

Seedling growth and root morphology of plants with different life-histories

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SUMMARY

Differences among plant species in morphology and patterns of growth are assumed to influence their ability to acquire resources and, consequently, their competitive ability. Despite the acknowledged importance of below-ground resources for plant growth, our knowledge of species differences in root morphology of non-agricultural plants is limited. Comparisons of root morphology, growth rate and topology of seedlings of 12 herbaceous plant species that occur in early to mid-successional fields revealed significant differences among species that were largely related to life history. Annuals grew faster and produced longer and more branched roots than did biennials and perennials. Only among the annuals was there a positive correlation between seed mass and root growth. The grasses allocated proportionately more biomass to roots than the dicots, but did not differ in root length or branching pattern. As seedlings, all 12 species exhibited a herringbone topology; although after 10 d there were significant differences in topology between annuals and perennials indicating that the annuals had begun to develop a more dichotomously branched root system. The possible effects of early differences in root morphology among life-history types in acquiring soil resources in heterogeneous and successional environments are discussed.

Key words: Root systems, morphology, architecture, topology, life-history, succession.

INTRODUCTION

Plant ecologists have long been interested in relating morphological differences among plants to competitive ability. Over the past decade considerable insight has been gained as to how differences between species in above-ground morphology, canopy structure, and leaf form relate to competition for light in plants (e.g. Horn, 1971; Givnish, 1986). However, we know very little about how species differences in below-ground morphology relate to the acquisition of soil resources (cf. Fitter, 1985; Caldwell & Richards, 1986). Most studies considering mechanisms of competition for soil resources have focused on differences in allocation pattern (see Tilman, 1988; Gleason & Tilman, 1990) or rooting depth and density (Parrish & Bazzaz, 1976; Berendse, 1982; Caldwell, 1987). However, species differences in root system morphology and architecture (pattern of branching) may also affect competitive ability for soil

resources (Fitter, 1985, 1987; Caldwell & Richards, 1986; Caldwell, 1987).

Recent studies by Fitter (1987; Fitter, Nichols & Harvey, 1988) have suggested that differences in root system architecture can affect the exploration and exploitation of soil resources. In a laboratory study comparing root system architecture of several species, Fitter *et al.* (1988) found that annual and perennial species exhibited consistent differences in root system architecture and suggested that these differences could influence their ability to acquire soil resources in nutrient rich and poor habitats. All of the annual species they studied exhibited near-dichotomously branched root systems, which in earlier studies Fitter (1987) had suggested would be advantageous in high resource environments. In contrast, the perennials had a herringbone architecture which is predicted to be more efficient when resource levels are low (Fitter, 1987). However, relatively few species were compared in this study and all of the annual species studied occur in relatively fertile habitats, whereas the perennials

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Table 1. Characteristics of 12 species used in the experiment. Species are grouped by life-history type and life-form. Mean seed mass was determined from 50 randomly selected seeds from a bulk collection from local populations. Nomenclature for species follows Gleason & Cronquist (1963)

Species	Life-history	Life-form	Mean Seed mass (mg)
<i>Ambrosia artemisiifolia</i> L.	Annual	Herb	5.35
<i>Chenopodium album</i> L.	Annual	Herb	0.51
<i>Amaranthus retroflexus</i> L.	Annual	Herb	0.20
<i>Setaria glauca</i> (L.) Beauv.	Annual	Grass	2.01
<i>Panicum capillare</i> L.	Annual	Grass	0.15
<i>Daucus carota</i> L.	Biennial	Herb	0.69
<i>Oenothera biennis</i> L.	Biennial	Herb	0.32
<i>Centaurea maculosa</i> Lam.	Perennial	Herb	2.04
<i>Potentilla recta</i> L.	Perennial	Herb	0.17
<i>Achillea millefolium</i> L.	Perennial	Herb	0.13
<i>Bromus inermis</i> Leyss.	Perennial	Grass	3.63
<i>Phleum pratense</i> L.	Perennial	Grass	0.51

grow in sites with poor soils (Fitter *et al.*, 1988). Thus, it is not clear whether the patterns observed by Fitter *et al.* (1988) are a consequence of the species' life-history or the fertility of the sites in which they typically occur. Different root growth patterns may be advantageous in different environments.

