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Root System Differences Among Species: Implications for Early Successional Changes in Forests of Western Oregon

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ABSTRACT.—Differences in root systems among species may contribute to compositional changes during succession. We excavated all belowground parts of species in an early successional community 2–3 yr after logging and burning of an old *Pseudotsuga menziesii* forest. Annual species had a similar overall root system morphology, but varied in characteristics such as rooting depth and root/shoot ratio. Seedlings of perennial species generally had higher root/shoot ratios than did annuals. Mature perennials had extensive root systems with high root/shoot ratios and most species were clonal. Species typical of later successional stages had more extensive and deeper root systems than did species of earlier stages, a factor that may influence compositional change. Some species that persist throughout succession may do so because their root systems are flexible, changing in origin and distribution. Differences in root systems among species are consistent with their successional roles and habitat affinities, and thus, are important in understanding species replacement during secondary succession.

INTRODUCTION

Root systems vary greatly among species in ways that can influence species' interactions and, ultimately, changes in abundance during succession (Weaver, 1958; Parrish and Bazzaz, 1976; Fitter *et al.*, 1988; Gleeson and Tilman, 1990). Interspecific competition is often an important mechanism of compositional change (Tilman, 1985), and competitive success can be mediated by root distribution (Parrish and Bazzaz, 1976; Manning and Barbour, 1988; Tyler and D'Antonio, 1995). Rapid development of deep roots in woody species is often critical in the successional replacement of herbaceous species by woody ones (Williams and Hobbs, 1989; Brown and Archer, 1990). In addition, distributions of roots and perennating buds are fundamental in determining survival through disturbance. For example, differential survival of species is related to root depth during drought (Weaver, 1958), depth of perennating structures during forest fires (Flinn and Pringle, 1983; Flinn and Wein, 1988) and patterns of rhizome growth following burial by volcanic tephra (Antos and Zobel, 1985a, b).

Early post-logging succession has been studied extensively in the Pacific Northwest (Dyrness, 1973; Halpern, 1988, 1989; Halpern and Franklin, 1990; Halpern and Spies, 1995). The seral vegetation is composed of forest understory species that survive disturbance, as well as annual and perennial taxa that establish subsequently but dominate the early stages of succession. Species turnover, changes in species abundance and changes in plant size are rapid during this period. Although early successional stages are often brief relative to the potential length of the sere, they are critical in maintaining ecosystem functions (Bormann and Likens, 1979) and in shaping patterns of tree establishment and growth (De Steven, 1991; Gill and Marks, 1991). Despite the extensive body of research on early suc-

cession in this region, we have limited knowledge of the basic characteristics of root systems (*e.g.,* rooting depth, lateral spread) of early successional plants. This may be a significant gap in understanding if successional change is causally related to species-specific differences in root system characteristics.

The ecological significance of root systems has received relatively little attention in general in the Pacific Northwest. Belowground structures have been studied in herbs in old-growth forests (Antos and Zobel, 1984; Antos, 1988), in dominant shrubs (Tappeiner *et al.,* 1991; Huffman *et al.,* 1994) and in a diversity of species following volcanic disturbance (Antos and Zobel, 1985a, b), but these studies provide little insight into the dynamics of herbaceous species during early secondary succession. The work described in this paper represents one component of a broader set of field experiments that address the roles of species' interactions in early successional change (Halpern *et al.,* 1992, 1997). Here we compare the basic root system characteristics of plants on a recently clear-cut site and consider how differences in root systems may influence species' distributions and successional roles.

STUDY AREA

The study was conducted in the Western Cascade Mountains on a recently clear-cut site (the Starrbright timber sale, henceforth Starrbright) ca. 25 km S. of the Andrews Experimental Forest near Blue River, Oregon. Starrbright was selected to be similar to sites on the Andrews Experimental Forest where long-term studies of secondary succession have been conducted since 1962 (Dyrness, 1973; Halpern, 1988, 1989). The 4-ha clear-cut is at 730 m elevation on a gentle E-facing slope in the *Tsuga heterophylla* zone (Franklin and Dyrness, 1973). The climate is strongly Mediterranean with cool wet winters and warm dry summers. At this elevation, winter snowpack is intermittent. At a similar elevation in the Andrews Experimental Forest, annual precipitation averages 235 cm, and July and January temperatures average 17.8 C and 0.6 C, respectively (Bierlmaier and McKee, 1989). Soils at Starrbright were formed from deep layers of volcanic ash and contain few rocks, which greatly facilitates excavation of root systems.

