Growth and carbon allocation of *Agropyron desertorum* following autumn defoliation

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Summary. Growth and carbon allocation of a cool-season bunchgrass, *Agropyron desertorum*, following defoliation in early autumn and later in the autumn and 1986 and 1989 were investigated. Tiller density and mortality, reproductive shoot density, root density, biomass, incremental tiller weight, carbon allocation, and soil water depletion were used to evaluate the response of *A. desertorum* to autumn grazing. Tiller recruitment was lower in the autumn-defoliated treatment in both years compared with the control because of the cessation of tiller development following autumn defoliation. Autumn defoliation also significantly reduced the movement of ^{14}C to the roots in 1989 but not in 1988. Soils were cooler and drier in 1989. Other plant growth measurements and soil water depletion were very non-different between treatments. Autumn defoliation in 1989 did not influence tiller recruitment in the following autumn. If re-vegetation was of autumn defoliation did not affect tiller recruitment or mortality, or peak standing crop of *A. desertorum* the following spring.

Key words: Allocation – Defoliation – Tiller – Roots – Crested wheatgrass – $\delta^{14}C$

Summary. Growth and carbon allocation of a cool season tussock grass, *Agropyron desertorum,* following defoliation of newly initiated tillers in the autumn of 1988 and 1989 were investigated. Tiller density and mortality, reproductive shoot density, root density, biomass, individual tiller weight, carbon allocation, and soil water depletion were used to evaluate the response of *A. desertorum* to autumn grazing. Tiller recruitment was lower in the autumn-defoliated treatment in both years compared with the control because of the cessation of tiller development following autumn defoliation. Autumn defoliation also significantly reduced the movement of ^{13}C to the roots in 1988 but not in 1989. Soils were cooler and drier in 1989. Other plant growth measurements and soil water depletion rates were not different between treatments. Autumn defoliation in 1988 did not influence tiller recruitment in the following autumn. Two consecutive years of autumn defoliation did not affect tiller overwinter mortality or peak standing crop in 1990.

Key words: Allocation – Defoliation – Tiller – Roots – Crested Wheatgrass – $\delta^{13}C$

Tiller recruitment predominately occurs in the autumn for several cool-season grasses (Richards and Caldwell 1985; Mueller and Richards 1986; Olson and Richards 1988). Mueller and Richards (1986) reported the majority of tillers for *Agropyron desertorum* (Fisch. ex Link) Schult. and *A. spicatum* (Pursh.) Scribn. and Smith present in the spring were produced the previous autumn following late summer or autumn precipitation. In eastern Oregon, precipitation is generally adequate to initiate tiller growth in September or October. Over a 5-year period, 80 to 90% of all *A. desertorum* tillers present in the spring were produced the previous autumn (Squaw Butte file data, Burns, Oregon, USA). When autumn conditions were dry (September and October), tiller re-cruitment was observed in November. Autumn tillers can become photosynthetically active in the winter if conditions are suitable. *A. desertorum* leaves are capable of photosynthesis and carbohydrate production near 0° C (Nowak and Caldwell 1984; Chatterton et al. 1988). Early photosynthetic activity in autumn-produced shoots may reduce demands for stored carbohydrates during initial spring growth. Hyder and Sneva (1959) reported that use of carbohydrate reserves in *A. desertorum* for initial spring growth was lower than expected. For some species current assimilate is apparently more important for growth than are carbon reserves (Ryle and Powell 1975; Richards and Caldwell 1985). The presence of green leaves early in the growing season may also provide a competitive advantage for acquisition of water and nutrients. Miller (1988) reported that *Artemisia tridentata* Nutt., a semi-deciduous shrub, was better able to capitalize on soil moisture early in the growing season than were associated decidous species.

