The dependence of root system properties on root system biomass of 10 North American grassland species

J. M. Craine[1,5], D. A. Wedin[2], F. S. Chapin, III[3] & P. B. Reich[4]

[1]*Department of Integrative Biology, University of California, Berkeley, CA 94720, USA.* [2]*School of Natural Resource Sciences, University of Nebraska, Lincoln, NE 68583, USA.* [3]*F. S. Chapin, III: Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA.* [4]*P. B. Reich: Department of Forest Resources, University of Minnesota, St. Paul, MN 55108 USA.* [5]*Corresponding author**

Abstract

Dependence of the properties of root systems on the size of the root system may alter conclusions about differences in plant growth in different environments and among species. To determine whether important root system properties changed as root systems aged and accumulated biomass, we measured three important properties of fine roots (tissue density, diameter, and C:N) and three biomass ratios (root:shoot, fine:coarse, and shallow:deep) of monocultures of 10 North American grassland species five times during their second and third years of growth. With increasing belowground biomass, root tissue density increased and diameter decreased. This may reflect cortical loss associated with the aging of roots. For non-legumes, fine root C:N decreased with increasing root biomass, associated with decreases in soil solution NO_3^- concentrations. No changes in fine root C:N were detected with increasing belowground biomass for the two legumes we studied. Among all 10 species, there were generally no changes in the relative amounts of biomass in coarse and fine roots, root:shoot, or the depth placement of fine roots in the soil profile as belowground biomass increased. Though further research is needed to separate the influence of root system size, age of the roots, and changes in nutrient availability, these factors will need to be considered when comparing root functional traits among species and treatments.

Abbreviations: SRL – specific root length; PVC – polyvinylcholride

Introduction

The structure and function of root systems play a critical role in carbon and nutrient dynamics of ecosystems and affect species interactions (Caldwell and Richards, 1986; Fisher et al., 1994; Jackson et al., 1997; Nepstad et al., 1994; Norby, 1994; Tilman and Wedin, 1991; Van Noordwijk et al., 1994). If root system properties are stable with increasing plant/stand biomass, measurements at a single point in time can be used in dynamic models of plant growth and ecosystem processes or for comparisons of treatments or species. The dependence of plant properties on plant biomass has been shown to alter conclusions regarding differences in plant traits among environments (McConnaughay and Coleman, 1999; Poorter and Garnier, 1996; Tjoelker et al., 1998; Walters et al., 1993) and may explain differences in plant properties between seedlings and larger, older plants (Gleeson and Tilman, 1994). If root system properties are dependent on the amount of belowground biomass, then models and tests of differences among and between species become more complex, requiring inclusion of differences in individual/stand biomass.

There are many properties of root systems whose importance in plant growth and ecosystem N cycling merit determining whether these properties change as

plants grow and stands accumulate biomass. Specific root length (SRL, length per unit mass of root) and its components, root diameter and tissue density, are key traits that influence the potential for acquisition of soil resources under low-nutrient conditions (Nye and Tinker, 1977). In addition, these traits are important components of economic analyses of the production and mortality of root systems (Eissenstat and Yanai, 1997; Ryser, 1996) and they determine inter-root distance and therefore inter- and intra-plant competition (Caldwell and Richards, 1986; Coutts, 1987; Fitter, 1991; Nye and Tinker, 1977). Fine root C:N, an important factor in the nitrogen economy of an ecosystem, could also change as plant biomass increases due to changes in the balances between N availability and N demand. Yet, it is unknown whether root C:N and N availability change as stands accumulate biomass belowground.

Root system construction, distribution and allocation also affect plant, community and ecosystem properties and it is important to know if they change as plant biomass increases. For example, coarse roots are primarily for storage, transport, vegetative reproduction, and mechanical support, whereas fine roots primarily acquire water and nutrients (Coutts, 1987; Eissenstat, 1997; Jackson et al., 1997; Körner, 1984). Because fine and coarse roots serve different purposes and may have different turnover rates (Jackson et al., 1997; Weaver and Zink, 1945), knowing how the ratios of fine and coarse roots change as plants grow allows better estimations of belowground productivity and root system uptake and storage potential. Of similar importance, placement of root biomass in the soil profile affects resource acquisition and redistribution (Caldwell and Richards, 1986; Jobbágy and Jackson, 2000).

