ECOLOGICAL IMPLICATIONS OF BELOWGROUND MORPHOLOGY OF NINE CONIFEROUS FOREST HERBS

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The morphology of forest herbs was examined to determine how variation in growth form could relate to growth and survival in the forest. Five to 10 plants of nine herbaceous species were totally excavated in old-growth forests in the central Oregon Cascade Mountains. Underground parts were mapped, measured, oven-dried, and weighed. Additional information was derived from sites in the southern Washington Cascades. Achlys triphylla, Clintonia uniflora, and Smilacina stellata maintain extensive rhizome systems with both short and long shoots. This growth form allows these species flexibility in exploiting the forest environment. The three species differed in rate of extension growth and rooting depth. Arnica latifolia spreads by long rhizomes, which persist for only a few years; thus, extensive interconnected stem systems do not develop. Rubus lasiococcus and Linnaea borealis have extensive stolon systems with greater potential rates of spread than the three rhizomatous species. Although they expand rapidly under favorable conditions, they may be displaced by taller herbs. Rubus has larger and deeper roots than Linnaea. Tiarella trifoliata, Valeriana sitchensis, and Erythronium montanum have minimal vegetative spread. Plants of these three species often included the original seedling structure, indicating that seedling establishment is relatively frequent. On the six species with extensive vegetative spread, we never found a seedling source; genets are older than 5-36 yr, and new genet establishment appears to be uncommon. The differences in growth form among the species help to explain their ability to survive and coexist in the heterogeneous forest floor environment.

Introduction

The ecological implications of plant characteristics are poorly understood for most species of forest herbs (BIERZYCHUDEK 1982), as are mechanisms that allow coexistence. There are many possible types of niche segregation among forest herbs; characteristics of underground organs may allow species to exploit resources differently. The nature of underground structures controls vegetative expansion and reproduction of many species as well as their nutrient and water uptake. Root systems vary among species, especially in their vertical distribution (WEAVER 1919; HOLCH et al. 1941). Much of this variation can be explained in relation to environment and the partitioning of resources among species (WEAVER 1958a, 1958b). The horizontal growth of underground stems produces vegetative spread, and appropriate rhizome geometry facilitates colonization of an area (WATT 1940; BELL 1974; BELL and TOMLINSON 1980). Many plant populations can be considered as a group of modules that result primarily from spread of rhizomes or stolons (HARPER and BELL 1979).

Vegetative reproduction is especially important in forest herbs (SALISBURY 1942; WHITFORD 1949; ABRAHAMSON 1980; WINN and PITELKA 1981), which vary in their extent, method, and pattern of expansion. Moreover, the life span of rhizomes varies, leading to morphologies ranging from sin-

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Address for correspondence and reprints: JOSEPH A. ANTOS, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331. gle isolated shoots to large, interconnected shoot systems. Some herbs reproduce vegetatively, and others are fixed in position and reproduce strictly by seed (BIERZYCHUDEK 1982).

We examined underground characteristics of nine herbs of contrasting growth form growing in coniferous forests. Our specific objectives were (1) to document the underground morphology of the species, and (2) to evaluate the possible significance of the various morphologies in relation to the growth and survival of the species in the forest.

Material and methods

The nine species we examined are Achlys triphylla (Berberidaceae), Arnica latifolia (Asteraceae), Clintonia uniflora (Liliaceae), Linnaea borealis (Caprifoliaceae), Rubus lasiococcus (Rosaceae), Smilacina stellata (Liliaceae), Tiarella trifoliata var. unifoliata (Saxifragaceae), Valeriana sitchensis (Valerianaceae), and Erythronium montanum (Liliaceae). They were chosen because of their differences in growth form and their common occurrence in subalpine coniferous forests of the Cascade Range.