Our study was designed to compare and contrast patterns of growth, above- and below-ground, of species with different life-histories. The species studied all occur in early to mid-successional old fields throughout the midwestern USA. All 12 species can colonize newly abandoned agricultural fields, if propagules are present at the time of abandonment (Gross & Werner, 1982; Gross, unpublished). They differ, however, in their ability to persist in these communities. Annual species are rapidly replaced (generally within two years) by biennial and perennial species in successional fields in southwestern Michigan (Gross & Werner, 1982), although they persist for several years on sites in the midwestern United States with nutrient poor, sandy soils where vegetation cover is low and bare soil remains available for colonization (Inouye *et al.*, 1987).

The 12 species studied encompass a broad range of seed sizes and include both grasses and herbaceous dicots (herbs) (Table 1). These characteristics were of interest to us because other studies have suggested they might influence root growth or development patterns. Baker (1972) suggested that seed size might be important in seedling establishment in xeric habitats because large seeds have greater root allocation. Grasses and dicots, typically have different rooting patterns as adults (Klepper, 1987). Our goal was to determine whether there were consistent differences among these species in root growth and development that could be related to life history or whether other traits, unrelated to life-

history, specifically seed size and life form, might be more strongly correlated with root traits.

MATERIALS AND METHODS

Seeds of the 12 species (see Table 1) were collected in October 1987 from local populations at the W. K. Kellogg Biological Station, Hickory Corners, Michigan, and were stored in an unheated garage over winter. In June 1988, fifty seeds of each species were selected at random from these bulk collections for the experiment. An additional set of 50 seeds was weighed individually to determine mean seed mass.

Several species were given a pre-treatment to promote rapid, synchronous germination. The annual dicot species were cold-stratified in the dark at 4 °C for 1 wk. Seeds of *Setaria glauca* were scarified in sulphuric acid. Seeds of each species were placed in separate 15 cm Petri plates lined with wet filter paper in a heated glasshouse to germinate. Ten newly germinated seeds, with the radicle just emerging, were randomly selected from those that had germinated and used for the experiment. All seedlings for a species were planted on the same day, between 27 June and 5 July 1988.

Each seedling was planted individually in a soil-filled plastic Petri plate (15 cm diameter by 1.5 cm deep) placed on edge, of which 2 cm had been cut off the 'top' edge to allow shoot growth. A small hole (3 mm) was drilled in the bottom of the plate to allow drainage. Each plate was filled with moistened soil-less seedling mix (Fison's Sunshine Seedling Mix no. 3) and one surface of the plate was sealed with cloth tape to block light to the soil. The other surface of the plate was left uncovered to provide a window for viewing and mapping root growth. The plates were placed on edge in styrofoam boxes (25 × 39 × 29 cm) at a 40° angle from horizontal to encourage root growth against the window side of

the plate. Each box contained ten plates, arranged in two rows of five plates. Sets of five plates of each species were assigned randomly to two different boxes. Damp paper towels were placed around the plates to provide additional insulation and to minimize temperature fluctuations around the seedlings. The top of the box was left open to provide light for the seedlings.

Plates were checked daily for new root growth beginning the day after planting. New roots were mapped on the plate window with a permanent marker colour-coded for each day. The seedlings were grown until the main root hit the bottom of the plate or until they had been mapped for 12 d and then harvested to determine above- and below-ground biomass. The 12 d period was chosen arbitrarily in order to compare seedlings of similar developmental stage.

To preserve the whole root system intact when harvested, the roots and soil were placed in a shallow pan and the roots gently washed free of soil. The actual number of branches on the root system was then counted to compare to the number of mapped root branches. The shoots and roots were then pressed and dried at 65 °C for a minimum of 48 h, and dry biomass determined on a Cahn electro-balance to the nearest microgram. Because of differences in the date of harvest, data on total and below-ground biomass and root length are expressed on a per day basis.