In order to test whether root system properties change as root systems age and accrue biomass, we examined relationships between belowground biomass and root system properties of 10 North American grassland species over their second and third years of growth in monoculture. The specific goals of our experiment were to determine if the following parameters changed as the belowground biomass of the monocultures increased:

1. Root functional traits (tissue density, diameter, specific root length, and nitrogen concentration of fine roots).

2. Relative amounts of aboveground and belowground biomass, coarse belowground biomass and fine root biomass, shallow and deep fine root biomass.

3. Relationships between fine root biomass and soil solution NO_3^-.

Material and methods

Experimental design

Thirty replicates of each of 10 grassland species were grown in monoculture. The species included 3 C_3 grasses (*Agropyron repens, Bouteloua gracilis, Koeleria cristata*), 3 C_4 grasses (*Andropogon gerardii, Bouteloua gracilis, Schizachyrium scoparium*), 2 non-leguminous forbs (*Achillea millefolium, Solidago rigida*), and 2 legumes (*Lespedeza capitata, Petalostemum villosum*). Eight of the species are native to the North American tallgrass biome; two (*A. repens* and *P. pratensis*) are Eurasian species that are common in many North American grasslands. Monocultures were contained in polyvinylchloride (PVC) tubes, 20 cm in diameter and 96 cm high. Soil for the monocultures was obtained from the top 10 cm of soil from an abandoned agricultural field at the Cedar Creek Natural History Area, Minnesota, USA and was sandy (94% sand, 6% silt plus clay), with low soil carbon (0.45% C). The bottom of each tube was fitted with a plastic cap that had a 2.5 cm hole into which polyester fibers were placed to facilitate drainage.

Monocultures were seeded in early June of 1997 at 12 g seed m^{-2}. All monocultures were watered frequently during the first 6 weeks of the first growing season. Monocultures were maintained in six 1-m deep trenches. During the 1997–98 winter, the trench was filled with straw to decrease temperature fluctuations. During the 1998–99 winter, remaining trenches were filled with soil to the level of the soil surface of the monocultures. The straw or soil was removed from the trenches surrounding the monocultures at the beginning of each growing season to allow access to minirhizotron tubes that were present in the PVC tubes and leachate collectors. Monocultures that were to be harvested in the first three harvests were randomly assigned to one of three trenches; the last two harvests randomly assigned to one of two different trenches.

Half of the tubes of each species were amended with 4 g N m^{-2} yr^{-1} in the form of NH_4NO_3 during the 1998 and 1999 growing season, applied during May, July and September each year. Our nitrogen treatment was moderate, only increasing total plant

biomass by approximately 20% on average and not significantly affecting any other traits or relationships analyzed in this study more than would have been expected by chance (data not shown). As such, although we have included the nitrogen treatment in statistical analyses, we do not further report the results of the nitrogen treatment.

Measurements

At each of five dates during the second and third years of growth, six replicate monocultures of each species were harvested. Harvests were begun on days 151, 207, 251 in 1998 (May 31, July 26, September 8) and days 151 and 246 in 1999 (May 31 and September 3). At each harvest, all aboveground biomass of a monoculture was clipped and sorted into dead and live fractions. The live fractions included any leaf, stem or reproductive biomass that was at least partially green. For three harvests (first, second and fourth), after removal of aboveground biomass we extracted a 2.5 cm diameter, 20 cm deep core to determine extractable inorganic nitrogen concentrations in the soil solution. Soils were kept at 5 °C for no more than 24 h prior to extraction with 0.01 M KCl. Extractable soil NO_3^- and NH_4^+ were determined according to Wedin and Tilman (1993). Because NH_4^+ concentrations were consistently low and rarely responded significantly to any treatment, only the NO_3^- results will be discussed.

Within 3 days of the aboveground biomass harvest, each tube was cut into three strata, 0–24 cm, 24–56 cm and 56–96 cm in depth. Root biomass was washed free of soil under running water over a 1.3 mm screen. Root samples were stored at 5 °C before being separated into coarse, fine, and crown biomass fractions within 48 h. For non-grasses and rhizomatous grasses, the 'crown' category included the bases of stems, i.e. interface between above- and belowground parts, which include up to 1 cm of aboveground biomass and 1 cm of belowground biomass. All non-crown root segments and rhizomes greater than 1 mm in diameter were classified as 'coarse roots' and those less than 1 mm in diameter were considered fine roots. We estimate that the coarse root biomass fraction contained no more than 1% fine root biomass.