Most plants were excavated at 1,400 m elevation in the H. J. Andrews Experimental Ecological Reserve (Andrews EER) in the central Oregon Cascade Mountains. The vegetation represents the *Abies amabilis* zone, where temperatures are cool and deep winter snowpacks accumulate (FRANKLIN and DYR-NESS 1973; ZOBEL et al. 1976). The climate is wet maritime with a relatively dry summer. The site was on a ca. 10° northwest slope in old-growth forest dominated by *Abies amabilis*, *A. procera*, Pseudotsuga menziesii, and Tsuga heterophylla. Many species of herbs, ca. 10 of which were common, provided complete cover over much of the area. Small trees of A. amabilis were numerous, but shrubs were sparse. Some plants were excavated in similar forests a few kilometers away, and E. montanum, which does not occur in the Andrews EER, was excavated 45 km farther north at Monument Peak, Oregon. The forest at Monument Peak was younger but in other ways similar to that at the Andrews EER.

A secondary study location was in old-growth forests of the A. *amabilis* zone northeast of the volcano Mount St. Helens, Washington. The tree canopy was not seriously damaged by the 1980 volcanic eruption, but 150 mm of volcanic aerial ejecta were deposited on the forest floor. We use data only from plant parts that formed prior to the 1980 eruption and should not have changed as a result of the volcanic deposit. Data from this area are used only to augment observations from the Oregon sites.

At the Oregon sites we completely excavated 10 plants of each of five species and between five and nine plants of the other four species. About half of the plants were excavated in September 1981, the others in September 1982. We chose shoots that were relatively free of herbivore or other damage. Starting at the shoot, we carefully excavated all connected plant parts by hand, using various small digging implements. Some plants included only a short rhizome with one or two aerial shoots, while in others an extensive rhizome or stolon system had many attached shoots. We mapped the rhizome (stolon) system of all plants, noting yearly growth increments and the positions of aerial shoots and major roots. The term "segment" refers to an annual length growth increment. We recorded root length, depth, and extent of branching; rhizome depth, diameter, and length; aerial shoot height, number of leaves, and leaf area; and total area covered by the entire plant. For all plants we estimated leaf area in the field; for about half of these, we also obtained area of dried leaves with a leaf area meter. The values were similar, and we have chosen to use the field estimates. All measurements were made in the field: plants were washed, separated into major parts, and frozen within a few hours of excavation. Plants were eventually ovendried at 70 C to constant weight (ca. 24 h in most cases) and weighed.

At the Mount St. Helens sites, plants were excavated during the summers of 1981 and 1982 and oven-dried immediately. We successfully excavated all rhizome and stolon tissue on plants used in the analysis; excavating the entire root systems proved impractical. Much of the root mass was lost for two species with very brittle roots.

All nomenclature follows HITCHCOCK and CRON-QUIST (1973).

Results

PLANT FORM AND SIZE

The nine species vary greatly in growth form and size (table 1). Achlys triphylla, Clintonia uniflora, and Smilacina stellata have long rhizomes, which often persist for many years (table 2), and ephemeral aerial shoots. Rhizomes of Arnica latifolia also elongate rapidly but are shorter in total length. The long stems of Rubus lasiococcus and Linnaea borealis result from rapidly growing stolons that persist for many years. Tiarella trifoliata and Valeriana sitchensis have short rhizomes and very limited vegetative spread. Erythronium montanum has a short cormlike structure that is fixed in position.

The three species that maintain extensive rhizome systems (A. triphylla, C. uniflora, and S. stellata) have dimorphic annual segments. Short rhizome segments produce leaves in approximately the same position annually. Long rhizome segments expand the plant into new areas. Short shoots can occur as side branches of long segments, can produce a long segment, and are occasionally terminal to a long segment. For these three species, we never found a segment that seemed to have been produced when the plant was a seedling.

Plant size, as indicated by rhizome length, number of shoots, number of leaves, number of roots, and weight of the different parts, varies greatly both among and within species (table 1). For most species, size varies among plants by over an order of magnitude. In many species, plant size is skewed, with the mean greater than the median, often because of one to three exceptionally large plants (fig. 1). This is especially clear with *Clintonia* and *Smilacina*.

