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Clipping effects on root architecture and morphology of 3 range grasses

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Abstract

Although defoliation is known to affect root growth in range plants, little information is available concerning the effect of defoliation on root architecture and its relationship to root morphological characteristics. This study evaluated the influence of clipping on root architecture and morphology of 3 range grasses from the Intermountain West: 'Whitmar', a cultivar of bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve]; 'Hycrest', a cultivar of hybrid crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult. × *A. cristatum* (L.) Gaert.]; and cheatgrass (*Bromus tectorum* L.). Greenhouse-grown seedlings were clipped once or twice at 3 intensities of defoliation (0, 50, and 70 %). The topology (pathlength-slope index), geometry (link length and root diameter), and morphology (total root length and specific root length) of roots of the 3 grasses were evaluated 28, 35, and 42 days after planting. Root topology (*Pe*-slope index) did not vary among defoliation treatments but did vary among species across harvests. Root branching of the grazing-tolerant Hycrest decreased through time, while root branching of the grazing-sensitive Whitmar increased through time. Cheatgrass maintained a highly branched root system throughout the experiment. Specific root length in Hycrest and Whitmar decreased through time, indicating that roots became coarser with age. Similar to its topological response, cheatgrass did not exhibit changes in specific root length through time. There were apparent tradeoffs between link lengths of the main axis and lateral roots of the seminal root, which may lead to important changes in root branching density, root production costs, and probably root function.

Key Words: root topology, link length, defoliation, bluebunch wheatgrass, crested wheatgrass, cheatgrass

Resumen

Es conocido que la defoliación afecta el crecimiento radical en plantas de pastizales, sin embargo existe poca información acerca del efecto de la defoliacion en la arquitectura y características morfológicas de las raíces. En este estudio se evaluó la influencia de defoliación sobre la arquitectura y morfología de 3 gramineas de los pastizales Intermontañosos del Oeste de los Estados Unidos; 'Whitmar' un cultivar de bluebunch wheatgrass [Pseudoroegneria spicata (Pursh) A. Löve]; 'Hycrest', un cultivar hibrido de crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult. × *A. cristatum* (L.) Gaert.]; y cheatgrass (*Bromus tectorum* L.). Bajo condiciones de pastoreo, plántulas de estas especies se defoliaron 1 ó 2 veces a 3 intensidades de defoliación (0, 50 y 70%). Se evaluó la topología (pendiente de pathlength), geometría (diámetro y distancias entre raices laterales) y morfología (longitud total y específica de la raíz) en tres fechas diferentes; 28, 35, y 42 dias despues de germinación. La topología no varió entre los tratamientos de defoliación, sin embargo se observaron diferencias entre especies y fechas. Así, la complejidad de ramificación de Hycrest la cual es una especie que tolera pastoreo, se redujo con el tiempo, en cambio Whitmar una especie sensible a pastoreo, incremento su complejidad con tiempo. Cheatgrass por su parte, mantuvo un sistema radical muy ramificado durante todo el estudio. La longitud específica de la raíz en Hycrest y Whitmar disminuyó con tiempo, lo cual indica que las raices se volvieron mas gruesas con la edad de la plántula, mientras cheatgrass no mostró cambios en esta característica. Se observaron aparentes trueques de la longitud de las distancias de raices laterales entre el eje primario y las raíces laterales de primer orden, lo cual puede acarrear importantes cambios en la densidad de ramificación, costos de producción y posiblemente el funcionamiento de las raices.

The seedling stage represents a critical stage for the successful establishment of rangeland plants (Johnson 1986). Post-planting grazing restrictions are usually recommended for new seedings to allow the stand to become better established before grazing (Horton 1989). Deferred grazing of these newly established stands, however, represents a significant economic cost for many ranchers (Evans and Workman 1994). As a result, understanding seedling root development and its response to defoliation may aid in the development of improved rangeland species that can be grazed earlier.

Plant species differ in their ability to tolerate defoliation (Dahl and Hyder 1977). Recovery of foliage after shoot removal is influenced by meristematic characteristics of the plant and flexibility in reallocation of plant resources (Dahl and Hyder 1977, Richards and Caldwell 1985). In general, tolerance to defoliation

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has been associated with rapid regrowth of foliage following defoliation (Detling et al. 1979, Richards and Caldwell 1985). Defoliation frequently reduces root growth in some species (Crider 1955, Davidson and Milthorpe 1966, Richards 1984) and may be a mechanism by which species preferentially allocate carbon resources to aboveground growth (Richards 1984). Defoliation also may reduce carbon allocation to the root system, thus slowing root elongation and root development. In addition, reduced leaf area may improve soil water conditions (Wraith et al. 1987) and affect ion diffusion (Nye 1966, Clarke and Barley 1968, Burns 1980), perhaps changing soil solution concentrations, and eventually affecting root morphology.

