Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington

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Abstract: Variation in belowground traits of herbaceous species may influence their ability to persist and spread during and after the closed-canopy period of forest development. In 40- to 60-year-old closed-canopy, coniferous forests of the Olympic Peninsula, Washington, we excavated root and rhizome systems of 11 herbaceous species to compare morphology, vegetative spread, and proportion of biomass in belowground structures. All species were perennial and most were rhizomatous; four species were nonclonal. Of the seven clonal species, only two (*Maianthemum dilatatum* and *Oxalis oregana*) spread extensively (mean lateral spread >50 cm) by belowground perennating structures. The proportion of total biomass in belowground structures varied considerably among species (21–85%) and was higher for deciduous than for evergreen species. High variability in belowground traits suggests that multiple strategies may contribute to survival during closed-canopy conditions. For species with a high proportion of belowground biomass, we suggest that the ability to store resources or to acquire new resources through lateral spread may contribute to persistence in dense coniferous forests.

Key words: biomass allocation, canopy closure, forest understory plants, rhizomes, root systems, succession.

Résumé : Une variation des caractères hypogés des espèces herbacées peut influencer leur aptitude à persister et à s’étendre pendant et après la période de fermeture de la canopée (couvert forestier) au cours du développement forestier. Dans des forêts conifériennes à canopées fermées, âgées de 40–60 ans, de la péninsule Olympia, Washington, les auteurs ont extrait les systèmes racinaires et les rhizomes de 11 espèces herbacées afin de comparer la morphologie, la propagation végétative et la proportion de la biomasse dans les structures hypogées. Toutes les espèces sont pérennes et la plupart possèdent des rhizomes; quatre espèces ne sont pas clonales. Sur les sept espèces clonales, seulement two (*Maianthemum dilatatum* et *Oxalis oregana*) s’étendent extensivement (soit une propagation latérale >50 cm) par des structures hypogées pérennes. La proportion de la biomasse totale dans les structures hypogées varie considérablement selon les espèces (21–85%), et est plus importante pour les espèces sempervirentes. La forte variabilité des caractères hypogés suggère que plusieurs stratégies peuvent contribuer à la survie sous des conditions de canopée fermée. Pour les espèces ayant une forte proportion de biomasse hypogée, les auteurs suggèrent que la capacité d’emmagasiner des réserves, ou d’obtenir de nouvelles ressources par la propagation latérale, pourrait contribuer à leur persistence dans les forêts conifériennes denses.

Mots clés : allocation de la biomasse, fermeture de la canopée (couvert forestier), plantes du parterre forestier, rhizomes, systèmes racinaires, succession.

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Introduction

Following stand-replacing disturbance, young forests often develop through a dense, closed-canopy stage (Harcombe 1986; Oliver and Larson 1996), during which vascular understory plants are greatly reduced in abundance or eliminated locally (Alaback 1982). Species that survive this period may play an important role in subsequent re-initiation of the forest understory during natural stand development or after silvicultural thinning. However, little is known about the life-history traits of surviving species or the potential of these species to spread vegetatively once conditions improve.

Aboveground traits (e.g., photosynthetic systems, leaf physiology, shoot morphology, and phenology) are frequently cited as the key adaptations to shade (Menges 1987; Yoshie 1995; Henry and Aarssen 1997), but forest herbs also possess belowground organs that may facilitate their survival and growth under low-light, closed-canopy conditions. These structures enable plants to produce new ramets, capture and store resources, and spread to new environments (Sobey and Barkhouse 1977; Antos and Zobel 1984, 1985; Carlsson et al. 1990; Fitter 1991; Meyer and Hellwig 1997). In coniferous forests of the Pacific Northwest, some shrub species survive the closed-canopy stage of forest development, presumably because they possess extensive rhizome systems (storing resources and buds) established during ear-

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Table 1. Physical and forest stand characteristics of sampling sites in young, coniferous forests of the Olympic Peninsula, Wash.

