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COSTS AND BENEFITS OF CONSTRUCTING ROOTS OF SMALL DIAMETER[1]

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ABSTRACT: Roots represent a considerable carbon cost for plants. Furthermore, plants vary considerably in how carbon is expended for belowground processes. One attribute that varies widely among species is the investment of root biomass in the production of root length. Relatively thin roots have a high specific root length (SRL) or length: dry weight ratio. Since water and nutrient uptake is based more upon root length than mass, one might conclude that species of high SRL invest their root biomass more efficiently than species of low SRL. This, however, ignores many other functional attributes of roots that may permit coarse lateral roots to be more adaptive than fine lateral roots under certain environmental conditions. In leaves, studies on the relationship of structure and function suggest that evergreen plants with greater leaf longevity commonly have thicker leaves, lower photosynthetic capacity, and lower respiration rates than deciduous plants. These kinds of relationships may also be true for thick roots (low SRL). Limited evidence suggests that species of high SRL tend to have greater plasticity in root growth, greater physiological capacity for water and nutrient uptake, but less root longevity and less mycorrhizal dependency than species of low SRL. More study is needed before the physiological traits associated with variation in length-biomass ratio are understood.

IMPORTANCE OF FINE ROOTS

The fine root system is the principal pathway for water and nutrient absorption. Roots also represent a substantial cost to a plant's overall carbon

economy. In a wide range of ecosystems, from wet tundra to deciduous forests, root biomass production exceeds 50% of total biomass production (8). Maintenance costs of fine root biomass are also high. Lambers (44) reviewed data collected from plants grown in pots under favorable conditions and suggests that 12 to 29% of photosynthetically fixed carbon is used for root respiration, 5% is lost as exudates, and 7 to 10% may be used to support the mycorrhizal symbiosis. During unfavorable conditions, the percent of photosynthate used for maintaining the roots may be much greater (67, 68). This large allocation of carbon to support the root system is at the expense of carbon that could be reinvested in leaf growth. Even small changes in allocation to new leaves dramatically affect the maximum potential whole-plant growth rate (59). Under conditions of water or nutrient stress, carbon may have little value relative to the value of the most limiting resource (17). Under these conditions, large amounts of carbon may be allocated to acquire the most limiting resource. This apparent "excessive" use of carbon does not imply that carbon is used inefficiently to optimize growth or reproduction of the plant. For long-lived plants adapted to environments of variable water and nutrient supply, this may entail sizeable carbon investment in roots to insure survival of the unusually harsh periods. Consequently, roots should have evolved in form and function so as to utilize carbon in such a manner that aids a plant's overall fitness.

A paradox in this carbon optimization hypothesis is that carbon allocation for root length production varies widely among species even though root length is probably the most important plant property influencing water and nutrient acquisition (53,56). In this paper, I will review the relationship of specific root length (SRL) or the length of roots divided by their weight to various root functions to help reconcile this apparent contradiction to the efficient use of carbon for water and nutrient uptake.

Physiological ecologists have long been interested in aerial plant parts and the relationship of their composition, structure, and longevity to their defense from herbivores, water and nutrient use, and photosynthetic capacity (4). In leaves, their longevity, dark respiration rate, photosynthetic capacity, and thickness are commonly interrelated (13,16,45,76). In general, deciduous leaves have greater specific leaf area (SLA) or area-to-mass ratio, greater photosynthetic capacity, and also greater potential dark respiration rates than evergreen leaves.

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[1] Florida Agricultural Experiment Station Journal Series No. R-00488.economy.

Similarly, SRL may be fundamentally linked to general differences in how carbon is expended for acquisition of belowground resources. A complete analysis of root photosynthate requirements (costs) needs to include not only tissue synthesis, but also maintenance costs of the root and its symbionts over the lifetime of the root relative to the water and nutrients that it absorbs (benefits). Different environmental conditions will likely favor different methods of carbon expenditure (6,17).