Data for the analysis of root length growth pattern was determined from the maps of daily root growth using a video-image analysis system ('ROOTS') developed by one of us (K.S.P.). The mapped plates were video-recorded and the images from the tape digitized. Daily increments of growth on all branches were individually digitized and measured to obtain total daily root growth rates. The image analysis system allowed the precise measurement of growth of all visible root branches and the main root. For each root, daily length extension (to the nearest 0.1 mm) and numbers of new branches (external links) were tabulated.

The proportion of the total root system (number of branches) which was mapped on the plates differed among species ($F_{11,108} = 5.26$, $P < 0.0001$) and ranged from 77% (*Oenothera biennis*) to 25% (*Bromus inermis*). To account for these differences, the total root length determined from the maps was adjusted for species differences in the proportion of the root system mapped (adjusted length = measured length/proportion mapped). The adjusted length data were used for all comparisons involving total or daily root length.

The number and pattern of branching at 5 and 10 d after planting also was tabulated from the root maps. These data were used to determine the topological characteristics (magnitude and altitude)

of each species, following methods of Fitter (1987). Magnitude was measured as the total number of external links and altitude as the length (in link units) of the longest path.

Root growth patterns and biomass were analysed by analysis of variance (ANOVA) using the General Linear Model (GLM) procedure of SAS (version 5). Differences among species in daily growth, morphological and topological variables were determined by one-way ANOVAs using individuals within species as replicates. To examine if these differences were related to life history or life form, separate ANOVAs were calculated using species means as the unit of replication and combining species into groups as indicated in Table 1. Differences among groups were tested using Tukey's Studentized Range Test ($P < 0.05$). The data were transformed prior to analysis to eliminate skewness in the distributions. Data are reported as untransformed means ± 1 SE.

RESULTS

Comparisons of species, life history and life form

There were significant differences among species for all of the growth and root characteristics measured (Figs 1–3). Grouping species by life-history and life-form revealed differences related to life-history for several of the parameters examined and few differences between life-forms (Tables 2–4). Annuals consistently had higher rates of daily biomass accumulation than perennials and biennials (Fig. 1, Table 2). There were no significant differences related to life history in daily root mass growth, although the annuals produced on average 2–3 times more root biomass on a daily basis than perennials and biennials (Table 2). The daily root length produced by annuals was marginally significantly greater ($P = 0.08$) than that of biennials and perennials (Fig. 1, Table 2), but there was no relation between life-history and root allocation or specific root length (Table 3).

Total and root biomass growth did not differ for grasses and dicots; although the grasses produced root biomass at nearly twice the rate as the dicots (0.20 vs. 0.09 mg d⁻¹). As a consequence there was a marginally significant difference in proportional allocation to roots between grasses and dicots (Table 3). The grasses also had somewhat higher average rates of daily root length growth than dicots (Table 2), but no difference in specific root length (Table 3). Variation in root length growth among the four grass species studied spanned nearly the whole range observed (1.8–8.5 cm d⁻¹; Fig. 1).

There were significant differences among species in the time of initiation and rate of branching (Fig. 3). Among life-history types, the annuals initiated branches 1–2 d earlier than biennials and perennials (Table 4). Five and ten days after planting, the root systems of annuals had greater magnitude (number