The effects of defoliation on cool-season grass species during the spring and summer (Sampson and McCarty 1930; McCarty and Price 1942; McIlvanie 1942; Cook et al. 1958; Hyder and Sneva 1963; Caldwell et al. 1981; Richards 1984; Olson and Richards 1988) are well documented. Very little work, however, has focused on the defoliation of active leaf tissue in the autumn. Development of new shoot tissue in the autumn provides a source of high quality forage for many wild and domestic herbivores prior to winter. Trlica and Cook (1972) reported carbohydrate concentrations decreased with the onset of autumn growth and were not replenished before winter dormancy. They also concluded that removal of new leaf tissue in the autumn had little effect on growth and carbohydrate concentrations in *A. desertorum* the following spring. However, others have found that autumn growth can replenish carbohydrate reserves prior to winter quiescence (El Hassan and Krueger 1980; Chatterton et al. 1988). Autumn leaf removal of *Lolium perenne* L. significantly depletes total carbohydrate reserves (El Hassan and Krueger 1980). No work to date has evaluated the effects of autumn defoliation on tiller replacement and survival, root growth, or carbon allocation.

Our goal was to ascertain the effects of defoliating photosynthetically active replacement tillers in the autumn. Our hypotheses were that autumn defoliation of new replacement tillers would: (1) increase winter tiller mortality, (2) decrease root growth and carbon allocation to the roots, and (3) decrease peak standing crop the following growing season.

Methods

The study site was located at the Squaw Butte Experimental Range in southeastern Oregon, 67 km west of Burns, on the northern fringe of the Great Basin (119 43′W Lat., 43 29′N Long.). The experiment was repeated during the autumn and spring of 88–89 and 89–90. The 39-year mean annual precipitation for this area is 283-mm. Precipitation during the 88–89 and 89–90 crop years (September–August) was 302 and 189 mm, respectively. Approximately 90% of the precipitation occurs between September and June, primarily as snow. The mean winter temperature is $-0.6°$ C with the daily minimum averaging $-4.8°$ C. The mean summer temperature is $17.6°$ C with the daily maximum averaging $26.8°$ C. Soils at the study site are coarse-loamy, mixed, frigid Orthic Durixerols approximately 600-mm deep (Lentz and Simonson 1986). The site was seeded to *A. desertorum* in the late 1960s and has not been grazed by livestock since then.

Treatments were applied to 20, 6-m × 6-m plots arranged in a completely randomized design. The same plots were used in consecutive years without rerandomization. During summer dormancy in August of 1988 and 1989, the previous seasons standing crop was mowed to a 30-mm stubble height. No autumn precipitation had occurred by mid September 1988, so 25-mm of water was sprinkled on the plots over a 24-h period. In 1989, 38-mm of precipitation was received during September, so plots were not irrigated. In 10 plots, autumn-initiated tillers were defoliated during mid October in 1988 and 1989 to a height of 50-mm. Most tillers were in the 3-leaf stage at the time of defoliation. The remaining 10 plots were used as a control.

Tiller density was recorded in one, 3-m × 40-mm permanent subplot established within each plot. Tiller density was recorded just prior to autumn defoliation in mid October and again in early spring (April). Ten tillers were permanently marked within each of the permanent subplots, concurrent with autumn density measurements. Winter survival of tillers in defoliated and control plots was estimated by counting the number of live-marked tillers remaining during early-spring growth. The number of reproductive tillers was recorded during late flowering in each subplot both years. At peak standing crop in the second year, the 3-m × 40-mm subplots were clipped to a 30-mm stubble height. Plant material was dried for 48-hours at 60° C and weighed. In the spring of 1990, dry weight removed was divided by total number of tillers in each subplot, to estimate mean tiller weight. Aboveground biomass was determined by clipping a 2-m² plot in each 6-m × 6-m plot during senescence in both years. Plots were clipped to a 30-mm stubble height.

Rooth growth was monitored during autumn and spring both years using a root periscope (Richards 1984; Brown and Upchurch 1987). A Pyrex minirhizotron access tube, marked at 50-mm increments, was buried in each plot adjacent to the permanent tiller density subplots. Tubes were installed at a 30° angle from the vertical to depth of bedrock, approximately 0.5 m. Root density was recorded biweekly in the autumn until mid November, and biweekly in the spring just prior to initiation of above-ground growth through early senescence. Only young, light-colored unsuberized roots intersecting the marked increments were counted within a 180° arc on the upper surface of the tube.