After washing and sorting, a subsample of fine root biomass was selected from each 0–24 cm stratum and digitally scanned. Each subsample was suspended in 1 cm of water in a 10 × 15 cm clear acrylic tray and then scanned at 600 dots per inch (0.04 mm resolution)

with a Hewlett Packard Scanjet 4c. After scanning, each subsample was dried for 72 h at 65 °C. Each digital root image was processed with the WinRhizo root analysis program (Régent Instruments, Quebec, Canada) to determine the subsample's average diameter, volume, and length were determined in order to calculate specific root length (length per unit mass) and tissue density (mass per unit volume).

All other biomass was dried at 50 °C until constant mass, generally 7 days, and then weighed to the nearest mg. After weighing, fine roots were composited over the 3 depths, ground with a Udy cyclone mill (Udy Corporation, Fort Collins, CO, USA), and analyzed for C and N concentration with a Leco CN 2000 analyzer.

Statistical analyses

Belowground biomass results were scaled to g m^{-2} for the entire 96 cm volume, adjusting the measured mass of the 0–24 cm strata to take into account the amount of root biomass present in the 2.5 cm cores that was removed before harvest. All statistical analyses were performed in JMP 3.0 (SAS Institute, Cary, North Carolina, USA).

When stands are establishing, the amount of biomass and the age of the stand are correlated. In this case, the two were too confounded to be separated statistically (data not shown). As such, we analyze and present our data on root system properties relative to biomass rather than some metric of stand age, but can not separate the influence of biomass, average root age, and other correlated factors on traits.

We regressed each of four root traits (diameter, tissue density, specific root length, and fine root nitrogen concentration) against total belowground biomass. For each root trait, one model was run for each species. We also determined whether any of the root-system or whole-plant traits changed with increasing belowground biomass. These included relationships between: (1) above- and belowground biomass, (2) coarse belowground biomass (coarse roots + crowns) and fine root biomass, and (3) deep and shallow fine root biomass. For each relationship, we ran one linear multiple regression model for each species. Because the analyses of ratios can inflate variance and create other statistical problems, we treated one parameter (e.g. belowground biomass) as a predictor and one parameter (e.g. aboveground biomass) as a response variable in examining each relationship. The explanatory variables of each model included the main pre-
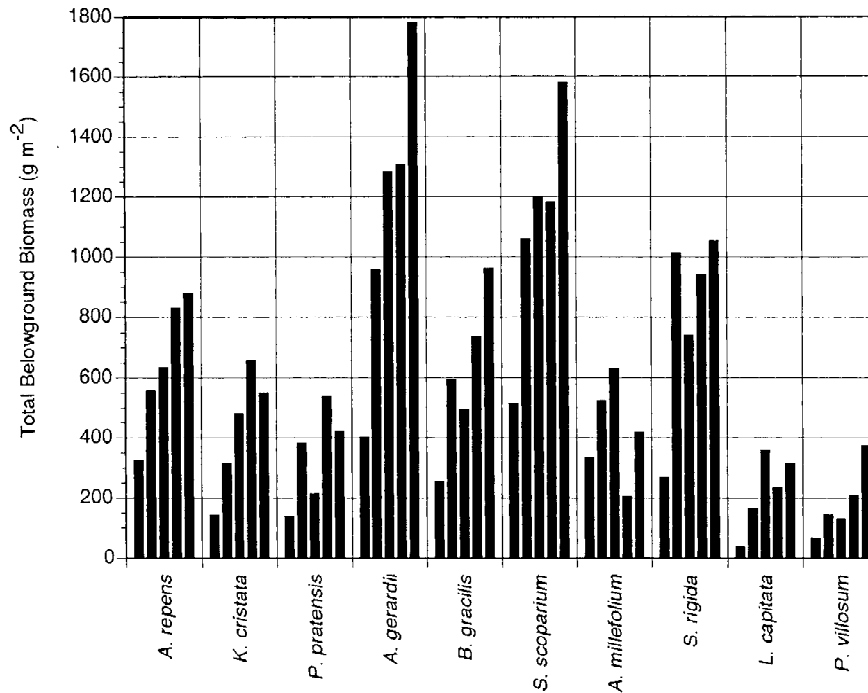
Figure 1. Average root system biomass of 10 species over five harvests (May 31, 1998; July 26, 1998; September 8, 1998; May 31, 1999 and September 3, 1999).

dictor data centered at the mean for a species (to test for constant ratio between parameters) and the square of the centered predictor data (for change in ratios with an increase in the predictor).