Starrbright was logged during May and June 1991 and broadcast-burned with a moderate intensity fire in September 1991. Before harvest the site supported a mature to old-growth forest of *Pseudotsuga menziesii, Tsuga heterophylla* and *Thuja plicata.* The understory was dominated by an evergreen shrub layer of *Berberis nervosa, Gaultheria shallon* and *Rhododendron macrophyllum.* Vegetation was sparse the year following burning, consisting of re-sprouting forest understory plants and colonizing species (Halpern *et al.,* 1996, 1997). By the 2nd season, annual species, especially *Epilobium paniculatum* and *Senecio sylvaticus,* were dominant. Annuals, invading perennials, and resprouting forest species were all common on the site by the 3rd growing season (Halpern *et al.,* 1996). This diversity of plant types combined with the occurrence of seasonal water limitation makes the study site especially favorable for examining relationships between root system architecture and early successional changes. Nomenclature follows Hitchcock and Cronquist (1973).

METHODS

All sampling was conducted during the 2nd and 3rd seasons following disturbance (1993 and 1994). Emphasis was placed on annual species and seedlings of perennials because these were the most common during the period of study, and because seedling establishment and early growth are critical stages in the life history of perennials. Frequency and cover values for major species at the site, including almost all of those studied here, are provided in Halpern *et al.* (1996).

We completely excavated 10 individuals of most species selected for study; for some perennial species, time constraints limited sample sizes. For two dominant annual species, *Epilobium paniculatum* and *Conyza canadensis,* we sampled 10 individuals in each year, because there was considerable size variation between years. For the dominant perennial herb, *Epilobium angustifolium,* we sampled both seedlings and 2–3-yr-old plants. For all species, aerial shoots were chosen to represent well-developed plants commonly found on the site. All living plant parts attached to the selected shoot were carefully excavated using small hand tools, as done previously for herbs and shrubs in the Cascade Mountains (Antos and Zobel, 1984, 1985a, b; Antos, 1988). For clonal species, all parts attached via rhizomes, stolons and roots were excavated and collected. Root distributional patterns, including maximum lateral spread and depth, were determined for each plant, and a diagram was drawn of the root system. Notes were made on the density of roots per unit volume of soil, which often varied greatly both within the root zone of a plant and among species. Other belowground traits, such as rhizome depth and root branching pattern, were recorded as appropriate for the different species. Plant height and number of shoots were recorded for aboveground parts of each individual. Excavated plants were cleaned, oven-dried at 70 C, and weighed to determine root/shoot (belowground/aboveground) ratios. Most plants excavated were in flower, except for *Epilobium paniculatum* and *Conyza canadensis,* which were generally sampled just before anthesis.

The significance of differences in traits among annual species, among seedlings of perennial species, and between these two groups were examined using one-way ANOVA. For the annuals, *Epilobium paniculatum* and *Conyza canadensis,* only the well-developed plants present in 1993 were included in the analyses. All statistical analyses were conducted using Statistix (Analytical Software, Tallahassee, Florida).

RESULTS

Annual species.—Root system morphology was similar among annual species, but many aspects of root system size were significantly different (root depth, P = 0.010; root spread, P = 0.029; root system weight, P = 0.000; root/shoot ratio, P = 0.000). These differences were apparent despite considerable variation in plant weight within species (Table 1). Most annual plants had taproots, with varying amounts of lateral root development. However, the relationship between root depth and lateral spread varied considerably both within and among species (Fig. 1). In general, the proportion of the root system composed of lateral roots increased with plant size. Species are described in order of increasing root depth.

