. Pitelka (1984) suggested that clonal species that are highly integrated physiologically regulate shoot densities to minimize intraspecific competition.

REPRODUCTIVE EFFORT

There have been several studies of patterns of biomass allocation in woodland herbs since Bierzychudek (1982a) concluded that the only generalization that could be made was that woodland herbs allocated less biomass to sexual reproduction than species in grasslands or early successional habitats. Biomass of most woodland herbs is allocated between sexual reproductive effort (SRE) and asexual propagation, referred to as vegetative reproductive effort (VRE). Both SRE and VRE have been measured in few species. The mean variation of VRE in *Aster acuminatus* was

large (28.2%–35.2%) compared with 5.0%–13.4% for SRE (Pitelka et al. 1980). VRE for *Solidago caesia* (8.3%–33.3%) and *Aster lateriflorus* (11.1%–56.3%) was also highly variable (Gross et al. 1983). Most recent SRE data fall within the range of values reported by Bierzychudek (1982a), but they show that SRE can be highly variable. A highly variable SRE, for example, has been found in the sex-switching genus *Arisaema* (Lovett Doust et al. 1986, Clay 1993). SREs of staminate, carpellate, and monoecious individuals were similar (ca. 15%), but large carpellate plants allocated 44% of the biomass to sexual reproduction, a value much higher than the SRE reported for the species by Bierzychudek (1982a). Factors acting independently or in combination that influence SRE are light (Gross et al. 1983, Jurik 1983, Pitelka et al. 1985a), pollination, and fruit success (Snow & Whigham 1989). Although several authors have demonstrated that fruit and seed production in woodland herbs is often limited (Flanagan & Moser 1985a, Davis 1986, Barrett & Helenurm 1987, Lubbers & Lechowicz 1989, Snow & Whigham 1989, Primack & Hall 1990, Robertson & Wyatt 1990, Bertin & Sholes 1993, Agren & Willson 1992, Primack et al. 1994, Rockwood & Lobstein 1994, Irwin 2000), few studies have examined the impacts of sexual reproduction on SRE or VRE. The most significant impacts of pollinator limitations on fruit and seed set appear to be on future growth and reproduction (Snow & Whigham 1989, Primack & Hall 1990, Gerber et al. 1997b, Matsumura & Washitani 2000).

SEED DISPERSAL AND GERMINATION

Bierzychudek (1982a) found that most forest herbs lack “special dispersal mechanisms,” that seeds of most species require a cold treatment, and that dormancy typically lasts less than 6 months (i.e., there is no seed bank). A review by Pickett & McDonnell (1989) supports her conclusion, but several woodland herbs, including weedy species, persist in the seed bank (Baskin & Baskin 1992, Baskin et al. 1993, Leckie et al. 2000).

There have been additional studies of seed germination of woodland herbs (e.g., Lewis & Zenger 1982; Smith 1983b; Matlack 1987; Syrjänen & Lehtilä 1993; Traveset & Willson 1997; Baskin & Baskin 1998, 2002; Kalisz et al. 1999; Bender et al. 2003). Germination characteristics of selected woodland herbs are summarized in Table 4 and a larger listing can be found in table 10.18 in Baskin & Baskin (1998). Seeds of some species are not dormant at maturation (Baskin & Baskin 1998), but most are dormant, and a common dormancy syndrome is morphophysiological (i.e., embryos are both morphologically and physiologically dormant). Embryos of some species mature during a period of warm temperature and germinate in the autumn (Baskin & Baskin 1983, Smith 1983b).

Most seed germination studies have used relatively large seeds. Some woodland herbs (e.g., ferns, parasitic plants, and orchids), however, have very small seeds or spores. “Dust” seeds of terrestrial orchids are dormant when they are dispersed, and germination is spatially and temporally variable (Rasmussen & Whigham

TABLE 4 Seed characteristics of woodland herbs

Species (Family)	Seed weight (mg)	Number seeds per fruit	Seed longevity	Germination	Source
<i>Actaea spicata</i> (Ranunculaceae)	5.9 ^a	NA ^d	NA	NA	Ehrlén & Eriksson 2000
<i>Allium ursinum</i> (Liliaceae)	5.4 ^a	NA	NA	Winter or spring after cold treatment	Ernst 1979
<i>Arisaema triphyllum</i> (Araceae)	NA	NA	NA	NA	Braun & Brooks 1987
<i>Asarum canadense</i> (Aristolochiaceae)	6.8–14.2 ^b	2–30 ^c	1 year?	Epicotyle dormancy (radicle growth in autumn, shoot growth following spring)	Baskin & Baskin 1986, Cain & Damman 1997, Heithaus 1981, Smith et al. 1989a
<i>Campanula americana</i> (Campanulaceae)	0.1 ^a	20–40	NA	Autumn or spring depending on phenology of mother plant	Galloway 2002
<i>C. latifolia</i>	0.1 ^a	NA	NA	NA	Ehrlén & Eriksson 2000
<i>Convallaria majalis</i> (Convallariaceae)	17.0 ^a	NA	NA	NA	Ehrlén & Eriksson 2000
<i>Floerkea proserpinacoides</i> (Limnanthaceae)	NA	1	Several years	No dormancy, controlled by environment	Smith 1983b
<i>Hepatica acutiloba</i> (Ranunculaceae)	2.4 ^a	9.9 ^a	NA	NA	Smith et al. 1989b

<i>Jeffersonia diphylla</i> (Berberidaceae)	3.4–36.8 ^b (Embryos undeveloped when seeds dispersed)	~20–40 ^c	NA	Spring following dispersal	Baskin & Baskin 1989; Smith et al. 1986, 1989a; Heithaus 1981
<i>Lathyrus vernus</i> (Fabaceae)	12.0 ^a	NA	NA	NA	Ehrlén & Eriksson 2000
<i>Paris quadrifolia</i> (Trilliaceae)	4.6 ^a	NA	NA	NA	Ehrlén & Eriksson 2000
<i>Panax quinquefolia</i> (Araliaceae)	NA	1.9 ^a	2 years?	18–22 months after dispersal	Lewis & Zenger 1982
<i>Podophyllum peltatum</i> (Berberidaceae)	NA	NA	NA	NA	Braun & Brooks 1987
<i>Polygonatum multiflorum</i> (Convallariaceae)	28.6 ^a	NA	NA	NA	Ehrlén & Eriksson 2000
<i>Sanguinaria canadensis</i> (Papaveraceae)	15.7 ^a	11.2–31.0 ^b	NA	NA	Pudlo et al. 1980, Heithaus 1981
<i>Hyacinthoides</i> (= <i>Scilla</i>) <i>nonscripta</i> (Liliaceae)	NA	NA	NA	June–July. Seeds require high temperature conditioning, germinate in autumn	Thompson & Cox 1978
<i>Silene dioica</i> (Caryophyllaceae)	0.7–1.2 ^b	NA	Several years	No dormancy (controlled by environment)	Matlack 1987
<i>Trientalis europaea</i> (Primulaceae)	41.1–64.7 ^c	0–14 ^c	Several years	Autumn or following spring	Hirsalmi 1969

(Continued)

TABLE 4 (Continued)

Species (Family)	Seed weight (mg)	Number seeds per fruit	Seed longevity	Germination	Source
<i>Trillium erectum</i> (Liliaceae)	4.1 ^a	9.6-21.6 ^b	NA	NA	Davis 1981, Gunther & Lanza 1989
<i>T. grandiflorum</i>	6.5 ^b	NA	NA	NA	Gunther & Lanza 1989
<i>T. kamtschaticum</i>	2.9 ^a	38-216 ^c	NA	NA	Ohara & Higashi 1987, Ohara & Kawano 1986
<i>T. nivale</i>	2.8 ^a	31.4 ^a	NA	NA	Smith et al. 1989a
<i>T. tschonoskii</i>	3.5 ^a	28-168 ^c	NA	NA	Ohara & Higashi 1987, Ohara & Kawano 1986
<i>T. undulatum</i>	5.7 ^a	NA	NA	NA	Gunther & Lanza 1989
<i>Uvularia perfoliata</i> (Liliaceae)	NA	NA	NA	Double dormancy (radicle in first year, epicotyl in second)	Webb & Willson 1985, Whigham 1974
<i>Viola mirabilis</i> (Violaceae)	2.48-2.56 ^b	17.0-19.9 ^b	NA	NA	Mattila & Salonen 1995
<i>V. sororia</i>	7.8-9.3 ^b	20-54 ^c	Unknown but >1 year	Require cold treatment, germinate in spring	Solbrig 1981

^aMean^bRange of means^cRange^dInformation not provided in original source material.

1993, 1998b; Whigham et al. 2002). Seeds of many woodland orchids will not germinate unless an appropriate mycorrhizal fungus is present (Rasmussen 1995, Whigham et al. 2002), but others germinate without fungi (Baskin & Baskin 1998) and the spatial variation in fungal distribution may determine where successful germination will occur (Rasmussen & Whigham 1998b).

To the list of seed dispersers (Table 5) can be added spiders (Gunther & Lanza 1989), yellow jackets (Zettler et al. 2001), turtles (Braun & Brooks 1987), rabbits (Knight 1964), and both brown and black bear (Traveset & Willson 1997). Long distance dispersal of seeds has also been documented (Willson 1993, Cain et al. 1998, Vellend et al. 2003), and hedgerows that connect forest patches provide intermediate scale corridors for dispersal (Corbit et al. 1999). Although a variety of vertebrates and invertebrates disperse woodland herb seeds (Handel et al. 1981, Vellend et al. 2003), ants are the most common dispersal agent (table 10.21 in Baskin & Baskin 1998). Interactions between ants and other animals can play a critical role in seed dispersal (Webb & Willson 1985; Smith et al. 1989a,b; Valverde & Silvertown 1995). Ground beetles, for example, eat elaiosomes on *Trillium* seeds, resulting in lower rates of ant seed dispersal (Ohara & Higashi 1987). Seed dispersal by ants is also influenced by seed density (Smith et al. 1986), and studies of *Trillium* species have shown that ant-seed interactions are very complex (Gunther & Lanza 1989, Higashi et al. 1989).

