Defoliation of Thurber needlegrass: herbage and root responses

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Abstract

Thurber needlegrass (*Stipa thurberiana* Piper) is an important component of both forested and shrub-steppe communities of the Pacific Northwest and Great Basin regions, and little is known of its tolerance to defoliation. A study was conducted on the Squaw Butte Experimental Range to determine the response of containerized Thurber needlegrass to single defoliations (2.5-cm stubble) throughout the growing season. Dates of treatment spanned vegetative through quiescent stages of phenology. Response variables included: summer regrowth, number of reproductive stems, fall growth, and subsequent spring herbage production, change in basal area, and root mass. Vigor of Thurber needlegrass was reduced most by defoliation during the early-boot stage of development. Impacts were successively less severe from vegetative, late-boot, and anthesis treatments, respectively. Cumulative herbage production the year of treatment was reduced from 38 to 64% by defoliation at the early-boot stage. The same treatment reduced subsequent spring growth by 46 to 51% and root mass the next spring by 34 to 45%. Treatment effects were somewhat reduced when temperature and moisture regimes allowed substantial regrowth after defoliation. Defoliation during or after anthesis had little effect on plant response. Managers should be aware that a single defoliation, particularly during the boot stage, can significantly reduce subsequent herbage production and root mass and possibly lower the competitive ability of Thurber needlegrass.

Key Words: *Stipa thurberiana*, clipping, grazing tolerance, herbage production, roots

Thurber needlegrass (*Stipa thurberiana* Piper) is a component of several steppe, shrub-steppe, and forest communities from central Washington to California and east to southwest Montana and northeast Wyoming (Hitchcock and Cronquist 1974, Franklin and Dyrness 1973). It may dominate the herbaceous layer (Culver 1964, Hironaka et al. 1983) or exist as a subordinant in communities where the vegetation is characterized by bluebunch wheatgrass [*Agropyron spicatum* (Pursh)Scribn. & Smith; recently revised nomenclature is *Pseudorogneria spicata* (Pursh)A. Love by Barkworth et al. 1983], Idaho fescue (*Festuca idahoensis* Elmer), or needle-and-thread grass (*Stipa comata* Trin. & Rupr.) (Daubenmire 1970). Thurber needlegrass is valuable forage for livestock and wildlife, and its cured foliage maintains a slightly higher crude protein content than other bunchgrasses sharing the same environment (Hickman 1975). Only 3 reports have addressed the sensitivity of this species to defoliation or grazing. Tüeller (1962) found Thurber needlegrass decreased with grazing, and while monitoring recovery of grasses from a severe 1-year drought, Ganskopp and Bedell (1981) found a significant reduction in height of Thurber needlegrass plants with a history of heavy, summer use. In a community dominated by Thurber needlegrass, Eckert and Spencer (1987) detected significant reductions in basal areas of plants heavily grazed during a single growing season and subsequently deferred for 4 growing seasons. Where more moisture was available and Thurber needlegrass shared the environment with bluebunch wheatgrass, there were no reductions in basal area (Eckert and Spencer 1987).

Defoliation of other cool-season bunchgrasses is typically most injurious during the middle portion of their rapid growth period when substantial regrowth is prevented by inadequate moisture (McIlvanie 1942, Stoddart 1946, Blaisdell and Pechanec 1949, Blaisdell 1958, Cook et al. 1958). Given the sparsity of information available on responses of Thurber needlegrass to defoliation, a study was initiated in 1982 to evaluate herbage and root responses of this species to 1-time defoliations at various phenological stages during the spring–summer growing season. The objective was to identify at which phenological stage defoliation most adversely affected regrowth and subsequent spring growth and root mass.