The architectural analysis of root systems proposed by Fitter (1985, 1987) makes it possible to test hypotheses regarding the functional advantages of root architecture with respect to the efficiency of exploitation of soil resources (volume of soil exploited per unit volume of root, Fitter et al. 1991), the potential of soil exploitation (volume of soil exploited, Berntson 1994), and the carbon cost and acquisition efficiency of root systems (Nielsen et al. 1994). Because some defoliated plants divert most of their available carbon and nutrient resources to shoot regrowth, root systems of these plants may be limited by the availability of resources. Thus, root systems must optimize available resources to maintain their functions when defoliated. As a result, new roots will be required to enhance uptake as well as to optimize carbon investment.

We chose 3 important grasses that commonly occur on rangelands of the Intermountain West of the U.S.A. for this study including 'Whitmar', a cultivar of bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve); 'Hycrest', a cultivar of hybrid crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult. × *A. cristatum* (L.) Gaert.); and cheatgrass (*Bromus tectorum* L.), an exotic annual grass. Hycrest exhibits similar characteristics as *Agropyron desertorum*, a grazing-tolerant species that reduces root growth following shoot defoliation, and bluebunch wheatgrass is a grazing-sensitive species that maintains root growth after severe defoliation (Caldwell et al. 1981, Richards 1984, Richards and Caldwell 1985). The annual cheatgrass was included in the study as a basis for comparison because of its prevalence and competitive ability as a weedy species on many rangelands in western North America. Cheatgrass can withstand grazing at an early age and survives more frequent grazing than bluebunch wheatgrass (Pyke 1987). Cheatgrass also has faster root growth and more rapid root development than *P. spicata* and *A. desertorum* (Harris 1967, Buman et al. 1988, Aguirre and Johnson 1991a, 1991b, Johnson and Aguirre 1991).

The objective of this study was to evaluate the influence of defoliation intensity and frequency on seedling root architecture and morphology of 3 important range grasses.

Materials and Methods

The study was conducted in a greenhouse at Logan, Ut., during March through May 1993. No artificial light was provided, and air temperatures were maintained between about 20 and 30° C. Seeds of cheatgrass, which were obtained from a site near Pullman, Wash., Whitmar, and Hycrest were germinated on moistened blotter paper. Five germinated seeds exhibiting a 1- to 2-cm long radicle were transplanted in each plastic pot (20 cm height, 20 cm diameter), which contained 8 kg of fine washed sand (particle size < 0.1 mm). Seedlings were thinned to 1 plant per pot after the second leaf emerged.

Sand in the pots was saturated with 2 liters of 32.2% Rorison nutrient solution containing 56 mg liter^{-1} N-NO$_3$ $^-$, 31 mg Liter^{-1} P-PO$_4$$^{- - -}$, 78 mg Liter^{-1} K$^+$, 80 mg Liter^{-1} Ca^{++}, 32 mg Liter^{-1} S-SO$_4$$^{- -}$, and microelements (Hewitt 1966). After saturation, sand was maintained at field capacity by daily additions of 50 to 100 ml of the same nutrient solution. Three weeks after transplanting, the grasses were subjected to 3 defoliation intensities (0, 50, and 70% shoot removal) and 2 defoliation frequencies (clipped once or twice). Defoliation intensities of 50 and 70% can reduce root growth of range grasses (Crider 1955). Successive defoliations on the same plant were made 21 and 26 days after transplanting. Seedlings were harvested at 30, 37, and 44 days after transplanting by washing the sand from the roots. The shoot was separated from the root, and the shoot was oven dried at 70°C to constant weight. The root system was stored in a cold room at 4°C until further processing.

From each root system the seminal root was selected (Rose 1983), dyed with toluidine blue, and were immersed in water between 2 pieces of glass. Root diameters were measured at the root axis and first order laterals (roots initiated on the axis) of the seminal root. Three measurements at 3 distances from the point of attachment to the shoot (5, 10, and 15 cm) were taken using a 7x magnifying lens equipped with a 0.1 mm scale. The number of first order lateral roots was also recorded at the same 3 distances. Then the complete, previously dyed root axis of the seminal root was spread on a transparent acetate sheet using dissecting needles. Total root length of the remaining roots was measured using a root scanner (Comair, Inc., Melbourne, Australia), and root dry weight of these remaining roots was determined as above. Values of specific root length were derived from values of root length and root biomass of the entire root system (seminal and adventitious roots).