Seed dispersal distances vary widely, and data in Table 5 are probably minimum values because no wind-dispersed species (e.g., terrestrial orchids) are included. Mammals (Vellend et al. 2003) and birds can disperse seeds for long distances, but movements of seeds over long distances are difficult to assess. Rodents disperse seeds of woodland herbs (e.g., Valverde & Silvertown 1995), but they also destroy many seeds (Smith et al. 1989a,b).

Models have also been used to test generalities and evaluate the importance of seed dispersal and factors that influence it. Patterns of seed dispersal (Ehrlén & Eriksson 2000) and disturbance to the forest canopy influence woodland herb community diversity (Fröberg & Eriksson 1997, Valverde & Silvertown 1997b), and dispersal of seeds away from parent plants can be beneficial (Cipollini et al. 1993) or harmful (Valverde & Silvertown 1997a).

NUTRIENT STORAGE AND NUTRIENT CYCLING

Herbs account for a relatively small amount of the biomass and nutrient standing stocks in deciduous forests, but nutrient uptake and cycling by herbs can account for significant amounts of total ecosystem nutrient flux (Peterson & Rolfe 1982). The importance of herbs in nutrient cycling processes in forests is, however, undoubtedly related to their patterns of distribution in forests, as the distribution of most species is strongly influenced by nutrient availability and habitat heterogeneity (Crozier & Boerner 1984; Gilliam 1988; Lechowicz et al. 1988; Klinka et al. 1990; Vellend et al. 2000a,b; Miller et al. 2002; Beatty 2003; Small & McCarthy 2003).

TABLE 5 Seed dispersal and predation characteristics of woodland herbs^a

Species	Dispersal agent	Dispersal distance (m)	Predator	Percent predation	Source
<i>Allium ursinum</i> (Liliaceae)	Gravity and flowering stalks falling over	0.19–0.27	NA ^b	NA	Ernst (1979)
<i>Asarum canadense</i> (Aristolochiaceae)	Ants	Mean = 1.54, Max = 35	Rodent (<i>Peromyscus leucopus</i>)	Little to ~50	Heithaus 1981, Smith et al. 1989b, Cain & Damman 1997, Cain et al. 1998
<i>Arabis laevigata</i> var. <i>laevigata</i> (Brassicaceae)	Gravity	<0.5	NA	NA	Bloom et al. 2002a
<i>Arisaema triphyllum</i> (Araceae)	Turtle (<i>Terrapene carolina</i>)	NA	NA	NA	Braun & Brooks 1987
<i>Carex communis</i> (Cyperaceae)	Ants, mature culms bend toward ground	0.25	NA	NA	Handel 1978
<i>C. platyphylla</i>	May, flower stalks bend when mature	0.01–0.29	NA	NA	Handel 1978
<i>C. umbellata</i>	Ants	0.02–0.16	NA	NA	Handel 1978
<i>Claytonia virginica</i> (Portulacaceae)	Ants, mature inflorescence reflexes toward ground	NA	NA	NA	Handel 1978
<i>Endymion onscriptus</i> (Liliaceae)	Passive expulsion of seeds, rabbits	Mean = 0.40, Max = 0.81	N	NA	Knight 1964
<i>Floerkea proserpinacoides</i> (Limnanthaceae)	Gravity	Up to 0.05	None	NA	Stamp & Lucas 1983
<i>Geranium maculatum</i> (Geraniaceae)	Explosive (e.g., ballistic)	Mean = 3.02, Max = 4.55	NA	NA	Stamp & Lucas 1983
<i>Hepatica acutiloba</i> (Ranunculaceae)	Ants	NA	Rodents	Seed predation is rare	Smith et al. 1989a
<i>Impatiens capensis</i> (Balsaminaceae)	Explosive (e.g., ballistic)	Mean = 0.24, Max = 3.5	NA	NA	Stamp & Lucas 1983, Primack & Miao 1992

Species	Ants	NA	Rodents	37-54 of capsules prior to dehiscence	Heithaus 1981, Smith et al. 1986, 1989b
<i>Jeffersonia diphylla</i> (Berberidaceae)	Ants	NA			
<i>Lucula campestris</i> (Juncaceae)	Ants	1	NA	NA	Handel 1978
<i>Panax quinquefolium</i> (Araliaceae)	Gravity	<0.1	Rodents?	NA	Lewis & Zenger 1982
<i>Oxalis acetosella</i> (Oxalidaceae)	Explosive (e.g., ballistic)	Range: 0.6-4.5	NA	NA	Berg 2000
<i>Phytolacca americana</i> (Phytolaccaceae)	Birds	>33	NA	NA	Hoppes 1988
<i>Podophyllum peltatum</i> (Berberidaceae)	Turtle (<i>Terrapene carolina</i>)	NA	NA	NA	Braun & Brooks 1987
<i>Primula vulgaris</i> (Primulaceae)	Ants (<i>Myrmica rubra</i>) ca. 20%, rodents ca. 75%	Ants = 0.037-0.099, rodents = unknown	NA	NA	Cahalan & Gliddon 1985; Valverde & Silvertown 1995, 1997a,b
<i>Sanguinaria canadensis</i> (Papaveraceae)	Ants (<i>Aphaenogaster ruidis</i> , <i>Formica subsericea</i> , <i>Lasius alienus</i> , <i>Myrmica punctiventris</i> , <i>Stenamma</i> sp.)	0 in disturbed habitats, 17 in undisturbed areas. Mean = 1.38	Rodents	Predispersal consumption of seeds to >65 of post-dehiscence seeds	Padlo et al. 1980, Heithaus 1981
<i>Silene dioica</i> (Caryophyllaceae)	Gravity	<0.7	NA	NA	Matlack 1987
<i>Siretopus amplexifolius</i> (Liliaceae)	American robin (<i>Turdus migratorius</i>); varied through (<i>Ixoreus naevius</i>); brown bear (<i>Ursus arctos</i>); black bear (<i>Ursus americanus</i>)	NA	NA	NA	Traveset & Willson 1997
<i>Trillium cuneatum</i> , <i>T. erectum</i> , <i>T. grandiflorum</i> , <i>T. undulatum</i> (Liliaceae)	Ants (<i>Myrmica punctiventris</i>) and harvestmen (<i>Arachnida</i>), white-tailed deer, yellow jackets (<i>Vespula</i> sp.)	<1 to >3000	Slugs and harvestmen eat seeds	NA	Gunther & Lanza 1989, Kalisz et al. 1999, Zeitler et al. 2001, Vellend et al. 2003
<i>T. kamischaticum</i>	Ants (<i>Aphaenogaster mythiesi japonica</i> , <i>Myrmica rugimodis</i>)	0.30-3.30	Elaeosomes eaten by ground beetles	85	Ohara & Higashi 1987, Higashi et al. 1989

(Continued)

TABLE 5 (Continued)

Species	Dispersal agent	Dispersal distance (m)	Predator	Percent predation	Source
<i>T. niveale</i>	Ants	NA	Rodents	Seed predation is rare	Smith et al. 1989a
<i>T. tschonoskii</i>	Ants (<i>Aphaenogaster smythiesi japonica</i> , <i>Myrmica ruginodis</i> , <i>Lasius niger</i>)	0.01–2.7	Elaeosome eaten by ground beetles	85	Ohara & Higashi 1987
<i>Uvularia grandiflora</i> (Liliaceae)	Ants (<i>Myrmica americana</i> , <i>M. aphaenogaster</i> , <i>Camponotus pennsylvanicus</i> , <i>Formica phenolepis</i>)	<0.1 to >2	<i>Peromyscus leucopus</i> , <i>Tamias striatus</i>	NA	Webb & Wilson 1985, Kalisz et al. 1999
<i>U. perfoliata</i>	Ants	≤2	NA	NA	D.F. Whigham, personal observation
<i>Viola</i> sp., <i>Viola mirabilis</i> (Violaceae)	Ants	Mean = 0.01–2.1, Max. 0.02–5.4	NA	NA	Beattie & Lyons 1975, Mattila & Salonen 1995
<i>V. pedata</i>	Ants, ballistic	0.25–5.1 Mean = 0.35	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978
<i>V. pensylvanica</i>	Ants, ballistic	0.72–1.2	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978
<i>V. rostrata</i>	Ants, ballistic	0.1–4.2	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978
<i>V. striata</i>	Ants, ballistic	0.2–3.3	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978, Stamp & Lucas 1983

^aDispersal distances are given as ranges or, where indicated, as mean or maximum distances.

^bInformation not provided in source material.

Nutrient cycling is also related to patterns of resource allocation. The majority of woodland herbs are perennial, and most biomass and nutrients are stored in roots, rhizomes, bulbs, and corms (Kawano 1975, Muller 1979, Gross et al. 1983, Piper 1989, Kawano et al. 1992). The seasonal pattern of biomass and nutrient allocation in *Allium tricoccum* seems to be typical of many perennial woodland herbs (e.g., Whigham 1974, Nault & Gagnon 1988). Early in the growing season, carbon and nutrients stored belowground are allocated to aboveground biomass, peaking in leaves and reproductive structures in the spring or early summer. As the growing season progresses, nutrients are resorbed and accumulate in belowground structures, declining in aboveground structures as leaves senesce and fruits and seeds develop. In clonal species, belowground biomass and nutrients are allocated to new ramets, as well as to older structures (Pitelka et al. 1980, Boerner 1986, Benner & Watson 1989, Wijesinghe & Whigham 1997).

Nutrient resorption has been investigated in a few species. DeMars & Boerner (1997) found significant differences in phosphorus and nitrogen resorption and suggested that differences among species were due to phenological characteristics, topographic differences, and nutrient and moisture availability. In *Polystichum acrostichoides*, an evergreen fern, there were no seasonal differences in nutrient resorption, indicating that leaves were maintained during the cold period to allow the species to fix carbon whenever climatic conditions were suitable (Minoletti & Boerner 1993).

Patterns of nutrient uptake and resorption by woodland herbs led to the "vernal dam hypothesis" (Muller 1979, Muller 2003) that described the ability of woodland herbs to immobilize nutrients in biomass that would otherwise be lost from the ecosystem. Others (e.g., Peterson & Rolfe 1982) examined this hypothesis and concluded that plants have the potential to immobilize nitrogen but have little impact on other nutrients. Zak et al. (1990) evaluated the hypothesis in the context of competition for nutrients between the spring geophyte *Allium tricoccum* and microbes. They concluded that microbes immobilized more nitrogen than the spring geophyte, but that microbes and *A. tricoccum* together retained significant amounts of nutrients.