	Study site		
Stand characteristic	Bait	Fresca	Clavicle
Elevation (m)	190–230	150	490–520
Soil texture	Silt loam	Very gravelly sandy loam	Silt loam
Years since harvest	41	55	60
Major overstory species	Tshe, Psme	Tshe, Pisi	Tshe, Pisi
Overstory stem density (no./ha)	840–1574	498–775	590–1327
Basal area (m^2/ha)	49–70	66–73	72–98
Major understory species	Pomu, Oxor, Gash	Pomu, Oxor	Pomu, Oxor

Note: Tree species are ordered by relative basal area. Tshe, *Tsuga heterophylla*; Pisi, *Picea sitchensis*; Psme, *Pseudotsuga menziesii;* Pomu, *Polystichum munitum*; Oxor, *Oxalis oregana*; Gash, *Gaultheria shallon.* Source: C. Harrington, unpublished data; Snyder et al. (1969).

lier times (Messier and Kimmins 1991; Tappeiner et al. 1991; Huffman et al. 1994). However, very little comparable information is available on herbaceous species in these forests (but see Tappeiner and Alaback 1989).

Comparative studies of root and rhizome morphology (Parrish and Bazzaz 1976; Gross et al. 1992; Antos and Halpern 1997), vegetative spread (Prach and Pyšek 1994), and biomass distribution (Gleeson and Tilman 1990) have been used to explain colonization patterns of herbs during early succession. In this study, we compared the belowground traits of 11 herbaceous species that persist through a second critical stage of understory development in dense, closed-canopy forests of the western Olympic Peninsula. We examined (*i*) the presence and type of perennating structures, (*ii*) the extent of clonality and lateral vegetative spread, and (*iii*) the degree to which species show similar patterns of biomass allocation and root system development. We use the results of these comparative analyses to suggest possible mechanisms by which these traits facilitate survival through canopy closure and vegetative spread following silvicultural thinning or natural opening of the forest canopy.

Methods

Study sites

Root and rhizome systems of herbaceous species were examined at three sites on the western Olympic Peninsula, Washington, U.S.A. Sites are in low-elevation (150–520 m) forests of the *Picea sitchensis* and *Tsuga heterophylla* vegetation zones (Henderson et al. 1989). Precipitation in this region averages 250 to >300 cm annually, falling primarily as rain from October through April; mean January and July temperatures are ca. 4 and 15–17°C, respectively (Henderson et al. 1989; Western Regional Climate Center 1999). Study sites occupy flat to gentle terrain (0–25%) and are characterized by gravelly sandy loam or silty loam soils of moderate to high productivity (Table 1).

The three study sites are among a larger set of sites that constitute the Olympic Habitat Development Study (C.A. Harrington and A.B. Carey, unpublished study plan), a silvicultural experiment in which variable intensity thinning and manipulation of coarse woody debris will be used to promote late-successional forest characteristics in relatively young forests. These are also the locations of a companion study of soil seed banks (Halpern et al. 1999). These densely stocked forests originated following clear-cut logging and slash burning ca. 40–60 years ago and are dominated by *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii* (Mirbel) Franco. var. *menziesii*, and (or) *Picea sitchensis* (Bong.) Carr. (Table 1). Understory vegetation is typical of the *Polystichum munitum – Oxalis oregana* or *Gaultheria shallon – Oxalis oregana* plant associations (Henderson et al. 1989) but is poorly developed, with total vascular plant cover averaging <21% at all sites. *Vaccinium parvifolium* Smith, *Oxalis oregana* Nutt., and ferns compose most of the sparse cover of vascular understory species. Bryophytes and decaying stumps and logs cover much of the ground surface. Thickness of the organic horizon measured beneath excavated plants ranged from ca. 1 to 5 cm.

Plant sampling

We sampled 11 herbaceous species that are common in low-elevation forests on the west side of the Olympic Peninsula (Henderson et al. 1989) and that occurred with relatively high frequency at one or more sites (Halpern et al. 1999). These species are among the few that are found during maximum canopy closure. Four are dicots (*Montia sibirica* (L.) Howell, *Oxalis oregana*, *Pyrola uniflora* L., and *Viola sempervirens* Greene), four are monocots (*Disporum smithii* (Hook.) Piper, *Listera caurina* Piper, *Maianthemum dilatatum* (Wood) Nels. & Macbr., and *Trillium ovatum* Pursh), and three are ferns (*Blechnum spicant* (L.) Roth., *Dryopteris austriaca* (Jacq.) Woynar, and *Polystichum munitum* Roth). Nomenclature follows Hitchcock and Cronquist (1973).