Relative dry weight of the three major parts of the plants varies considerably (fig. 2). *Clintonia*, *Rubus*, and the two short-rhizomatous species have the largest relative root weight; *Erythronium* has minimal roots. The long-rhizomatous species generally have the lowest percentage dry weight in leaves.

STEMS AND LEAVES

The large leaves of A. triphylla arise directly from subterranean rhizomes; stems emerge aboveground only when a rhizome tip turns upward to yield an inflorescence. First-year rhizome segments are uniformly white, while older segments are longitudinally striped and brownish. Internodes are often ca. 10 mm long and are easily delineated on younger rhizome segments by the small scales at the nodes. Annual segments are indicated by a group of short internodes. On older rhizomes, annual increments can be hard to distinguish because few scales are present. Our conservative estimate indicates plants at the Andrews EER averaged 14 yr of live rhizomes. One had 36 annual rhizome segments (ta-

	Achlys triphylla (no. = 9) ^a		Clintonia uniflora (no. = 10)		Smilacina stellata (no. = 7)			Arnica latifolia (no. = 9)			
Rhizome, stolon, or									· · · ·		
corm length (m)	3.55	±	.77	2.46	±	.82	8.06	±	3.15	.75	± .17
No. aerial shoots	5.4	±	1.1	4.9	±	1.4	21	±	8	1.8	±.4
No. leaves	5.4	±	1.1	10.0	±	2.9	201	±	63	7.9	± 1.4
No. roots	247	±	42	34	±	9	1,300	±	500	14	± 3
Maximum root length							,			-	-
(m)	.21	±	.02	.35	±	.04	.25	±	.03	.22	± .03
Maximum root depth											
(m)	.19	±	.02	.29	±	.04	.23	±	.02	.18	± .03
No. of roots per meter of rhizome,											
stolon, or corm	84	±	8	17	±	2	168	±	23	21	± 3
(stolon or corm)											
diameter (mm)	1.2	±	.1	.9	±	.1	2.1	±	.1	1.0	± .1
(stolon or corm)											
diameter (mm)	2.7	±	.3	1.4	±	.2	3.9	±	.1	2.1	± .2
Rhizome, corm, or											
stolon dry wt (g)	4.88	±	1.08	1.10	±	.41	12.37	±	4.63	.50	± .09
Root dry weight (g)	1.15	±	.24	.94	±	.29	2.66	±	.86	.15	± .06
Leaf dry weight (g)	1.28	±	.26	.61	±	.21	2.30	±	.96	.23	± .03
Leaf area (m^2)	.049	±	.011	.024	±	.008	. 105	±	.044	.010	± .002
Rhizome, stolon, or corm dry wt per											
unit length (g/m)	1.40	±	.06	.41	±	.02	1.58	±	.15	.69	± .09
Maximum leaf height											
(m)	.26	±	.01	.05	±	.01	.18	±	.01	.12	± .01

TABLE 1 Means of plant values (± SE) for comparable characteristics among the species examined

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NOTE.---ND = not determined. * No. plants excavated.

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TABLE 2
CHARACTERISTICS OF LONG-RHIZOMATOUS SPECIES AT ANDREWS EER, OREGON, AND MOUNT ST. HELENS, WASHINGTON

	ACHLYS TRIPHYLLA		CLINTON	IA UNIFLORA	Smilacina stellata	
	Andrews $(no. = 9)$	St. Helens $(no. = 8-10)$	Andrews $(no. = 10)$	St. Helens $(no. = 8-11)$	Andrews $(no. = 7)$	St. Helens $(no. = 17)$
Rhizome segments which are						
short (%) Average long segment	ND	ND	57 ± 4	53 ± 9	59 ± 2	54 ± 3
length (m) Maximum long segment	.17 ± .01	.17 ± .03	.14 ± .01	.08 ± .01	.15 ± .01	.10 ± .01
length (m)	.35 ± .03	.40 ± .07	.21 ± .01	.14 ± .01	.25 ± .02	.19 ± .01
depth (mm) Maximum rhizome	14 ± 4	ND	14 ± 2	ND	9 ± 4	ND
depth (mm) No. of new long rhizome segments	114 ± 17	ND	69 ± 8	ND	89 ± 8	ND
per plant per year No. of years represented by	1.8 ± .6	ND	.9 ± .4	ND	7.7 ± 2.5	ND
rhizome segments	14 ± 3	13 ± 1	12 ± 2	17 ± 1	14 ± 1	13 ± 1

NOTE.—Means \pm SE for the number of plants indicated. ND = not determined.