MYCORRHIZAE

Every woodland herb that has been examined has been shown to develop mycorrhizal associations, and the primary benefit to the herb partner is increased nutrient uptake (e.g., Widden 1996, Whitbread et al. 1996, Lapointe & Molard 1997). There appear to be differences in levels of mycorrhizal activity among species, with slow growing species having lower levels of mycorrhizal infection (Brundrett & Kendrick 1990a,b). Differences in mycorrhizal activity also occur across moisture, nutrient, and successional gradients; woodland herbs in wet and nutrient-rich habitats have lower levels of mycorrhizal activity (DeMars & Boerner 1995) and species in late successional habitats have higher levels of vesicular, arbuscular, and ectomycorrhizal activity (Boerner 1992, Boerner et al. 1996).

Terrestrial orchids are an interesting group because they develop mycorrhizal associations that apparently only benefit the orchid partner (Rasmussen 1995). Some woodland orchids are achlorophyllous (e.g., *Corallorhiza* sp.) and obtain all their carbon and other nutrients from mycorrhizae, thus requiring fungal interactions at all life history stages (Zelmer & Currah 1995). Mycorrhizae are also important for woodland orchids that produce leaves but are able to persist below-ground for one to many years without forming leaves (Mehrhoff 1989, Gill 1996, Shefferson et al. 2001).

A variety of techniques for studying seed germination and protocorm development in the field portend to expand our understanding of mycorrhizal interactions in terrestrial orchids (Rasmussen & Whigham 1993, 1998a,b, 2002). Much of our knowledge comes from laboratory studies (e.g., Rasmussen 1995), but more recent efforts have included field-based approaches. Seeds of some species, as previously noted, require mycorrhizae for germination, whereas interactions between seeds and mycorrhizal fungi appear to be facultative for other species (Baskin & Baskin 1998; Rasmussen 1995, 2002; Rasmussen & Whigham 1998b; Whigham et al. 2002). Protocorms, the life history stage that follows seed germination, obtain all their resources through mycorrhizal interactions (Rasmussen 1995, 2002). Some woodland orchids (e.g., species of *Corallorhiza*) associated with fungi that form ectomycorrhizal interactions and are indirectly parasitic on trees (Zelmer & Currah 1995).

POPULATION STRUCTURE AND STABILITY

Since 1982, there have been few age structure studies of woodland herbs, and most have employed stage-based models to simulate age-based characteristics (e.g., Bierzychudek 1982b; Meagher & Antonovics 1982a,b; Hara & Wakahara 1994; Bierzychudek 1999; Jolls 2003). Some species have been shown to have stable population structure (Meagher & Antonovics 1982a; Inghe & Tamm 1985; Kawano et al. 1986, 1992), but for most species, population structure is temporally variable (Inghe & Tamm 1985, Matlack 1987, Scheiner 1988, Whitman et al. 1998) due to variation in factors such as weather, disturbance, and levels of nutrient availability (Whigham et al. 1993, Fröberg & Eriksson 1997). Population size may also vary spatially, as has been shown for the rare orchid *Isotria medeoloides* (Mehrhoff 1989). Population trends may also be directional. Diekmann & Dupré (1997), for example, found long-term declines in populations due to regional acidification and eutrophication.

More recent publications suggest that flowering rates may be greater and more variable than the 1%–25% range reported in the 1982 review. Flowering may be size dependent, and once a minimum size is reached, individuals can flower yearly independent of the level of reproductive effort (Lewis & Zenger 1982, Mehrhoff 1989, Cain & Damman 1997). Other species switch back and forth between flowering and nonflowering depending on the level of reproductive effort

(Bierzychudek 1982b, Snow & Whigham 1989, Gerber et al. 1997a). Variability in flowering also appears to be influenced by factors such as genetics (Meagher & Antonovics 1982a), herbivory (Snow & Whigham 1989), weather (Inghe & Tamm 1985), disturbance (Whigham et al. 1993, Primack et al. 1994, Gill 1996), and the costs of producing flowers and fruits (Snow & Whigham 1989, Whigham & O'Neill 1991, Primack & Hall 1990, Falb & Leopold 1993, Gerber et al. 1997b).

GENETIC VARIABILITY

Relatively few studies have examined genetic variability of woodland herbs, and even fewer studies have been based on measurements of genetic identities of plants within or among populations. The most important conclusion thus far is that most populations of clonally reproducing species typically contain more than one genet (e.g., Smith et al. 2002). Patches of some species (e.g., *Clintonia borealis* and *Podophyllum peltatum*) contain few, perhaps one or two, genets (Policansky 1983, Pitelka et al. 1985b). Patches of other woodland herbs (e.g., *Asarum canadense*) contain numerous genotypes (Eriksson 1989, Cain & Damman 1997), and genetic substructuring has been demonstrated for clonal species (Cahalan & Glidden 1985, Kudoh et al. 1999, Ziegenhagen et al. 2003). Some woodland herbs have both high and low genetic diversity, depending on rates of outcrossing and seed set (Ohara et al. 1996).

Uvularia perfoliata (Kudoh et al. 1999) is probably representative of many clonal woodland herbs. An *Uvularia* patch in an area where tree gaps had previously occurred had a high level of genetic variability at small (centimeter) and large (meter) scales. Ramets of different genets intermingled, and there was no evidence of competition between genets. Kudoh et al. (1999) also found genetic substructuring of a few genets with many ramets, and of many genets with few ramets. They attributed this pattern to a few founder genets and subsequent establishment of new genets from seeds that were produced from within-patch outcrossing.

RESPONSES TO DISTURBANCE

Canopy Gaps

Disturbance plays an important role in the dynamics of forests (Pickett & White 1985, Webb 1999), and a close linkage exists between canopy disturbance and dynamics of understory vegetation (Gilliam & Roberts 2003). Collins et al. (1985) reviewed the literature on woodland herb responses to gaps and suggested that herbaceous species can be divided into three guilds (Table 6) and that various physiological, morphological, and ecological responses of species could be predicted for each guild. Woodland herbs clearly respond to changes in light conditions in canopy gaps, but microhabitat heterogeneity may be equally important (Bratton

TABLE 6 Predicted responses (first column) of woodland herbs in gap habitats (Collins et al. 1985). The predicted responses are positive (+), none (0), or negative (-)

Responses	Sun herbs	Light flexible herbs	Shade herbs
Water uptake	0	+	+
Nutrient uptake	+/0	+/0	0
Seedling establishment	+	+	0/-
Leaf duration	+/0	+/0	0/-
Assimilation	+/0	+	-
Pollination	+/0	+	+
Flowering	+/0	+	0/+
Seed set	+/0	+	0
Clonal growth	+/0	+	0/-
Architectural shift	0	+	0
Survivorship	0	+	-

1976). Pits and mounds associated with treefalls, for example, provide a high degree of microhabitat variability and may have a higher species diversity and greater herb cover than adjacent undisturbed areas (Peterson & Campbell 1993). Mounds and logs created during treefalls are sites for colonization by woodland orchids (Rasmussen & Whigham 1998a). Pits and mounds have also been shown to have characteristic species assemblages, depending to a large degree on the dominant tree species (Beatty 1984).

Although microhabitat conditions are important, changes in light quality and quantity associated with gaps generate the greatest responses in understory herbs because most species are light limited (Table 6). Most woodland herbs experience increased growth and reproduction in response to increased light (Collins & Pickett 1988, Neufeld & Young 2003). Positive responses to gaps are related to gap size, but positive responses can be partially offset by negative impacts associated with competition (Hughes 1992).

Individual species have shown a range of responses to increased light in gaps. Gap size has a positive influence on population size (Scheiner 1988), growth rates, and frequency of flowering (Dahlem & Boerner 1987, Whigham et al. 1993, Griffith 1996, Wijesinghe & Whigham 1997). Recently, models have been used to evaluate a range of species responses to gap habitats. Valverde & Silvertown (1997a, 1998) concluded that *Primula vulgaris* formed metapopulations in response to gaps and that local populations formed and became extinct in response to changing habitat conditions associated with light gaps. Cipollini et al. (1993) and Whigham et al. (1993) found similar results for *Cynoglossum virginianum*, a nonclonal woodland herb that persists in a vegetative state for long periods under closed canopy

conditions. When gaps form, individuals increase in size and flower until light levels decline, eventually returning to a vegetative state.

Herbivory

Woodland herbs (e.g., ferns) produce chemicals that deter herbivores, but herbivory appears to have a negative impact on most species (Brunet 1993). The impacts of herbivory on growth and reproduction of woodland herbs appears to be, in part, species dependent (Rockwood & Lobstein 1994), but other factors are also important. Plant size (Davis 1981, Rooney & Waller 2001), sex (Delph et al. 1993), and nutritional quality (Ericson & Oksanen 1987) are important. The plant parts attacked by herbivores (Ericson & Oksanen 1987), herbivore-feeding patterns (Ehrlén 1995, Matlack 1987), the phenological status of the plant (de Kroon et al. 1991, Watson 1995, Whigham & Chapa 1999), and the degree of physiological integration in clonal species (Ashmun et al. 1982, Price et al. 1992) are also important.

As might be expected, the greater the amount of tissue removed the greater the impacts on growth and reproduction, but other factors (e.g., the pattern of leaf removal) also influence plant responses to herbivory (Whigham 1990, Price & Hutchings 1992). Perhaps most importantly, most woodland herbs do not produce new aboveground tissues in response to herbivory, which suggests that the timing and amount of herbivory would influence short- and long-term plant responses. Complete or partial leaf removal can result in cessation of or decreased flowering (Whigham 1990, Syrjänen & Lehtilä 1993, Primack et al. 1994). Partial defoliation can, however, also have no effect on growth and reproduction (Agren & Willson 1992).

Most herbivory studies have only considered aboveground plant parts. Herbivores also consume belowground tissues (Ericson & Wennström 1997). Rodent herbivory of underground corms of *Tipularia discolor*, for example, had a greater impact on the long-term dynamics of populations than any other factor (Whigham & O'Neill 1991).