For each species, we excavated, measured, and collected 10–30 plants (10–11 per site, with most species found at only one or two sites) between July and August 1995. Our unit of comparison was the clonal fragment, consisting of all live plant parts (e.g., rhizomes, stolons, roots, buried apical buds, and aerial shoots) connected to an initially selected, undamaged aerial shoot. Aerial shoots were subjectively chosen so as not to include atypically large or small plants. Each clonal fragment was carefully excavated with fingers and small hand tools as in previous studies (e.g., Antos and Zobel 1984). The following measurements were taken in the field on each clonal fragment using rulers and calipers: (*i*) maximum lateral spread by rhizomes and stolons or by vegetatively sprouting lateral roots (measured before removing the plant from the substrate); (*ii*) root and rhizome dimensions including maximum root length and maximum level of root branching, total rhizome length, and maximum rhizome diameter; (*iii*) maximum depths of roots and minimum and maximum depths of rhizomes (from the upper surface of the organic horizon); (*iv*) maximum stem heights; and (*v*) number of ramets per clonal fragment (based on the number of connected aerial shoots). Each clonal fragment was mapped to show the distribution of ramets and roots and the branching pattern of rhizomes.

Plants were transported to the laboratory, washed to remove soil and organic debris, and frozen. To assess root to shoot ratios (the ratio of all belowground to all aboveground dry mass) and percent biomass below ground, we separated clonal fragments into aboveground portions (fronds or aboveground stems, petioles, reproductive tissue, stolons, and leaves) and belowground structures (roots, rhizomes, and buried apical buds). Plant components were dried at 65°C for at least 48 h and weighed to the nearest 0.01 g.

Data summary and analyses

Our goal in sampling multiple sites was to capture some of the variability in species traits found in closed-canopy forests of the region rather than to compare differences among sites. Because data distributions were non-normal and variances were generally not homogeneous, we used nonparametric Kruskal–Wallis or Mann–Whitney rank tests to determine if species' traits differed enough among sites to justify separate site-level analyses (Zar 1984; SPSS Inc. 1996). Among the many species-by-traits tests performed, few significant differences ($p \leq 0.05$) were found among sites, and no evidence was found that multiple traits within a particular site differed in a consistent direction. Consequently, all samples for a given species were combined, and mean, minimum, and maximum values were calculated to characterize the range of species performance. To compare trends among growth forms, species were classified as perennial (possessing multiple annual shoot scars) or annual, and as clonal (possessing multiple, potentially independent ramets) or nonclonal.

Results

Presence and type of perennial organs

All 11 species were perennial, and individuals of most species consistently had multiple aerial shoot scars, decay at the oldest portion of the rhizome, and (or) persistent adventitious roots indicating growth over a number of years. *Montia* was an exception; it generally appeared to be short-lived and occasionally flowered in its 1st year. Nearly all species possessed rhizomes; however, the extent of rhizome development (e.g., rhizome length, diameter) varied greatly among species (Table 2). *Pyrola* lacked rhizomes but produced new ramets from spreading, perennial roots. *Viola* had stolons in addition to rhizomes.

Clonality and vegetative spread

Species differed greatly in their lateral vegetative spread and in the number of interconnected ramets per clonal fragment (Table 2). Of the 11 species, 4 were nonclonal (*Montia*, *Listera*, *Trillium*, and *Disporum*); rhizome extension associated with annual shoot renewal accounted for little or no vegetative spread in these species (Fig. 1A). Although seven species were clonal (i.e., sometimes formed interconnected ramets), only three (*Maianthemum*, *Oxalis*, and *Pyrola*) spread extensively (Fig. 1B) and typically had more than one ramet per clonal fragment (Table 2).

Biomass distribution

The mean proportion of total biomass in belowground structures ranged from 21 to 85% among species, with considerable variation within some species (Table 3). Four species (*Oxalis*, *Maianthemum*, *Disporum*, and *Trillium*) had a high proportion of biomass in belowground structures (means >80% and minima largely >60%), and two species (*Pyrola* and *Montia*) had a low proportion of biomass below ground (means <25% and maxima <55%). The four evergreen species (*Blechnum*, *Pyrola*, *Polystichum*, and *Viola*) had lower proportions of biomass in belowground structures than did six of the other seven species. Mean total plant bio-

Table 2. Characteristics of rhizomes, roots, and shoots for 11 understory species in young coniferous forests of the Olympic Peninsula, Wash.

