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Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope

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Summary. Root growth responses to defoliation were observed in the field with an improved root periscope technique, which is described. The grazing tolerant, Eurasian bunchgrass, *Agropyron desertorum*, was compared with the very similar but grazing sensitive, North American bunchgrass, *A. spicatum*. Root length growth of clipped *A. desertorum* was about 50% of that of intact plants, while root elongation of clipped *A. spicatum* continued relatively unabated during ninety days of regrowth following severe defoliation. The reduced root growth in *A. desertorum* was correlated with the allocation of relatively more resources to aboveground regrowth, thus aiding reestablishment of the root:shoot balance. This balance was apparent in similar root mortality patterns of clipped and control *A. desertorum* plants in the season following defoliation. In clipped *A. spicatum*, however, root mortality increased in the winter following the season in which the clipping was done and continued into the subsequent growing season. Reduction of root growth following defoliation appears to be an effective mechanism to aid reestablishment of the photosynthetic canopy and the root:shoot balance. As such it contributes to both herbivory tolerance and maintenance of competitive ability.

Introduction

Root growth is an important process for water and nutrient uptake (Caldwell 1976, 1979), especially at low soil water potentials (Cowan 1965; Gardner 1960) and in the case of immobile soil nutrients, such as phosphorus (Bhat and Nye 1973, 1974). Defoliation usually results in immediate reductions in root growth (Crider 1955; Jameson 1963; Davidson and Milthorpe 1966), which might reduce the ability of a defoliated plant to regrow since both nutrient and water uptake would be reduced. Differences between species in amount or duration of root growth inhibition might thus be an important mechanism by which defoliation affects the competitive balance in natural communities and pastures. Alternatively, root growth reductions might be a mechanism to reduce belowground carbon demand in defoliated plants and would thus allow greater allocation of carbon to the shoot resulting in more rapid reestablishment of the canopy and return to root:shoot equilibrium. In this paper results of experiments designed to test the hypothesis that following defoliation root growth in the grazing-sensitive *Agropyron spicatum* (Pursh) Scribn. and Smith[1] is reduced to the same extent as in the grazing-tolerant *A. desertorum* (Fisch. ex Link) Schult. are reported and discussed. These two species were chosen for study because of their morphological and phenological similarity, their importance on nutrient poor, semiarid rangelands, and their large difference in tolerance of defoliation (Caldwell et al. 1981).

Study of root growth under natural conditions is extremely difficult. Most techniques are either destructive, preventing study of the same root or root system through time, or introduce largely artificial conditions or constraints on roots (Böhm 1979). Some of the observations reported in this paper were made possible by improvements in a root observation technique proposed by Bates (1937), Waddington (1971) and Böhm (1974). These improvements allow rapid, quantitative observation of root length growth of relatively undisturbed plants growing under field conditions. In this study additional plants were excavated and root system biomass determined to verify the observations made with the improved root periscope.

Materials and methods

Ten plants each of crested wheatgrass (*A. desertorum*) and bluebunch wheatgrass (*A. spicatum*) were chosen randomly from stands of these species which had been established two years previously at an experimental site 4 km northeast of Logan, Utah (41° 45′ N, 111° 48′ W, 1460 m a.s.l.). Sagebrush (*Artemisia tridentata* ssp. *vaseyana* Rydb.) Beetle had also been planted in the experimental plots to provide a uniform competitive background. Further description of the site, soils, climate and planted stands is given in Caldwell et al. (1981). Plants chosen for root growth study were randomly assigned to control (5 each species) or treatment (5 each species). The treatment was a severe defoliation (85% foliage removal) repeated twice, on April 30 and on May 13, during the 1980 growing season. This simulated the pattern and timing of defoliation commonly experienced by these bunchgrasses (Norton and Johnson 1983).

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[1] Recent taxonomic revisions make *Pseudoroegneria spicata* (Pursh) Löve (Löve 1980) and *Elytrigia spicata* (Pursh) D.R. Dewey (Dewey 1983) synonymous with *A. spicatum*