Rubus lasiococcus (no. = 10)	Linnaea borealis (no. = 5)	Tiarella trifoliata (no. = 10)	Valeriana sitchensis (no. = 10)	Erythronium montanum (no. = 10)
$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$5.84 \pm 1.4641 \pm 8325 \pm 7229 \pm 9$	$.12 \pm .04$ $1.2 \pm .1$ 7.1 ± 1 $14 \pm .3$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
.45 ± .04	.28 ± .03	.36 ± .04	.25 ± .01	.08 ± .01
31 ± .03	.25 ± .02	.21 ± .03	.22 ± .01	.12 ± .01
14 ± 2	5 ± 1	176 ± 33	323 ± 79	280 ± 37
.9 ± .1	.6 ± 0	$1.3 \pm .1$	2.1 ± .2	ND
1.6 ± .1	1.5 ± 0	$3.2 \pm .3$	4.5 ± .3	ND
$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	$.31 \pm .1$ $.27 \pm .06$ $.18 \pm .02$ $.007 \pm .001$	$\begin{array}{rrrrr} .75 & \pm & .18 \\ .80 & \pm & .14 \\ .69 & \pm & .19 \\ .022 & \pm & .005 \end{array}$	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
.53 ± .05	.35 ± .03	$2.25 \pm .26$	3.56 ± .46	4.03 ± .37
.06 ± 0	.07 ± 0	.08 ± .01	.14 ± .01	.07 ± .01



AT ANDREWS EER, OREGON

FIG. 1.—Total rhizome (stolon) lengths of plants at Andrews EER, Oregon.

ble 2), the oldest datable live tissue we found. The genet age cannot be determined since dead rhizome segments decompose in 2 yr or less.

The rhizome system of *Achlys* can be complex (fig. 3). Leaves do not necessarily form at the end of a long or short rhizome every year. On one plant all leaves were on short shoots on an older rhizome, while a vigorously growing rhizome had none. The rhizomes are tough, flexible, and difficult to break. They generally occurred 0.01-0.12 m deep but sometimes reached 0.2 m. An average plant annually produced just under two new, long rhizome segments and five leaves (tables 1, 2).

New rhizome segments on *C. uniflora* are ca. 2 mm in diameter, but they soon slough part of the cortex to become thin, tough strands ca. 1 mm in diameter. Annual segments have no scales or other markings and may represent a single internode. The end of each segment is distinctly swollen. The segments are much shorter, and weight per unit of rhizome length is less than for *Achlys* (tables 1, 2).

Rhizomes on *Clintonia* are a mixture of short and long shoots (fig. 4). Plants at Andrews EER average 40 total segments, of which 24 are short. Living rhizomes average 12 yr at the Andrews EER and 17 at Mount St. Helens (table 2). The plants average fewer than one new long rhizome segment



FIG. 2.—Percentage of oven-dry weight contained in leaves; rhizomes, stolons, or corms; and roots for the nine species examined at Andrews EER or Monument Peak, Oregon.

(table 2). Under adverse conditions the rhizomes apparently fail to elongate, and the plants persist with leaves confined to short shoots. One to three leaves are almost always produced at the end of new segments, in contrast to the frequent lack of



FIG. 3.—Map of a slightly larger than average Achlys triphylla at Andrews EER. Number of roots per segment is indicated by the numerals. A dot on the rhizome indicates the end of an annual growth increment. Thicker lines indicate a series of short segments. \bigcirc , the locations of leaves.