	Rhizome					Root	
Species	Total length (cm)*	Max. diam. (mm)	Lateral spread (cm)†	No. of ramets	Plant height (cm)‡	Max. length (cm)	Max. spread (cm)§
Nonclonal species							
Montia sibirica (10)	1.3 (0–2.4)	1.7 (0–3.0)	0.9 (0–1.7)	1.0	7.7 (3.0–12.0)	15.2 (3.5–41.0)	12.7 (3.5–30.0)
Listera caurina (11)	2.0 (0.5–4.0)	1.5 (0.5–2.0)	0.7 (0.1–2.0)	1.0	8.4 (4.0–12.5)	9.9 (6.5–14.5)	5.9 (3.0–11.0)
Trillium ovatum (10)	2.7 (1.2–5.0)	9.5 (5.0–16.5)	1.9 (0.5–4.0)	1.0	14.0 (9.0–20.0)	41.4 (20.5–98.0)	31.0 (15.0–60.0)
Disporum smithii (21)	6.8 (1.0–19.0)	3.2 (1.5–6.0)	4.4 (0.8–9.0)	1.0	14.9 (5.0–31.0)	43.1 (13.5–79.0)	30.4 (5.0–65.0)
Clonal species							
Blechnum spicant (21)	5.9 (1.8–16.0)	12.1 (6.0–24.0)	3.7 (1.0–11.0)	1.4 (1–2)	13.8 (4.0–31.0)	43.6 (17.0–100.0)	29.3 (10.5–50.0)
Polystichum munitum (20)	5.9 (1.5–17.0)	23.7 (5.5–62.0)	3.9 (1.0–10.0)	1.1 (1–2)	37.6 (15.0–74.0)	46.6 (18.5–145.0)	39.6 (14.0–110.0)
Dryopteris austriaca (10)	6.7 (2.0–19.5)	12.1 (4.0–20.0)	4.2 (0.5–11.0)	1.3 (1–2)	16.0 (8.0–46.0)	29.7 (12.0–55.0)	23.3 (12.0–36.0)
Viola sempervirens (20)	4.1 (0.5–17.5)	1.9 (1.0–3.0)	6.9 (0.2–24.0)	1.2 (1–3)	4.8 (0.5–9.0)	19.0 (11.0–36.0)	13.6 (4.5–38.0)
Pyrola uniflora (10)	97.3 (20.0–242.0)	ND	31.7 (11.0–55.0)	3.6 (1–9)	5.5 (3.0–8.0)	ND	ND
Maianthemum dilatatum (20)	133.5 (25.0–344.0)	1.2 (0.5–2.2)	70.2 (18.0–175.0)	2.0 (1–5)	11.8 (4.0–26.0)	8.7 (2.5–18.0)	5.7 (2.0–11.0)
Oxalis oregana (30)	137.4 (13.5–759.0)	1.8 (0.9–6.0)	56.7 (11.0–160.0)	4.8 (1–16)	8.4 (5.0–13.0)	14.5 (6.0–25.0)	11.5 (2.0–24.0)

Note: Species are ordered by degree of lateral spread. Numbers beside species names are number of clonal fragments excavated. Values are means per clonal fragment with ranges in parentheses. ND, no data.

*Rhizome length is the total additive length of rhizomes, spreading roots (for *P. uniflora*), or stolons plus rhizomes (for *V. sempervirens*).

†Lateral spread is the maximum distance of vegetative horizontal spread via rhizomes, or roots (for *P. uniflora*), or rhizomes and stolons (for *V. sempervirens*).

‡Plant height is the maximum height to leaf, stem, or frond.

§Max. root spread is the greatest horizontal distance from the junction of a root and rhizome to the farthest root tip.

Fig. 1. Maximum lateral vegetative spread versus maximum root depth of clonal fragments for (A) nonclonal species and (B) clonal species. See Table 2 for full names.