Both *Collomia heterophylla* and *Madia gracilis* had low root/shoot ratios and shallow root systems (Table 1). Their root systems were diffuse with a higher concentration of fine roots near the soil surface. The taproot of *C. heterophylla* was poorly developed and the root system consisted mostly of lateral roots, especially on larger plants. In contrast, for *M. gracilis,* the lateral spread of roots was much less than the root depth. Plants of *C. heterophylla* were short with many primary stems; most other annual species had a single main stem.

Conyza canadensis also had a shallow root system, averaging <20 cm deep (Table 1). The taproot was the dominant feature of the root system except in larger plants, which had considerable lateral root development, especially near the soil surface. In the smaller plants of *C. canadensis* sampled in 1994, lateral spread of root systems was greatly reduced (Table 1).

Root systems of *Epilobium paniculatum* and *Senecio sylvaticus* averaged ca. 25 cm in depth, but differed in root density and lateral spread. As in *Conyza canadensis,* the smaller plants of *E. paniculatum* sampled in 1994 had root systems with reduced lateral spread (Table 1). *Epilobium paniculatum* had a very diffuse root system. In contrast, *Senecio sylvaticus* had

TABLE 1.—Means and ranges (in parentheses) of characteristics of plants excavated in a 2- to 3-yr-old clear-cut in western Oregon. Year excavated is the number of years following disturbance (2 = 1993; 3 = 1994). Plant height is the maximum height attained by any part of the plant (leaves, stems or flowers). Root depth is the maximum depth any root reached below the soil surface. Root lateral spread is the maximum lateral spread of the root system (including rhizomes) from the base of an aerial shoot. Values for above- and belowground biomass are oven-dried weights. Root/shoot ratio is the ratio of the oven dry weight of all belowground plant parts (including rhizomes) to all aboveground plant parts. Seedlings are plants less than 1 yr old

Species	Year excavated	n	Plant height (cm)	Root depth (cm)	Root lateral spread (cm)	Aboveground biomass (g)	Belowground biomass (g)	Root/shoot ratio
Annual species								
Collomia heterophylla	2 and 3	10	16 (11–23)	16 (5–26)	16 (2–30)	1.91 (0.18–10.19)	0.11 (0.02–0.37)	0.08 (0.04–0.13)
Conyza canadensis	2	10	39 (5–96)	19 (5–33)	13 (2–28)	1.50 (0.02–9.11)	0.35 (0.01–2.01)	0.25 (0.20–0.33)
	3	10	7 (3–11)	10 (6–14)	2 (1–4)	ND*	ND	ND
Crepis capillaris	3	10	33 (17–52)	31 (14–51)	17 (4–42)	0.88 (0.08–1.86)	0.22 (0.01–0.57)	0.25 (0.13–0.44)
Epilobium paniculatum	2	10	39 (15–67)	25 (5–52)	18 (3–35)	0.85 (0.02–2.81)	0.18 (0.01–0.61)	0.19 (0.12–0.28)
	3	10	20 (12–25)	20 (11–31)	3 (1–7)	0.07 (0.01–0.14)	0.01 (0.01–0.02)	0.19 (0.14–0.25)
Madia gracilis	3	10	48 (25–73)	17 (9–23)	9 (2–20)	0.95 (0.11–3.87)	0.18 (0.01–0.73)	0.15 (0.08–0.25)
Senecio sylvaticus	2	10	62 (34–89)	26 (9–42)	25 (5–50)	4.64 (0.28–17.06)	1.07 (0.03–3.71)	0.21 (0.11–0.29)
Perennial species								
Berberis nervosa	2	5	9 (4–20)	44 (11–80)	93 (28–217)	2.82 (0.04–6.77)	22.53 (1.58–47.57)	20.30 (3.45–39.50)
Epilobium angustifolium seedlings	2	10	14 (4–30)	19 (5–27)	12 (2–25)	0.40 (0.02–1.14)	0.13 (0.01–0.49)	0.31 (0.15–0.56)
2- to 3-yr-old plants	3	10	32 (17–60)	43 (19–92)	59 (3–120)	4.42 (0.51–18.39)	8.37 (0.19–29.61)	1.88 (0.37–5.17)