FIG. 4.—Map of a large *Clintonia uniflora* (5.1 m, total rhizome length) at Andrews EER. Dashed lines indicate roots with the length (cm) indicated at the end of each. A dot on the rhizome indicates the end of an annual growth increment. O, the locations of leaves. A thick line represents a part of the rhizome system that is composed of short shoots; the number of short shoot segments is indicated.

leaf formation in Achlys. Clintonia produces an aboveground stem only during flowering.

Smilacina stellata plants are the largest of the species we studied (table 1). One plant from Andrews EER has a total rhizome length of 26 m (fig. 5). The rhizomes are robust and from 2 to 4 mm in diameter (table 1). In contrast to Achlys and Clintonia, Smilacina produces vegetative aerial stems. These determinate, annual shoots normally bear seven to nine leaves, occasionally produce flowers at the tip, and leave a large distinctive scar on the rhizome. Aerial shoots are produced on both long and short rhizome segments in most years.

Instead of determinate, ephemeral, aerial shoots, A. latifolia forms aerial shoots from upturned rhizome tips, which may persist for a number of years. New rhizomes arise from the base of the vertical part of old rhizomes. Age of aerial shoots can be determined with fair reliability, but age of rhizomes is difficult to determine. It appears that most plants included less than 10-yr-old rhizomes.

Arnica plants have much smaller rhizome systems than Achlys, Clintonia, or Smilacina (table 1), largely because of shorter rhizome life. The other three species have tough, flexible rhizomes, but



FIG. 5.—A very large *Smilacina stellata* with 26 m of rhizome, 58 shoots, 432 leaves, and 21 new long rhizome segments. The plant, apparently in a favorable microsite where extensive branching was possible, represents 17 yr of growth. The numbers of annual segments in rhizome sections composed of short shoots are indicated by the numerals. A dot indicates the end of an annual rhizome increment. O, the locations of determinate aerial shoots.

Arnica rhizomes are weak and brittle. Arnica rhizomes do not produce short shoots; the persistent aerial shoots are the closest analogue.

In contrast to the preceding four species, R. lasiococcus and L. borealis spread vegetatively by stolons, which grow on the soil surface and have persistent leaves. Their stolons grow more rapidly than any of the long rhizomes (tables 2, 3). The annual increments can be discerned for the first 1-3 yr, after which the pattern is obscured in part by their limited secondary growth. The stolons, generally 1-1.5 mm in diameter (table 1), eventually become covered by litter (table 3): 35% of the *Rubus* stolon length was above the litter, compared to >50% for *Linnaea*. We estimate that the deeply buried stolon parts are 10 yr or older. Main branches with rapidly growing tips form when a short branch starts to grow rapidly. Frequent short stolons, with one to two leaves, occur along younger long segments of *Rubus* (fig. 6). These short stolons normally die, but occasionally they grow out to form new long, rapidly growing stolons. *Linnaea borealis* had over three times the total stolon length of *Rubus* (table 1), 40% attributable to the frequent, short side branches. *Linnaea* stolons weighed the least per unit stem length of any species examined (table 1).

Tiarella trifoliata and V. sitchensis do not spread appreciably by vegetative means. Their rhizomes are short (table 1). Tiarella rhizomes are more slender, weigh less per unit length, branch less, and produce fewer aerial shoots than Valeriana (table 1). Although the new rhizome tip of both species remains at the soil surface, the older parts of the rhizome become buried by litter, Tiarella to an average depth of 34 mm (maximum observed = 80 mm), deeper than for Valeriana (10 mm), Rubus, or Linnaea. Annual increments are not distinguishable on the rhizome of Valeriana and Tiarella, so age cannot be determined. The original seedling source, as indicated by a very small rhizome end, was present on 70% of Tiarella and 40% of Valeriana plants; the oldest part of other plants was dead. Most rhizome internodes of Tiarella are very short, but burial by litter may induce occasional long internodes. One plant produced a series of long internodes under a piece of fallen bark. Branching of Valeriana occurs when a rhizome tip turns up to form an inflorescence; new rhizomes then form from lateral buds on the upturned rhizome. On Tiarella, inflorescences come from lateral rhizome buds.