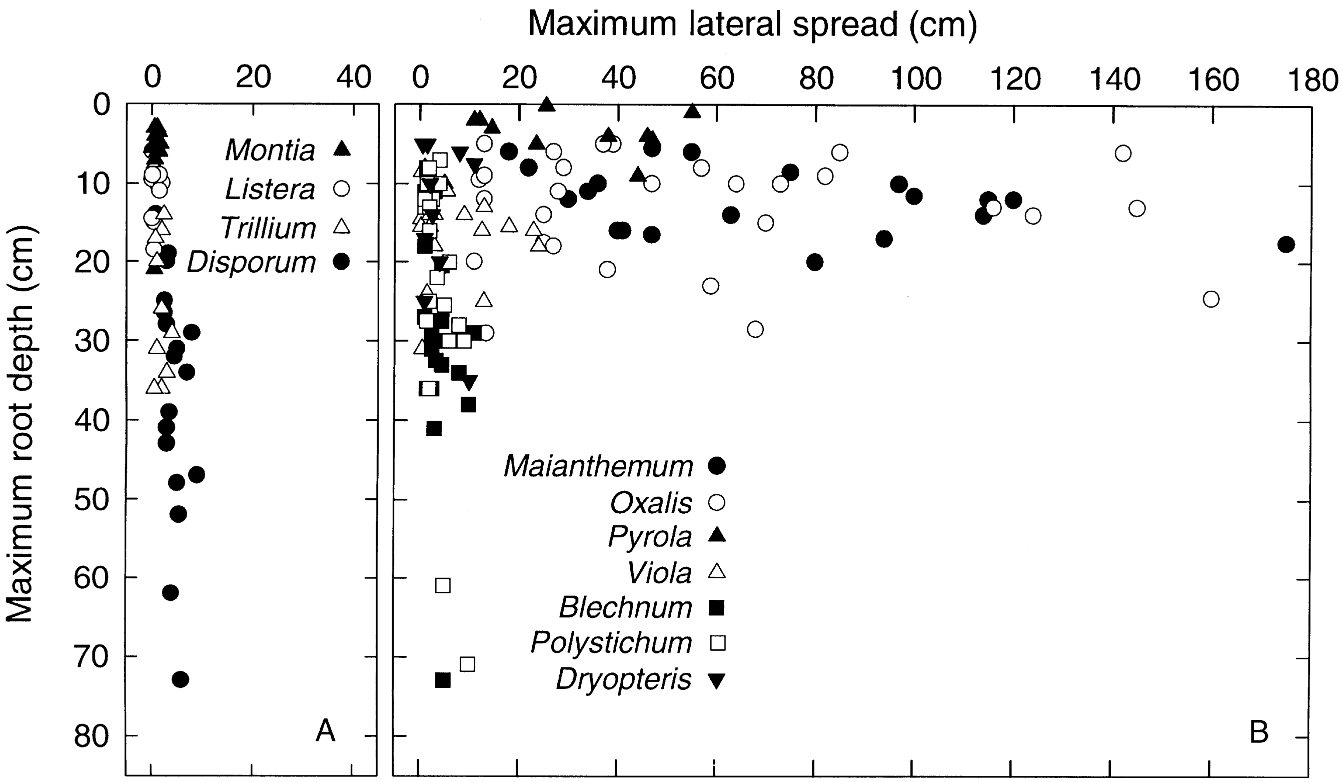


Table 3. Biomass characteristics of 11 understory species of young, coniferous forests of the Olympic Peninsula, Wash.

Species	Total plant dry wt. (g)	Root to shoot ratio	% of total dry wt. below ground
Nonclonal species			
Montia sibirica	0.11 (0.03–0.34)	0.4 (0.1–1.0)	24.0 (8.9–50.0)
Listera caurina	0.15 (0.06–0.44)	2.6 (1.0–10.0)	65.6 (50.0–90.9)
Trillium ovatum	0.85 (0.43–2.01)	5.8 (4.5–8.5)	85.0 (82.0–89.5)
Disporum smithii	1.53 (0.13–4.99)	6.9 (1.7–22.4)	83.6 (63.1–95.7)
Clonal species			
Blechnum spicant	4.31 (0.49–21.68)	1.1 (0.4–3.2)	49.1 (30.6–75.9)
Polystichum munitum	36.31 (1.49–178.31)	0.8 (0.3–3.2)	40.2 (23.5–76.4)
Dryopteris austriaca	1.60 (0.16–4.83)	2.1 (1.3–3.3)	67.0 (55.6–76.8)
Viola sempervirens	0.18 (0.05–0.68)	1.2 (0.3–7.5)	44.9 (21.1–88.2)
Pyrola uniflora	0.19 (0.04–0.65)	0.3 (0.1–1.2)	21.5 (7.7–54.5)
Maianthemum dilatatum	0.75 (0.07–2.62)	7.8 (0.9–37.0)	83.7 (48.2–97.4)
Oxalis oregana	1.36 (0.16–6.00)	5.2 (1.7–22.8)	80.9 (63.2–95.8)

Note: Species are ordered by degree of lateral spread. Sample sizes are indicated in Table 2. Values are clonal fragment means with ranges in parentheses.

mass differed by >300-fold among species and was highest for the three fern species (Table 3).