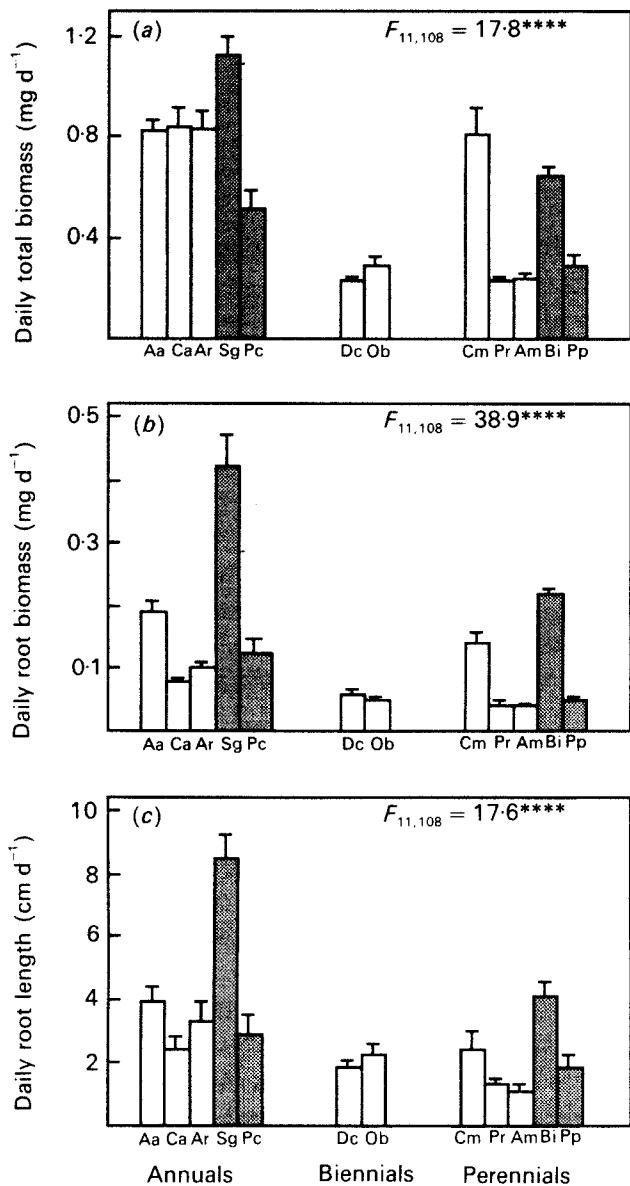


Figure 1. Summary of total and root growth patterns of 12 early to mid-successional species compared in these experiments. Species are arranged in life-history groups in order of decreasing seed mass within life-forms (dicots open bars; grasses shaded bars) in the same order as in Table 1. Values are mean \pm 1 SE. $n = 10$ for each species. F statistics are given for each variable for a one-way ANOVA comparing species; significance levels are as listed in Table 2. (a) Daily total biomass (mg d^{-1}), (b) daily root biomass (mg d^{-1}), (c) daily root length (cm d^{-1}).

of external links) than those of biennials or perennials (Table 4). Of the annuals, *Ambrosia* and *Setaria* had by far the highest rates of branching (Fig. 3). (All the *Ambrosia* seedlings were harvested 6 d after planting because of their high root growth rates, so this species is not included in the tabulation at 10 d.) The differences in magnitude among life-history types are still significant if these two extremely rapidly growing species are excluded from the analyses (day 5 – magnitude: $F_{2,7} = 5.79$, $P < 0.03$; day 10 – magnitude: $F_{2,7} = 11.3$, $P < 0.007$).

All 12 species exhibited a herringbone pattern of root growth (magnitude = altitude; Fitter, 1985) at 5 d after planting. However, by day 10, the annual species had root systems with altitude less than magnitude, and the ratio of these variables (altitude/magnitude) was significantly different among life-