In general, roots of high SRL will have small average diameter, which assumes of course that density of the root tissue is constant. Even the term, "fine" roots, is deliberately ambiguous. The average diameter of "fine" roots varies widely among species, between plants of the same species, and even within the root system of the same individual. For instance, in trifoliate orange *(Poncirus trifoliata)*, young roots (< 10 weeks) that exhibited no secondary thickening ranged from 400 to 1500 um in diameter, although most roots had diameters of 500 to 750 pm (Fig. 1). Furthermore, root diameter can be quite plastic, changing in response to many soil conditions, including aeration, temperature, nutrient status, physical impedance, and infection by microorganisms (30,48,62). In addition to the variability in root diameter within a plant and shifts in root diameter in response to changes in environmental conditions, different species have substantially different average root diameters of their "fine" lateral roots (Table 1). Graminoids tend to have the smallest- and tree species, especially evergreens, the largest diameter roots. This variation in root diameter of the fine roots and the closely analogous property, SRL, has important implications regarding tradeoffs in root construction.

Root acquisition of water and nutrients is based more upon root length or root surface area than mass (53,56). Root length is especially important in relatively dry soil and for relatively immobile nutrients (Fig. 2). Barber and Silberbush (2) simulate the effect of changing root diameter under conditions where root volume (*i.e.*, biomass) and soil volume are kept constant using their mechanistic model of nutrient uptake. Root length density increases exponentially with a decrease in root diameter, and concomitantly, nutrient uptake, which is based on root surface area, increases exponentially. Differences in uptake of N, P, and K are mainly due to their differences in rates of diffusion and buffering capacity in the soil. Assuming that variation in biomass reflects variation in carbon costs of tissue synthesis (16), plants that invest less biomass to produce root length (high SRL) should be able to increase the length of their total root system more readily than those with low SRL. Thus, plants with high SRL gain an advantage in water and nutrient acquisition over those of low SRL (27,28).

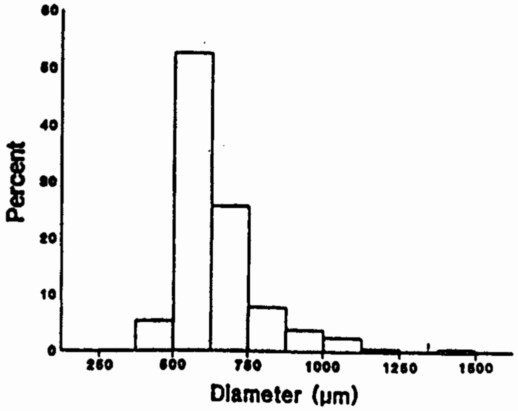

FIGURE 1. Frequency distribution of the diameter of "fine" roots of Poncirus trifoliata. Roots were less than 10 weeks old and were sampled from disturbed sandy soil in a mature rootstock trial with 'Valencia' sweet orange (Citrus sinensis) as the scion. Diameter determinations were made from 320 1-cm root pieces sampled from 8 different trees (after 25).

Although this is a compelling reason why small-diameter roots (high SRL) are advantageous, it is simplistic to ignore many other attributes of roots. As indicated by the wide range in average "fine" root diameter among species (Table 1), there is presumably no optimal SRL for all environmental conditions. Implicit in this line of reasoning is that there are specific physiological attributes associated with a particular root-length construction.

SRL AND ROOT FUNCTION

There has been little examination of functional attributes associated with SRL. There is fragmentary evidence that roots of high SRL (small diameter) are more plastic in lateral root proliferation in fertile parcels of soil (26) and may possibly have greater specific rates of water and nutrient uptake than roots of low SRL. On