For those traits or relationships that depended on root system biomass, we ran an additional linear model that predicted the parameter with species identity, total root biomass, and their interaction. We examined the relative sums of squares of the different components of the model to determine the relative explanatory power of species-specific relationships between total root biomass and the parameter in explaining variance.

Regressions were used to examine the relationships between fine root biomass and extractable soil nitrogen levels across all species and whether these relationships changed with increasing belowground biomass or with fertilization. Because of the reduced number of replicates (these parameters were only measured three times), we use harvest identity as a covariate instead of biomass, since there was often insufficient variation in biomass within species to test for differences in relationships among species. This analysis then provides the relationship between fine root biomass and soil available N across all species

for each harvest. For the model of soil NO_3^-, fine root biomass was log-transformed and the resultant transformed data then centered at its mean. The model tests for separate relationships between fine root biomass and soil NO_3^- between the two nitrogen treatments and among the three harvests for which data on soil moisture were collected. A few of the values for inorganic nitrogen concentrations were lower than our control blanks, resulting in measured concentrations that were negative. In order to determine quantitative relationships between the two paraameters for all measurements, we included all data, whether negative or not, and added a constant to all inorganic nitrogen concentration data to make all values positive, before log-transformation.

Results

Between the first and the last harvest, total belowground biomass increased on average by 586 g m^{-2}, approximately a factor of four, though there were large variations in the pattern of biomass accumulation among species (Figure 1). Generally for each species, as belowground biomass increased, tissue

Table 1. Relative explanatory power of species identity, total belowground biomass, and their interaction for fine root tissue density, fine root diameter, and fine root C:N

Parameter	r^2	n	Species		TBB		Species*TBB	
			SS	Prob $> F$	SS	Prob $> F$	SS	Prob $> F$
Tissue density	0.40	265	0.35	<0.05	0.18	<0.001	0.20	<0.001
Root diameter	0.71	267	0.0046	<0.001	0.0002	<0.001	0.0002	ns
Fine root C:N	0.82	264	25684	<0.001	5175	<0.001	5606	<0.001

density increased while root diameter decreased, with little resultant effect on SRL. Tissue density increased significantly with increasing total belowground biomass for *A. gerardii*, *L. capitata* and *P. villosum*, and the other 7 species had non-significant trends for increasing tissue density with increasing belowground biomass (average rate of increase = 0.00010 g root biomass cm^{-3} g^{-1} root biomass m^{-2}). The average diameter of root systems decreased significantly ($p<0.05$) with increasing belowground biomass for 6 species (*A. gerardii, B. gracilis, K. cristata, P. pratensis, S. scoparium, S. rigida*) (average rate of change in diameter per unit increase in root biomass $= -3.2 \times 10^{-6}$ mm diameter g^{-1} root biomass m^{-2}). Offsetting changes in diameter and tissue density led to constant SRL with increasing belowground biomass for all but one species (average rate of change in SRL $= -0.0018$ cm g^{-1} root g^{-1} root biomass m^{-2}).

Species identity was associated with 48% of the explained variation in tissue density (total $r^2 = 0.40$) while root biomass and the species-biomass interaction was associated with 25 and 27%, respectively (Table 1). Although diameter decreased with increasing belowground biomass, most of the explained variation in root diameter (total $r^2 = 0.71$) among samples was associated with species identity (92%) (Table 1).