Effects of autumn defoliation on carbon allocation were determined by using the stable isotope ^{13}C (Svejcar et al. 1990). Five plots in each treatment were labeled 24 h after defoliation. Chambers (300-mm × 450-mm × 300-mm) were placed over the plots early

in the day for approximately 1/2-hour. An LI 6000 portable infrared photosynthesis system was used to monitor CO_2 concentration inside the chambers. A gas-tight syringe was used to inject 40-mL of 99 atom % $^{13}CO_2$. Total CO_2 inside the chambers increased to 460 ppm following injection, decreasing to less than 200 ppm at the end of the labeling period. After labeling, root and current year's shoot material were collected from each labeled plot at 1, 24 and 120 hours in 1988, and 1, 24 and 72 h in 1989. Roots were collected to a depth of 250-mm. Five additional unlabeled plants were collected to measure baseline ^{13}C levels. Plants were separated into roots and shoots, and prepared as described by Svejcar et al. (1990). Samples were analyzed for δ^{13}C vs PDB (Pee Dee Belemnite) at the Stable Isotopes Laboratory at the University of Utah, and results are expressed as ‰ relative to PDB (δ_{13}C).

Air temperatures, soil temperatures averaged across three depths (50, 250, and 500 mm), and precipitation were continuously monitored by an automated weather station at the study site. Soil water content was determined gravimetrically from samples collected several times during the autumn and following spring at 20–200 and 200–400 mm depths in each plot. Moisture release curves were developed for each of the two soil depths and were used to estimate soil water potential.

Tiller density, tiller mortality, tiller weight, reproductive shoot density, plant biomass, soil water availability prior to treatment, and mean air and soil temperatures were analyzed using analysis of variance (ANOVA) at $p \leq 0.05$. When measurements were recorded over time for carbon allocation and soil water depletion, time was set as a variable in addition to treatment. Root density data was analyzed using repeated measures procedure. Means were separated using least significant differences (LSD) at $p \leq 0.05$.

Results

Environmental conditions

Mean air and soil temperatures, and soil moisture were higher in the autumn of 1988 than in 1989 (Table 1). Mean soil temperatures during carbon labeling and sampling were $2.4°$ C higher in 1988 than 1989. Soil water content during autumn and early spring was not significantly different between defoliation treatments.

Tillers

Spring tiller densities were lower in autumn defoliated plots than in control plots. Tiller densities declined between autumn defoliation and early spring (% change), whereas tiller densities in control plots increased during

Table 1. Soil water potential at the initiation of autumn growth, mean soil temperatures across 50, 250 and 500 mm depths, and air temperatures during the first 72-hr period following ^{13}C labeling

	1988	1989
Soil Water (MPa)		
0–200 mm	-0.36^a	-0.51^b
200–400 mm	-0.39^a	-0.76^b
Average soil temperature (°C)	15.8^a	13.4^b
Average air temperature (°C)	12.6^a	10.0^b

Means followed by similar lower case letters are not significantly different between years ($p \leq 0.05$)

Table 2. Tiller and biomass responses of *Agropyron desertorum* under two autumn defoliation treatments over a 2-year period

	Control	Defoliated
Tiller Density (#/m²)		
88–89		
Autumn[1]	2765[A]	2494[A]
Spring	3098[A]	2074[A]
% Change	11.3[Aa]	−14.8[Ab]
89–90		
Autumn	2983[A]	2620[A]
Spring	3045[A]	2256[A]
% Change	2.7[Ba]	−18.0[Ab]
Overwinter Mortality (%)		
1989	8.7[Aa]	9.4[Aa]
1990	9.0[Aa]	10.0[Aa]
Reproductive Shoots (#/m²)		
1989	119[a]	117[a]
1990	0	0
Grams/Tiller 1990	0.054[a]	0.060[a]
Biomass (g/m²)		
1989	22.4[Aa]	21.6[Aa]
1990	20.0[Aa]	19.7[Aa]

Means followed by similar lower case letters are not significantly different between treatments ($p \leq 0.05$).
Means followed by similar upper case letters are not significantly different between years within each parameter ($p \leq 0.05$)
[1] Prior to defoliation

this same period (Table 2). Tiller densities are a function of recruitment and mortality. Although tiller densities declined in the defoliated plots, overwinter mortality was not different between treatments (Table 2). Thus, the primary affect of autumn removal of green-leaf tissue was the cessation of additional tiller development. If we account for winter mortality in the control plots, 20.0% and 11.7% of the 1989 and 1990 spring tiller crop, respectively, were developed after mid October in the control plots. Autumn defoliation did not affect individual tiller weight, reproductive shoot density, or peak standing crop the following growing season (Table 2).