A digitized image of the root axis was obtained with a flatbed scanner (Silverscanner, LaCie, Portland, Ore., USA) at a resolution of 28.54 pixels cm^{-1}. The architecture of the seminal root image was analyzed with Branching v1.52ß software (Berntson 1992), which estimates topological parameters following the nomenclature and algorithms presented by Fitter (1985, 1986, 1987), which is similar to the method of Werner and Smart (1973). In essence, the topological system of classification consists of a description of branching networks, using the link, which is the segment of root between a meristem and a branching point or between 2 branching points, as the unit of the system. Links are classified as external if they end in a meristem or internal if they do not. Smart (1978) proposed a further classification of links based on the type of links they join. Thus, 'EE' are external links that join other external links, 'EI' are external links connected to internal links, 'IE' are internal links attached to external links, and 'II' are internal links. Other parameters such as magnitude, 'μ' (number of exterior links in the system); altitude, '*a*' (largest path of links from the base to an exterior link meristem); and total exterior pathlength '*Pe*' (the sum of all the paths from each meristem to the base) are calculated from this link distribution (Fitter 1985, 1986, 1987). The pathlength-slope index (log *Pe* on log μ) was then calculated from these parameters. This index classifies root system topology as dichotomous if values are near 1 and herringbone if values are near 2.

Link length was estimated for each link category including EE, EI, IE, and II (Smart 1978). For each link type the average length was calculated by averaging all links of the same type independently of their location in the system. To ascertain possible differences in link length distribution within the root system, links along the root axis (hereafter referred to as interbranch distance) were also evaluated at 3 sampling depths (0–5, 5–10, and 10–15 cm from the base). Interbranch distances included both II and IE links; however, II and IE exhibited a localized distribution along the axis. Interbranch distances of the root axis in the 0–5 and 5–10 cm sampling depths were mostly II links, while those located in the 10–15 cm sampling depth were mainly IE links. Because interbranch distances were similar among sampling depths, only the 10–15 cm level is presented here. The average IE link length for the system, which in this case is the seminal root, was estimated by averaging all IE links of the seminal root including also those located in the root axis, which were usually found at the deepest sampling depth. This average length represented mainly IE links from lateral roots.

Statistical Analysis

All data were tested for normality using normal probability plots of residuals, stem-and-leaf diagrams, and the Shapiro-Wilk test (Zar 1984). Non-normal data were logarithm and square-root transformed to correct for deviations from normality. Data were analyzed as a factorial analysis of variance in a randomized complete block design with 4 replications. Because the experiment was an incomplete factorial design, the analysis was separated into 2 models (GLM procedure, SAS Institute, Inc. 1988) with blocks as a random factor in the models. The first model averaged observations across defoliation frequencies to test differences due to defoliation intensity (0, 50, and 70%). The second model eliminated the 0% defoliation intensity to test differences between defoliation frequencies (once and twice) and their interaction with the 50 and 70% defoliation intensities. A third model was used when comparisons involved a control treatment (0% defoliation) (e.g., species X defoliation frequency interaction). Means were separated by Fisher's protected least significant difference (LSD) test. Analysis of covariance was used when needed to correct for the dependence of architectural variables on root system magnitude, with the log of magnitude as the covariate (Fitter and Stickland 1991). Linear regressions between log path-length and log of magnitude were used to estimate the topological index (*Pe*-slope) Heterogeneity of slopes was tested with a linear model, using log of magnitude as the regressor and factors as independent variables for each treatment combination group (Littell et al. 1994). Individual slopes were compared using the Tukey-Kramer test (Sokal and Rohlf 1981).

Results and Discussion

Root Architecture: Root System Topology

Normally, the development of root systems involves a gradual increase in branching complexity as lateral roots of different order are initiated. These increases in root branching complexity are represented by a decrease in the *Pe*-slope index, which tends toward a value of 1. The index can vary among genotypes (Lynch and van Beem 1993) and can also be modified by environmental factors (Fitter and Stickland 1991, Schellenbaum et al. 1991, Berntson and Woodward 1992). The index can reach a constant value, which may indicate that morphological or environmental characteristics constrain further increases in branching complexity (Fitter 1986, Fitter and Stickland 1992).