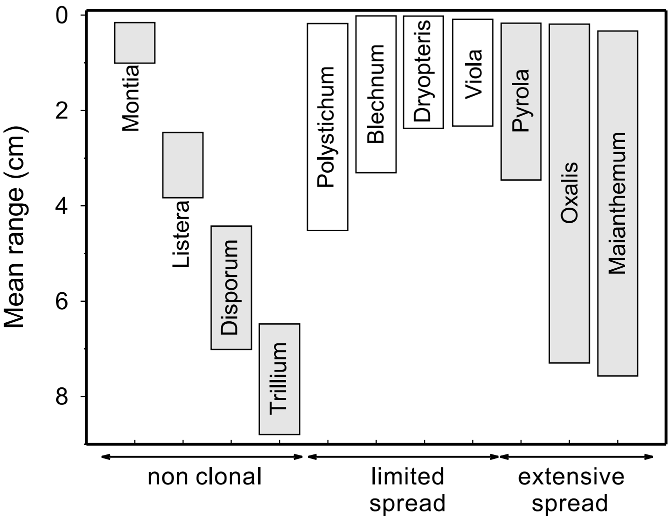
Root system development: individual species characteristics

Species' root systems differed in morphology, depth in the soil profile, and dimensions of roots and rhizomes (Table 2; Fig. 2). However, some species exhibited similar suites of traits. For example, species with extensive lateral spread were also among those with the shallowest rooting depths (Fig. 1B). In contrast, maximum depths of rooting and perennating structures among nonclonal species varied greatly (Fig. 1A, Fig. 2). Among nonclonal species, rooting depth increased with plant stature (cf. Fig. 1A and Table 2). We describe similarities and differences in root system development among species, with taxa grouped by their potential for clonal spread.

Nonclonal species

Four nonclonal, deciduous species (*Montia*, *Listera*, *Disporum*, and *Trillium*) had very short rhizomes but varying patterns of rhizome depth and belowground biomass distri-

Fig. 2. Mean ranges in depth (mean minimum to mean maximum) of perennating organs for the 11 species. See Table 2 for full names.



bution. With the exception of *Montia*, perennating buds of these species were buried deeper below the organic surface than the rhizomes were long (cf. Fig. 2 and Table 2).

Montia and *Listera*, with short rhizomes and roots, had the smallest total biomass of all species sampled (Table 3). *Montia* exhibited two forms of belowground development: 1st-year plants possessed a cluster of succulent stems and petioles supported by a thin, branched tap root with little biomass below ground. Older plants had fibrous roots emerging from a superficial rhizome. *Montia* also flowered frequently (80% of clonal fragments) in contrast with most of the other species sampled. *Listera*, an orchid, had the perennating portion of its rhizome buried ca. 2 cm below the organic surface (i.e., minimum rhizome depth; Fig. 2) and possessed fleshy, generally unbranched roots. At least half of its biomass occurred in belowground structures.

Trillium and *Disporum* had short rhizomes that were either thickened (*Trillium*) or knotty (*Disporum*) and deeper on average than those of the other species (Fig. 2). *Disporum* spread laterally more than other nonclonal species by adding annual sympodial rhizome segments. Both species possessed longer and deeper roots than did the other angiosperm species (Fig. 1A; Table 2) and had >83% of their biomass in belowground structures (Table 3).

Clonal species with limited lateral spread

The four species with limited lateral spread (*Polystichum*, *Blechnum*, *Dryopteris*, and *Viola*) had branched roots, shallow perennating buds (Fig. 2), and intermediate proportions of biomass below ground (Table 3). Although all four species were clonal, most plants consisted of a single rhizome segment that thickened with the production of new fronds or leaves. Among the ferns, 5% (*Polystichum*) to 38% (*Blechnum*) of the clonal fragments had more than one ramet emerging from a branched rhizome (Table 2). Some clonal fragments of *Dryopteris* had dimorphic rhizomes consisting of short, cornucopia-shaped perennating rhizomes connected by slender, scaly segments with long internodes. Roots of the ferns were wiry and densely branched, primarily spreading laterally through the upper organic horizon (Table 2); only a portion of the roots of most ferns extended deep into mineral soil.

Evergreen *Viola* formed new ramets via leafy stolons, but each ramet also possessed a short scaly rhizome. Although plants spread up to 24 cm, lateral spread averaged only 7 cm because <50% of the plants possessed stolons and interconnected ramets. *Viola* had the greatest variability among species in the proportion of biomass below ground (21–88%) because of variation in stolon production and rhizome length and poor development of rhizomes and roots on “daughter” ramets. Adventitious roots of mature plants were relatively long and few (2–7) with short, second-order branches.