Erythronium montanum has no means of vegetative spread. The plants have one or two leaves,

TAB	LE 3

Means \pm SE for characteristics of three species with stolons or long rhizomes that emerge aboveground

	Arnica latifolia	Rubus lasiococcus	Linnaea borealis
Stem length above litter (%) Maximum rhizome (stolon)	12 ± 3	35 ± 7	51 ± 4
depth (mm) Number of rapidly growing	80 ± 14	31 ± 4	27 ± 4
rhizome or stolon tips Maximum current year extension	$2.3 \pm .5$	$2.6 \pm .5$	$2.2 \pm .5$
growth (m)	ND	.40 ± .09	.38 ± .07
Average root length (m)	.09 ± .01	.13 ± .01	.11 ± .01

NOTE.—Data are from Andrews EER, Oregon. ND = not determined.



FIG. 6.—Map of *Rubus lasiococcus* of approximately average size (1.71 m of stolon). A circle at the end of a dotted line represents a leaf. Dashed lines represent roots, and the number at the end indicates the root length (cm). DE = Dead end (stolon that has died back).

which come from a vertical to coiled corm ca. 60-90 mm below the surface. The corms, ca. 70 mm long, consist of two parts: (1) a current segment largely composed of a fleshy bulblike scale, and (2) a chain of old, isodiametric segments. The latter part constitutes about half the total length. The corm segments represent annual growth increments, so it is possible to obtain the age of living material and a minimum estimate of plant age. At the oldest end of the corm, ca. 10% of the plants have a small linear segment that indicates the seedling. The Monument Peak plants have an average of 13 live segments and an average minimum age of 15 yr, including attached dead segments. The St. Helens plants have an average minimum age of 17 yr, with one plant reaching 39 yr; the number of live corm segments reached 25.

ROOTS

Achlys roots are distributed all along the rhizome, both at the nodes and on the internodes. They are often absent on the new white segments but appear to reach full size in the second year. There appears to be little, if any, subsequent growth, even though the roots persist for years. The roots are thin, well branched, and radiate in all directions from the rhizome. Roots are short (table 1), rarely exceeding 0.2 m deep. Roots tend to be concentrated on the new parts of the rhizome system.

Clintonia normally produces two new roots at the end of each new rhizome segment; no roots are produced within an annual segment. Roots grow mostly during the first two seasons, averaging 0.15 m long with few branches. The roots are longer and deeper than for the other long-rhizomatous plants (table 1).

The roots on *Smilacina* are dimorphic. A large root that grows straight downward occurs at the junction between some segments; numerous small roots emanate in all directions from the rhizome. The large roots constitute less than 4% of the roots but reach at least 0.34 m long and may survive many years. Roots appear to develop fully in the first year or two and then gradually die so that old rhizome segments bear few or none. The small roots exceeded 200/m of rhizome during the first 3 yr, but by year 7 dropped below 100/m.

Arnica root development is more variable than in Achlys, Clintonia, or Smilacina. As with the rhizomes, the roots are brittle and do not give the impression of durability.

Rubus lasiococcus often has many small roots and a few much larger ones (fig. 6), the latter usually on the older stolon. Average maximum root length and depth exceed that of the other species we studied (table 1). On one of the St. Helens plants a root reached 0.85 m long and 0.5 m deep. The roots appear to grow in length and diameter as long as they live and can reach 2 mm in diameter, the same size as the largest stolon. Many plants had one to three large roots on thick stolon segments.

Linnaea roots are scattered all along the stolons. Large roots occur on the older stolons. Sometimes there is a large root at the oldest end of the plant, but not as frequently as with *Rubus*. The roots extend both down and laterally from the stolons. The number of roots per unit length of stolon or rhizome (5/m) is the lowest of any of the species examined (table 1).