Two consecutive years of autumn defoliation did not affect tiller overwinter mortality or peak standing crop in 1990. Autumn tiller densities within each treatment were similar in 1988 and 1989 (Table 2). However, tiller recruitment following the mid October defoliation dates (% change) was greater in 88–89 than 89–90 in the control plots.

Carbon allocation

Tillers readily absorbed and allocated carbon in the autumn of both years. Movement of ^{13}C to the roots occurred within 1 h of labeling (Fig. 1). However, leaf uptake and carbon allocation to roots in the autumn were significantly less in 1989 than in 1988. In 1988, significantly more ^{13}C carbon moved to the roots in the control compared with the defoliation treatment.
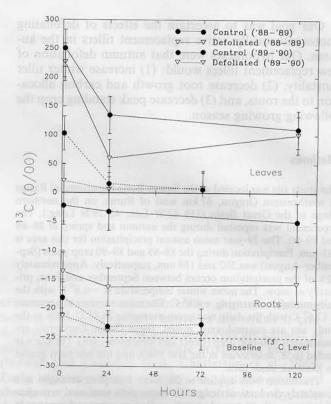

Fig. 1. $\delta^{13}C$ concentrations in shoots and roots of labeled *Agropyron desertorum* for defoliated and control plants following after labeling in 1988 and 1989. Bars around the means are one standard deviation at the 95% confidence interval
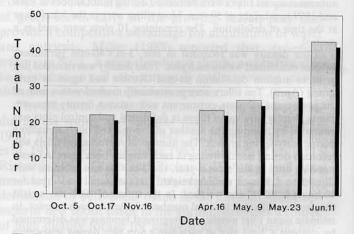

Fig. 2. Total number of light colored unsuberized roots intersecting the lines scribed at 50-mm increments in the minirhizotron access tube across both treatments during the autumn and spring of 89–90

Greater concentrations of ^{13}C in the roots were maintained throughout the 5-day sampling period in the control treatment. In 1989, autumn defoliation did not significantly effect carbon allocation. Concentration of ^{13}C was maintained above baseline in the shoots during the 3-day sampling period for both treatments. In the roots, however, ^{13}C increased immediately following labeling, but rapidly declined to near baseline levels within 24 h of labeling.

Roots

Root growth data were not analyzed for the 88–89 growth period because of poor root contact on newly established minirhizotron tubes. Active root growth was observed the second year at the onset of autumn soil moisture. No net increase in root densities occurred from late November through April 30, 89–90 (Fig. 2). Soil temperature during the April 30 root observations was 7.6° C. As soil temperatures increased in the spring, new roots increased. Autumn defoliation did not significantly reduce root densities in the autumn or following spring.

Discussion

The cessation in tiller recruitment was the only consistent response to autumn defoliation over the 2-year period. If we combine the increase in tillers in the control plots with the decline in the autumn-defoliated plots, autumn-defoliated plants produced 25% and 21% fewer tillers than control plants in 88–89 and 89–90, respectively. However, the decline in tillers was not a result of an increase in winter mortality, but the cessation of tiller development immediately following autumn defoliation. This contrasts with a late spring defoliation which did not influence the number of tillers developed in the autumn but did increase winter mortality (Olson and Richards 1988). Autumn defoliation in 1988 also did not affect tiller recruitment the following fall. We reject the hypothesis that autumn defoliation of replacement tillers increases winter tiller mortality.

Factors which influence tiller development include increased red/far-red light reaching the plant base (Deregibus et al. 1982), growing degree-day (Frank and Ries 1990), removal of apical dominance in the spring, resource availability within and between tillers, and leaf or root produced growth regulators (Richards et al. 1988). Removal of apical dominance by defoliation is not a factor in the autumn since the growing point remains near ground level. Light quantity and quality reaching the crown probably had little influence in the autumn. Because standing dead material had been previously removed in this study, newly formed leaf area within tussocks was probably not high enough to influence light quantity or quality. However, our data indicate that the reduction of leaf area in the autumn was followed by a cessation of tiller recruitment. Factors which autumn leaf removal could affect include levels of carbon assimilation, production of leaf produced growth regulators, and temperature within the tussock. Past work by Caldwell et al. (1981) showed that *A. desertorum* continues to allocate current photosynthate to the shoots following a spring defoliation, at the expense of the roots. However, in our study autumn defoliation appeared to have a different effect. Labeled carbon continued to be translocated to the roots (although at reduced levels in 88–89) following defoliation, possibly at the expense of the shoots.