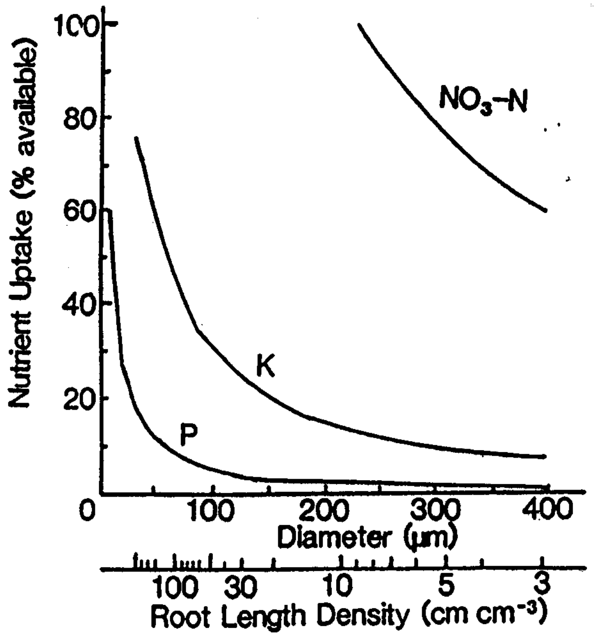

FIGURE 2. The effect of changing root diameter while holding root volume and soil volume constant on phosphorus, potassium, and nitrate-nitrogen uptake. Uptake is expressed as the percent of the total nutrient diffusible that is taken up in a 5-day period (Redrawn from 2).

the other hand, roots of low SRL may often be more dependent on mycorrhizae and have greater longevity (9,33,43,65). All these possible relationships to SRL deserve further study. Despite the considerable carbon invested in root systems, the relationship of SRL and root function is poorly understood.

SRL and Mycorrhizae: Plants invest carbon below ground into absorbing structures other than roots; most notably mycorrhizal fungi, nitrogen-fixing bacteria, and root hairs. Although I know of no apparent relationship of SRL with root hairs or N fixation, there tends to be a relationship with mycorrhizae.

Mycorrhizal infection of terrestrial plant roots is exceedingly common (55) and can appreciably increase the maintenance cost of roots (22,58,69,73). Since

TABLE 1. Approximate Diameter, Rounded to the Nearest 50 µm, of the Laterals (i.e., Highest Order) in a Range of Plant Species. All Plants Were Grown in Soil and All Root Diameters Were Measured Optically.

	Diameter (µm)	Reference
Graminoids		
Cereals		
Oryza sativa cv. Norin 11	100	(77)
Zea maize cv. Golden Cross Bantan	250	(77)
Agropyron spp.	200	(10)
Lolium perenne	150	(51)
Lolium rigidum	150[a]	(7)
Carex aquatilis	150	(18)
Legumes		
Trifolium repens	200	(21)
Lotus pendunculatus	200	(21)
Centrosema pubescens	300	(21)
Stylosanthes guyansis	300	(21)
Trifolium subterranean	300[a]	(7)
Trifolium pratense	300	(51)
Shrubs		
Chaparral		
Adenostoma fasiculatum	250	(43)
Arctostaphylos glauca	300	(43)
Ceanothus greggi	350	(43)
Rhus ovata	300	(43)
Cold desert		
Atriplex confertifolia	100	(29)
Ceratoides lanata	350	(29)
Artemisia tridentata	350	(29)
Trees		
Deciduous		
Liquidambar styracifolia	200	(66)
Lirodendron tulipfera	600	(66)
Quercus rubra	150[b]	(46)
Acer rubrum	250[b]	(47)
Conifers		
Picea sitchensis	500	(32)
Pinus radiata	550	(52)
Pinus taeda	500	Simmons unpubl.
Pseudotsuga menziesii	500	(63)
Broadleaf evergreens		
Citrus spp.	650	(33)
Poncirus trifoliata	600	(33)

[a] Sufficient P.
[b] Root tips.

many plant species and associated mycorrhizae probably have co-evolved (60), interpreting relationships of form and function in roots without including the mycorrhizal component is unwise.