TABLE 1.—Continued

| Species	Year excavated	n	Plant height (cm)	Root depth (cm)	Root lateral spread (cm)	Above-ground biomass (g)	Below-ground biomass (g)	Root/shoot ratio
Epilobium watsonii seedlings	2	10	31 (4–61)	15 (5–23)	12 (2–27)	0.50 (0.11–1.09)	0.08 (0.01–0.19)	0.17 (0.08–0.25)
Gnaphalium microcephalum seedlings	2	10	4 (3–7)	18 (9–30)	7 (2–22)	0.14 (0.04–0.62)	0.05 (0.01–0.17)	0.40 (0.25–0.55)
Lupinus latifolius seedlings	2	5	9 (3–13)	38 (32–52)	10 (3–25)	0.21 (0.05–0.29)	0.18 (0.06–0.29)	0.92 (0.62–1.20)
Pseudotsuga menziesii seedlings	3	10	4 (2–6)	14 (8–22)	2 (1–3)	ND	ND	ND
Whipplea modesta 2–3-yr-old plants	2 and 3	6	12 (7–18)	49 (32–65)	45 (17–65)	6.47 (0.94–18.42)	2.02 (0.59–4.49)	0.53 (0.24–1.26)

* No data
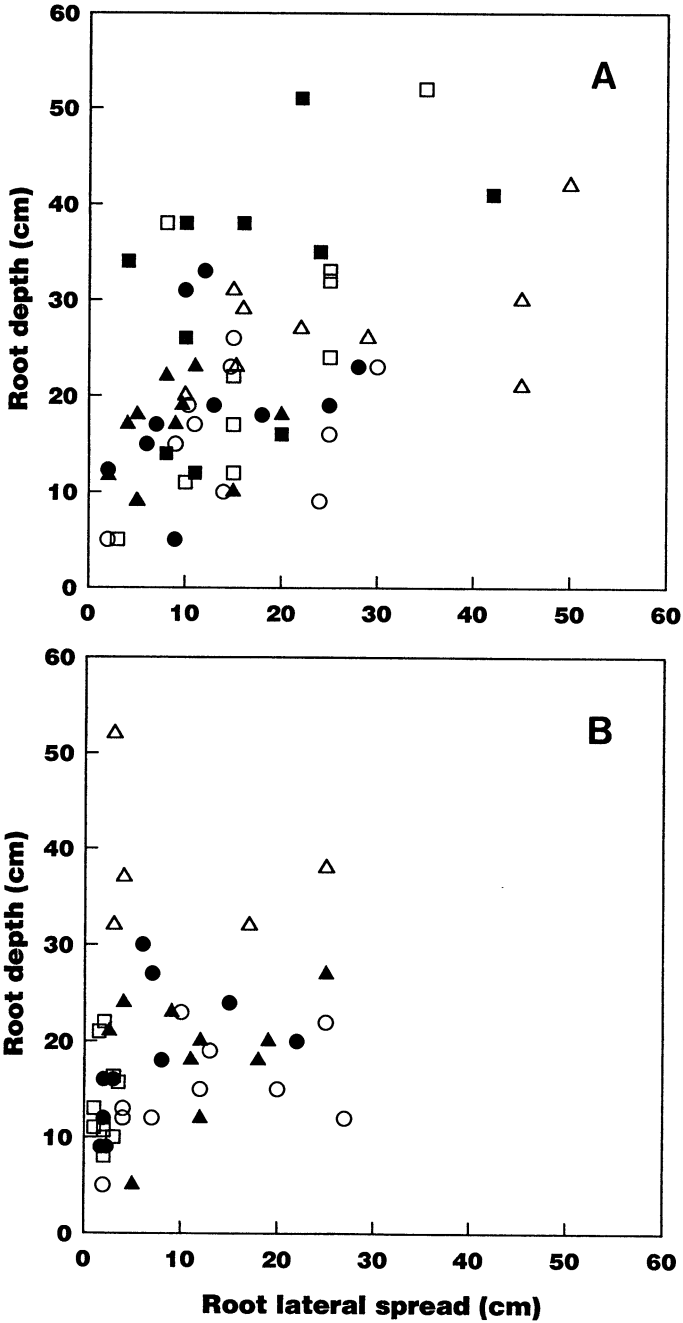
FIG. 1.—Maximum lateral root spread from a stem vs. maximum root depth for annual species (A) and seedlings of perennial species (B) excavated on the Starrbright study site 2 and 3 yr after disturbance (1993 and 1994). Data points are for individual plants. For A: *Collomia heterophylla* (open circles), *Conyza canadensis* (closed circles), *Crepis capillaris* (closed squares), *Epilobium paniculatum* (open