The *Pe*-slope index for categorizing root system topology did not vary with harvests, species, defoliation intensity, or defoliation frequency (Table 1). The harvest x species interaction was the only significant interaction for the *Pe*-slope index ($P \leq 0.10$). There were significant increases in the *Pe*-slope index for Hycrest and cheatgrass between Harvests 1 and 3 (Fig. 1a), indicating that Hycrest, and to a lesser extent cheatgrass, exhibited reduced root branching complexity through time. The *Pe*-slope index decreased for Whitmar, indicating an increase in root branching complexity through time.

Hycrest was bred and selected for improved seedling vigor and competitive ability (Asay et al. 1985). Its low *Pe*-slope index for Harvest 1 and 2 is the result of its rapid seedling root development, which was similar to that of cheatgrass (Fig. 1a). At Harvest 3 root branching complexity for Hycrest decreased (higher *Pe*-slope index). Because defoliation intensity or frequency did not significantly affect root system topology (Table 1, $P > 0.10$), the change in *Pe*-slope index may be related to density-dependent mechanisms by which roots reduce inter-root competition

Table 1. ANOVA, associated mean squares, and significance levels for *Pe*-slope index (*Pe*-slope), specific root length (SRL), internal-external link length (IE), interbranch distance (Int. dist.), axis diameter of the seminal root (axis diam.), and diameter of first order lateral roots of the seminal root (Lat. root diam.). Column for *Pe*-slope index only presents mean squares for slope comparisons; intersect comparisons were not included.

Source of variation	df	*Pe*-slope	SRL	IE	Int. dist.	Axis diam.	Lat. root diam.
			(m g^{-1})	(cm)	(cm)	(mm)	(mm)
Harvests (H)	2	0.0063	1.0940**	0.0062	0.0076	0.0464	0.0099**
Species (S)	2	0.0206	0.2257**	0.3363**	0.0870*	0.0848**	0.0101**
H × S	4	0.0269*	0.1582**	0.0085	0.0417	0.0292	0.0002
Intensity (I)	2	0.0128	0.1506**	0.0050	0.1114	0.0011	0.0010
I × H	4	0.0153	0.0652*	0.0106	0.0042	0.0054	0.0004
I × S	4	0.0093	0.0074	0.0073	0.0107	0.0418*	0.0042*
I × S × H	8	0.0046	0.0066	0.0080	0.0339	0.0129	0.0012
Frequency (F)	1	0.0004	0.1379 *	0.0364*	0.0168	0.1154 *	0.0047
F × H	2	0.0058	0.0537	0.0122	0.0481	0.0285	0.0016
F × S	2	0.0263	0.0424	0.0996**	0.5097**	0.0002	0.0001
F × I	2	0.0047	0.0322	0.0085	0.0022	0.0151	0.0001
F × S × H	4	0.0114	0.0166	0.0108	0.0434	0.0083	0.0009
F × I × H	2	0.0134	0.0425	0.0084	0.0090	0.0119	0.0029
F × I × S	2	0.0105	0.0764 *	0.0153	0.0100	0.0174	0.0009
F × I × S × H	4	0.0070	0.0302	0.0124	0.0249	0.0153	0.0027

*, ** indicate significant differences at $P \leq 0.10$ and $P \leq 0.01$, respectively.