Description of Study Area and Methods

The study was conducted at the Squaw Butte Experimental Range (119° 43'W, 43° 29'N) approximately 72-km west-southwest of Burns, Oregon. Mean annual precipitation is 27.6 cm with peak accumulations in November, December, January, and May (ranging between 2.9 and 3.6 cm); and a minimal accumulation (0.8 cm) in July (NOAA 1986). Herbaceous plant yield is most strongly correlated with September–June precipitation accumulations (Sneva

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1982). Mean annual temperature is 7.6° C with recorded extremes of -29 to 42° C (NOAA 1952–1986). Overstory dominants of major plant communities include western juniper (*Juniperus occidentalis* Hook.), low sagebrush (*Artemisia arbuscula* Nutt.), and 3 subspecies of big sagebrush (*Artemisia tridentata* Nutt.) including basin big sagebrush (subsp. *tridentata* Nutt.), Wyoming big sagebrush (subsp. *wyomingensis* Beetle), and mountain big sagebrush (subsp. *vaseyana* (Rydb.) Beetle). Understory dominants include bluebunch wheatgrass, Idaho fescue, Thurber needlegrass, Sandberg's bluegrass (*Poa sandbergii* Vasey), and cheatgrass (*Bromus tectorum* L.).

In August 1982 after quiescence, 150 plants were excavated from sites supporting a Wyoming big sagebrush-Thurber needlegrass community. Descriptions of vegetation and soils of the community are provided by Doescher et al. (1984) and Lentz and Simonson (1986). An effort was made to preserve soil-root integrity of plants to a 15-cm depth. Bunches were transported to a common garden, trimmed to approximately equal dimensions (7.5-cm diameter), and replanted in polyethylene bags with a 25-cm diameter and 61-cm depth. The 61-cm dimension was selected because it approximated the depth of unweathered bedrock in the plants' natural habitats (Lentz and Simonson 1986).

Bags were constructed by cutting sections from a continuous tube of polyethylene material, folding 1 end 3 times, and securing the folds with heavy duty staples. This closure allowed water to drain from the bottom but excluded outside roots. Sifted alluvium (6.4-mm mesh) was used as a potting soil to facilitate later removal of roots. Particle composition of the soil was 77% sand, 9% silt, and 14% clay. Filled bags were placed vertically in 61-cm deep trenches and exterior voids filled with sifted soil. After planting, a 1-time irrigation of approximately 2 liters of water per plant was provided to enhance soil:root contact and facilitate soil settling. When settling occurred, additional soil was provided to create a continuous surface across the top of the bags and the surrounding soil. September through June precipitation for the ensuing establishment, treatment, and harvest years (1983–1987) was 109, 119, 77, 111, and 97% of the long-term average (25.2 cm, NOAA 1986). Emerging weeds were removed when necessary.

One-half of the plants were scheduled for defoliation treatments in 1985 and total plant harvest in 1986, with the remainder designated for a replication of the study in 1986 through spring of 1987. This provided 2 and 3 growing seasons, respectively, for plants to recover from the rigors of transplanting and acclimate to containers. Plants scheduled for 1985 treatments were clipped to a 2.5-cm height in October 1984 to remove standing litter. Plants scheduled for replication of the study in 1986 were similarly clipped in October 1985.

A treatment consisted of a single defoliation (2.5-cm stubble) on 1 of 7 dates during the spring–summer growing season. Biweekly treatments spanned the vegetative through quiescent stages of phenology. Treatment 1 (24 April) occurred when plants were in a vegetative stage of growth. Treatments 2 and 3 (8 May and 22 May) were applied during the early and late-boot stages of development, respectively. As apical meristems began to elevate, bases of reproductive tillers became visibly swollen during the early-boot stage. In the late-boot stage, uppermost awns were emerging from the boot, but remaining portions of reproductive stems were still concealed by protective sheathing. Treatment 4 occurred during anthesis (5 June), and treatment 5 (19 June) occurred when seeds were filling and just beginning to harden. Most seed had hardened, some had fallen from the plant, and portions of the foliage were beginning to senesce when treatment 6 was applied (3 July). A count of seed stalks was also conducted on this date to provide an index of reproductive tiller development in all treatments. Treat-

Table 1. Biomass (mg/cm² basal area) of pretreatment herbage production, regrowth (harvested 31 July), fall growth (harvested 15 Oct.), and herbage and roots the subsequent spring (harvested 5 May) of Thurber needlegrass plants defoliated on 1 of 7 dates spanning the spring-summer growing seasons of 1985 and 1986. Plants of the 17 July treatment grew uninhibited and were viewed as controls. Means in rows sharing a common letter are not significantly different ($P>0.05$).