Deer browsing can result in the almost complete elimination of woodland herbs, except for a few unpalatable species (Tilghman 1989). In addition, species that can survive on microsites (e.g., refuges such as mounds, boulders, and logs) that are unavailable to deer can also avoid browsing (Rooney & Dress 1997a). If species can survive browsing, however, there is some evidence that they can recover following elimination of deer browsing (Albert & Barnes 1987).

Waller & Alverson (1997) agreed with McShea & Rappole (1992) in concluding that deer are keystone species with impacts well beyond reducing herb diversity in forests. Deer browsing reduces or eliminates tree regeneration (e.g., Nomiya et al. 2002), and browsing results in the loss of bird species that specialize in the forest understory (Casey & Hein 1983). Deer browsing can also reduce invertebrate diversity (Miller et al. 1992), and increased deer abundance has been linked to Lyme disease (Jones et al. 1998). The evidence seems clear that deer abundance

and management will continue to be a major threat to the diversity of woodland herbs in forests of eastern North America.

Urbanization and Forest Conversion

Researchers have examined the fate of woodland herbs in urban settings, concluding that we may not be able to conserve the original species diversity in urban forests (Robinson et al. 1994, Drayton & Primack 1996). Similarly, several studies (Peterken & Game 1984, Falinski et al. 1988, Brunet 1993, Hermy et al. 1993, Hermy 1994, Singleton et al. 2001, Bellemare et al. 2002, Vellend 2003, Verheyen et al. 2003) have shown that it will take long periods of time, perhaps centuries, for herb diversity to recover in forests that developed on lands that had previously been cleared and used for agricultural production. For example, forested areas in the Vosges Mountains that had been cleared and used to support crops, gardens, pastures, or tree plantations had similar species diversity of woodland herbs, but none of them were characteristic of ancient forests (Koerner et al. 1997).

Logging

Woodland herb diversity may be lower in logged forests, and it may never again reach levels found in old-growth forests (Meier et al. 1995). Comparison of different logging activities showed that woodland herbs were negatively impacted by clearcuts (Albert & Barnes 1987, Duffy & Meier 1992) and completely eliminated by clearcutting followed by herbicide application (Kochenderfer & Wendel 1983). Duffy & Meier (1992) concluded that it was unlikely that the herb community would recover in the clearcut stands within normal (40–150 years) cutting cycles. Selective logging had less of an impact on herb diversity in Canada (Reader 1987, 1988; Meier et al. 1995), and Reader & Bricker (1992) suggested that selective logging could be used as a management tool to conserve woodland herbs.

CONCLUSIONS AND RECOMMENDATIONS

Woodland herbs include species of diverse phylogenetic origin that have evolved a wide range of life history adaptations that allow them to persist and flourish in an environment that is often light limited. Light is clearly the most important factor limiting the growth and reproduction of woodland herbs, but some life history strategies (e.g., spring ephemerals, wintergreen species, parasites, etc.) have evolved that allow individuals to complete most of their growth and reproduction prior to full development of the tree canopy and resultant low light conditions.

Although much more has been learned about the ecology of woodland herbs since Bierzychudek's (1982a) review, only a small percentage of the species have been studied in detail, and, at best, we can still offer only broad generalizations about the ecology of woodland herbs. What types of studies will most likely benefit future efforts to understand the ecology of woodland herbs and also support

conservation and restoration efforts? Individual species will undoubtedly continue to attract the attention of researchers, and those types of efforts should be encouraged. The most effective studies, however, are likely to be those that use a synthetic approach in which functional groups (e.g., Givnish 1982, Kawano 1985) are identified and used as the basis for testing ideas that further our understanding of woodland herbs as well as support conservation and restoration efforts.

As indicated, only a few broad generalizations about the ecology of woodland herbs are, however, possible because only a limited number of species and have been studied in detail. First, it is clear that most species are adapted to take advantage of canopy disturbances, which result in higher light conditions for a few years or more and higher levels of other resources. Canopy gaps often have higher herb diversity because they have a greater range of microhabitats (e.g., pits and mounds, coarse wood in various stages of decomposition), but light is still the key to success of most species. Most woodland herbs have increased growth, sexual reproduction and asexual propagation in gaps, and seedling recruitment also appears to be more common in gap habitats. It is difficult, however, to evaluate species responses to gap disturbances without either long-term studies or experimental manipulations. Matrix models offer the opportunity to explore broader questions about the range of responses of woodland herbs to gap disturbances. To date, however, matrix models have been applied to few species, and a useful approach would be to use them to address questions related to functional groups. The incorporation of spatially explicit models into studies of woodland herb populations would also be useful because of the high degree of spatial heterogeneity found in forest habitats.

A second broad generalization is that all woodland herbs are mycorrhizal. What are the ecological consequences of mycorrhizal interactions beyond those that have been associated with nutrient uptake? We still know very little about the importance of mycorrhizal interactions in the establishment and growth of seedlings of woodland herbs, especially species that require mycorrhizal associations for germination and survival.

A third generalization is that herbivores and pathogens affects the short- and long-term dynamics of woodland herb populations. Herbivores and pathogens probably influence woodland herbs much more than have been identified to date. Additional studies are needed on the growth and reproductive responses of woodland herbs to pathogens and herbivores, especially the responses of belowground tissues.

Conservation issues have only begun to be addressed, and future research needs to focus on the maintenance and restoration of woodland herbs in landscapes influenced more directly by human activities (e.g., clearcutting and fragmentation of forests) or indirectly (e.g., deer browsing, invasion of alien species). Little research has been conducted on management approaches that might be used to reintroduce species into forests from which they have been eliminated.

Finally, more effort should be placed on long-term population studies of woodland herbs. Inevitably, long-term studies provide valuable information that can be used to design experiments, develop realistic parameters for modeling efforts, and

open new lines of investigation. Long-term studies reveal previously unknown facts about woodland herb ecology and the many important interactions that woodland herbs have with other organisms. Although difficult to fund and sustain, long-term studies have low start-up and maintenance costs and are ideal for demonstrating ecological phenomena in teaching environments. Small colleges and universities throughout the eastern United States own or have access to sites that would be ideal for conducting long-term studies of woodland herbs. Datasets that expand from year to year with relatively little effort can be very useful in teaching ecological principles. Hopefully, this review will encourage others to start both short- and long-term studies using this interesting group of plants as models to embellish scientific knowledge and educate the public and future scientists.

In closing, space limitations required me to restrict the number of references cited in the review. A larger list of relevant documents can be found at http://www.serc.si.edu/labs/plant_ecology/biblio.jsp, and additional references are in Gilliam & Roberts (2003).

ACKNOWLEDGMENTS

The review was written while the author was a Bullard Fellow at Harvard Forest. I extend thanks to the staff of the Harvard Forest, especially David Foster, Glen Mozkin, and Ruth Kern for reading early versions and for discussions related to it. I thank Matt Baker, Jerry Baskin, Candy Feller, Anne Innis, Ann Lubbers, Jay O'Neill, Ryan King, Melissa McCormick, Glen Mozkin, Dag-Inge Øien, Mark Vellend, and Dushyantha Wijesinghe for comments on various drafts. The Smithsonian's Environmental Sciences and Scholarly Studies programs have supported the author's research on woodland herbs. Smithsonian Fellowship and Visiting Scientist programs provided funding for post-docs and visitors who work on woodland herbs (Martin Cipollini, Hans de Kroon, Heidrun Huber, Hiroshi Kudoh, Melissa McCormick, Hanne Rasmussen, Allison Snow, Dushyantha Wijesinghe, Jess Zimmerman). The Smithsonian Work-Learn program supported many student interns over a 20-year period. The long-term influence of Shoichi Kawano is much appreciated, as are grants from the Smithsonian Institution and the Japanese government, which have provided resources for long-term interactions between our labs. Finally, special thanks to Jan for her support during the preparation of the manuscript.

**The Annual Review of Ecology, Evolution, and Systematics is online at
<http://ecolsys.annualreviews.org>**

LITERATURE CITED

- | | |
|--|--|
| <p>Agren J, Willson MF. 1992. Determinants of seed production in <i>Geranium maculatum</i>. <i>Oecologia</i> 92:177-82</p> <p>Albert DA, Barnes BV. 1987. Effects of</p> | <p>clearcutting on the vegetation and soil of a Sugar Maple-dominated ecosystem, Western Upper Michigan. <i>For. Ecol. Manag.</i> 18: 283-98</p> |
|--|--|