There is a general tendency for species with small-diameter roots to be less dependent on mycorrhizae than large-diameter species (33,61) which is felt to be related to the ability of these species in the nonmycorrhizal condition to take up phosphorus. Factors, such as long root hairs (3) or slow inherent growth rates (35), influence the relationship between SRL and mycorrhizal dependency (defined as the plant growth response with mycorrhizae divided by the growth response without mycorrhizae) and decrease the benefit derived by the host plant from a symbiosis with mycorrhizae. The percentage of a plant's root system infected by mycorrhizae and the mycorrhizal dependency of that species are not necessarily related. Consequently, whether or not differences among species in their mycorrhizal dependency relates to the amount of carbon they use to support their symbionts is unclear.

Although the hyphae of mycorrhizal fungi are of considerably smaller diameter than roots, hyphae cost roughly 10% more to construct than that of roots (37). Furthermore, maintenance of mycorrhizae may require up to 12% of available photosynthate (22,58,69). Consequently, mycorrhizal infection is commonly beneficial for plant growth when P supply is limiting more than carbon supply. This can be brought about by limited root length, high shoot-P demand, and low soil supply of P. Mycorrhizal infection may cause growth reductions under conditions where carbon is more limiting than nutrients (particularly P). This can be caused by low light or high soil supply of P per unit root length (31,50,70).

SRL and Root Extension: In general, species of high SRL produce root length more rapidly and obtain greater root length densities than species of lower SRL (10,36,51). This is an important reason why species of high SRL tend to be very successful competitors (10,51).

The relationship of high SRL and rapid root extension of the total "fine" (*e.g.*, < 1 mm) root system of a plant is in contrast to the relationship of low SRL to rapid root extension observed in *individual* large-diameter (> 1 mm) roots. Using root-observation boxes or trenches in which roots in the soil can be viewed with glass windows, Head (38) found that individual "coarse" roots of cherry trees are thicker and tend to grow more rapidly and to a greater extent than those of apple.

Comparisons among roots of different orders in the same plant yielded similar results (42,49). One explanation is that fewer large-diameter roots are supported by a greater supply of photosynthate for growth. Furthermore, large-diameter roots can often withstand greater soil impedance before they buckle (75). This may be why cultivars of *Festuca arundinacea* that produce a greater proportion of large-diameter (> 3.4 mm) roots have been more successful in penetrating "compacted" soil than those with fewer coarse roots (71). Consequently, plants with many large-diameter roots may be more capable of extensive root growth by increasing their total soil volume by lateral and vertical spread of their root system, whereas plants that invest in few "coarse" roots and many "fine" roots of small diameter may be better adapted for intensive root growth and high root length densities in close vicinity of the shoot.

SRL and Root Plasticity: The considerable cost of root production and maintenance may be offset if roots grow preferentially into soil volumes in which there is greater return in terms of water and nutrient for the carbon investment. For instance in sugar beet, Weaver (74) illustrates how root growth is primarily in the fertile clay layers at 50 and 120 cm and not in the fine sandy loam in between (Fig. 3). In 1926, Weaver (74) writes "It has been known for a long time that plants grown in soils with alternate layers enriched in nutrient solution branch much more profusely in these layers." Drew et al. (24) supports this observation that root proliferation in zones of localized nutrient enrichment is normally accomplished by rapid initiation of new laterals. Furthermore, roots in nutrient-rich patches often have greater SRL than roots in the unenriched surrounding soil (30).

Despite the obvious importance of this opportunistic root growth, until recently, there has been little attention given to differences among species in the ability to respond to fertile patches (11,12,20,26,28,64). Eissenstat and Caldwell (26) examined rates of root proliferation of two *Agropyron* tussock grasses into volumes of soil enriched with concentrated nutrient solution in the spring. Using minirhizotrons (clear plastic or glass tubes), roots were observed congregating only in the zones of enrichment and not elsewhere. The species of greater SRL, *Agropyron desertorum*, tended to have more rapid root proliferation than *Agropyron spicatum*. Subsequent experiments indicated that just one day following fertilization, *A. desertorum* and to a much lesser extent *A. spicatum* could respond to localized fertilization (39). Similar differences in the two species