	Dates of defoliation						
	24 April	8 May	22 May	5 June	19 June	3 July	17 July
Phenology	Vegetative			Anthesis	Hard seed		
		Boot			Soft dough	Seed shatter	
				1985 treatments			
Pretreatment herbage	40a	54a	116b	128bc	171c	227d	232d
Regrowth (31 July)	79c	31b	46b	33b	1a	<1a	<1a
Fall growth (15 Oct.)	5a	4a	9a	11a	4a	8a	10a
Total herbage	124ab	89a	171b	172b	176b	235c	242c
				Harvested 5 May 1986			
Spring growth	123a	83a	84a	126a	133a	150a	158a
Roots (0–20 cm)	259abc	189a	227a	346c	349c	325bc	351c
Roots (20–40 cm)	43a	48ab	75bcd	55ab	57abc	88d	85c
Roots (40–60 cm)	38a	31a	40a	55a	53a	50a	53a
Total roots	340ab	268a	342a	456b	459b	463b	489b
				1986 treatments			
Pretreatment herbage	15a	23a	45a	116b	159bc	220c	219c
Regrowth (31 July)	151c	123c	124c	118c	57b	58b	19a
Fall growth (15 Oct.)	6a	6a	6a	9a	6a	4a	9a
Total herbage	172ab	152a	175ab	243bc	222abc	282c	247bc
				Harvested 5 May 1987			
Spring growth	110ab	87a	126abc	160bc	163bc	175c	171c
Roots (0–20 cm)	597ab	569a	601ab	874c	850bc	994c	896c
Roots (20–40 cm)	239a	180a	240a	234a	225a	265a	267a
Roots (40–60 cm)	170a	156a	173a	176a	171a	222a	209a
Total roots	1006a	905a	1014a	1284a	1246a	1481a	1381a

ment 7, applied on 17 July when all seed had shattered and all foliage was brown, was viewed as a control. Material harvested in the progressive application of treatments (pretreatment herbage production) was retained and dry weights obtained to provide an index of seasonal growth patterns.

Immediately after application of a treatment, basal areas of treated plants were ascertained by measuring (to the nearest 1 mm) major and minor axes of the crowns and later solving for the area of an ellipse. Individual portions were measured and the derived areas totaled if a crown had fractured into obvious components. After acquisition of crown dimensions, soil samples (5 to 40-cm depth) were collected from 5 bags and soil water content measured gravimetrically. Attempts to sample soil moisture at lower depths of the column were confounded by contamination from the drier and often unstable upper portions.

Response variables in this study included: regrowth, seed stalk density, fall growth, total herbage production during the year of treatment (= sum of pretreatment herbage, regrowth, and fall growth), and the subsequent spring's herbage production, root mass, and change in basal area between treatment application and final harvest.

Regrowth was harvested from all treatments on 31 July when most foliage had turned brown. Fall growth occurred in both years that treatments were applied, and was harvested in mid-October.

Spring growth of all treatments was harvested to ground level on 5 May (late-vegetative phenology), and live crown dimensions remeasured on all plants. Root bags were excavated, severed into 3 increments (0–20, 20–40, 40–61 cm) and roots manually washed free of soil over a 5-mm mesh screen. Additional detritus was removed by floating and agitating roots in a shallow pan of water. Because plant crowns were extremely compact in nature, and dead and foreign material could not be satisfactorily removed, crowns were severed from the uppermost root mass.

All harvested materials were oven dried at 60° C for 48 hours and weighed. When first transplanted, all bunches were trimmed to approximately equal dimensions. During the years allowed for plant establishment, however, variations in growth and rodent damage inconsistently altered basal areas. To compensate for variations in plant size all weights were expressed on a mg/cm^2 basal area basis. Pretreatment herbage, regrowth, fall growth, and density of reproductive stems are based on the initial measure of basal area; and spring growth and root weights based on the final measure of basal area. Root weights from the 3 different increments were also converted to percent of total root mass to test the hypothesis that relative distribution of root mass was altered by treatments.