- Angevine MW, Handel SN. 1986. Invasion of forest floor space, clonal architecture, and population growth in the perennial herb *Clin-tonia borealis*. *J. Ecol.* 74:547-60
- Antos JA. 1988. Underground morphology and habitat relationships of three pairs of forest herbs. *Am. J. Bot.* 75:106-13
- Ashmun JW, Thomas RJ, Pitelka LF. 1982. Translocation of photoassimilates between sister ramets in two rhizomatous forest herbs. *Ann. Bot.* 49:403-15
- Barrett SCH, Helenurm K. 1987. The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Can. J. Bot.* 65: 2036-46
- Baskin CC, Baskin JM. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. New York: Academic
- Baskin CC, Baskin JM. 2002. Achene germination ecology of the federally threatened floodplain endemic *Boltonia decurrens* (Asteraceae). *Am. Midl. Nat.* 147:16-24
- Baskin CC, Baskin JM, Chester EW. 1993. Seed germination ecology of two mesic woodland winter annuals, *Nemophila aphylla* and *Phacelia ranunculaceae* (Hydrophyllaceae). *Bull. Torrey Bot. Club* 120:29-37
- Baskin JM, Baskin CC. 1983. Germination ecology of *Collinsia verna*, a winter annual of rich deciduous woodlands. *Bull. Torrey Bot. Club* 110:311-15
- Baskin JM, Baskin CC. 1986. Seed germination ecophysiology of the woodland herb *Asarum canadense*. *Am. Midl. Nat.* 116:132-39
- Baskin JM, Baskin CC. 1988. The ecological life cycle of *Cryptotaenia canadensis* (L.) DC. (Umbelliferae), a woodland herb with monocarpic ramets. *Am. Midl. Nat.* 119:165-73
- Baskin JM, Baskin CC. 1989. Seed germination ecophysiology of *Jeffersonia diphylla*, a perennial herb of mesic deciduous forests. *Am. J. Bot.* 76:1073-80
- Baskin JM, Baskin CC. 1992. Role of temperature and light in the germination ecology of buried seeds of weedy species of disturbed forests I. *Lobelia inflata*. *Can. J. Bot.* 70:589-92
- Bawa KS, Keegan CR, Voss RH. 1982. Sexual dimorphism in *Aralia nudicaulis* L. (Araliaceae). *Evolution* 36:371-78
- Beattie AJ, Lyons N. 1975. Seed dispersal in *Viola* (Violaceae): adaptations and strategies. *Am. J. Bot.* 62:714-22
- Beatty SW. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406-19
- Beatty SW. 2003. Habitat heterogeneity and maintenance of species in understory communities. In *The Herbaceous Layer in Forests of Eastern North America*, ed. FS Gilliam, MR Roberts, pp. 177-97. New York: Oxford Univ. Press
- Bell AD. 1974. Rhizome organization in relation to vegetative spread in *Medeola virginiana*. *J. Arnold Arb.* 55:458-68
- Bellemare J, Motzkin G, Foster DR. 2002. Legacies of the agricultural past in the forest present: an assessment of historical land-use effects on rich mesic forests. *J. Biogeogr.* 29:1401-20
- Bender MH, Baskin JM, Baskin CC. 2000. Ecological life history of *Polymnia canadensis*, a monocarpic species of the North American temperate deciduous forest. *Plant Ecol.* 147:117-36
- Bender MH, Baskin JM, Baskin CC. 2002. Phenology and common garden and reciprocal transplant studies of *Polymnia canadensis* (Asteraceae), a monocarpic species of the North American temperate deciduous forest. *Plant Ecol.* 161:15-39
- Bender MH, Baskin JM, Baskin CC. 2003. Seed germination ecology of *Polymnia canadensis* (Asteraceae), a monocarpic species of the North American Temperate Deciduous Forest. *Plant Ecol.* 168:221-53
- Benner BL, Watson MA. 1989. Developmental ecology of mayapple: seasonal patterns of resource distribution in sexual and vegetative rhizome systems. *Funct. Ecol.* 3:539-47
- Berg H. 2000. Differential seed dispersal in *Oxalis acetosella*, a cleistogamous perennial herb. *Acta Oecol.* 21:109-18

- Bertin RI, Sholes ODV. 1993. Weather, pollination and phenology of *Geranium maculatum*. *Am. Midl. Nat.* 129:52–66
- Bierzychudek P. 1982a. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytol.* 90:757–76
- Bierzychudek P. 1982b. The demography of Jack-in-the-pulpit, a forest perennial that changes sex. *Ecol. Monogr.* 52:335–51
- Bierzychudek P. 1999. Looking backwards: assessing the projections of a transition matrix model. *Ecol. Appl.* 9:1278–87
- Bloom TC, Baskin JM, Baskin CC. 2001. Ecological life history of the facultative woodland biennial *Arabis laevigata* variety *laevigata* (Brassicaceae): survivorship. *J. Torrey Bot. Soc.* 128:93–108
- Bloom TC, Baskin JM, Baskin CC. 2002. Ecological life history of the facultative woodland biennial *Arabis laevigata* variety *laevigata* (Brassicaceae): seed dispersal. *J. Torrey Bot. Soc.* 129:21–28
- Boerner REJ. 1986. Seasonal nutrient dynamics, nutrient resorption, and mycorrhizal infection intensity of two perennial forest herbs. *Am. J. Bot.* 73:1249–57
- Boerner REJ. 1992. Plant life span and response to inoculation with vesicular-arbuscular mycorrhizal fungi. III. Responsiveness and residual soil P levels. *Mycorrhiza* 1:169–74
- Boerner REJ, DeMars BG, Leicht PN. 1996. Spatial patterns of mycorrhizal infectiveness of soils along a successional chronosequence. *Mycorrhiza* 6:79–90
- Boyd M, Silvertown J, Tucker C. 1990. Population ecology of heterostyle and homostyle *Primula vulgaris*: growth, survival and reproduction in field populations. *J. Ecol.* 78:799–813
- Bratton SP. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. *Am. Nat.* 110:679–93
- Braun J, Brooks GR Jr. 1987. Box turtles (*Terrapene carolina*) as potential agents for seed dispersal. *Am. Midl. Nat.* 117:312–18
- Brundrett M, Kendrick B. 1990a. The roots and mycorrhizas of herbaceous woodland plants I. Quantitative aspects of morphology. *New Phytol.* 114:457–67
- Brundrett M, Kendrick B. 1990b. The roots and mycorrhizas of herbaceous woodland plants II. Structural aspects of morphology. *New Phytol.* 114:469–79
- Brunet J. 1993. Environmental and historical factors limiting the distribution of rare forest grasses in south Sweden. *For. Ecol. Manag.* 61:263–75
- Cahalan CM, Gliddon C. 1985. Genetic neighbourhood sizes in *Primula vulgaris*. *Heredity* 54:65–70
- Cain ML, Damman H. 1997. Clonal growth and ramet performance in the woodland herb, *Asarum canadense*. *J. Ecol.* 85:883–97
- Cain ML, Damman H, Muir A. 1998. Seed dispersal and the Holocene migration of woodland herbs. *Ecol. Monogr.* 68:325–47
- Cain ML, Dudle DA, Evans JP. 1996. Spatial models of foraging in clonal plant species. *Am. J. Bot.* 83:76–85
- Casey D, Hein D. 1983. Effects of heavy browsing on a bird community in a deciduous forest. *J. Wildl. Manag.* 47:829–36
- Cipollini ML, Whigham DF, O'Neill J. 1993. Population growth, structure, and seed dispersal in the understory herb *Cynoglossum virginianum*: a population and patch dynamic model. *Plant Species Biol.* 8:117–29
- Clay K. 1993. Size-dependent gender change in green dragon (*Arisaema dracontium*: Araceae). *Am. J. Bot.* 80:769–77
- Collins BS, Dunne KP, Pickett STA. 1985. Responses of forest herbs to canopy gaps. See Pickett & White 1985, pp. 218–34
- Collins BS, Pickett STA. 1988. Response of herb layer cover to experimental canopy gaps. *Am. Midl. Nat.* 119:282–90
- Cook RE. 1983. Clonal plant populations. *Am. Sci.* 71:244–53
- Cook RE. 1988. Growth in *Medeola virginiana* clones. I. Field observations. *Am. J. Bot.* 75:725–31
- Corbit M, Marks PL, Gardescu S. 1999. Hedgerows as habitat corridors for forest herbs in central New York, USA. *J. Ecol.* 87:220–32

- Crozier CR, Boerner REJ. 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. *Oecologia* 62:337-43
- Culver DC, Beattie AJ. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *J. Ecol.* 66:53-72
- Dahlem TS, Boerner REJ. 1987. Effects of canopy light gap and early emergence on the growth and reproduction of *Geranium maculatum*. *Can. J. Bot.* 65:242-45
- Davis M. 1981. The effect of pollinators, predators, and energy constraints on the floral ecology and evolution of *Trillium erectum*. *Oecologia* 48:400-6
- Davis RW. 1986. The pollination biology of *Cypripedium acaule* (Orchidaceae). *Rhodora* 88:445-50
- de Kroon H, Hutchings MJ. 1995. Morphological plasticity in clonal plants: the foraging concept reconsidered. *J. Ecol.* 83:143-52
- de Kroon H, Whigham DF, Watson MA. 1991. Developmental ecology of mayapple: effects of rhizome severing, fertilization and timing of shoot senescence. *Funct. Ecol.* 5:360-68
- Delph LF, Lu Y, Jayne LD. 1993. Patterns of resource allocation in a dioecious *Carex* (Cyperaceae). *Am. J. Bot.* 80:607-15
- DeMars BG, Boerner REJ. 1995. Mycorrhizal dynamics of three woodland herbs of contrasting phenology along topographic gradients. *Am. J. Bot.* 82:1426-31
- DeMars BG, Boerner REJ. 1997. Foliar phosphorus and nitrogen resorption in three woodland herbs of contrasting phenology. *Castanea* 62:43-54
- Diekmann M, Dupré C. 1997. Acidification and eutrophication of deciduous forests in north-western Germany demonstrated by indicator species analysis. *J. Veg. Sci.* 8:885-64
- Dieringer G. 1982. The pollination ecology of *Orchis spectabilis* L. (Orchidaceae). *Ohio J. Sci.* 82:218-24
- Drayton B, Primack RB. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894-1993. *Conserv. Biol.* 10:30-39
- Duffy DC, Meier AJ. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conserv. Biol.* 6:196-201
- Ehrlén J. 1995. Demography of the perennial herb *Lathyrus vernus*. I. Herbivory and individual performance. *J. Ecol.* 83:287-95
- Ehrlén J, Eriksson O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81:1667-74
- Ericson L, Oksanen L. 1987. The impact of controlled grazing by *Clethrionomys rufocanus* on experimental guilds of boreal forest floor herbs. *OIKOS* 50:403-16
- Ericson L, Wennström A. 1997. The effect of herbivory on the interaction between the clonal plant *Trientalis europaea* and its smut fungus *Urocystis trientalis*. *OIKOS* 80:107-11
- Eriksson O. 1989. Seedling dynamics and life histories in clonal plants. *OIKOS* 55:231-38
- Eriksson O. 1992. Population structure and dynamics of the clonal dwarf-shrub *Linnaea borealis*. *J. Veg. Sci.* 3:61-68
- Ernst WHO. 1979. Population biology of *Allium ursinum* in northern Germany. *J. Ecol.* 67:347-62
- Falb DL, Leopold DI. 1993. Population dynamics of *Cypripedium candidum* Muhl. ex Willd., Small White Ladystipper, in a western New York fen. *Nat. Areas J.* 13:76-86
- Falinski JB, Canullo R, Bialy K. 1988. Changes in herb layer, litter fall and soil properties under primary and secondary tree stands in a deciduous forest ecosystem. *Phytocoenosis* 1:1-49
- Flanagan LB, Moser W. 1985a. Flowering phenology, floral display and reproductive success in dioecious, *Aralia nudicaulis* L. (Araliaceae). *Oecologia* 68:23-28
- Flanagan LB, Moser W. 1985b. Pattern of ¹⁴C assimilate distribution in a clonal herb, *Aralia nudicaulis*. *Can. J. Bot.* 63:2111-14
- Fröberg H, Eriksson O. 1997. Local colonization and extinction of field layer plants in a deciduous forest and their dependence upon life history features. *J. Veg. Sci.* 8:395-400