very dense roots in the upper 10 cm of soil near the base of the stem, with a few long lateral roots extending considerably beyond this dense root mass. *Senecio sylvaticus* was substantially larger (*i.e.*, taller with greater mass) than the other annual species, with a root depth approximately equal to the distance of root lateral spread from the stem. For all other species except *Collomia heterophylla,* root lateral spread was less than root depth (Table 1). *Crepis capillaris* had the deepest root system among the annual species sampled (Table 1), with a pronounced taproot and occasional large, lateral roots. Its root/shoot ratio was relatively high.

Perennial species.—Seedlings of perennial species varied in root system morphology; some resembled annuals whereas others had deep taproots and high root/shoot ratios (Table 1). For example, seedlings of *Epilobium watsonii* were similar to annuals: they generally flowered the 1st yr and had a low root/shoot ratio with relatively shallow root systems averaging 15-cm deep (Table 1). The taproot was poorly developed and the root system largely consisted of a few spreading, lateral roots. In contrast, seedlings of *E. angustifolium* had much more extensive root development, with a pronounced taproot and a root/shoot ratio almost twice as high as that of *E. watsonii*.

As a group, seedlings of perennials had significantly smaller root spread (P = 0.000) and larger root/shoot ratios (P = 0.000) than did annuals. However, root systems differed considerably among seedlings of perennial species (Fig. 1b), with significant differences among species in root depth (P = 0.000), lateral spread (P = 0.015) and root/shoot ratio (P = 0.000).

Root systems of perennial species that established after logging and burning changed rapidly as plants developed beyond the seedling stage. Within 2-3 yr the root system of *Epilobium angustifolium* had become much deeper and the root/shoot ratio much greater (six times that of seedlings), as the extensive root system and clonal growth typical of mature plants started to develop (Table 1). Seedlings of both *Gnaphalium microcephalum* and *Lupinus latifolius* had pronounced taproots and only small rosettes of leaves. However, *L. latifolius* seedlings had a much deeper taproot and a higher root/shoot ratio than did *G. microcephalum* (Table 1). Although seedlings of *L. latifolius* have limited lateral root development, observations of 2 to 3-yr-old plants unearthed during excavations of other taxa indicate that *L. latifolius* soon develops an extensive, and often deep, lateral root system, and can spread vegetatively from root sprouts. The roots of both seedlings and older plants had abundant nodules. Observations made during excavations of other taxa indicate that *G. microcephalum* also develops an extensive lateral root system within 2-3 yr, but does not spread vegetatively.

Berberis nervosa and *Whipplea modesta* are present during most or all of the successional sequence in these forests. Although these species differ considerably in growth form, both are clonal. Almost all of the biomass of *B. nervosa* was belowground, in contrast to all other species examined (Table 1). This low-growing, evergreen shrub survives through fire and resprouts from persistent, woody rhizomes. In contrast, most individuals of *W. modesta* were eliminated by burning. Post-disturbance plants began as seedlings with taproots and gradually metamorphosed into stoloniferous subshrubs with adventitious roots. Two to 3-yr-old plants had a double root system with extensive, diffuse roots originating from the taproot

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squares), *Madia gracilis* (closed triangles), *Senecio sylvaticus* (open triangles). For B: *Epilobium watsonii* (open circles), *Epilobium angustifolium* (closed triangles), *Gnaphalium microcephalum* (closed circles), *Lupinus latifolius* (open triangles), *Pseudotsuga menziesii* (open squares)

and numerous adventitious roots emanating from the stoloniferous stems. The root system was deep and widespread (Table 1).