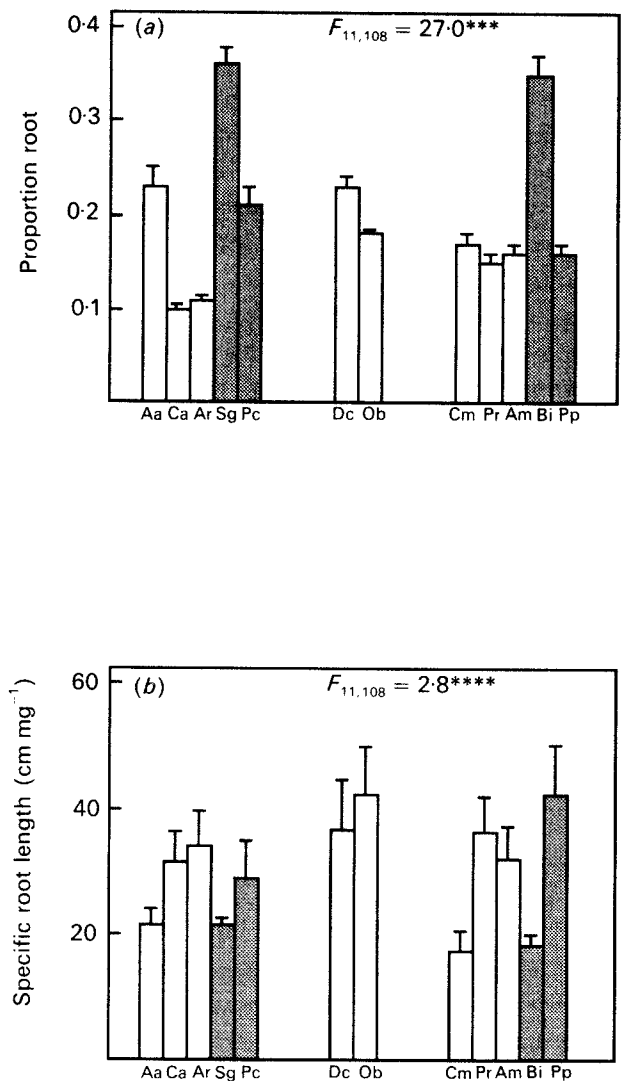


Figure 2. Comparison of species differences in (a) proportion root at harvest, (b) specific root length (cm mg^{-1}). Species arranged as in Figure 1.

history types (Table 4). This suggests that the annuals had begun to deviate from a strictly herringbone architecture toward a more dichotomously branched root system. This result is not solely a function of the larger-size (= greater magnitude) of the root system of the annuals, as *O. biennis* (biennial) and *C. album* (annual) had identical magnitude (Fig. 3).

There were no differences between dicots and grasses in the rate or pattern of branching (Table 4). However, 10 d after planting, *Setaria glauca* (an annual grass) had the highest number of branches (= external links) of any species studied (Fig. 3). A lower proportion of the roots of grasses were mapped on the plates than the dicots ($F_{1,10} = 21.8$; $P < 0.001$) but, there was no difference in branching rate (actual number of tips produced per day) determined at harvest between grasses and dicots. Based on the root system that was mapped, both the grasses and dicots produced a herringbone root system over this period of seedling development (Table 4).