The study was arranged in a completely randomized design with 7 treatments and 8 replications. Years were analyzed separately. The extra plants provided replacements if rodent damage or plant mortality occurred prior to scheduled treatment dates. When significant differences were detected among treatments, mean separation tests were made using least significant difference (LSD) procedures. Significance was assumed at $P<0.05$.

Results

Phenological development of plants was similar between 1985 and 1986, but timing of herbage accumulation varied somewhat between the 2 growing seasons. Herbage production for control plants, clipped on 17 July, was nearly identical between the 2 years, however. Pretreatment herbage data of Table 1 can be visualized as the growth curve of Thurber needlegrass. In 1985, growth was most rapid during the boot stage (9 May–22 May) when there was a 214% increase in herbage. In 1986, a 257% increase occurred during the late-boot through anthesis stage (23 May–5 June). During the early portion of the 1986 growing season (25 April–22 May), mean daily temperatures ((maximum + minimum)/2) averaged 3.7° C degrees cooler than in 1985, which probably depressed herbage production. In the late boot through early anthesis portion of 1986, however, mean daily temperatures were 7.2° C above those of the same period in 1985 (NOAA 1986). Because soil moisture levels were generally greater during the 1986 growing season than in 1985 (Fig. 1), higher levels of regrowth were exhibited by the 1986 treatments.

Thurber needlegrass root and shoot biomass were most adversely affected by defoliation during the early-boot stage of development during both years plants were treated. Plants defoliated during the early-boot stage generally had lower regrowth, total herbage, spring growth, and total roots than plants defoliated at earlier or later phenological stages (Table 1).

As would be expected in an environment where deep soil moisture is a product of winter precipitation, soil water content was gradually depleted as the growing season advanced, and potential for regrowth after defoliation progressively declined. In 1985, regrowth exceeded pretreatment production only when plants were clipped in the vegetative stage (Table 1). By 19 June 1985 soil moisture content was reduced to 4.2%, and plants defoliated on or after that date produced only trace amounts of regrowth. Across all treatments in 1985, regrowth constituted roughly 16% of total herbage production. The greater moisture availability in 1986, however, allowed a greater accumulation of regrowth in even the latest treatments. Regrowth exceeded pretreatment production for the vegetative through anthesis treatments, and contributed sufficient biomass to the 3 July treatment to exceed the control plants in total herbage production. Averaged across all treatments, regrowth constituted 44% of total herbage production in 1986.

Among all treatments and years, fall growth constituted only 3 to 4% of total yearly standing crop (Table 1). No significant treatment effects were detected, and no consistent trends were apparent across treatments.

Significant treatment effects were detected in total herbage production in both years (Table 1). In 1985, defoliation at any time from the vegetative through soft-dough stages caused significant reductions in total herbage. Most severe, compared to the controls, was a 63% reduction in total herbage when plants were defoliated during the early-boot stage. Due to the greater contribution of regrowth to total herbage in 1986, differences between treatments were less apparent, but defoliation during the early boot stage was again responsible for the greatest reduction in total herbage (46% less compared to 3 July treatment).

Despite a two-fold difference across treatments, no significant effects could be detected in spring growth of plants treated in 1985 (Table 1). In the 1986 treatments, however, spring growth of plants defoliated during the early-boot stage was significantly less than for those treated during or after anthesis, and plants defoliated during the vegetative stage produced significantly less spring growth than those clipped at seed-shatter.

Responses of roots mirrored those of the above ground components. Root mass of all treatments was nearly 3 times higher in 1987 compared to 1986. Across treatments and years, roughly 68% of the total root mass was concentrated in the upper 20 cm of the soil, and significant effects were detected in this portion of the roots during both years (Table 1). Middle and lower portions of the roots averaged 18 and 14% of the total, respectively, and treatment effects were not consistently apparent within these portions of the root mass. When root weights from the 3 sections were converted to relative values (percent), no significant differences were found among treatments, indicating the distribution of roots remained relatively constant across treatments.

Plants defoliated during the boot stage in 1985 exhibited significantly less root mass in the 0-20-cm profile than in subsequent treatments (Table 1). Although treatment effects were significant in the 20-40-cm depth, the only clear separations of means were between the first-2 and last-2 treatments. When total roots were considered, the reduced mass in the early-boot stage treatment differed significantly from treatments during or after anthesis.