- Galen C, Plowright RC, Thomson JD. 1985. Floral biology and regulation of seed set and seed size in the lily, *Clintonia borealis*. *Am. J. Bot.* 72:1544–52
- Galloway LF. 2002. The effect of maternal phenology on offspring characters in the herbaceous plant *Campanula americana*. *J. Ecol.* 90:851–58
- Gerber MA, de Kroon H, Watson MA. 1997a. Organ preformation in mayapple as a mechanism for historical effects on demography. *J. Ecol.* 85:211–23
- Gerber MA, Watson MA, de Kroon H. 1997b. Organ preformation, development, and resource allocation in perennials. In *Plant Resource Allocation*, ed. FA Bazzaz, J Grace, pp. 113–41. New York: Academic
- Gill DE. 1996. The natural population ecology of temperate terrestrials: Pink Lady's-Slippers, *Cypripedium acaule*. In *North American Native Terrestrial Orchids, Propagation and Production*, ed. C Allen, pp. 91–106. Germantown, MD: N. Am. Native Terr. Orchid Conf.
- Gilliam FS. 1988. Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor Coastal Plain forest. *Bull. Torrey Bot. Club* 115:265–71
- Gilliam FS, Roberts MR. 2003. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford Univ. Press
- Givnish TJ. 1982. On the adaptive significance of leaf height in forest herbs. *Am. Nat.* 120:353–81
- Givnish TJ. 1983. Biomechanical constraints on crown geometry in forest herbs. In *On the Economy of Plant Form and Function*, ed. TJ Givnish, pp. 525–83. New York: Cambridge Univ. Press
- Givnish TJ. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* 106:131–60
- Griffith C, Jr. 1996. Distribution of *Viola blanda* in relation to within-habitat variation in canopy openness, soil phosphorus, and magnesium. *Bull. Torrey Bot. Club* 123:281–85
- Gross KL, Berner T, Marschall E, Tomcko C. 1983. Patterns of resource allocation among five herbaceous perennials. *Bull. Torrey Bot. Club* 110:345–52
- Gunther RW, Lanza J. 1989. Variation in attractiveness of *Trillium* diaspores to a seed-dispersing ant. *Am. Midl. Nat.* 122:321–28
- Handel SN. 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae), a new North American myrmecochore. *Am. J. Bot.* 63:1071–79
- Handel SN. 1978. New ant-dispersed species in the genera *Carex*, *Luzula*, and *Claytonia*. *Can. J. Bot.* 56:2925–27
- Handel SN, Fisch SB, Schatz GE. 1981. Ants disperse a majority of herbs in a mesic forest community in New York state. *Bull. Torrey Bot. Club* 108:430–37
- Hannan GL, Prucher HA. 1996. Reproductive biology of *Caulophyllum thalictroides* (Berberidaceae), an early flowering perennial of eastern North America. *Am. Midl. Nat.* 136:267–77
- Hara T, Wakahara M. 1994. Variation in individual growth and the population structure of a woodland perennial herb, *Paris tetraphylla*. *J. Ecol.* 82:3–12
- Harder LD, Cruzan MB, Thomson JD. 1993. Unilateral incompatibility and the effects of interspecific pollination for *Erythronium americanum* and *Erythronium albidum* (Liliaceae). *Can. J. Bot.* 71:353–58
- Heithaus ER. 1981. Seed predation by rodents on three ant-dispersed plants. *Ecology* 62:136–45
- Hermly M. 1994. Effects of former land use on plant species diversity and pattern in European deciduous woodlands. In *Biodiversity, Temperate Ecosystems, and Global Change*, ed. TJB Boyle, CEB Boyle, pp. 123–44. Berlin: Springer-Verlag
- Hermly M, Honnay O, Firbank L, Grashof-Bokdam C-J, Lawesson J-E. 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol. Conserv.* 91:9–22
- Hermly M, van den Bremt P, Tack G. 1993.

- Effects of site history on woodland vegetation. In *European Forest Reserves*, ed. MEA Broekmeyer, W Vos, H Koop, pp. 219–31. Wageningen, Neth.: Pudoc Sci.
- Higashi S, Tsuyuzaki S, Ohara M, Ito F. 1989. Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). *OIKOS* 54:389–94
- Hiirsalmi H. 1969. *Trientalis europaea* L. A study of the reproductive biology, ecology, and variation in Finland. *Ann. Bot. Fenn.* 6:119–73
- Holland PG. 1974. The growth behavior, ecology, and geography of *Erythronium americanum* in northeast North America. *Can. J. Bot.* 52:1765–72
- Hoppes WG. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69:320–29
- Hori Y, Yokoi T. 1999. Population structure and dynamics of an evergreen shade herb, *Ainsliaea apiculata* (Asteraceae), with special reference to herbivore effects. *Ecol. Res.* 14:39–48
- Hughes JW. 1992. Effect of removal of co-occurring species on distribution and abundance of *Erythronium americanum* (Liliaceae), a spring ephemeral. *Am. J. Bot.* 79:1329–36
- Hutchings MJ, de Kroon H. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* 25:160–238
- Hutchings MJ, Mogie M. 1990. The spatial structure of clonal plants: control and consequences. In *Clonal Growth in Plants: Regulation and Function*, ed. J van Groenendael, H de Kroon, pp. 57–76. The Hague: SPB Academic
- Inghe O, Tamm CO. 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–1981. *OIKOS* 45:400–20
- Irwin RE. 2000. Morphological variation and female reproductive success in two sympatric *Trillium* species: evidence for phenotypic selection in *Trillium erectum* and *Trillium grandiflorum* (Liliaceae). *Am. J. Bot.* 87:205–14
- Jasieniuk M, Lechowicz MJ. 1987. Spatial and temporal variation in chasmogamy and cleistogamy in *Oxalis montana* (Oxalidaceae). *Am. J. Bot.* 74:1672–80
- Jolls CL. 2003. Populations and threats to rare plants of the herb layer: more challenges and opportunities for conservation biology. In *The Herbaceous Layer of Forests of Eastern North America*, ed. FS Gilliam, MR Roberts, pp. 105–59. New York: Oxford Univ. Press
- Jones CG, Ostfeld RS, Richard MP, Schauber EM, Wolff JO. 1998. Chain reactions linking acorn to gypsy moth outbreaks and Lyme disease risk. *Science* 279:1023–26
- Jurik TW. 1983. Reproductive effort and CO₂ dynamics of wild strawberry populations. *Ecology* 64:1329–42
- Jónsdóttir IS, Watson MA. 1997. Extensive physiological integration: an adaptive trait in resource-poor environments? In *The Ecology and Evolution of Clonal Plants*, ed. H de Kroon, J van Groenendael, pp. 109–36. Leiden, Neth.: Backhuys
- Kalisz S, Hanzawa FM, Tonsor SJ, Thiede DA, Voigt S. 1999. Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. *Ecology* 80:2620–34
- Kawano S. 1975. The productive and reproductive biology of flowering plants. II. The concept of life history strategy in plants. *J. Coll. Lib. Arts Toyama Univ.* 8:51–86
- Kawano S. 1985. Life history characteristics of temperate woodland plants in Japan. In *The Population Structure of Vegetation*, ed. J White, pp. 515–49. Dordrecht: Dr. W. Junk
- Kawano S, Ohara M, Utech FH. 1986. Life history studies on the genus *Trillium* (Liliaceae) II. Reproductive biology and survivorship of four eastern North American species. *Plant Species Biol.* 1:47–58
- Kawano S, Ohara M, Utech FH. 1992. Life history studies on the genus *Trillium* (Liliaceae) VI. Life history characteristics of three western North American species and their evolutionary-ecological implications. *Plant Species Biol.* 7:21–36

- Klimés L, Klimesová J, Hendriks R, van Groenendael J. 1997. Clonal plant architecture: a comparative analysis of form and function. In *The Ecology and Evolution of Clonal Plants*, ed. H de Kroon, J van Groenendael, pp. 1–29. Leiden, Neth.: Backhuys
- Klinka K, Wang Q, Carter RE. 1990. Relationships among humus forms, forest floor nutrient properties, and understory vegetation. *For. Sci.* 36:564–81
- Knight GH. 1964. Some factors affecting the distribution of *Endymion Nonscriptus* (L.) Garcke in Warwickshire Woods. *J. Ecol.* 52:405–56
- Kochenderfer JN, Wendel GW. 1983. Plant succession and hydrologic recovery on a deforested and herbicided watershed. *For. Sci.* 29:545–58
- Koerner W, Dupouey JL, Dambrine E, Benoit M. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *J. Ecol.* 85:351–58
- Kudo H, Shibaie H, Takasu H, Whigham DF, Kawano S. 1999. Genet structure and determinants of clonal structure in a temperate deciduous woodland herb, *Uvularia perfoliata*. *J. Ecol.* 87:244–57
- Landa K, Benner B, Watson M, Gartner J. 1992. Physiological integration for carbon in mayapple (*Podophyllum peltatum*), a clonal perennial herb. *OIKOS* 63:348–56
- Lapointe L, Molard J. 1997. Cost and benefits of mycorrhizal infection in a spring ephemeral, *Erythronium americanum*. *New Phytol.* 135:491–500
- Lau RR, Young DR. 1988. Influence of physiological integration on survivorship and water relations in a clonal herb. *Ecology* 69:215–19
- Laverty TM, Plowright RC. 1988. Fruit and seed set in Mayapple (*Podophyllum peltatum*): influence of intraspecific factors and local enhancement near *Pedicularis canadensis*. *Can. J. Bot.* 66:173–78
- Lechowicz MJ, Schoen DJ, Bell G. 1988. Environmental correlates of habitat distribution and fitness components in *Impatiens capensis* and *Impatiens pallida*. *J. Ecol.* 76:1043–54
- Leckie S, Vellend M, Bell G, Waterway MJ, Lechowicz MJ. 2000. The seed bank in an old-growth, temperate deciduous forest. *Can. J. Bot.* 78:181–92
- Leimu R, Syrjänen K, Ehrlén J. 2002. Pre-dispersal seed predation in *Pirmula veris*: among-population variation in damage intensity and selection on flower number. *Oecologia* 133:510–16
- Lewis WJ, Zenger VE. 1982. Population dynamics of the American Ginseng *Panax quinquefolium* (Araliaceae). *Am. J. Bot.* 69:1483–90
- Lovett Doust L, Lovett Doust J, Turi K. 1986. Fecundity and size relationships in Jack-in-the-Pulpit *Arisaema triphyllum* (Araceae). *Am. J. Bot.* 73:489–94
- Lubbers AE, Lechowicz MJ. 1989. Effects of leaf removal on reproduction vs. belowground storage in *Trillium grandiflorum*. *Ecology* 70:85–96
- Marino RC, Eisenberg RM, Cornell HV. 1997. Influence of sunlight and soil nutrients on clonal growth and sexual reproduction of the understory perennial herb *Sanguinaria canadensis* L. *J. Torrey Bot. Soc.* 124:219–27
- Martin MC. 1965. An ecological life history of *Geranium maculatum*. *Am. Midl. Nat.* 73:111–49
- Matlack GR. 1987. Comparative demographies of four adjacent populations of the perennial herb *Silene dioica* (Caryophyllaceae). *J. Ecol.* 75:113–34
- Matsumura C, Washitani I. 2000. Effects of population size and pollinator limitation on seed-set of *Primula sieboldii* populations in a fragmented landscape. *Ecol. Res.* 15:307–22
- Mattila T, Salonen V. 1995. Reproduction of *Viola mirabilis* in relation to light and nutrient availability. *Can. J. Bot.* 73:1917–24
- McCall C, Primack RB. 1987. Resources limit the fecundity of three woodland herbs. *Oecologia* 71:431–35
- McCarthy BC. 2003. The herbaceous layer of