For the non-legumes, as root system biomass increased, biomass accumulation increased faster than N accumulation, causing the C:N of roots to increase (Figure 2). The relationship between total root biomass and fine root C:N was significant for 6 of 8 non-legumes, and the non-significant trends for *A. millefolium* and *P. pratensis* were positive also (Figure 2; average rate of change in C:N for non-legumes = 0.021 g^{-1} root biomass m^{-2}). Across and within species, most of the explained variation (total $r^2 = 0.82$) was associated with species identity (70%), with equal amounts of variance explained by total root biomass and the interaction between total root biomass and species identity (Table 1). For the legumes, there was
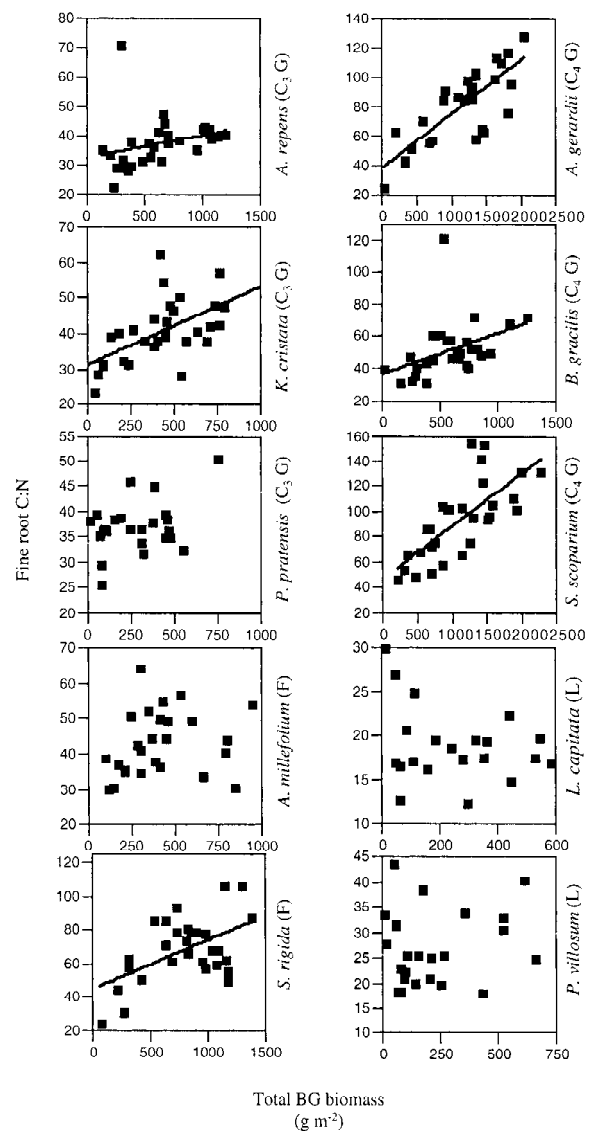

Figure 2. Fine root C:N of 10 species plotted against total belowground biomass. The presence of a black line indicates a statistically significant ($p < 0.05$) relationship between the two parameters.
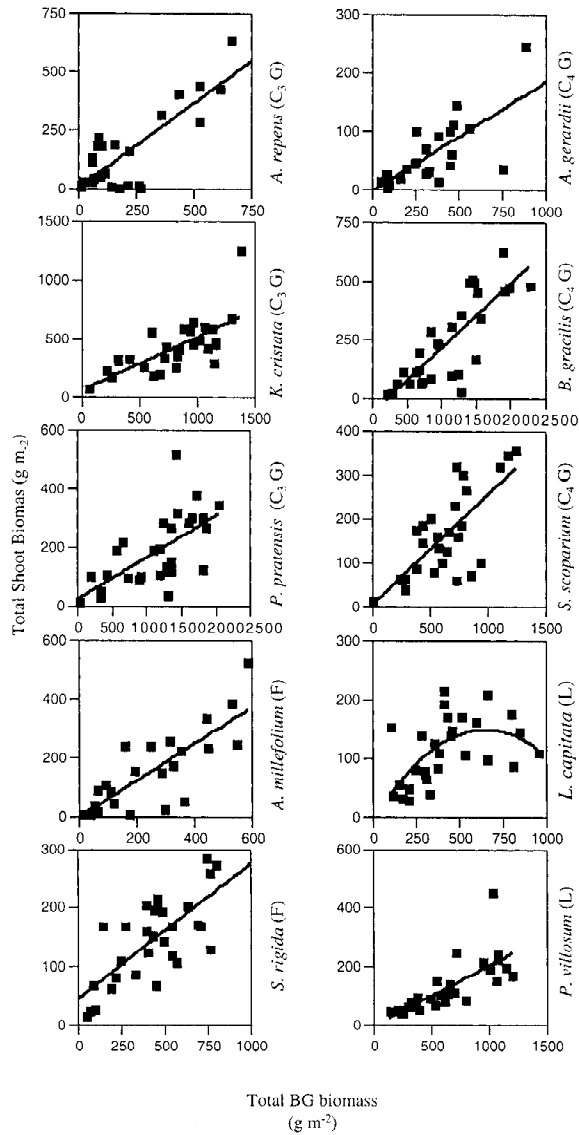
Figure 3. Shoot biomass of ten species plotted against total belowground biomass. The presence of a best fit line indicates a statistically significant ($p < 0.05$) relationship between the two parameters; the presence of a quadratic line indicates a change in the relationship with increasing biomass.