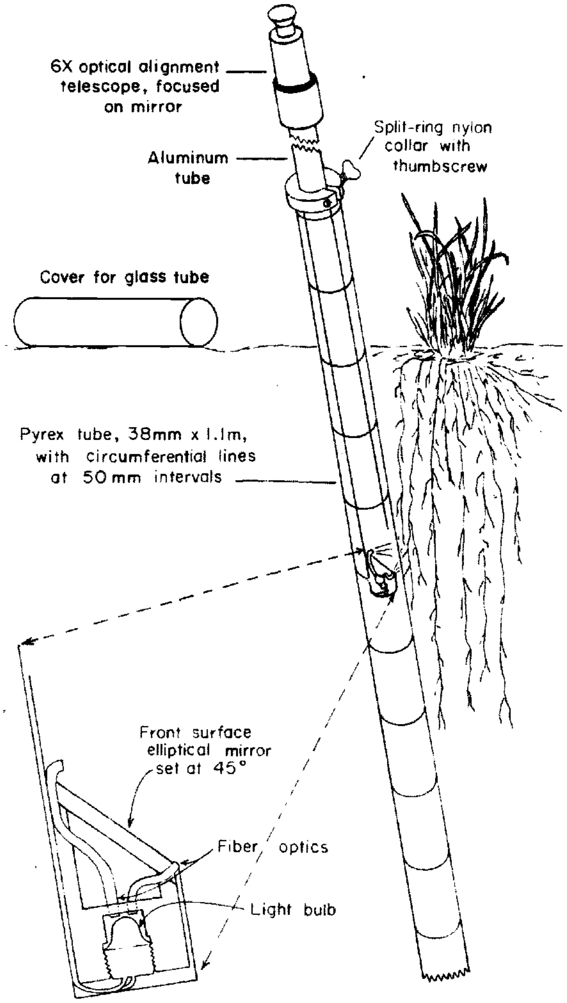

Fig. 1. Schematic illustration of the root periscope developed for observing roots through the wall of a glass root observation tube installed in the soil beneath a bunchgrass plant. Roots intersecting lines scribed at 5 cm depth increments on the tube were counted at intervals to determine net root growth. The glass tubes were kept covered to exclude light and prevent overheating when observations were not being made. Each observation, to 1 m depth, required approximately 20 min

In April 1980 a 4 cm diameter hole was augered into the soil to a depth of 1 m directly beneath each bunchgrass. The soil extracted was sieved to remove stones and used as backfill when the root observation tubes were installed in the holes. Glass tubes (38 mm O.D. × 1.1 m, Pyrex) were scribed with circumferential lines at 5 cm intervals and a rubber stopper was placed in one end before installation. During installation the backfill soil was mixed with water to form a thick slurry and poured into the holes to completely fill the spaces (~7 mm) around the tube. Aluminum covers, painted white to minimize heating, were placed over the portion of the tubes (~15 cm) which extended above the soil surface to exclude light, precipitation, and small animals. The relationship of an installed root observation tube and a bunchgrass plant is shown in Fig. 1.

Observations of root growth were made with a periscope which is also shown schematically in Fig. 1. The periscope consisted of a 1.6-m aluminum tube (27 mm O.D.) machined to accept an illumination source and mirror at one end and an optical alignment telescope (6 ×, Edmund Scientific) on the other. The telescope was focused on a front-surface, eliptical mirror (Edmund Scientific) which was mounted at 45° at the base of the periscope (see Fig. 1). A 10W 6V quartz halogen lamp (Gilway Technical Lamps, Inc.; No. L8017) provided light which was directed at the plane viewed by the mirror by two glass fiber optics (American Optical). Oblique illumination by one of the fiber optics provided better resolution of small translucent roots. A small voltage regulated power supply (not shown in Fig. 1) was mounted on the upper end of the aluminum tube and power was supplied to the bulb by wires set in narrow grooves machined along the outside of the aluminum tube. A rechargeable 12V Ni-Cd battery was used as a power source. The periscope was fitted with an adjustable nylon collar (Fig. 1), which, when resting on the top of the glass tube, allowed the periscope to be held firmly at any depth.

Observations were made by counting the number of roots intersecting each circumferential line of each tube. The medium to dark brown sagebrush roots were distinguishable from the light tan to white bunchgrass roots and were not counted. Most bunchgrass roots grow verticaly; thus they crossed the circumferential lines at angles near the perpendicular. In cases where roots are growing horizontally, vertical lines should be scribed on the glass tubes and roots intersecting them counted. Counts were made at intervals starting in early June 1980, 38 days following the first defoliation, until the end of the next growing season (1981). The number of intersections was converted to root length visible per unit depth using an equation adapted from Newman (1966) and Tennant (1975).

In this paper, root length visible per unit depth was averaged over the 1 m depth profile and is presented as relative root length. Gregory (1979), Köpke (1981) and Bragg et al. (1983) have compared the tube method, similar to that described here, with other methods for measuring root growth. They found that this technique is good for comparative purposes, and for long-term root growth studies, although it underestimates root density at shallow depths. This may be due to more horizontal root growth near the surface, or to localized modification of the soil temperature, water or nutrient regime.