Active root growth was observed in the autumn, however, the density of young roots was 47% higher in the

spring. Root growth during the autumn of 1989 and into the following spring was not affected by defoliation of newly recruited tillers. Continued allocation of carbon to the roots and a reduced aboveground carbon sink, due to the cessation of tiller development, may lessen the effect of autumn defoliation on root development. A reduced aboveground carbon sink may be important for maintenance of root growth since the carbon source for root growth is from current assimilate, not reserves (Caldwell et al. 1981; Richards and Caldwell 1985). We reject the hypothesis that autumn defoliation reduces root growth, at least under less than ideal growing conditions as in 1989. However, autumn defoliation did reduce carbon flow to the roots in the autumn of 1988, when carbon uptake and allocation to the roots was significantly greater than the autumn of 1989. In the autumn of 1989 plants were less biologically active than the autumn of 1988, reflected by lower tiller development activity after mid October and lower carbon uptake by the leaves and movement of carbohydrates to the roots. Autumn defoliation may influence root growth under more optimal growing conditions, reducing the ability of *A. desertorum* to compete for soil resources. Under more optimal growing conditions in the spring, defoliation of *A. desertorum* reduces root growth by 50% (Richards 1984).

Defoliation of autumn tillers did not alter soil water depletion rates, possibly because of low evapotranspiration demands due to short photoperiods, cool temperatures and low leaf areas. Wraith et al. (1987) and Miller et al. (1990) reported reductions in soil water depletion rates on spring defoliated plants. However, differences were only detected when plants were defoliated during rapid growth in the spring (Miller et al. 1990).

During autumn tiller development, current assimilates were actively translocated to the roots both years. However, significantly more carbon was translocated below ground under warmer and moister soil conditions in the autumn of 1988. Plant water deficits have been demonstrated to decrease carbohydrate translocation (Wiebe and Wirheim 1962; Hartt 1967). In western Oregon, where the autumn climate is wetter and warmer than eastern Oregon, the primary period of carbohydrate reserve accumulation in perennial ryegrass occurs in the autumn (El Hassan and Krueger 1980). Under colder and drier conditions carbohydrate concentrations decline in the autumn (McIlvanie 1942; Trlica and Cook 1974). However, root growth or carbohydrate pool size were not considered in these studies. El Hassan and Krueger (1980) reported below ground pool size affects the magnitude of total available carbohydrates in a plant more than carbohydrate concentration. Carbohydrate concentrations may initially decrease in the autumn with the onset of root and shoot growth. As autumn growth progresses, however, current assimilate will probably become more important for shoot and root growth. Current assimilate of shoot growth is the most important, and under most conditions, the sole carbon source for growth (Richards and Caldwell 1985).

Our work showed autumn defoliation had little effect

on subsequent aboveground biomass, root growth, winter mortality of tillers, and the density of reproductive shoots. However, the degree to which autumn-defoliation affects *A. desertorum* may be influenced by the level of biological activity in the autumn, determined by soil water content and temperature. Trlica and Cook (1972) reported both *A. desertorum* and *Elymus junceus* Fisch. were adapted to autumn grazing based on the response of biomass the following year. But they stated that grazing during any period when plants are rapidly replenishing reserves can seriously decrease total available carbohydrate reserves and new growth. Olson and Richards (1989) reported heavy use during culm elongation decreased tiller recruitment below stand maintenance levels. They also observed an increase in weedy species in the stand, attributed to a decline in competition. Stout et al. (1981) found that four consecutive years of grazing *Calamagrostis rubescens* Buckl. during the same time of year decreased tiller numbers by 50%. For a bunchgrass to maintain its position in a plant community it must replace each tiller with one or more new tillers each year (Olson and Richards 1988). However, although defoliation of autumn initiated tillers in October 1988 decreased tiller numbers the following spring, it did not effect tiller numbers initiated the following autumn. Two consecutive years of autumn defoliation did not appear to detrimentally effect *A. desertorum*.

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