no relationship between belowground biomass and the C:N ratio of roots (Figure 2), most likely due to nitrogen fixation providing sufficient nitrogen to maintain C:N ratios as belowground biomass increased.

In general, as belowground biomass increased, species maintained constant ratios of aboveground and belowground biomass (Figure 3), fine and coarse root biomass (significant positive linear relationship for all 10 species, 2 species significant quadratic term (*A.*

repens, *L. capitata*) and shallow and deep root biomass (significant positive linear relationship for 8 of 10 species, non-significant increases for *K. cristata*, *P. pratensis*). For a few species, there were significant changes in the relationships between biomass and these parameters, but these relationships were often determined by a small number of highly influential individual points (data now shown).

Over all three harvests, soil inorganic nitrate concentrations decreased with increasing fine root biomass ($F = 122$, $p < 0.001$), with only slight differences in these relationships among the three harvests ($F = 3.1$, $p < 0.05$; Figure 4). Consequently, as belowground biomass increases, soil NO_3^- declined, but the ratio of fine root biomass to soil NO_3^- remained constant. This constant ratio of fine root biomass and soil NO_3^- implies equivalent relationships between plant uptake per unit biomass and microbial mineralization over the range of biomass and times that we sampled.

Discussion

To varying degrees, fine root tissue density, fine root diameter, fine root C:N, and soil extractable NO_3^- underneath plants changed as belowground biomass increased. Most likely, belowground biomass does not directly affect functional traits, but instead serves as a proxy for other factors such as root age or carbon inputs into the decomposition cycle. Further research that examines the proximal causes of changes in functional traits is clearly necessary in order to separate confounding factors that all change as root system biomass increases.

The inability to separate root system age, nitrogen availability, and the amount of biomass complicates the interpretation of results here. For example, the decreases in root diameter and increases in root tissue density with increasing belowground biomass could be explained by the aging of roots. As roots age, the cortex is often shed (Eissenstat and Yanai, 1997), decreasing the diameter of the root and leaving the denser stele tissue. On the other hand, more recently produced roots may have smaller diameter and greater tissue density and represent plant response to decreases in N availability. Ryser and Lambers (1995) found that for one species of grass, average root diameter was greater under higher nutrient supply, which may reflect differences in the need for root systems
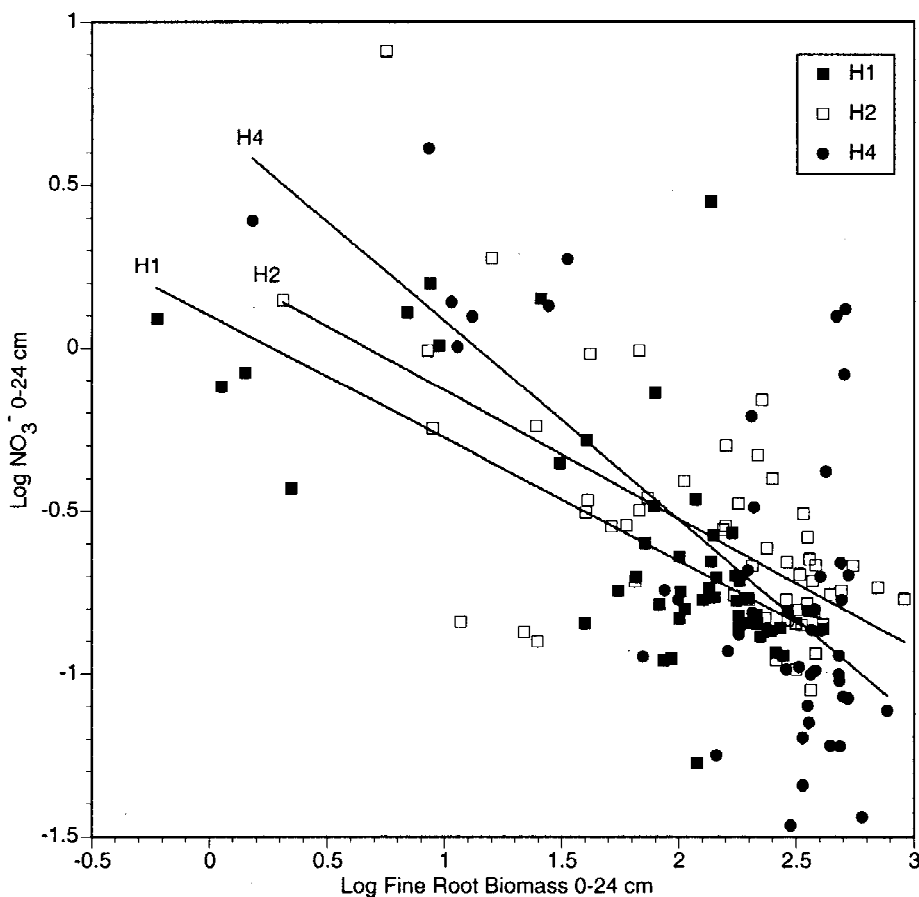
Figure 4. Relationships between log fine root biomass 0–24 cm and log inorganic NO₃⁻ 0–24 cm for three harvests (H1= May 31, 1998; H2= July 26, 1998; H4= May 31, 1999).