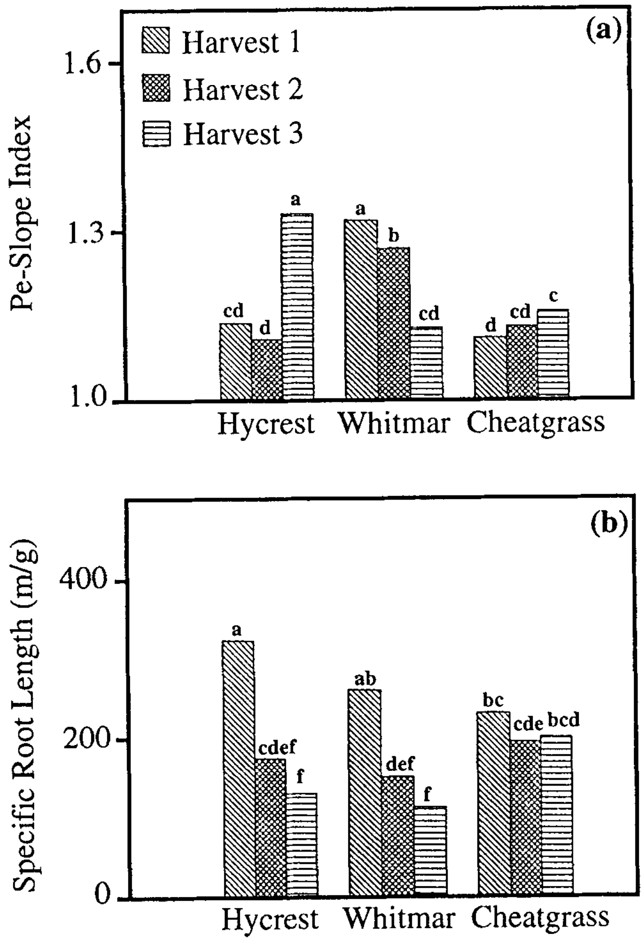

Fig. 1. ***Pe*-slope index (a) and specific root length (b) for Hycrest, Whitmar, and cheatgrass across 3 harvests.Values are averaged across 3 defoliation intensities and 2 frequencies of defoliation. Bars with different lower case letters on top indicate significant differences among species and harvests at $P \leq 0.10$.**

(Robinson and Rorison 1983). In our study, the root mass of Hycrest increased from 9 mg for Harvest 1 to 127 mg for Harvest 3; total root density also increased (data not shown). The decrease in branching complexity for Hycrest at Harvest 3 (higher *Pe*-slope index), which coincided with increases in root mass and density, indicated possible inhibition in branching initiation as volume of the root system increased.

Root development in Whitmar was slower than for Hycrest and cheatgrass, as evidenced by the high *Pe*-slope index (1.34) at Harvest 1 (Fig. 1a). At each consecutive harvest, however, the *Pe*-slope index for Whitmar decreased as branching complexity of the root system increased, in contrast to the patterns exhibited by Hycrest and cheatgrass. This slow root development may postpone interbranch competition in Whitmar. The slower root development of Whitmar is consistent with the results of Aguirre and Johnson (1991b).

Despite a significant increase in the *Pe*-slope index between Harvests 1 and 3, cheatgrass exhibited a relatively low *Pe*-slope index for the 3 harvests (Fig. 1a), an indication that cheatgrass was able to maintain its highly branched topology. Maintenance of such a highly branched system may aid the absorption of nutrients and water, thus sustaining rapid growth and development during the short life cycle of cheatgrass.

Root Morphology: Specific Root Length

The root length produced by a unit of root biomass (m g^{-1}) is defined as specific root length, an indication of how much biomass plants invest in a given root length and how efficiently plants invest carbon to acquire soil resources (Barber and Silberbush 1984, Fitter 1985). Assuming that changes in biomass reflect changes in carbon costs of tissue synthesis (Chapin 1989), plants that invest less biomass in root length (high specific root length) should increase total root length more than plants with a low specific root length (Eissenstat 1992); thus a high specific root length will confer an advantage in capturing soil resources. However, other morphological and physiological attributes associated with root morphology such as root hairs, nutrient uptake kinetics, etc. also are important.

Significant differences in specific root length were observed across harvests, species, defoliation intensities, and defoliation frequencies (Table 1, $P \leq 0.10$). The harvest × species, defoliation intensity × harvest, and defoliation frequency × defoliation intensity × species interactions were also significant for specific root length. Specific root length decreased with seedling age (273, 175, and 147 m g^{-1} for Harvests 1, 2, and 3, respectively), when averaged across species; however, there were significant reductions in specific root length only in Hycrest and Whitmar between Harvests 1 and 3 (Fig. 1b). The reduction in specific root length with seedling age observed for Hycrest and Whitmar means that construction costs per unit root length increased for these species, perhaps because seedlings initiated coarser roots at foliar nodes (adventitious roots). These coarse roots may reduce the proportion of fine roots within the root system and subsequently lead to lowered specific root length. Other root attributes including root longevity (Fernandez and Caldwell 1975), extension of individual roots (Eissenstat 1992), and specific rates of water and nutrient uptake (Hamblin and Tennant 1987, Mengel and Steffens 1985) may have changed to compensate for the increased construction costs. Cheatgrass, in contrast, maintained a uniform specific root length across harvests, and specific root length did not change with defoliation. Cheatgrass develops rapidly (Harris 1967), has high relative growth rates (unpublished data, Arredondo et al.), and consequently has a large nutrient demand. Maintaining a constant specific root length may let cheatgrass continue to exploit soil resources and maintain rapid growth.

