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ECOLOGY OF WOODLAND HERBS IN TEMPERATE DECIDUOUS FORESTS*

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■ **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

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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, Inghe & 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
Ainsliaea apiculata (Asteraceae)	+	Rhizome	NA[c]	NA	NA	NA	NA	Hori & Yokoi 1999
Athyrium filix-femina (Aspidiaceae)	+	Rhizome	<1.0	NA	NA	NA	NA	Sobey & Barkhouse 1977
Dryopteris phegopteris (Aspidiaceae)	+	Rhizome	1.5–3.0	Irregular	NA	NA	NA	Sobey & Barkhouse 1977
D. spinulosa	+	Rhizome	<1–4	NA	NA	NA	NA	Sobey & Barkhouse 1977
Lycopodium lucidulum (Lycopodiaceae)	+	Rhizome	1–3	Irregular	NA	NA	NA	Sobey & Barkhouse 1977
L. annotinum	+	Rhizome	0.1–8	Frequent	Fully integrated	NA	1	Sobey & Barkhouse 1977, Jónsdóttir & Watson 1997
L. clavatum	+	Rhizome	8–74	Frequent	NA	NA	1–4	Sobey & Barkhouse 1977
L. obscurum	+	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
L. flabelliforme	+	Rhizome	17–31	Frequent	Highly integrated–intermediate	NA	1	Sobey & Barkhouse 1977, Lau & Young 1988, Jónsdóttir & Watson 1997
L. tristrachyum	+	Rhizome	ca. 15	NA	NA	NA	NA	Sobey & Barkhouse 1977
Osmunda claytoniana (Osmundaceae)	+	Rhizome	<0.5	Very infrequent	NA	NA	1–75	Sobey & Barkhouse 1977
Polystichum acrostichoides (Aspidiaceae)	+	Rhizome	<1.0	Infrequent	NA	NA	NA	Sobey & Barkhouse 1977
Pteridium aquilinum (Pteridiaceae)	+	Rhizome	15–30	Frequent	Fully integrated	NA	1	Sobey & Barkhouse 1977, Jónsdóttir & Watson 1997

[a] Sobey & Barkhouse 1977.

[b] per year or as otherwise provided.

[c] NA = 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
Aralia nudicaulis (Araliaceae)	June	Self-incompatible	Dioecious	Yes/No	Bumblebees, solitary bees, syrphids	Barrett & Helenurm 1987, Flanagan & Moser 1985a
Anemone nemorosa (Ranunculaceae)	NA[a]	Mainly self-compatible	Hermaphrodite	NA	NA	Müller et al. 2000
Carex pedunculata (Cyperaceae)	April	Self-compatible	Monoecious	NA	NA	Handel 1976
Caulophyllum thalictroides (Berberidaceae)	Late April–mid-May	Self-compatible	Hermaphrodite	Yes	Diotera, hemiptera, hymenoptera	Hannan & Prucher 1996
Chamaelirium luteum (Liliaceae)	Mid-May	NA	Dioecious	NA	NA	Meagher & Antonovics 1982a,b
Chimaphila umbellata (Pyrolaceae)	Late July	Partially self-incompatible	Hermaphrodite	Yes	Syrphids	Barrett & Helenurm 1987
Claytonia virginica (Portulacaceae)	Late March–early May	Self-compatible, **Self-incompatible**[b]	Hermaphrodite	Yes	24 sp, Andrenid was primary pollinator	Schemske 1977