to acquire nutrients vs. transport nutrients or water quickly.

Using root system biomass as a operational proxy for other factors that may have been changing during stand development, the relationships of root functional traits on the amount of belowground biomass indicates that interpretation of their patterns among species and ecosystems may need to consider total plant or stand biomass and/or root age. For example, analysis of differences in nitrogen concentrations in plant parts among species may be ultimately due to differences in the biomass of the species, not due to anything inherently different in the manner by which species allocate nitrogen to biomass. Although most of the variance in traits that changed with increasing belowground biomass was explained by species identity, for fine root tissue density, half of the explained variation was associated with belowground biomass.

In general, due to the dependence of these traits on belowground biomass, measurement of some belowground properties of plants and ecosystems may not be reliably extrapolated to systems with differences in belowground biomass and/or assumed to be a direct result of the cause of the differences in biomass between ecosystems.

Besides the lack of a relationship between fine root biomass and fine root C:N for legumes, no one functional classification or species stands out as being markedly different in their relationships between root system properties and biomass. As the biomass of the non-legumes increased, the nitrogen concentrations of fine root biomass declined. This increase in root C:N may also correspond to root aging and N resorption, although there is no evidence of nitrogen resorption from roots during senescence (Nambiar, 1987). More likely, as belowground biomass

increases, N limitation may increase if plant uptake and microbial immobilization increase relative to mineralization. Consequently, soil NO_3^- levels decline, uptake decreases relative to production and fine root C:N declines.

Biomass ratios appear to be relatively insensitive to the amount of belowground biomass, though more research with longer observation periods and at different resource supply rates is necessary to better understand the variation among species, experiments, and sites for traits such as the ratio of aboveground to belowground biomass. Studies differ in conclusions about the effect of plant age on allocation of biomass above- vs. belowground and the resulting effects on biomass ratios above- and belowground. Craine et al. (in press) observed that relative allocation aboveground was similar among mature stands of species that varied in above- to belowground ratios, supporting data from seedlings (Gleeson and Tilman, 1994). Craine et al. hypothesized that as plants grow, allocation remains constant and differences in the relative amount of above- and belowground biomass arise as biomass disproportionately accumulates belowground due to the greater belowground longevity. Yet, in the present study, above- to belowground biomass ratios did not increase as biomass accumulated belowground. As absolute and relative amounts of biomass and production for a given species vary greatly among studies (Craine et al., in press; Reynolds and D'Antonio, 1996), more research is needed on the determinants of biomass ratios where sequential harvests include seedlings and are continued long enough to incorporate turnover of aboveground and belowground biomass.

Acknowledgements

References

Caldwell M M, Dawson T E and Richards J H 1998 Hydraulic lift: Consequences of water efflux from the roots of plants. Oecologia 113, 151–161.

Caldwell M M and Richards J H 1986 Competing root systems: morphology and models of absorption. *In* On the Economy of Plant Form and Function. Ed. T J Givnish. pp. 251–273. Cambridge University Press, Cambridge.