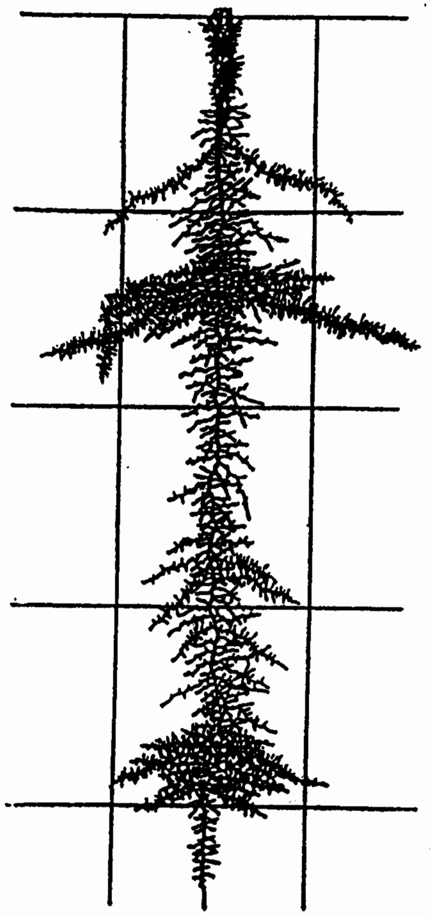

FIGURE 3. Root distribution of sugar beet in which root proliferation occurred in layers of clay in otherwise fine sandy loam soil. Grid marks ca. 30 cm apart (after 74).

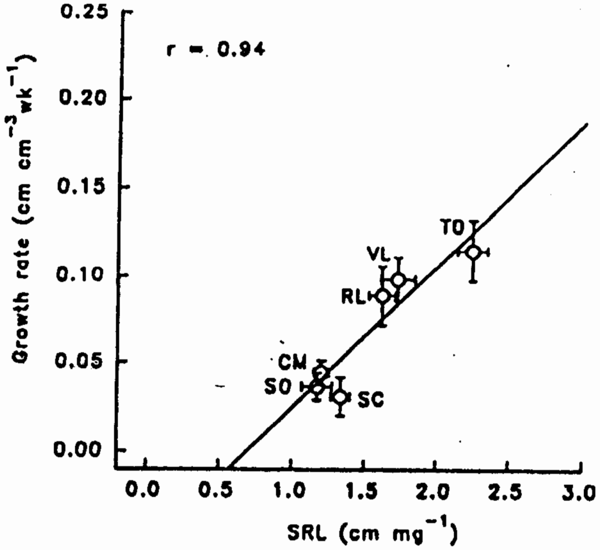

FIGURE 4. The relationship of root growth (extension) rate to the average rootstock specific root length (SRL) in disturbed soil. Growth rates were determined by sampling the disturbed soil at 5, 10, and 19 weeks after disturbance. Specific root length was determined from the total length divided by the root dry wt at each sampling. The rootstocks, sour orange (*Citrus aurantium*), Swingle citrumelo (*Poncirus trifoliata* x *Citrus paradisi*), Cleopatra mandarin (*Citrus reshni*), rough lemon (*Citrus jambhiri*), volkamer lemon (*Citrus volkameriana*), and Trifoliate orange (*Poncirus trifoliata*) were all budded to 'Valencia' sweet orange (*Citrus sinensis*). Trees were 13 yr old. Bar represents two SE (after 25).

of *Agropyron* were found for root invasion and proliferation in disturbed soil (28).