Seedlings of the long-lived tree, *Pseudotsuga menziesii,* were very small compared to seedlings of perennial herbs or annuals (Table 1). Although the taproot was well-developed and lateral roots were very short, root depth averaged only 14 cm—considerably less than in most of the species studied.

DISCUSSION

Annual species.—Some differences of possible ecological importance occur among the annual species studied, although their basic root system morphologies are similar. The small, shallow root systems (and low root/shoot ratios) of *Madia gracilis* and *Collomia heterophylla* likely lead to early seed production and senescence before the driest part of the summer. These native annuals are common in dry open habitats (Hitchcock and Cronquist, 1973), and can be considered spring or early summer ephemerals. Reduced allocation to roots may facilitate rapid growth of aboveground structures when soil water is abundant in the spring, thus allowing completion of seed production before the pronounced summer drought characteristic of the region. *Conyza canadensis,* a widespread, native, weedy annual, also had a shallow root system, but a higher root/shoot ratio. Dense, shallow roots may contribute to its abundance on recently disturbed sites, where nutrients and water can be abundant in upper soil layers. However, its late phenology probably limits its occurrence on dry, naturally open sites. At Starrbright, *C. canadensis* had just begun to flower when *Collomia heterophylla* and *Madia gracilis* were in fruit and senescent. The relatively deep taproot of *Crepis capillaris,* an exotic annual weed, may contribute to its continuing increase on the site when other annuals were declining. As plant community biomass increases with time, and soil moisture declines with increasing transpiration (Gholz *et al.,* 1985), deep roots should be of greater advantage.

Senecio sylvaticus and *Epilobium paniculatum* had the highest cover among annuals on the site in 1993, the 2nd growing season after disturbance. In the 3rd yr, *S. sylvaticus* declined dramatically, as is typical following logging and burning in the Pacific Northwest (West and Chilcote, 1968; Dyrness, 1973; Halpern, 1989; Geyer, 1995; Halpern *et al.,* 1997). Although *E. paniculatum* remained abundant in yr 3, plants were much smaller than in previous years. Although the root depth and the root/shoot ratio of the two species are similar, the concentration of fine roots near the base of the stem in *S. sylvaticus* may explain, in part, its brief dominance after disturbance. Following logging and burning, *S. sylvaticus* may be very efficient at nutrient uptake from high concentrations released near the soil surface. However, it may be at a disadvantage subsequently as nutrient concentrations decline. Although it has been reported to require high levels of nutrients (West and Chilcote, 1968; Kumler, 1969), other work fails to support this conclusion (Van Andel and Vera, 1977; Van Andel and Nelissen, 1979; Geyer, 1995). In contrast, *E. paniculatum,* with a more diffuse root system, may be more efficient at obtaining nutrients dispersed throughout a larger soil volume. A native winter annual, *E. paniculatum* commonly occurs on a variety of disturbed sites and in naturally open, dry habitats (Hitchcock and Cronquist, 1973; Geyer, 1995).

The overall pattern of root system development appeared fairly uniform within annual species. For example, root systems of the very small plants of *Epilobium paniculatum* and *Conyza canadensis* present in 1994 were similar to those of the large plants present in 1993, except that lateral roots were less well-developed relative to the taproot in the smaller plants. This reflects the general pattern of root development in the annual species examined; a taproot develops first and the proportion of the root system composed of lateral roots increases as plants become larger. This developmental sequence would allow plants to re-

duce mortality as surface soils dry out, then tap a larger volume of the upper soil layers for nutrients.