Correlations with seed size

The observed differences in growth patterns among

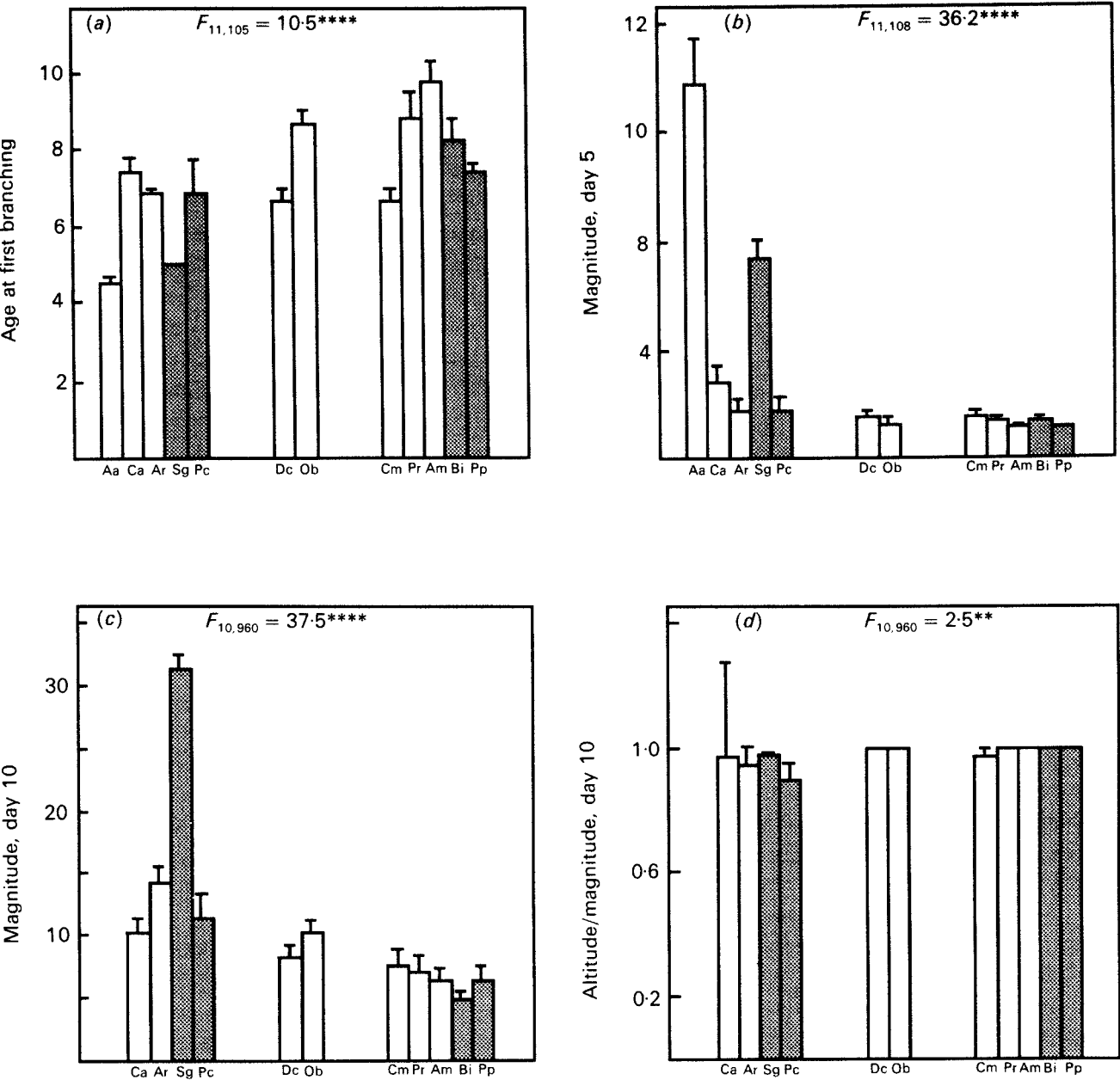


Figure 3. Comparison of branching rates and topological characteristics of species used in these experiments. Species arranged as in Figure 1. (a) Age at first branching; (b) magnitude, day 5; (c) magnitude, day 10; (d) altitude/magnitude, day 10.

Table 2. Mean daily growth in total and below-ground biomass and root length for life-history types and life-forms based on species means combined as indicated in Table 1

	Daily total biomass (mg d ⁻¹)	Daily root biomass (mg d ⁻¹)	Daily root length (cm d ⁻¹)
Life-history			
Annuals	0.83 ± 0.10 a	0.18 ± 0.06	4.2 ± 0.5
Biennials	0.26 ± 0.03 b	0.05 ± 0.01	2.4 ± 0.3
Perennials	0.43 ± 0.12 a, b	0.10 ± 0.04	2.3 ± 0.2
F _{2,9}	6.03*	1.85 n.s.	2.9(*)
Life-form			
Herbs	0.54 ± 0.11	0.09 ± 0.02	2.8 ± 0.1
Grasses	0.65 ± 0.18	0.20 ± 0.08	4.9 ± 0.7
F _{1,10}	0.41 n.s.	2.37 n.s.	3.1 n.s.

Values given are untransformed means ± 1 SE. Sample sizes are: annuals (*n* = 5), biennials (*n* = 2), perennials (*n* = 5), herbs (*n* = 8), grasses (*n* = 4). Results of ANOVA for each analysis (d.f. in parentheses) are given with significance levels indicated: (*) 0.05 < *P* < 0.10; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001; n.s., not significant, *P* > 0.10. Means followed by different letters are significantly different (*P* < 0.05; Turkey's Studentized Range Test).

Table 3. Average root allocation characteristics of life-history types and growth forms

	Proportion root	Specific root length (cm mg ⁻¹)
Life-history		
Annuals	0.20 ± 0.05	27.4 ± 2.7
Biennials	0.21 ± 0.03	39.6 ± 2.8
Perennials	0.20 ± 0.04	29.3 ± 5.0
F _{2,9}	0.05 n.s.	1.5 n.s.
Life-form		
Herbs	0.17 ± 0.05	31.5 ± 2.1
Grasses	0.27 ± 0.05	27.2 ± 2.8
F _{1,10}	4.63(*)	1.15 n.s.