The relationship of high SRL to increased opportunistic root growth was also indicated by the response of 6 different citrus rootstocks (Fig. 4). These data were collected by removing soil cores from beneath the tree canopy and replacing the soil, sieved free of roots, in an open-mesh container which was then placed back in the hole. New root length, dry weight, diameter, and soil water content were monitored over a 40-week period in the disturbed soil and in nearby undisturbed soil. Disturbed soil was wetter than undisturbed soil at every sampling date (data not shown). The average root extension rate expressed per unit of disturbed soil (cm/cm^3/wk) was clearly correlated with average SRL of the roots (Fig. 4). Since each point represents the average of two cores/tree averaged over eight trees, average genetic differences in SRL and root growth rate could be separated from the well-known environmental factors affecting roots in individual cores. An increase in SRL from 1.3 to 2.3 cm mg was associated with a 2.5-fold increase in average root extension rate. One reason for differences in root extension rate was apparently due to SRL. For the same biomass invested, plants of high SRL could extend their roots faster than plants of low SRL. There was also an indication of differences in opportunistic root growth, since root growth rates based on root dry wt (mg/cm^3/wk) were also greatest for plants of high SRL and least for those of low SRL ($r = 0.74$).

SRL and Specific Rates of Water and Nutrient Uptake: Field data of specific rates of water and nutrient uptake (uptake per unit length) indicate that rates are often greater in the coarse roots of dicots than the fine roots of graminoids (36,51). Factors contributing to this difference may include greater shoot demand per unit root length and less axial resistance of the xylem vessels of dicots than monocots.

However, if specific rates of root uptake are examined at saturating levels of resource supply and shoot demand is standardized, a different relationship may result. Graham and Syvertsen (33) provide evidence that root hydraulic conductivity or the capacity to conduct water per unit length in wet soil increases with an increase in SRL (Fig. 5). Root hydraulic conductivity was determined by pressurizing the entire root system and measuring rates of xylem exudation from the cut stem. These data were generated for 60 mycorrhizal and nonmycorrhizal plants growing under uniform soil conditions. Note that these data express conductivity per unit root length. On a unit mass basis, differences in hydraulic conductivity between species of low and high SRL would be even greater. One possible explanation for the relationship of SRL to g_{root} is that since radial resistance in the root is an important limitation to water uptake (23), roots of small average diameter will have a shorter path length for water movement to the xylem than large-diameter roots. Another possible explanation is that there are specific anatomical differences associated with SRL. Preliminary data (Achor and Eissenstat, unpublished) suggest that citrus rootstock cultivars of high SRL have a less suberized and less lignified hypodermis than those of low SRL, possibly reflecting tradeoffs between high hydraulic conductivity and protecting the root against pathogens and dessication.

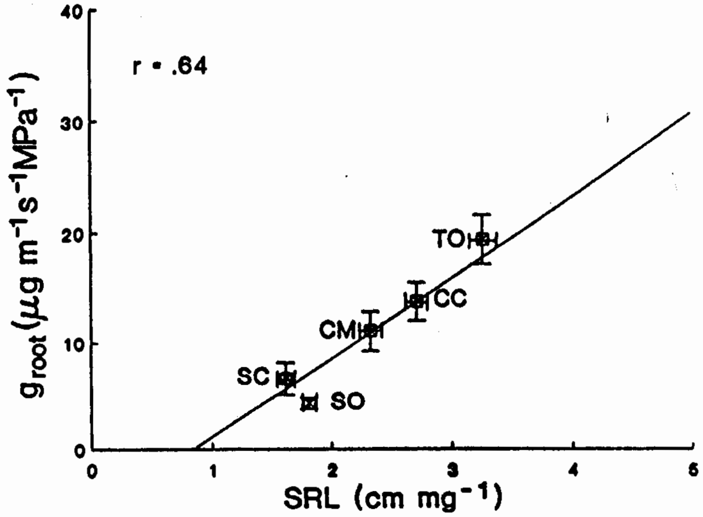

FIGURE 5. The relationship of SRL to root hydraulic conductivity (g_{root}) of seedlings of five citrus genotypes (SO = sour orange, SC = swingle citrumelo, CM = Cleopatra mandarin, CC = Carrizo citrange, and TO = trifoliate orange). The correlation is based upon 60 mycorrhizal and nonmycorrhizal seedlings (10 per genotype) in pots with equivalent P nutrition (data from 33). Bar represents two SE.