Similar trends were exhibited with the root systems of plants excavated in 1987. Treatment effects, however, were significant only in the 0-20-cm depth. Defoliation during the early-boot stage reduced root production in the 0-20-cm depth by 33 to 43% when compared to treatments applied during or after anthesis. Summation of data from the top, middle, and lower depths, however, enhanced variation to such a degree that significant responses could not be detected in analysis of total root mass.

Maximum densities of reproductive stems and mature seed were attained by the July treatments which allowed seed to mature prior to defoliation (Table 2). In both years densities of reproductive stems were reduced nearly 50% by the 24 April clipping when plants were described as being in a vegetative stage of growth. Possibly, apical meristems were just beginning to elevate, and nearly 50% were removed by clipping, or tillers failed to differentiate or were aborted. By 8 May in both years, reproductive stems were visibly swollen, and 80 to 90% of the meristems were harvested. On 22 May, awns were just extending from the uppermost sheaths, and clipping removed all apical meristems in 1985. In 1986, however, when early growth rates were slowed by cool temperatures, a few reproductive meristems were low enough to escape the 22 May defoliation. June treatments removed all apical meristems in both years, and no replacements developed.

Basal areas of plants in all treatments declined during both years plants were defoliated. Declines averaged 45% for the 1985 treatments and 16% for the 1986 (Table 2). Trends suggested earlier treatments were most affected, but no significant differences among treatments were detected in either year.

Discussion and Conclusions

Responses of Thurber needlegrass to defoliation during the growing season paralleled those reported for other cool-season bunchgrasses common to the Pacific Northwest and Great Basin regions (Hanson and Stoddart 1940; Mueggler 1970, 1972; Branson 1956; Eckert and Spencer 1987). Clipping at any time prior to seed shatter depressed total herbage accumulation for the current year.

Due to a progressive depletion of soil moisture in late spring and early summer, greatest opportunities for regrowth were exhibited by the earliest treatment. Intuitively, one would expect an orderly decline in the production of regrowth as plants were defoliated on successively later dates. Early-boot stage treatments, however, exhibited depressed regrowth in both years when its production was aligned with earlier and subsequent treatments. Early-boot stage defoliation removed approximately 80% of aboveground material, and due to the compact nature of the crowns, probably an equivalent or greater proportion of photosynthetic tissue. Patterns of carbohydrate withdrawal and allocation vary among species (Jameson 1963, White 1973, Caldwell et al. 1981, Brown 1985), but data from other cool-season bunchgrasses suggest nonstructural carbohydrate pools are at their lowest concentration at this stage of phenology (McIlvanie 1942, Donart 1969). When grasses are severely defoliated and the small amounts of photosynthetic tissue remaining can not support development of new shoots, maintenance of the plant and regrowth of foliage initially depend on stored carbon (White 1973, Caldwell et al. 1981). Possibly, plants clipped at the early-boot stage were forced to initiate regrowth with less stored carbon than other treatments. More recent efforts (Richards and Caldwell 1985, Brown 1985) have found little correlation between carbohydrate levels and regrowth and suggest limitations of meristematic tissues or variations in carbon allocation patterns might be more important.

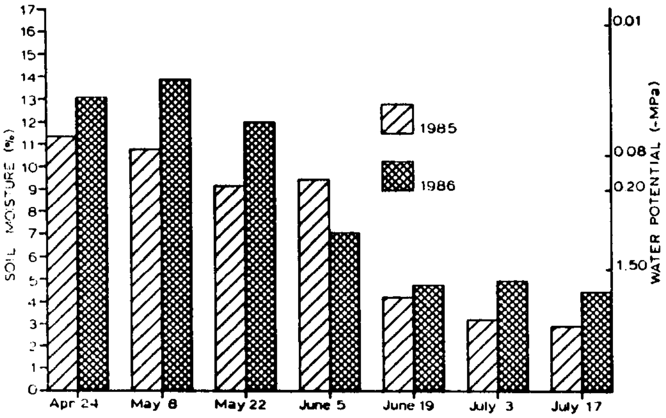

Fig. 1. *Mean gravimetric water content and water potential of soil (5-40-cm depth) in Thurber needlegrass containers on 7 dates when plants were defoliated in the 1985 and 1986 growing seasons (n=5).*

A 50% reduction in herbage production the subsequent spring further suggested plants were most heavily stressed by defoliation at the early boot stage. Treatment differences may have been alleviated if plants had been allowed to grow for a longer period, but past efforts by others indicate more than 1 growing season may be necessary for complete recovery of weakened grasses (Biswell and Weaver 1933, Hanson and Stoddart 1940, Eckert and Spencer 1987).