Values are untransformed means ± 1 SE; sample sizes and levels of significance as in Table 2.

these 12 species (weight, length and topology) were independent of initial seed mass. For none of the variables measured was there a significant correlation with the mean seed mass of the species; although the relationship between mean seed mass and mean daily root growth across all species was nearly significant ($r^2 = 0.35$, $F = 4.9$, $P = 0.06$). Subdividing the data by life-history type revealed that among the annuals ($n = 5$), there was a significant effect of seed mass on several root growth variables. Daily root growth in mass ($r^2 = 0.94$, $F = 33.4$, $P < 0.03$), daily root length ($r^2 = 0.93$, $F = 27.8$, $P < 0.03$), magnitude on day 5 ($r^2 = 0.98$, $F = 123.4$, $P < 0.01$) and day 10 ($r^2 = 0.90$, $F = 18.5$, $P < 0.05$) were all positively correlated with seed mass in the annuals. There was no effect of seed mass on any of the measured growth or root characteristics among perennials ($n = 5$), grasses ($n = 4$) or dicots ($n = 8$).

DISCUSSION

The differences among these 12 species in root growth, morphology and topology appear to be strongly related to life-history and independent of life-form. The five annual species exhibited higher rates of growth above- and below-ground, were more highly branched and initiated branching earlier than did the biennial and perennial species.

The differences observed between life-forms (grasses and herbaceous dicots) appear to be more related to allocation patterns than root system morphology. The grasses allocated a greater proportion of biomass to roots and tended to produce more root length per day than dicots. However, this did not result in a difference in seedling SRL or root system topology at this stage of development. Although grasses and dicots typically have different patterns of root growth and distribution (Klepper, 1987), these differences may arise later in development as a consequence of shifts in topology over time.

The observed lack of a seed mass effect on root and total growth may be a consequence of the relatively benign (high light, high nutrient, well-watered) conditions under which the seedlings were grown. Baker (1972) reported a positive correlation between seed size and habitat dryness (larger seeded species in more xeric habitats) in the California flora, and suggested larger seed size might be advantageous in xeric sites because of greater allocation to root in larger-seeded species. Weis (1982) found that root biomass increased with seed size in *Mirabilis hirsuta*, a short-lived prairie perennial herb, but there was no change in proportional allocation to components. Among the 12 species studied here, there was also no

Table 4. Mean topological characteristics of life-history types and life-forms 5 and 10 d after planting. Age of first branch (days), magnitude (number of external links) and altitude (longest path length) were determined from plate maps: the ratio of altitude to magnitude is expected to be 1 for strict herringbone topology

	Age at 1st branch	Day 5 Magnitude	Day 10	
			Magnitude	Altitude/magnitude
Life history				
Annuals	6.1 ± 0.6	5.5 ± 2.3 a	16.0 ± 5.0 a	0.95 ± 0.02 a
Biennials	7.6 ± 1.0	1.5 ± 0.2 a, b	9.3 ± 1.1 a, b	1.00 ± 0.0 a, b
Perennials	8.1 ± 0.6	1.3 ± 0.9 b	6.3 ± 0.5 b	0.99 ± 0.01 b
F	3.4(*)	4.3*	5.7*	7.6**
(d.f.)	(2, 9)	(2, 9)	(2, 8)	(2, 8)
Life-form				
Herbs	7.4 ± 0.6	3.2 ± 1.5	9.2 ± 0.5	0.98 ± 0.02
Grasses	6.9 ± 0.7	2.9 ± 1.5	13.5 ± 1.8	0.96 ± 0.01
F	0.3 n.s.	0.1 n.s.	0.1 n.s.	0.4 n.s.
(d.f.)	(1, 10)	(1, 10)	(1, 9)	(1, 9)

Values are means ± 1 SE; sample sizes as in Table 2. Degrees of freedom are given in parentheses below each F value. On day 5, magnitude = altitude for all groups. All *Ambrosia* seedlings were harvested by day 6, so the sample size for annuals and dicots is reduced for day 10.

evidence that seed size differences among species influenced proportional allocation to root.