- eastern old-growth deciduous forests. See Gilliam & Roberts 2003, pp. 163–76
- McCarthy BC, Bailey DR. 1996. Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. *Bull. Torrey Bot. Club* 123:350–65
- McShea WJ, Rappole JH. 1992. White-tailed deer as keystone species within forested habitats of Virginia. *Va. J. Sci.* 43:177–86
- Meagher TR, Antonovics JJ. 1982a. Life history variation in dioecious plant populations: a case study of *Chamaelirium luteum*. In *Evolution and Genetics of Life Histories*, ed. H Dingle, JL Hegmann, pp. 139–54. New York: Springer-Verlag
- Meagher TR, Antonovics JJ. 1982b. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. *Ecology* 63:1690–700
- Meekins JF, McCarthy BC. 2000. Responses of the biennial forest herb *Allaria petiolata* to variation in population density, nutrient addition and light availability. *J. Ecol.* 88:447–63
- Mehrhoff LA. 1989. The dynamics of declining populations of an endangered orchid, *Isotria medeoloides*. *Ecology* 70:783–86
- Meier AJ, Bratton SP, Duffy DC. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecol. Appl.* 5:935–46
- Miller SG, Bratton SP, Hadidian J. 1992. Impacts of white-tailed deer on endangered plants. *Nat. Areas J.* 12:67–74
- Miller TF, Mladenoff DJ, Clayton MK. 2002. Old-growth northern hardwood forests: spatial autocorrelation and patterns of understory vegetation. *Ecol. Monogr.* 72:487–503
- Minoletti ML, Boerner REJ. 1993. Seasonal photosynthesis, nitrogen and phosphorus dynamics, and resorption in the wintergreen fern *Polystichum acrostichoides* (Mich.) Schott. *Bull. Torrey Bot. Club* 120:397–404
- Motten AF. 1982. Autogamy and competition for pollinators in *Hepatica americana* (Ranunculaceae). *Am. J. Bot.* 69:1296–305
- Mukerji SK. 1936. Contributions to the autecology of *Mercurialis perennis* L. *J. Ecol.* 24:38–81
- Müller N, Schneller JJ, Holderegger R. 2000. Variation in breeding system among populations of the common woodland herb *Anemone nemorosa* (Ranunculaceae). *Plant Syst. Evol.* 221:69–76
- Muller RN. 1979. Biomass accumulation and reproduction in *Erythronium albidum*. *Bull. Torrey Bot. Club* 106:276–83
- Muller RN. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. See Gilliam & Roberts 2003, pp. 15–37
- Nault A, Gagnon D. 1988. Seasonal biomass and nutrient allocation patterns in wild leek (*Allium tricoccum* Ait.), a spring geophyte. *Bull. Torrey Bot. Club* 115:45–54
- Nesom GL, LaDuke JC. 1985. Biology of *Trillium nivale* (Liliaceae). *Can. J. Bot.* 63:7–14
- Neufeld HS, Young DR. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. See Gilliam & Roberts 2003, pp. 38–90
- Nomiya H, Suzuki W, Kanazashi T, Shibata M, Tanaka H, Nakashizuka T. 2002. The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. *Plant Ecol.* 164:263–76
- Ohara M, Higashi S. 1987. Interference by ground beetles with the dispersal by ants of seeds of *Trillium* species (Liliaceae). *J. Ecol.* 75:1091–98
- Ohara M, Higashi S. 1994. Effects of inflorescence size on visits from pollinators and seed set in *Corydalis ambigua* (Papaveraceae). *Oecologia* 98:25–30
- Ohara M, Kawano S. 1986. Life history studies on the genus *Trillium* (Liliaceae) I. Reproductive biology of four Japanese species. *Plant Species Biol.* 1:35–45
- Ohara M, Takeda H, Ohno Y, Shimamoto Y. 1996. Variations in the breeding system and the population genetic structure of *Trillium kamtschaticum* (Liliaceae). *Heredity* 76:476–84
- Packham JR, Willis AJ. 1982. The influence of

- shading and of soil type on the growth of *Gaieobdolon luteum*. *J. Ecol.* 70:491–512
- Peterken GF, Game M. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.* 72:155–82
- Peterson CJ, Campbell JE. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. *Bull. Torrey Bot. Club* 120:451–60
- Peterson DL, Rolfe GL. 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *Am. Midl. Nat.* 107:325–39
- Pickett FL. 1915. A contribution to our knowledge of *Arisaema triphyllum*. *Mem. Torrey Bot. Club* 16:1–55
- Pickett STA, McDonnell MJ. 1989. Seed bank dynamics in temperate deciduous forest. In *Ecology of Soil Seed Banks*, ed. MA Leck, TV Parker, RL Simpson, pp. 124–48. New York: Academic
- Pickett STA, White PS, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. London: Academic
- Piper JK. 1989. Distribution of dry mass between shoot and root in nine understory species. *Am. Midl. Nat.* 122:114–19
- Pitelka LF. 1984. Application of the $-3/2$ power law to clonal herbs. *Am. Nat.* 123:442–49
- Pitelka LF, Ashmun JW. 1985. Physiology and integration of ramets in clonal plants. In *Population Biology and Evolution of Clonal Organisms*, ed. JBC Jackson, LW Buss, RE Cook, pp. 399–435. New Haven, CT: Yale Univ. Press
- Pitelka LF, Ashmun JW, Brown RL. 1985a. The relationship between seasonal variation in light intensity, ramet size, and sexual reproduction in natural and experimental populations of *Aster acuminatus* (Compositae). *Am. J. Bot.* 72:311–19
- Pitelka LF, Hansen SB, Ashmun JW. 1985b. Population biology of *Clintonia borealis*. I. Ramet and patch dynamics. *J. Ecol.* 73:169–83
- Pitelka LF, Stanton DS, Peckham MO. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). *Am. J. Bot.* 67:942–48
- Policansky D. 1983. Patches, clones and self-fertility of mayapples (*Podophyllum peltatum* L.). *Rhodora* 85:253–56
- Price EAC, Hutchings MJ. 1992. Studies of growth in the clonal herb *Glechoma hederacea*. II. The effects of selective defoliation. *J. Ecol.* 80:39–47
- Price EAC, Marshall C, Hutchings MJ. 1992. Studies of growth in the clonal herb *Glechoma hederacea*. I. Patterns of physiological integration. *J. Ecol.* 80:25–38
- Primack RB, Hall P. 1990. Costs of reproduction in the Pink Lady's Slipper orchid: a four-year experimental study. *Am. Nat.* 136:638–56
- Primack RB, Miao SL. 1992. Dispersal can limit local plant distribution. *Conserv. Biol.* 6:513–19
- Primack RB, Miao SL, Becker KR. 1994. Costs of reproduction in the Pink Lady's Slipper orchid (*Cypripedium acaule*): defoliation, increased fruit production, and fire. *Am. J. Bot.* 81:1083–90
- Pudlo RJ, Beattie AI, Culver DC. 1980. Population consequences of changes in an ant-seed mutualism in *Sanguinaria canadensis*. *Oecologia* 146:32–37
- Ramsey GW, Leys CH, Wright RAS, Coleman DA, Neas AO, et al. 1993. Vascular flora of the James River gorge watersheds in the central Blue Ridge mountains of Virginia. *Cas-tanea* 58:260–300
- Rasmussen HN. 1995. *Terrestrial Orchids from Seed to Mycotrophic Plant*. Cambridge, UK: Cambridge Univ. Press
- Rasmussen HN. 2002. Recent developments in the study of orchid mycorrhiza. *Plant Soil* 244:149–63
- Rasmussen HN, Whigham DF. 1993. Seed ecology of dust seeds in situ: a new study technique and its application in terrestrial orchids. *Am. J. Bot.* 80:1374–78
- Rasmussen HN, Whigham DF. 1998a. Importance of woody debris in seed germination