Clintonia borealis (Liliaceae)	Early June	Partially self-incompatible	Hermaphrodite	Yes	Bumblebees, solitary bees	Barrett & Helenurm 1987, Galen et al. 1985
Cornus canadensis (*Cornaceae*)	Mid-June	Self-incompatible	Hermaphrodite	Yes	Bumblebees, solitary bees, beeflies, syrphids	Barrett & Helenurm 1987
Corydalis ambigua (Papaveraceae)	Late April–early May	Self-incompatible	Hermaphrodite	Yes	Honeybees, bumblebees	Ohara & Higashi 1994
Cypripedium acaule (Orchidaceae)	Mid-June	Self-incompatible	Hermaphrodite	Yes	Bumblebees	Barrett & Helenurm 1987, Davis 1986
Erythronium albidum (Liliaceae)	Late April	Self-compatible	Hermaphrodite	NA	Bees	Harder et al. 1993
E. americanum	Late April	Self-incompatible	Hermaphrodite	NA	Bees	Harder et al. 1993
Geranium maculatum (Geraniaceae)	May	Partially self-incompatible	Hermaphrodite	No	Halicted bees, flies, bumblebees, beetles, ants	McCall & Primack 1987
Hepatica americana (Ranunculaceae)	March–April	Self-compatible	Hermaphrodite	No	Mostly solitary bees, bee flies, halictid bees	Motten 1982
Jeffersonia diphylla (Berberidaceae)	April	Self-compatible (facultative autogamy)	Hermaphrodite	No	Halictids, honeybees	Smith et al. 1986
Linnaea borealis (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
Maianthemum canadense (Liliaceae)	Early June	Self-incompatible	Hermaphrodite	No	Solitary bees, bee flies, syrphids	Barrett & Helenurm 1987, McCall & Primack 1987
Medeola virginiana (Liliaceae)	Late June	Self-incompatible	Hermaphrodite	Yes	Flies?	Barrett & Helenurm 1987, McCall & Primack 1987
Oxalis montana (Oxalidaceae)	Early July	Partially self-incompatible	Hermaphrodite (Chasmogamous, cleistogamous)	Yes	Solitary bees, syrphids, flies, thrips, beetles	Barrett & Helenurm 1987, Jasieniuk & Lechowicz 1987
Orchis (= *Galearis*) *spectabilis* (Orchidaceae)	Late April–early June	Partially self-incompatible	Hermaphrodite Polygamodioecious	Yes	Bumblebees	Dieringer 1982
Panax quinquefolium (Araliaceae)	June–August	NA	Hermaphrodite	Yes?	NA	Lewis & Zenger 1982
Podophyllum peltatum (Berberidaceae)	May	Partially self-incompatibility	Polygamodioecious	Yes	Bumblebees	Policansky 1983, Laverty & Plowright 1988
Primula veris (Primulaceae)	May	Self-incompatible	Hermaphrodite (distylous)	NA	NA	Leimu et al. 2002
P. vulgaris	May	Self-incompatible	Hermaphrodite (distylous)	Yes	Bee-flies, bumble bees, butterflies	Boyd et al. 1990

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

[a] Information not provided in original source material.

[b] Bold 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
Actaea spicata (Ranunculaceae)	5.9^{a}	NA^{d}	NA	NA	Ehrlén & Eriksson 2000
Allium ursinum (Liliaceae)	5.4^{a}	NA	NA	Winter or spring after cold treatment	Ernst 1979
Arisaema triphyllum (Araceae)	NA	NA	NA	NA	Braun & Brooks 1987
Asarum canadense (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
Campanula americana (Campanulaceae)	0.1^{a}	20–40	NA	Autumn or spring depending on phenology of mother plant	Galloway 2002
C. latifolia	0.1^{a}	NA	NA	NA	Ehrlén & Eriksson 2000
Convallaria majalis (Convallariaceae)	17.0^{a}	NA	NA	NA	Ehrlén & Eriksson 2000
Floerkea proserpinacoides (Limnanthaceae)	NA	1	Several years	No dormancy, controlled by environment	Smith 1983b
Hepatica acutiloba (Ranunculaceae)	2.4^{a}	9.9^{a}	NA	NA	Smith et al. 1989b

Jeffersonia diphylla (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
Lathyrus vernus (Fabaceae)	12.0[a]	NA	NA	NA	Ehrlén & Eriksson 2000
Paris quadrifolia (Trilliaceae)	4.6[a]	NA	NA	NA	Ehrlén & Eriksson 2000
Panax quinquefolia (Araliaceae)	NA	1.9[a]	2 years?	18–22 months after dispersal	Lewis & Zenger 1982
Podophyllum peltatum (Berberidaceae)	NA	NA	NA	NA	Braun & Brooks 1987
Polygonatum multiflorum (Convallariaceae)	28.6[a]	NA	NA	NA	Ehrlén & Eriksson 2000
Sanguinaria canadensis (Papaveraceae)	15.7[a]	11.2–31.0[b]	NA	NA	Pudlo et al. 1980, Heithaus 1981
Hyacinthoides (= *Scilla*) *nonscripta* (Liliaceae)	NA	NA	NA	June–July. Seeds require high temperature conditioning, germinate in autumn	Thompson & Cox 1978
Silene dioica (Caryophyllaceae)	0.7–1.2[b]	NA	Several years	No dormancy (controlled by environment)	Matlack 1987
Trientalis europaea (Primulaceae)	41.1–64.7[c]	0–14[c]	Several years	Autumn or following spring	Hiirsalmi 1969