All 12 species exhibited a herringbone topology (magnitude = altitude) over the first 10 d of the experiment. The annuals had both a higher magnitude and altitude than biennial and perennial species, which reflected early differences in branching rate among the life-history types. Fitter (1985, 1987) has argued that a herringbone topology would be very effective in exploiting soil resources, but less efficient for resource transport. He also suggested that a herringbone root structure would be favoured in systems where water is limiting (Fitter, 1985). For many species, acquisition of moisture may be critical for seedling establishment and growth in the field. Thus, a herringbone pattern of root growth may be favoured at the seedling stage for many plant species.

As an individual matures, different growth patterns (morphology and topology) may develop in response to the availability and distribution of soil resources. The short-term nature of our experiments (5–12 d) prevented any such time-dependent or ontogenetic switches in topology from being observed among these species. However, we did detect significant differences among these species in root morphology and growth rate at these early stages. The apparent shift in topology among the annuals to a less herringbone architecture at 10 d, suggests that species topology may shift as it grows and perhaps may be developmentally plastic. Such differences might strongly influence seedling establishment and growth in different environments, or microsites within one environment.

Both seedling root growth rate and topology are likely to affect the ability to acquire soil resources. The relative importance of each of these factors in determining competitive ability may vary among environments, particularly in relation to the level and spatial distribution of soil resources. Based on results of simulation modelling (Fitter, 1987) and an experimental study (Fitter *et al.*, 1988), Fitter has suggested that different root branching and growth patterns would be advantageous in nutrient poor and rich habitats. He has also suggested that annuals, particularly weedy species, should exhibit a dichotomously branched root system because they occur in relatively nutrient rich habitats (Fitter, 1987).

However, for weedy and early successional plant species, competitive success may depend more on rapid exploitation of resources (above- and below-ground) than on efficiency (Parrish & Bazzaz, 1976; Bazzaz, 1979). For such plants, a herringbone root topology, especially when combined with a high below-ground growth rate, as observed among the annuals in this study may increase competitive ability by maximizing the exploitation of uncolonized soil volume (see also Harris & Wilson, 1970; Parrish & Bazzaz, 1976). Such a 'space-exploitative' growth pattern may be less effective for acquiring resources

when other species have colonized a site and/or soil resources are more spatially heterogeneous. Little is known from either experimental or modeling studies as to how root topology, growth rate, and plasticity in branching may affect acquisition of soil resources which are patchily distributed (but see Sibly & Grime, 1986; Jackson & Caldwell, 1989; Jackson, Manwaring & Caldwell, 1990).

The species compared in this study are dominant at different times in successional old-fields in the midwestern United States (cf. Gross & Werner, 1982; Inouye *et al.*, 1987), but all must colonize and establish as seedlings. Seedling establishment for both early- and later-successional species (particularly of small-seeded species) may be limited to a relatively 'narrow window' in time soon after abandonment. The ability of perennial species to persist in successful fields has been related to changes in soil fertility, biomass, growth form and root/shoot allocation patterns of competitors (Tilman, 1988). However, differences in root morphology or topology may also influence species abundance or distribution in successional (or other) communities (cf. Caldwell & Richards, 1986). The differences in root development rate observed in this study suggest that annuals might have a competitive advantage for soil resources when resource levels are high and exploitation of soil volume (e.g. site pre-emption) rather than efficient patch utilization, determines competitive ability. Whereas, the slower growth of perennials may reflect their greater efficiency and/or greater ability to encounter and exploit patches of resources in more heterogeneous environments.

Our studies of seedling growth and root morphology have shown that there are significant differences among species with different life-histories. Despite the short-term nature of these studies (5–12 d), we detected significant differences among annual and perennial species in several aspects of root growth and morphology. Seedlings of the annual species we studied tended to have higher root growth rates (length and mass) and had a greater number of branches than perennials of the same developmental stage. The small size of these root systems at the time of harvest (typically less than 10 branches), may have prevented us from detecting differences in architecture (herringbone *vs.* dichotomously branched), that have been predicted for species with different life-histories. However, there were significant differences in magnitude among life-history types after only 5 d growth. Such difference in root growth rate and development may be equally as important as architecture in determining the ability of a species to exploit soil resources. The ecological implications of such differences need to be explored in future studies.

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