Roots occur all along *Tiarella* rhizomes, but most roots, especially the larger ones, are concentrated on older parts of the rhizomes. Often two large roots occur at the oldest end of a rhizome, apparently the location of the original seedling. The roots are tough and finely branched. The largest roots exceeded 1 mm in diameter.

Valeriana roots radiate from the rhizome in all directions; most angle downward. Few roots remain in the litter layer. The roots are large, often 1 mm in diameter, and branch sparingly except near the end. Since the roots are brittle and difficult to excavate, lengths and depths (table 1) are minimum estimates.

Erythronium roots are even more brittle and hard to excavate. It is obvious, though, that Erythro-

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nium has less root development than the other species examined (table 1, fig. 2).

Discussion

The forest is a highly heterogeneous environment in both space and time, and herbs in forest understories may be inhibited by several different environmental factors (TOUMEY 1929; TOUMEY and KIENHOLZ 1931; ANDERSON et al. 1969). Given the variable nature of the tree canopy, especially in oldgrowth forests like those we sampled, the multiple ways in which the canopy affects herbs, and the variability of the substrate, the forest floor environment clearly is heterogeneous for more than one resource. The coexistence of herbaceous species of very different growth forms may, in part, relate to this heterogeneity; some growth forms may be more successful than others in a given microsite.

The nine studied species can be divided into four major morphological groups of apparent ecological importance: (1) species with rapidly growing rhizomes that develop long, complex rhizome systems (Achlys, Clintonia, Smilacina); (2) species with a shorter system of fast-growing but less durable rhizomes (Arnica); (3) species with extensive stolons that elongate rapidly (Linnaea, Rubus); and (4) species with limited or no capacity for vegetative spread (Tiarella, Valeriana, Erythronium).

Species varied both among and within morphological groups in several characteristics that can affect their ecological behavior. Some species have no form of vegetative expansion. Among species that proliferate vegetatively, differences occur in rate of spread, degree of connectedness maintained among aerial shoots, presence of long versus short rhizome segments, and consistency of production of aerial shoots by rhizome segments. Seedling reproduction and maximum age of genets appear to be inversely correlated. Rooting varies in depth, density of surface roots, and the duration of individual root growth. Leaves vary in longevity and height above the ground.

The five species that maintain extensive rhizome or stolon systems overlap considerably in distribution at Andrews EER (ZOBEL et al. 1976). Their distributions are centered at the cold end of the temperature gradient except for *Linnaea*, which is most abundant toward the warm end but occurs all across the gradient. Even though these species greatly overlap in habitats occupied, they have morphological differences that may be important in segregation among microhabitats within a stand.

MORPHOLOGICAL VARIATION

All three species with extensive rhizome systems have a dimorphic pattern of extension growth that is analogous to the long and short shoots of some woody plants. New long segments extend the plant into new areas, while short segments allow leaves to be produced in the same spot annually. Leaves can remain in particularly favorable microsites, while rhizomes cross at least 1 m of unfavorable habitat. This growth form provides flexibility in dealing with the variable environment of the forest floor—but at the cost of maintaining the rhizome system connections.

Achlys and Smilacina in general are similar. Although Achlys is more widespread in forests at Andrews EER (ZOBEL et al. 1976), it is restricted to forests of the Pacific Northwest, while S. stellata occurs in a wide range of habitats over much of North America. Its dimorphic root system may give Smilacina a considerable degree of flexibility; e.g., its roots reached 1 m deep in a gravel slide community (WEAVER 1919).

Clintonia differs in leaf height from *Achlys* and *Smilacina*, which have leaves well above the ground surface and often form dense patches. In contrast, the shorter leaves of *Clintonia* rarely form a continuous layer. *Clintonia*, extremely tolerant of shade and with fairly deep roots, can persist under dense tree or herbaceous canopies where light and summer surface moisture are reduced. Under adverse conditions, long rhizome segments are not produced; the plants simply persist until conditions improve. *Clintonia* appears to be highly stress tolerant sensu GRIME (1977).