- of *Tipularia discolor* (Orchidaceae). *Am. J. Bot.* 85:829–34
- Rasmussen HN, Whigham DF. 1998b. The underground phase: a special challenge in studies of terrestrial orchid populations. *Bot. J. Linn. Soc.* 126:49–64
- Rasmussen HN, Whigham DF. 2002. Phenology of roots and mycorrhiza in orchid species differing in phototrophic strategy. *New Phytol.* 154:797–807
- Reader RJ. 1987. Loss of species from deciduous forest understory immediately following selective tree harvesting. *Biol. Conserv.* 42:231–44
- Reader RJ. 1988. Using the guild concept in the assessment of tree harvesting effects on understory herbs: a cautionary note. *Environ. Manag.* 12:803–8
- Reader RJ, Bricker BD. 1992. Response of five deciduous forest herbs to partial canopy removal and patch size. *Am. Midl. Nat.* 127:149–57
- Robertson JL, Wyatt R. 1990. Reproductive biology of the yellow-fringed orchid, *Platanthera ciliaris*. *Am. J. Bot.* 77:388–98
- Robinson GR, Yurlina ME, Handel SN. 1994. A century of change in the Staten Island flora: ecological correlates of species losses and invasions. *Bull. Torrey Bot. Club* 121:119–29
- Rockwood LL, Lobstein MB. 1994. The effects of experimental defoliation on reproduction in four species of herbaceous perennials from northern Virginia. *Castanea* 59:41–50
- Rooney TP. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74:201–8
- Rooney TP, Dress WJ. 1997a. Patterns of plant diversity in overbrowsed primary and mature secondary hemlock–northern hardwood forest stands. *J. Torrey Bot. Soc.* 124:43–51
- Rooney TP, Dress WJ. 1997b. Species loss over sixty years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. *Nat. Areas J.* 17:297–305
- Rooney TP, Gross K. 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecol.* 168:267–77
- Rooney TP, Waller DM. 2001. How experimental defoliation and leaf height affect growth and reproduction in *Trillium grandiflorum*. *J. Torrey Bot. Soc.* 128:393–99
- Scheiner SM. 1988. Population dynamics of an herbaceous perennial *Danthonia spicata* during secondary forest succession. *Am. Midl. Nat.* 119:268–81
- Schemske DW. 1977. Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). *Bull. Torrey Bot. Club* 104:254–63
- Shefferson RP, Sandercock BK, Proper J, Beissinger SR. 2001. Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. *Ecology* 82:145–56
- Singleton R, Gardescu S, Marks PL, Gerber MA. 2001. Forest herb colonization of post-agricultural forests in central New York state, USA. *J. Ecol.* 89:325–38
- Slade AJ, Hutchings MJ. 1987. An analysis of the costs and benefits of physiological integration between ramets in the clonal perennial herb *Glechoma hederacea*. *Oecologia* 73:425–31
- Small CJ, McCarthy BC. 2003. Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. *Plant Ecol.* 164:37–48
- Smith BH. 1983a. Demography of *Floerkea proserpinacoides*, a forest-floor annual. I. Density-dependent growth and mortality. *J. Ecol.* 71:391–404
- Smith BH. 1983b. Demography of *Floerkea proserpinacoides*, a forest-floor annual. II. Dynamics of seed and seedling populations. *J. Ecol.* 71:413–25
- Smith BH, DeRivera CE, Bridgman CL, Woida JJ. 1989a. Frequency-dependent seed dispersal by ants of two deciduous forest herbs. *Ecology* 70:1645–48
- Smith BH, Forman PD, Boyd AE. 1989b. Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. *Ecology* 70:1649–56
- Smith BH, Ronsheim ML, Swartz KR. 1986. Reproductive ecology of *Jeffersonia diphylla* (Berberidaceae). *Am. J. Bot.* 73:1416–26

- Smith JL, Hunter KL, Hunter RB. 2002. Genetic variation in the terrestrial orchid *Tipularia discolor*. *Southeast. Nat.* 1:17–26
- Smith RG, Caswell D, Carriera A, Zielke B. 1996. Variation in the ginsenoside content of American ginseng, *Panax quinquefolius* L., roots. *Can. J. Bot.* 74:1616–20
- Snow A, Whigham DF. 1989. Cost of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70:1286–93
- Sobey DG, Barkhouse P. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick–Nova Scotia border region. *Can. Field Nat.* 91:377–83
- Solbrig OT. 1981. Studies on the population biology of the genus *Viola*. II. The effect of plant size on fitness in *Viola sororia*. *Evolution* 35:1080–93
- Stamp NE, Lucas JR. 1983. Ecological correlates of explosive seed dispersal. *Oecologia* 59:272–78
- Syrjänen K, Lehtilä K. 1993. The cost of reproduction in *Primula veris*: differences between two adjacent populations. *OIKOS* 67:465–72
- Thompson PA, Cox SA. 1978. Germination of the Bluebell (*Hyacinthoides non-scripta* (L.) Chouard) in relation to its distribution and habitat. *Ann. Bot.* 42:51–62
- Tilghman NG. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildl. Manag.* 53:524–32
- Tissue DT, Skillman JB, McDonald EP, Strain BR. 1995. Photosynthesis and carbon allocation in *Tipularia discolor* (Orchidaceae), a wintergreen understory herb. *Am. J. Bot.* 82:1249–56
- Traveset A, Willson MF. 1997. Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. *OIKOS* 80:89–95
- Uemura S. 1993. Patterns of leaf phenology in forest understory. *Can. J. Bot.* 72:409–14
- Valverde T, Silvertown J. 1995. Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment. *Funct. Ecol.* 9:942–50
- Valverde T, Silvertown J. 1997a. A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *J. Ecol.* 85:193–210
- Valverde T, Silvertown J. 1997b. An integrated model of demography, patch dynamics and seed dispersal in a woodland herb, *Primula vulgaris*. *OIKOS* 80:67–77
- Valverde T, Silvertown J. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *J. Ecol.* 86:545–62
- Vellend M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology* 84:1158–64
- Vellend M, Lechowicz MJ, Waterway MJ. 2000a. Environmental distribution of four *Carex* species (Cyperaceae) in an old-growth forest. *Am. J. Bot.* 87:1507–16
- Vellend M, Lechowicz MJ, Waterway MJ. 2000b. Germination and establishment of forest sedges (*Carex*: Cyperaceae): tests for home-site advantage and effects of leaf litter. *Am. J. Bot.* 87:1517–25
- Vellend M, Myers JA, Gardescu S, Marks PL. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84:1067–72
- Verheyen K, Guntenspergen GR, Biesbrouck B, Hermy M. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *J. Ecol.* 91:731–42
- Waller DM, Alverson WS. 1997. The white-tailed deer: a keystone herbivore. *Wildl. Soc. Bull.* 25:217–26
- Watson MA. 1995. Sexual differences in plant developmental phenology affect plant-herbivore interactions. *Trees* 10:180–82
- Webb SL. 1999. Disturbance by wind in temperate-zone forests. In *Ecosystems of Disturbed Ground*, ed. LR Walker, pp. 187–222. Amsterdam, Neth.: Elsevier
- Webb SL, Willson MF. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67:150–53

- Wennström A, Ericson L. 1994. The effect of the systemic smut *Urocystis carcinodes* on the long-lived herb *Actaea spicata*. *OIKOS* 71:111–18
- Whigham DF. 1974. An ecological life history study of *Uvularia perfoliata* L. *Am. Midl. Nat.* 91:343–59
- Whigham DF. 1984. Biomass and nutrient allocation patterns of *Tipularia discolor* (Orchidaceae). *OIKOS* 42:303–13
- Whigham DF. 1990. The effect of experimental defoliation on the growth and reproduction of a woodland orchid, *Tipularia discolor*. *Can. J. Bot.* 68:1812–16
- Whigham DF, Chapa AS. 1999. Timing and intensity of herbivory: its influence on the performance of clonal woodland herbs. *Plant Species Biol.* 14:29–37
- Whigham DF, O'Neill J. 1991. The dynamics of flowering and fruit production in two eastern North American terrestrial orchids, *Tipularia discolor* and *Liparis lilifolia*. In *Population Ecology of Terrestrial Orchids*, ed. TCE Wells, JH Willems, pp. 89–101. The Hague: SPB Academic
- Whigham DF, O'Neill J, Cipollini M. 1993. The role of tree gaps in maintaining the population structure of a woodland herb: *Cynoglossum virginianum* L. *Plant Species Biol.* 8:107–15
- Whigham DF, O'Neill J, McCormick M, Smith C, Rasmussen H, et al. 2002. Interactions between decomposing wood, mycorrhizas, and terrestrial orchid seeds and protocorms. In *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*, ed. P Kindlmann, JH Willems, DF Whigham, pp. 117–31. Leiden, Neth.: Backhuys
- Whitbread F, McGonigle TP, Peterson RL. 1996. Vesicular-arbuscular mycorrhizal associations of American ginseng (*Panax quinquefolius*) in commercial production. *Can. J. Bot.* 74:1104–12
- Whitman AA, Hunter ML Jr., Witham JW. 1998. Age distribution of ramets of a forest herb, wild sarsaparilla, *Aralia nudicaulis* (Araliaceae). *Can. Field Nat.* 112:37–44
- Widden P. 1996. The morphology of vesicular-arbuscular mycorrhizae in *Clintonia borealis* and *Medeola virginiana*. *Can. J. Bot.* 74:679–85
- Wijesinghe D, Hutchings MJ. 1997. The effects of spatial scale of environmental heterogeneity on the growth of a clonal plant: an experimental study with *Glechoma hederacea*. *J. Ecol.* 85:17–28
- Wijesinghe DK, Whigham DF. 1997. Costs of producing clonal offspring and the effects of plant size on population dynamics of the woodland herb *Uvularia perfoliata* (Liliaceae). *J. Ecol.* 85:907–19
- Wijesinghe DK, Whigham DF. 2001. Nutrient foraging in woodland herbs: a comparison of three species of *Uvularia* (Liliaceae) with contrasting belowground morphologies. *Am. J. Bot.* 88:1071–79
- Willson MF. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108:261–80
- Wilson JY. 1959. Vegetative reproduction in the bluebell, *Endymion nonscriptus* (L.) Garcke. *New Phytol.* 58:155–63
- Zak DR, Groffman PM, Pregitzer KS, Christensen S, Tiedje JM. 1990. The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. *Ecology* 71:651–56
- Zelmer CD, Currah RS. 1995. Evidence for a fungal liaison between *Corallorhiza trifida* (Orchidaceae) and *Pinus contorta* (Pinaceae). *Can. J. Bot.* 73:862–66
- Zettler JA, Spira TP, Allen CR. 2001. Yellow jackets (*Vespula* spp.) disperse *Trillium* (spp.) seeds in eastern North America. *Am. Midl. Nat.* 146:444–46
- Ziegenhagen B, Bialozyt R, Kuhlenkamp V, Schulze I, Ulrich A, Wulf M. 2003. Spatial patterns of maternal lineages and clones of *Galium odoratum* in a large ancient woodland: inferences about seedling recruitment. *J. Ecol.* 91:578–86