The root periscope described here has a number of advantages over previously described tube observation devices. Small diameter glass tubes (38 mm in contrast to 70–100 mm tubes used by Köpke (1981) and Gregory (1979), respectively) can be used, thus causing minimal disturbance during installation, which is of particular importance with perennial species. Small diameter glass tubes also avoid problems of accumulation of roots at the soil tube interface (see Böhm et al. 1977), and avoid problems of plastic effects on root growth (Taylor and Böhm 1976; Voorhees 1976). The telescope and improved illumination source allow consistent viewing (resolution of 0.1 mm) at all depths to >1 m (see Böhm 1974), and the periscope system is less expensive (~$500) than several described previously (Waddington 1971; Sanders and Brown 1978; Gregory 1979; Upchurch and Ritchie 1983).

Results and discussion

Severe defoliation caused a reduction of about 50% in root length visible and significantly reduced root length growth

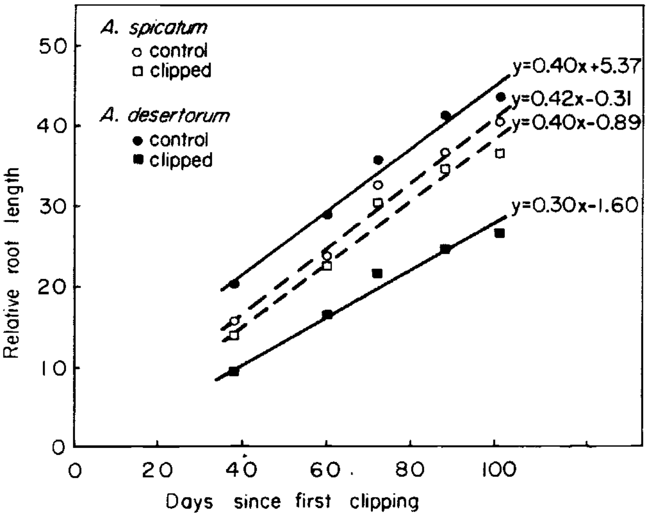

Fig. 2. Relative root length growth of control and clipped *A. desertorum* and *A. spicatum* for the first 100 days following severe defoliation. Clipped plants were defoliated on day 0 (April 30) and on day 13. Each point represents the mean of five plants. Lines are weighted least squares fits and all are significant at $p<0.029$, $0.44<r<0.84$; the fitted line for clipped *A. desertorum* has significantly lower slope ($p<0.005$) than the other three lines, which are not significantly different from each other

rate in *A. desertorum*, whereas severely defoliated *A. spicatum* plants had root length growth parallel that of controls (Fig. 2). The grazing-tolerant, more competitive species, *A. desertorum*, showed greater root growth reduction than the grazing-sensitive, less competitive species, *A. spicatum*. Reduced root growth in *A. desertorum* is probably related to that species' ability to preferentially allocate carbon resources to aboveground growth following defoliation, while the continued root growth of *A. spicatum* utilizes resources that might otherwise allow more rapid shoot replacement following defoliation. Thus aboveground recovery, i.e. foliage replacement, and reestablishment of the root:shoot balance (Drew and Ledig 1980; Richards 1978; Richards et al. 1979) is prevented.

Root length visible was slightly greater in *A. desertorum* control plants than in *A. spicatum* control plants at all sampling dates (Fig. 2). These relative data agree with the greater rooting density of *A. desertorum* determined by direct measurement of roots washed from known volumes of soil (Caldwell and Richards 1984). In both species root growth was rapid through June and July (days 28–88), a time when aboveground growth rate was declining (Caldwell et al. 1981), and continued in both species into late August when shoot xylem water potentials were below −2.5 MPa (Caldwell et al. 1981). Rapid root growth corresponded with the time of rapid water extraction (Richards et al., unpublished). Root growth observations were not made before June since adequate time had not elapsed for the backfilled soil to become permeated with roots (see Gregory 1979). Previous observations of root biomass changes showed that root growth also occurs in both species in late April and in May, when aboveground growth is most rapid (Caldwell et al. 1981).

Sequential destructive harvests of plants to determine root and shoot biomass also detected different postclipping allocation patterns in the two bunchgrass species (Table 1).

Table 1. Proportion of biomass belowground for control and defoliated (clipped) bunchgrasses harvested immediately following defoliation (13 May 1980, 18 May 1981) and at the end of the growing season (23 July 1980, 22 July 1981). Each value is the mean of three destructively harvested plants and within years those followed by different letters are significantly different at $p<0.05$. Analysis of variance utilized arcsine-square root transformed data and between cell differences were determined with a LSD test. Values for 1980 were calculated from data given by Caldwell et al. (1981).