There is also limited evidence to suggest that plants of high SRL have a greater capacity for nutrient uptake per unit root mass than plants of low SRL. Among graminoids from cold-stable and warm-fluctuating marshes, Chapin (14), using excised roots, found that those of small diameter (cold-stable) had greater phosphate absorption capacity (*e.g.*, V_{max}) at a given acclimation temperature than those of large diameter. Similar results were indicated by Pan et al. (57) in a study of nitrate uptake among decapitated seedlings of corn genotypes and by Jackson et al. (40) with two species of *Agropyron*.

SRL and Root Respiration: Carbon expended in root respiration may represent approximately 10 to 30% of net photosynthesis during favorable periods of growth and considerably more during unfavorable periods (44,67,68). Plants having different root structure may vary in this respect, although this has been rarely studied. Among three tundra graminoids, Billings et al. (5) indicated using excised roots that *Eriophorum angustifolium* had the highest root respiration rate [mg CO_2 g/(dry wt)/hr], *Dupontia fischeri* was intermediate, and *Carex aquatilis* was the lowest. The SRL (cm/mg) of these species reported by Shaver and Billings (65) was directly correlated to these rates. However, Chapin and Tyron (18) did not find a relationship between root respiration and SRL using excised roots of variable mycorrhizal status in a study of taiga graminoids and shrubs.

If there is a relationship of SRL with root respiration, it is likely complex. As a first approximation, root respiration per gram of root is likely to reflect nitrogen uptake per gram of root at high rates of N supply (17,41,72). Plants with high rates of nitrogen uptake per unit root mass presumably will have higher respiration rates than those with low specific rates of N uptake. At saturating levels of nitrogen supply, species of high SRL may have greater respiration rates than those of low SRL because of their differences in specific rate of N uptake (V_{max}). Under typical field conditions, where species of low SRL often have greater specific rates of N uptake than species of high SRL, root respiration may be greater for low SRL species. At very low rates of resource supply, presumably roots with the most enzymes (highest V_{max}) will have the greatest respiration rates, which may be more typical of species of high SRL.

Mycorrhizal infection will also influence the relationship of SRL and root respiration. At low P supply, mycorrhizae often increase specific rates of nutrient uptake of root systems of low SRL more than those of high SRL (33). Thus, it logically follows that especially at low P supply, mycorrhizae will affect the respiratory costs associated with nutrient uptake more in low SRL plants than high SRL plants. These costs are in addition to carbon directly required by the mycorrhizal symbiosis (1).

SRL and Root Longevity: Although the initial carbon investment for species of high SRL is less than plants of low SRL, the length of time before the root must be replaced may also be less. Limited comparisons of cold desert shrubs (9,29), chaparral shrubs (43), and tundra species (65) indicate that small-diameter roots of high SRL often die sooner than coarse roots. However, just as shade can alter the negative correlation of SLA and leaf longevity (76), environmental factors such as an increase in nutrients can cause a decrease in SRL (30) and a decrease in root longevity (19,54). Consequently, species comparisons of SRL and root longevity must be made under similar environmental conditions.

CONCLUSIONS

There are likely several functional attributes associated with SRL. In general, plants of low SRL are more mycorrhizal dependent than those of high SRL. Root extension as an intensive property (*i.e.*, increases in root length density) is generally greater for plants of high SRL than low SRL. The reverse relationship of SRL to root extension may be true for vertical and lateral spread of a root system. There is some evidence to suggest that compared to plants of low SRL, those of high SRL construct a more opportunistic root system which readily reallocates in favorable volumes of soil, more readily sheds roots in unfavorable soil, and has greater capacity for water and nutrient uptake. Similar relationships have been suggested for plants adapted to fertile as compared to infertile environments (15,34). There have been extremely few studies that have compared SRL to root function directly, despite the importance of carbon as a currency and length as a fundamental root property. More research is clearly needed.

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