Perennial species.—Seedlings of perennial species generally had higher root/shoot ratios than did annuals. The major exception was *Epilobium watsonii,* which in many respects resembled an annual: root systems were shallow and poorly developed, and most plants flowering in 1993 were 1st-yr seedlings. The shallow roots of *E. watsonii* are consistent with its typical occurrence on moist sites. In contrast, seedlings of *Lupinus latifolius* had a very high root/shoot ratio and a deep taproot. This species is common in meadows and dry forests, where the rapid production of a deep root may be essential for establishment in dense vegetation. The rapid development of an extensive lateral root system and initiation of clonal growth should allow *L. latifolius* to exploit resources effectively and thus succeed in a strongly competitive environment (*i.e.,* later in succession). Some *L. latifolius* plants were present in canopy gaps of the original forest, indicating its ability to succeed in a competitive environment. Seedlings of the weedy, native species, *Gnaphalium microcephalum,* have a shorter taproot, which probably limits establishment in dense vegetation. Although a fairly extensive root system develops the 2nd yr, the plants are nonclonal and short-lived; many individuals at Starrbright were monocarpic. Thus, the rooting habit of seedlings may limit the longer-term persistence of *G. microcephalum* as the post-disturbance community develops.

The widespread, circumboreal species, *Epilobium angustifolium,* occupies a variety of open habitats; in the Pacific Northwest it can dominate logged or otherwise disturbed sites for several to many years after disturbance (Myerscough, 1980; Halpern, 1989; Halpern *et al.,* 1990). The early development of horizontal roots observed on 1st-yr seedlings is fundamental to its rapid occupation of open sites. Extensive clonal growth via root sprouts is its primary mode of expansion (Van Andel, 1975; Myerscough, 1980), contributing to rapid attainment of dominance and long-term persistence in the seral community (Halpern, 1989).

Pseudotsuga menziesii was the most frequent conifer establishing at Starrbright. Of all the species studied, its seedlings were the smallest and had the shallowest roots, even though the taproot comprised most of the root system. Annual species on the site generally had much larger root systems. Given the great difference in root-system size and depth, it is not surprising that early seral vegetation can strongly inhibit conifer performance (*e.g.,* Cole and Newton, 1987).

Root systems and successional change.—Species common during different stages of succession differ considerably in root system morphology. The species that establish after disturbance vary from annuals to long-lived perennials that form large clones. Early colonizing annuals have low root/shoot ratios and small root systems. They are probably very efficient at acquiring soil nutrients released by disturbance, but ineffective at competing for belowground resources with perennials, which grow more slowly but eventually occupy the soil more thoroughly. Perennial species generally have greater root development than do annuals, which probably contributes to their ascendancy later in the successional sequence. In addition, annuals are at a disadvantage because with time, they have to establish root systems within soil that is increasingly occupied by the roots of perennials. Species with the greatest root development are among those that persist the longest. The clonal herbs and shrubs that dominate in old forests have a large proportion of their biomass below ground (Antos and Zobel, 1984; Antos, 1988; Tappeiner *et al.,* 1991; Huffman *et al.,* 1994), which confers an advantage under intense competition for nutrients or water on fully occupied sites. Furthermore, habitats are often highly variable at small spatial scales (Gross *et al.,*

1995), and the ability of clonal plants to integrate resources can be beneficial in patchy environments (*e.g.,* Stueffer *et al.,* 1994; Wijesinghe and Handle, 1994).

Some species may persist throughout the successional sequence because their root system morphologies and distributions change with time. For example, *Whipplea modesta,* common in mature and older forests but sensitive to fire, germinates after disturbance (probably from a persistent soil seedbank). Initially it forms a taproot, then it expands into a vegetatively spreading, stoloniferous subshrub, with an adventitious root system. Many other species are able to persist throughout the successional sequence because their root systems can survive disturbance and effectively use resources during all seral stages. However, it seems likely that the major biotic and abiotic changes associated with forest stand development lead to changes in the belowground characteristics of plants. Root system flexibility is integral to the survival of plants following burial by volcanic ash (Antos and Zobel, 1985a, b). We suggest that flexibility of root systems may lead to the broad successional amplitude of many forest species.

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