Overall specific root length was greater after 2 defoliations (219 m g^{-1}) than 1 defoliation (180 m g^{-1}) and increased with defoliation intensity (173, 208, and 214 m g^{-1} for 0, 50, and 70% defoliation intensities, respectively). Specific root length was greatest for Harvest 1 and at 50 and 70% defoliation intensities (Table 2, $P \leq 0.10$). Two defoliations at 50% defoliation intensity resulted in the highest specific root length for Hycrest and Whitmar; cheatgrass was not affected by defoliation (data not shown). A significant increase in specific root length at 50 and 70% defoliation intensities compared to no defoliation at Harvest

Table 2. Specific root length (m g^{-1}) for 3 defoliation intensities across 3 harvests.

Harvest	Defoliation intensity (%)		
	0	50	70
	(m g^{-1})		
Harvest 1	211 b	326 a	282 a
Harvest 2	167 bc	169 bc	188 bc
Harvest 3	143 c	130 c	174 bc

[1] Values with different lower case letters indicate significant differences among treatments ($P \leq 0.10$).

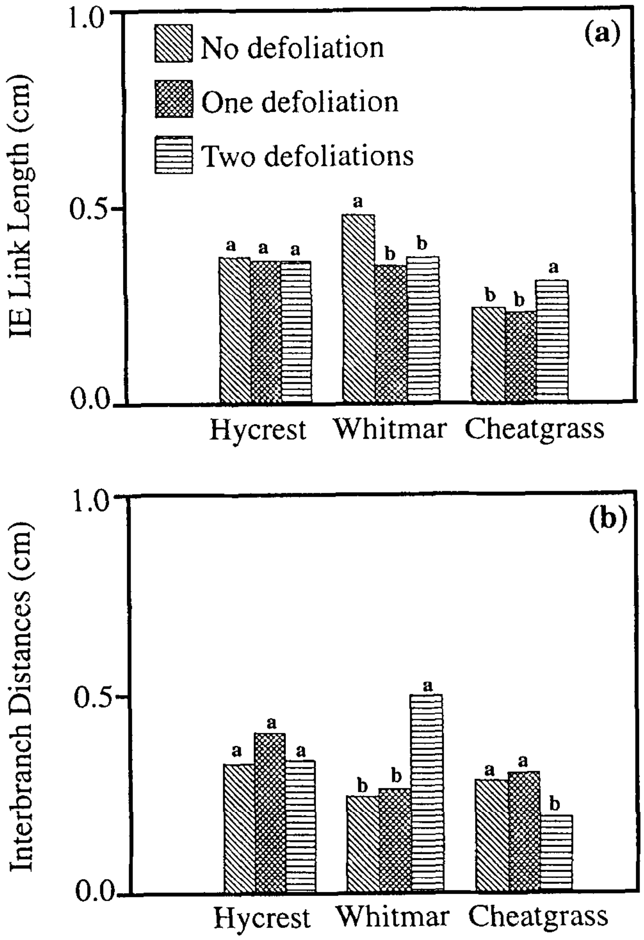

Fig. 2. Internal-external (IE) link lengths (a) and interbranch distances of the root axis at a sampling depth of 10–15 cm (b) with no defoliation (control), 1 defoliation, or 2 defoliations for Hycrest, Whitmar, and cheatgrass for Harvest 3. Bars with different lower case letters on top indicate significant differences among defoliation treatments within each species at $P \leq 0.05$. Values for 1 or 2 defoliations are averaged across 50 and 70 % defoliation intensities.

1 and a tendency for specific root length to increase at 70% defoliation intensity at Harvests 2 and 3 (Table 2) suggest that defoliation tended to reduce biomass per unit root length in these grasses. Investing less biomas per unit root length (high specific root length), may minimize production costs of root growth, thereby allowing defoliated plants to better cope with limited carbon resources following defoliation (Richards 1984).

Link Length and Interbranch Distances

The link length of IE (internal links attached to external links) varied significantly among species and defoliation frequencies; the species X defoliation frequency interaction was also significant (Table 1, $P \leq 0.10$). The IE links were longer in Hycrest and Whitmar than in cheatgrass (Fig 2a). Hycrest was not affected by defoliation intensity. One and 2 defoliations significantly decreased IE link length in Whitmar, indicating an increase in the number of second order laterals per unit of root length (first order laterals). In cheatgrass 2 defoliations significantly increased IE link length, indicating reduced density of second order lateral roots.