The two stoloniferous species, Rubus lasiococcus and Linnaea borealis, spread more rapidly than those with long rhizomes, perhaps because of greater ease of spread over the surface than through the soil. Also, stoloniferous species can use elevated substrates unavailable to rhizomes (rocks, recent logs, tree bases) and are not stopped by underground obstructions. Both stoloniferous species, especially Linnaea, have numerous short leafy shoots that develop into new long shoots; their branch growth is highly flexible and greatly dependent on local environmental conditions. The roots, especially on Rubus, continue to enlarge and to intensify their use of favorable soil conditions; in contrast, roots of the three long-rhizomatous species grow mostly in the first one or two seasons.

The two stoloniferous species differ in root development. Linnaea has little commitment to deep roots and probably persists on surface soil moisture to a large degree. It quickly colonizes favorable microsites, but its leaves can be easily overtopped by taller herbaceous species. This opportunistic growth pattern may account for its widespread but somewhat sporadic distributional pattern. Rubus lasiococcus also has leaves near the soil surface, but the plants die back under adverse conditions more often than Linnaea, have larger roots, and can survive under very dense canopies. With their deep roots, the plants are probably less dependent on growing season precipitation than is Linnaea.

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The long stolons connect leaves and roots separated by 2 m or more and can rapidly cross unfavorable spots.

The three remaining species have little capacity for vegetative spread. *Tiarella* and *Valeriana* both have short rhizomes, but the roots on *Tiarella* are more finely branched. *Erythronium* has a corm and minimal root development compared to all other species. *Erythronium* and *Valeriana* occur in both meadows and forest, but *Tiarella* is common in dense forests, and its distribution is similar to that of the species with extensive vegetative spread.

SIZE, AGE, AND REPRODUCTION

All three species with limited vegetative spread included apparent seedling segments on some rhizomes or corms and appear to bloom more frequently than the other species studied. Seedlings of E. montanum and T. trifoliata are frequent in the forest, in contrast to the paucity of seedlings for the other species studied. They are probably shorter-lived, on the average, than the species with extensive vegetative spread.

None of 129 plants excavated of the six species with rapid vegetative spread could be traced to a seedling source. Our method of selecting sample plants resulted in a bias for larger plants in species with multiple aerial shoots. Because we selected an individual shoot, prospects for selection were a direct function of the number of shoots on a plant; we were apt to miss plants with only a few shoots. Even with the size bias, seedling establishment of these species with extensive stem systems is uncommon; the 47 plants of C. uniflora and S. stellata (species whose age we could accurately determine) represented a grand total of 623 yr of segments; yet none of these segments began as a seedling. Seedlings may be both uncommon and restricted to specific microsites. We suspect that some genets of these six species may reach several hundred years in age.

Of species that spread vegetatively, some remain more connected than others (COOK 1979; NEWELL 1982). Many herbaceous plants with complex horizontal stem systems are composed of units containing an aerial shoot, an associated rhizome or stolon segment, and its roots. Although connections among such units can cost energy to maintain, they provide a number of potential benefits. Pooling of resources could be beneficial, especially under adverse conditions; excess resources derived from several connected units may be required to support a single new rhizome or a single inflorescence. Resources from a large shoot system could be concentrated to allow rapid expansion into a favorable microsite or for crossing unfavorable areas. Microsites with favorable soil conditions may be spatially separated from those with abundant light; thus, a connected system would allow combined use of these resources. Connections may allow damaged units to survive without greatly increasing the risk of mortality in undamaged parts. A unit causing a continuous drain on the system could be shed

Arnica latifolia lacks extensive rhizome connections and also has the weakest roots and rhizomes. Minimal energy may be invested in these structures initially or allocated to maintaining them. This could free energy for rapid growth under favorable conditions or maintenance in adverse situations. Shortlived, low-cost connections may be advantageous where microsites are temporarily stable or resources are not spatially separated.

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