Species with extensive lateral spread

Three species spread extensively by long, slender belowground organs, but only two of these species had rhizomes. All three placed perennating buds near the soil surface, but the maximum depth of perennating organs varied (Fig. 2).

Clonal fragments of the ericaceous evergreen herb *Pyrola* had the lowest proportion of biomass in belowground structures and spread about half as far as *Maianthemum* and *Oxalis*. *Pyrola* clonal fragments consisted of up to nine leafy shoots arising irregularly from a shallow, delicate, and highly branched root system (Goebel 1905), often spreading through substrates of decomposed wood or loose organic layers.

Among all seven clonal species, *Maianthemum* and *Oxalis* had the largest proportion of biomass below ground, the greatest potential for lateral spread, and the highest number of connected ramets (Tables 2 and 3). Both species expanded laterally through sympodial growth, producing new ramets at the tips of long horizontal rhizomes, while maintaining older leaf-producing ramets at scattered points throughout the clonal fragment. These ramets consisted of a series of annual rhizome segments with very short internodes (a short shoot), an annual flowering stem or leaf (*Maianthemum*) or cluster of leaves and flowers (*Oxalis*), and associated roots. Leaf senescence left clusters of scale-leaf scars (*Maianthemum*) or spirally stacked, swollen petiole bases (*Oxalis*) along these buried short shoots, providing evidence of ramet longevity (Lezberg 1998). Within both species, clonal fragments varied greatly in rhizome length and lateral spread (Table 2; Fig. 1B). Density of live ramets per length of rhizome averaged ca. 5/m for *Oxalis* and 2/m for and *Maianthemum*. Both species had relatively short roots (Table 2), but patterns of branching and emergence differed. The short, simple roots of *Maianthemum* emerged in whorls of 3–6 at nodes every 1–5 cm along the rhizomes. On *Oxalis* rhizomes, branched roots emerged singly at both nodes and internodes.

Discussion

Although we sampled only a subset of the herbaceous species found in these closed-canopy forests, we included the most common ones. Even among these, growth form, clonal spread, and biomass distribution varied markedly, with most species exhibiting unique combinations of traits. Similar variability in rhizome and stolon length, degree of spread and clonality, and biomass distribution have been found for herbaceous species in late-successional coniferous forests of western Oregon (Antos and Zobel 1984) and in deciduous or mixed hardwood forests (Sobey and Barkhouse 1977; Abrahamson 1979), but the explanations for this diversity remain obscure (Abrahamson 1979; Gross 1983). As none of the 11 species studied are restricted to young, closed-canopy forests, their root system traits may reflect adaptations to more heterogeneous environments of late-successional and disturbed forest habitats. The patchy but extreme shade that can occur in old-growth forest understories may have selected for a mix of below- and aboveground traits (Yoshie 1995; Henry and Aarssen 1997) that enhance resource exploitation in young dense stands.

Perennating organs

As in other temperate forests (Salisbury 1942; Sobey and Barkhouse 1977; Bierzychudek 1982; Antos and Zobel 1984), herbaceous species studied in these young, closed-canopy stands were mostly perennial and rhizomatous, although some possessed stolons or roots from which new shoots emerged. The perennial growth form allows for continuity of successful genotypes and may be critical for survival when sexual reproduction is limited, as was observed in these closed-canopy stands. Storage of resources and buds in rhizomes can facilitate resprouting of forest plants after disturbance and seasonal dormancy (Zobel and Antos 1987; Yoshie and Yoshida 1989; Alaback and Tappeiner 1991) or continuous leaf production during extreme light-limitations (Messier et al. 1989; Huffman et al. 1994). Four of our study species with both short and long perennating segments have flexible growth forms that allow herbaceous species to recover from burial by tephra and to exploit spatial and temporal variability in microsites (Antos and Zobel 1984, 1985; Carlsson et al. 1990).

Clonality, vegetative spread, and persistence

The sampled sites supported both nonclonal and clonal species, but most plants consisted of few interconnected ramets with low to moderate spread. Thus survival in dense, young coniferous forests appears not to be contingent on lateral mobility or clonal propagation, as shown by immobile species that have persisted under the relatively unfavorable conditions at our sites for many years.