Perhaps the most important response of Thurber needlegrass to defoliation during the early-boot stage was the reduction in root mass. While the present study detected no significant changes in the relative distribution of roots in the soil column, significant differences in mass intuitively imply differences in absorptive surfaces. Mass of roots in all treatments were nearly 3 times higher in 1987 compared to 1986. Under controlled conditions, Mohammad et al. (1982) noted reduced root production of plants exposed to increased water stress. One can only speculate, however, as to whether the disparity between years was a product of 3 years of undisturbed establishment time, a function of less moisture stress

Table 2. Density (number/cm² basal area) of reproductive stems (sampled on 3 July) and percent change in basal areas (between treatment date and 5 May the subsequent spring) of Thurber needlegrass defoliated to a 2.5-cm stubble on 1 of 7 dates spanning the spring-summer growing seasons of 1985 and 1986. Means in rows sharing a common letter are not significantly different ($P>0.05$).

	Dates of defoliation						
	24 April	8 May	22 May	5 June	19 June	3 July	17 July
Phenology	Vegetative			Anthesis	Hard seed		
		Boot			Soft dough	Seed shatter	
	Density of reproductive stems						
1985	0.4b	0.1ab	0.0a	0.0a	0.0a	0.8c	0.9c
1986	0.5bc	0.2ab	0.1a	0.0a	0.0a	1.0d	0.8cd
	% Change in basal area						
1985	-56a	-67a	-34a	-42a	-45a	-59a	-23a
1986	-21a	-26a	-19a	-17	- 7a	-10a	-12a

in 1986, or an interaction of the 2 factors.

Recent work has downplayed the importance of roots as a source of carbohydrate reserves (Marshall and Sager 1965, Caldwell et al. 1981). Nevertheless, their function as the primary means of water and nutrient absorption, makes them paramount to plant survival, particularly in arid environments. Grasses with weakened root systems suffer reductions in drought tolerance (Hanson and Stoddart 1940, Weaver and Albertson 1943, Crider 1955), cold and heat tolerance (Biswell and Weaver 1933, Julander 1945), and competitive ability (Weaver 1930).

Plants in this study existed in individual containers and were not exposed to competitive influences of other vegetation. Where there is no competition, or where growing pastures receive uniform grazing, defoliation may decrease moisture losses through transpiration, extend the retention of soil moisture, and thereby provide an improved moisture regime for the remaining foliage or regrowth (Svejcar and Christiansen 1987). The greater longevity of green foliage on regrowing plants in this study suggests this process may have occurred. Had this study been conducted under field conditions where neighboring grasses and shrubs could compete for unused resources, the potential for regrowth may have been reduced, and the negative aspects of defoliation even more enhanced (Weaver 1930, Mueggler 1970, 1972). An additional bias to this study was that no concerted effort was made to separate live and dead roots. Obvious dead and decaying roots were quite brittle and were shattered and washed away in the separation of roots and soil. Some dead roots were certainly included in samples, however, and presence of this material would lead to an understatement of treatment effects on the live component. With these biases in mind, extrapolation of these findings to field conditions should perhaps be made with even a more conservative approach than is suggested by these data.

Thurber needlegrass contributes substantially to the forage resource of the Pacific Northwest and Great Basin regions, and is obviously quite sensitive to defoliation during the growing season (Eckert and Spencer 1987). If we are to wisely manage this species, future efforts should address its sensitivity to repeated defoliations, the seasonality of its carbohydrate dynamics and root growth, and its competitive abilities and rate of recovery from severe or repeated defoliations.

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