Species	Treatment	Date	
		1980 13 May	23 July
Agropyron desertorum	control	0.70 cd	0.63 d
	severely clipped	0.92 a	0.81 b
Agropyron spicatum	control	0.77 bc	0.70 cd
	severely clipped	0.95 a	0.95 a
		1981 18 May	22 July
Agropyron desertorum	control	0.88 ab	0.73 c
	moderately clipped	0.94 a	0.86 b
Agropyron spicatum	control	0.87 ab	0.70 c
	moderately clipped	0.94 a	0.91 ab

After two and one-half months of regrowth the proportion of biomass belowground of clipped *A. spicatum* was not significantly reduced from the proportion immediately following defoliation. Clipped *A. desertorum* plants, however, allocated relatively more carbon aboveground causing the proportion of biomass belowground to be significantly reduced during regrowth. This occurred in 1980, following severe defoliation, and also in 1981 for a different set of plants subjected to moderate defoliation (50% foliage removal on 16 and 30 April and 15 May, 1981) and harvested in a manner similar to that described by Caldwell et al. (1981) (Table 1). Control plants of both species were similar in relative aboveground-belowground allocation in both years. These destructive harvest data corroborate the root periscope observations. *Agropyron spicatum* appears to inflexibly allocate carbon belowground, maintaining root growth, even when defoliation has caused a major imbalance in root:shoot biomass proportions. This inflexible allocation reduces carbon available for canopy reestablishment and contrasts sharply with the allocation pattern exhibited by defoliated *A. desertorum*.

Carbohydrates necessary for continued root growth in both species were primarily supplied by photosynthesis during regrowth rather than by carbohydrates synthesized before defoliation. Following severe defoliation total soluble carbohydrate pools in roots, crowns and regrowing shoots of both bunchgrass species were less than or equivalent to those produced during two to four days of photosynthesis during regrowth (Caldwell et al. 1981). Therefore, during the two and one-half month regrowth period most of the carbon utilized was derived from photosynthesis. Greater

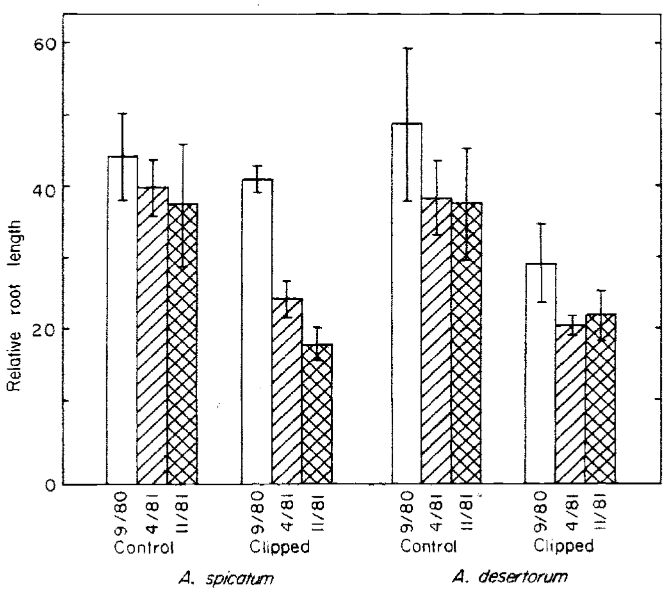

Fig. 3. Relative root length changes from the peak values reached during the 1980 season (September), in which two severe defoliations occurred, to values at the beginning of the following season (April 1981). Minimum values in November following the 1981 growing season are also shown. Mean ± 1 SE, $n=5$

relative allocation of current photosynthate to the shoot in *A. desertorum* resulted in more rapid increases in foliage area and whole-plant net assimilation rate in that species than in *A. spicatum* (Caldwell et al. 1981; Richards and Caldwell, unpublished).

If continued root growth in clipped *A. spicatum* prevents accumulation of adequate carbohydrates by the end of the growing season, the roots would be expected to suffer greater mortality in the following seasons. There was a greater decline in visible root length during the winter of 1980–1981 in clipped *A. spicatum* when compared with either control plants of the same species or with clipped plants of *A. desertorum* (Fig. 3). In the growing season following the clipping treatments root length continued to decline in *A. spicatum*, but began to recover in *A. desertorum*.

Immediately following defoliation root growth stops or is radically reduced (Crider 1955; Davidson and Milthorpe 1966). While root growth resumes after several days or weeks it may do so at a reduced rate, as in *A. desertorum*. Both immediate and continued reduction in root growth and productivity are usually considered to be detrimental to the survival and competitive ability of defoliated plants (Crider 1955; Jameson 1963). Reduced root growth during regrowth of *A. desertorum*, however, appears to be a mechanism contributing to more rapid reestablishment of the photosynthetic canopy and the balance between root and shoot. The similar but less grazing-tolerant and less competitive species, *A. spicatum*, suffered more long-term root mortality than *A. desertorum*, perhaps as a consequence of maintaining high root growth rates during regrowth. Root growth reductions thus may be an important component of the ability of *A. desertorum* to tolerate herbivory and maintain its competitive position in the rangeland plant community.

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