Among the nonclonal species, persistence may be achieved through very disparate life-history strategies. For species with short-lived rhizomes, such as *Listera* and *Montia*, sexual regeneration appears critical. In contrast, for *Trillium* or *Disporum*, in which we observed few signs of sexual reproduction, traits associated with a long life-span, such as successive resprouting of perennating buds, deeply buried rhizomes, and relatively long roots, are likely to be more important for survival in closed-canopy stands.

Plants with limited spread may reflect a compact growth form or a plastic response to environmental conditions. For example, the rhizomes of ferns spread by branching or thickening rather than by extensional growth, and thus the potential to form large clones appears to be morphologically constrained. On the other hand, large intraspecific variation in clonal spread (e.g., *Maianthemum*, *Oxalis*, and *Viola*) may indicate a plastic response to local changes in abiotic and biotic environments (e.g., nutrients, light, pathogens) or genetic variability within populations (Kana 1982). These spreading species are more likely than the nonclonal species to encounter new soil and light environments through vegetative spread. However, clonal growth of other forest herbs is known to decline under dense canopies or relatively low light compared with growth under more open canopies or higher light levels (Ashmun and Pitelka 1984; Tappeiner and Alaback 1989), suggesting that resource variability both within and among sites may influence the degree of clonality and spread of *Maianthemum*, *Oxalis*, and *Viola*. Nevertheless, the ability of *Maianthemum* to maintain older photosynthetic ramets at a given location when clonal growth is curtailed is an important element of persistence in closed-canopy stands (Lezberg 1998).

Biomass distribution

The species sampled were not characterized by a consistent pattern of biomass allocation. The smallest proportion (<25%) of belowground biomass observed is typical of annuals or short-lived perennials that dominate early successional sites (Antos and Halpern 1997) or old fields (Abrahamson 1979) and the highest values (>80%) are comparable to those of perennial herbs of late-successional forests in the region (Antos and Zobel 1984). Under dense forest canopies, low light should favor traits that enhance light absorption and thus should lead to relatively high allocation to aboveground structures (Abrahamson and Gadgil 1973; Menges 1987). Evergreen leaves may allow for efficient photoassimilation and storage in leaves (Chapin 1980; Sprugel 1989), and of five species with >50% of their biomass above ground, four were evergreen. However, the extremely low root to shoot ratio of *Pyrola* (0.3) may underestimate the true allocation of carbon to *Pyrola* roots, which have known associations with mycorrhizal fungi (Salisbury 1942; Robertson and Robertson 1985).

That 6 of 11 species had relatively high allocation of biomass to roots and rhizomes (means >50%) suggests that belowground resources may be equally or more limiting than light. Root competition from trees may contribute to nutrient limitations in these dense, closed-canopy forests (Toumey and Kienholz 1931). However, allocation to nutrient foraging structures (roots) was only one component of the large proportion of belowground biomass; rhizomes were also important. Relative to species of early successional sites, herbs of temperate forests often have higher proportions of biomass below ground, reflecting frequent vegetative propagation, cumulative growth below ground, and resource storage in their buried perennial organs (Abrahamson 1979; Gross 1983; Zobel and Antos 1987; Gleeson and Tilman 1990).

Significance of root system traits for understory reinitiation

As the canopies of dense, young forests open with time, or are thinned silviculturally, resource levels increase and can allow for greater development of the herb layer (Bailey et al. 1998; Thomas et al. 1999). Reinitiation of the understory is contingent on an adequate source of seeds or on vegetative reproduction of extant plants. However, most forest herbs are absent from the seed bank of these sites (Halpern et al. 1999) and woodland herbs generally are thought to possess limited dispersal capability (Cain et al. 1998). Residual species, rather than new species invading by seed, increased most in abundance following thinning of other young, coniferous forests (Alaback and Herman 1988). Thus, plant survival through stand closure should be critical to future understory development. However, the contribution of residual species to increases in understory cover depends on their ability to spread once resource conditions improve. Manipulative studies that quantify the vegetative spread of forest herbs in response to increased light are rare (Ashmun and Pitelka 1984, 1985; Marino et al. 1997) and will be necessary to determine their responses to thinning or natural canopy opening. Our results suggest that clonal species that typically produced multiple ramets in closed-canopy stands, such as *Maianthemum* and *Oxalis*, will be most successful; each module can initiate vegetative growth because it contains the roots, leaves, and buds needed to capture and utilize resources as they become available. However, for the many species with limited potential for vegetative spread, we expect that seed production and dispersal within site will be the primary mechanisms by which populations expand during understory reinitiation.

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