There were significant differences in interbranch distances among species (Table 1, $P \leq 0.10$). The defoliation frequency x species interaction was highly significant ($P \leq 0.01$) at each of the 3 sampling levels. Changes in interbranch distances in the root axis reflected changes in the density of first order lateral roots. Interbranch distances did not change among defoliation frequencies for Hycrest (Fig. 2b). For Whitmar, interbranch distances were significantly longer with 2 defoliations compared to 1 or no defoliation. Two defoliations significantly reduced interbranch distance in cheatgrass. Thus, 2 defoliations reduced the number of first order lateral roots per unit of root axis for Whitmar, but increased the density of first order lateral roots for cheatgrass.

Although Whitmar had the longest interbranch distances in plants defoliated twice (Fig. 2b), Whitmar exhibited shorter IE link lengths under 2 defoliations compared to no defoliation (Fig. 2a). A similar tradeoff was observed for cheatgrass, which exhibited shorter interbranch distances with 2 compared to 1 defoliation (Fig. 2b), but greater IE link lengths when defoliated twice (Fig. 2a). Apparently, changes in link length of roots may interact with root interbranch distances to regulate root branching density, which may subsequently affect root function. Increases in interbranch distances along the root axis may facilitate the spread of first order lateral roots, thus ameliorating interbranch competition. A reduction in the IE link length of lateral roots may increase the density of fine roots (second order lateral roots), thereby increasing root density, and improving exploitation potential rather than exploitation efficiency (Berntson 1994). On the other hand, decreases in interbranch distances of the root axis concomitant with increases of IE link length in first order laterals may help roots accommodate more first order laterals by reducing the density of second order lateral roots. Increases in IE link length in lateral roots, and thus the density of fine roots (second order lateral roots) would probably enhance the exploitation efficiency of the root system (Fitter 1985, 1987).

Berntson and Woodward (1992) reported trade-offs between branching angles and interior link lengths; increases in horizontal root growth trajectories were associated with shorter links, and vertical branching angles were associated with longer links. Predictions of Fitter (1986, 1987) and Fitter et al. (1991) suggested that link length is a static parameter. Our data, however, indicated that link length differs between the root axis and lateral roots. Understanding the trade-offs between geometrical features of root systems will help elucidate the functional significance and foraging tactics of root systems.

Root Diameter

Axis diameter of the seminal root varied significantly among species and defoliation frequencies (Table 1, $P \leq 0.10$). The defoliation intensity X species interaction was also significant ($P \leq 0.10$). Lateral root diameter varied significantly among harvests and species ($P \leq 0.01$), and the defoliation intensity X species interaction was significant ($P \leq 0.10$). Two defoliations reduced the diameter of the main axis of the seminal root more than 1 defoliation (0.29 and 0.32 mm for 2 and 1 defoliations, respectively). The diameter of lateral roots decreased with seedling age (0.14, 0.12, and 0.11 mm for Harvests 1, 2 , and 3, respectively). Defoliation intensity changed the root diameter of either the axis or lateral roots of the seminal root for Hycrest and cheatgrass, but not for Whitmar (Fig. 3a, 3b). For Hycrest, the diameter of the seminal root axis was significantly larger for the 70% defoliation intensity than control treatment. For cheatgrass, however, the diameter of