Coutts M P 1987 Developmental processes in tree root systems. Can. J. For. Res. 17, 761–767.

Craine J M, Tilman D G, Wedin D A, Reich P B, Tjoelker M J and Knops J M H in press The relationship between plant functional strategies and growth in a low-nitrogen habitat. Funct. Ecol.

Eissenstat D and Yanai R 1997 The ecology of root lifespan. Adv. Ecol. Res. 27, 2–60.

Eissenstat D M 1997 Trade-offs in root form and function. *In* Ecology in Agriculture. Ed. L E Jackson. pp. 173–199. Academic Press, Inc., San Diego, California, USA,

Fisher M J, Rao I M, Ayarza M A, Lascano C E, Sanz J I, Thomas R J and Vera R R 1994 Carbon storage by introduced deep-rooted grasses in the South American savannas. Nature 371, 236–238.

Fitter A 1991 The ecological significance of root system architecture an economic approach. *In* Plant Root Growth: An Ecological Perspective. Ed. D Atkinson. pp. 229–244. Blackwell Scientific Publications Ltd., Oxford, UK.

Gill R, Burke I C, Milchunas D G and Lauenroth W K 1999 Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. Ecosystems 2, 226–236.

Gleeson S K and Tilman D 1994 Plant allocation, growth rate and successional status. Funct. Ecol. 8, 543–550.

Habib R and Lafolie F 1991 Water and nitrate redistribution in soil as affected by root distribution and absorption. *In* Plant Root Growth: An Ecological Perspective. Ed. D Atkinson. pp. 131–146. Blackwell Scientific Publications, Ltd., Oxford, UK.

Jackson R B, Mooney H A and Schulze E D 1997 A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. USA 94, 7362–7366.

Jobbágy E G and Jackson R B 2000 The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol. Appl. 10, 423–436.

Körner C 1984 Biomass fractionation in plants: a reconsideration of definitions based on plant functions. *In* A Whole Plant Perspective on Carbon–Nitrogen Interactions. Ed. J Roy and E Garnier. pp. 173–185. SPB Academic Publishing, Inc., The Hague.

McConnaughay K D M and Coleman J S 1999 Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. Ecology 80, 2581–2593.

Nambiar E K S 1987 Do nutrients retranslocate from fine roots? Iufro (International Union Of Forestry Research Organization) Working Party Meeting On Roots In Forest Soils: Biology And Symbioses, Victoria, British Columbia, Canada, August 4–8, 1986. Can J For Res 17, 913–918.

Nepstad D C, De Carvalho C R, Davidson E A, Jipp P H, Lefebvre P A, Negreiros G H, Da Silva E D, Stone T A, Trumbore S E and Vieira S 1994 The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372, 666–669.

Norby R J 1994 Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. Plant and Soil 165, 9–20.

Poorter H and Garnier E 1996 Plant growth analysis: An evaluation of experimental design and computational methods. J. Exp. Bot. 47, 1343–1351.

Reynolds H L and D'Antonio C 1996 The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. Plant and Soil 185, 75–97.

Ryser P 1996 The importance of tissue density for growth and life span of leaves and roots: A comparison of five ecologically contrasting grasses. Funct. Ecol. 10, 717–723.

Ryser P and Lambers H 1995 Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. Plant and Soil 170, 251–265.

Tilman D and Wedin D 1991 Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology 73, 685–700.

Tjoelker M G, Oleksyn J and Reich P B 1998 Temperature and ontogeny mediate growth response to elevated CO2 in seedlings of five boreal tree species. New Phytologist 140, 197–210.

Van Noordwijk M, Brouwer G, Koning H, Meijboom F W and Grzebisz W 1994 Production and decay of structural root material of winter wheat and sugar beet in conventional and integrated cropping systems. Agric. Ecosyst. Environ. 51, 99–113.

Walters M B, Kruger E L and Reich P B 1993 Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: Species, light environment and ontogenetic considerations. Oecologia 96, 219–231.

Weaver J E and Zink E 1945 Extent and longevity of seminal roots of certain grasses. Plant Physiol. 21, 201–217.

Wedin D A and Tilman D G 1993 Competition among grasses along a nitrogen gradient: Initial conditions and mechanisms of competition. Ecol. Monogr. 63, 199–229.

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