(*Continued*)

TABLE 4 *(Continued)*

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

[a] Mean

[b] Range of means

[c] Range

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

Jeffersonia diphylla (Berberidaceae)	Ants	NA	Rodents	37–54 of capsules prior to dehiscence	Heithaus 1981; Smith et al. 1986, 1989b
Luzula campestris (Juncaceae)	Ants	1	NA	NA	Handel 1978
Panax quinquefolium (Araliaceae)	Gravity	<0.1	Rodents?	NA	Lewis & Zenger 1982
Oxalis acetosella (Oxalidaceae)	Explosive (e.g., ballistic)	Range: 0.6–4.5	NA	NA	Berg 2000
Phytolacca americana (Phytolaccaceae)	Birds	>33	NA	NA	Hoppes 1988
Podophyllum peltatum (Berberidaceae)	Turtle (*Terrapene carolina*)	NA	NA	NA	Braun & Brooks 1987
Primula vulgaris (Primulaceae)	Ants (*Myrmica rubra*) ca. 20%, rodents ca. 75%	Ants = 0.037–0.099, rodents = unknown	NA	NA	Cahalan & Gliddon 1985; Valverde & Silvertown 1995, 1997a,b
Sanguinaria canadensis (Papaveraceae)	Ants (*Aphaenogaster rudis, Formica subsericea, Lasius alienus, Myrmica punctiventris, Stenamma* sp.)	0 in disturbed habitats, 17 in undisturbed areas. Mean = 1.38	Rodents	Predispersal consumption of seeds to >65 of post-dehiscence seeds	Pudlo et al. 1980, Heithaus 1981
Silene dioica (Caryophyllaceae)	Gravity	≤0.7	NA	NA	Matlack 1987
Streptopus amplexifolius (Liliaceae)	American robin (*Turdus migratorius*); varied thrush (*Ixoreus naevius*); brown bear (*Ursus arctos*); black bear (*Ursus americanus*)	NA	NA	NA	Traveset & Willson 1997
Trillium cuneatum, T. erectum, T. grandiflorum, T. undulatum (Liliaceae)	Ants (*Myrmica punctiventris*) and harvestmen (*Arachnida*), white-tailed deer, yellow jackets (*Vespula* sp.)	<1 to >3000	Slugs and harvestmen eat seeds	NA	Gunther & Lanza 1989, Kalisz et al. 1999, Zettler et al. 2001, Vellend et al. 2003
T. kamtschaticum	Ants (*Aphaenogaster smythiesi japonica, Myrmica ruginodis*)	0.30–3.30	Elaiosomes 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
T. niveale	Ants	NA	Rodents	Seed predation is rare	Smith et al. 1989a
T. tschonoskii	Ants (*Aphaenogaster smythiesi japonica*, *Myrmica ruginodis*, *Lasius niger*)	0.01–2.7	Elaiosome eaten by ground beetles	85	Ohara & Higashi 1987
Uvularia grandiflora (Liliaceae)	Ants (*Myrmica americana*, *M. aphaenogaster*, *Camponotus pennsylvanicus*, *Formica phenolepis*)	<0.1 to >2	*Peromyscus leucopus*, *Tamius striatus*	NA	Webb & Wilson 1985, Kalisz et al. 1999
U. perfoliata	Ants	≤2	NA	NA	D.F. Whigham, personal observation
Viola sp., *Viola mirabilis* (Violaceae)	Ants	Mean = 0.01–2.1, Max. 0.02–5.4	NA	NA	Beattie & Lyons 1975, Mattila & Salonen 1995
V. pedata	Ants, ballistic	0.25–5.1 Mean = 0.35	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978
V. pensylvanica	Ants, ballistic	0.72–1.2	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978
V. rostrata	Ants, ballistic	0.1–4.2	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978
V. striata	Ants, ballistic	0.2–3.3	NA	NA	Beattie & Lyons 1975, Culver & Beattie 1978, Stamp & Lucas 1983

[a] Dispersal distances are given as ranges or, where indicated, as mean or maximum distances.

[b] Information 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 belowground 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, Fröborg & 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).

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