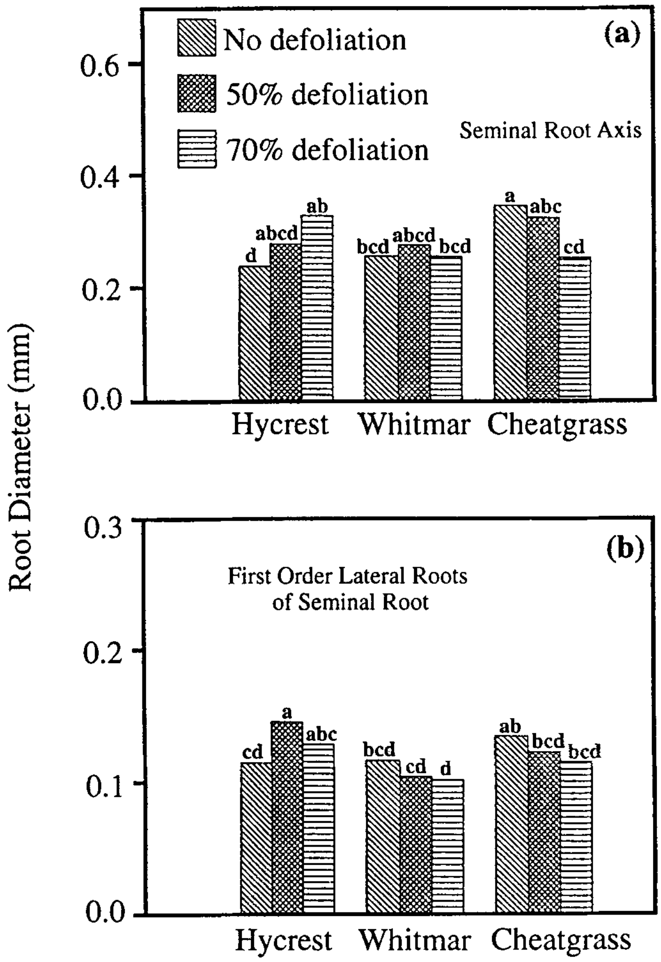

Fig. 3. Diameter of the root axis (a) and first order lateral roots (b) of the seminal root measured at the 10–15 cm sampling depth for Hycrest, Whitmar, and cheatgrass subjected to no defoliation (control) and 50 and 70% defoliation intensities. Means are averaged across 2 defoliation frequency treatments. Bars with different lower case letters indicate significant differences among all treatment combinations at $P \leq 0.05$.

the lower main root axis diameter decreased with 70% defoliation intensity. For Hycrest, the diameter of first order lateral roots was larger for the 50% defoliation intensity than the control treatment. Overall, the diameter of both seminal root types was smallest in Whitmar and largest in cheatgrass ($P \leq 0.05$). Aguirre and Johnson (1991b) reported that the diameters of the main axis and first-order lateral roots of the seminal root of Hycrest seedlings exceeded those of cheatgrass and Whitmar, which were similar. The degree of phenotypic plasticity in root diameter and the effect of genotype by environment interactions on root morphology in range grasses warrants additional study.

Changes in root diameter with defoliation intensity or time were generally not associated with equivalent changes in specific root length. Perhaps this was because changes in root diameter occurred only with some roots (i.e., seminal root), and therefore specific root length was not altered or variations in root diameter did not account entirely for variations in specific root length. This was also the case in 6 citrus rootstocks (Eissenstat 1991).

Root diameter is important in the consideration of cost-benefit relationships of root construction and nutrient uptake rates. Coarse roots require more biomass investment per unit root length than do thin roots. Coarse roots, however, may have a longer life span and higher specific nutrient uptake rates (uptake per unit length of root) than thin roots (Chapin 1989, Eissenstat 1991, 1992). The increased root diameter associated with increased defoliation intensity of Hycrest suggests that specific uptake rates may have increased. Such a strategy may have reduced carbon turnover rates because coarse roots have a long life span. *Agropyron desertorum*, a parent of Hycrest, is a grazing-tolerant species that reduces root growth after defoliation (Caldwell et al. 1981, Richards 1984). Survival after defoliation may depend on Hycrest's ability to recover its photosynthetic area, which depends on the carbon resources invested in root growth and the efficiency of roots in capturing soil nutrients. Reduction of root diameter in cheatgrass (Fig. 3a, 3b) probably involves decreased production costs of roots under carbon limitation.

Conclusions

The topological index (*Pe*-slope index), which is an indication of branching complexity of root systems, did not change with either defoliation intensity or frequency for Hycrest, Whitmar, and cheatgrass. However, the branching complexity of the 3 grasses differed with seedling age. In general, root branching was less complex in Hycrest and cheatgrass (high *Pe*-slope index) with time, and more complex in Whitmar (low *Pe*-slope index). The IE link length of roots changed with root interbranch distances, thereby controlling the root density of first and second order laterals. At a defoliation rate of 70 %, diameter of the main axis of the seminal root increased in Hycrest and decreased in cheatgrass. These changes in diameter were not associated with changes in specific root length. Thus, our study showed that seedling roots of 3 important range grasses responded to defoliation with both architectural and morphological changes, which may affect root demography and/or physiology. It must be emphasized that the results of our study are for young seedlings grown under controlled greenhouse conditions and that root architectural and morphological responses of mature, field-grown plants may be quite different than what we observed for seedlings. Nevertheless our study provides an initial attempt to apply recently developed computer technology to the analysis of how range grass root systems function.

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