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Impacts of defoliation on tiller production and survival in northern wheatgrass

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Abstract

Although northern wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.) is a dominant or co-dominant species that decreases under grazing in northern Mixed Prairie, little is known about its response to herbage removal at different times during the growing season. The objective of this research was to determine the effects of defoliation on the tiller production and survival of this native perennial on a clayey range site in mixed prairie in south-central Saskatchewan. Vegetation was subjected to a factorial experiment with an initial defoliation in early-May, June, July, or August and repeated at 2- or 6-week intervals until mid-September in the same plots for 3 years. An undefoliated control was also included. On average defoliation enhanced tillering (71%) and survival relative to the control, and tiller recruitment was greatest during June and September 1989. Generally tiller survival decreased as the date of emergence in the growing season was delayed. Numbers of tillers emerging was positively correlated with soil water (r=0.77). Some tillers of northern wheatgrass lived 5 years. The 2- and 6-week intervals of defoliation had little influence on tiller survival, but initiating defoliation near the time of tiller emergence reduced survival whereas delaying defoliation until August increased their survival. Increased tillering may be an adaptive feature enabling northern wheatgrass to tolerate defoliation by re-establishing lost photosynthetic area and maintaining or even increasing basal area. Thus, once released from grazing it may rapidly increase phytomass production in a relatively short time. Delaying grazing until August will maximize tiller survival of northern wheatgrass.

Keywords: *Agropyron dasytachyum* (Hook.) Scribn., grazing, Mixed Prairie, population dynamics, tillering, tiller demographics

Tillering responses to defoliation in grasses are extremely complex. Herbage removal of little bluestem (*Schizachyrium scoparium* (Michx.) Nash) extended the period of tiller recruitment, but the total number of tillers was unaffected (Butler and Briske 1988). Defoliation may also reduce the senescence of shoots (Crawley 1983), and tillering can increase or decrease following defoliation (Archer and Detling 1984, Willms 1988, Willms and Fraser 1992). A single defoliation of northern wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.) reduced tillering in a greenhouse study (Li and Redmann 1992). Lauenroth et al. (1985) reported that intensity and frequency of defoliation interactively influenced tillering in western wheatgrass (*Agropyron smithii* Rydb.) with densities reduced by repeated and heavy defoliation. With frequent defoliation grasses may undergo changes towards prostrate ecotypes that have high potential for tillering (Painter and Detling 1981). This change in growth form may help plants escape or tolerate defoliation through rapid tillering and leaf growth.

Tillering is a key process in the maintenance of populations for northern wheatgrass because it is rhizomatous and seldom produces seeds. However, it is difficult to assess the effects of disturbance on the population dynamics of rhizomatous grasses unless the focus is placed on tillers. Detailed studies of tiller dynamics are useful in predicting outcomes of different management activities (Jones and Mott 1980).

The objective of this study was to examine the recruitment and survival of northern wheatgrass tillers on a northern Mixed Prairie over a 3-year period to test the hypothesis that multiple defoliation regimes do not alter tillering and survival in this rhizomatous perennial.

Methods

Study Site Description

Research was conducted at the Matador Research Station of the University of Saskatchewan, approximately 70 km north of Swift Current (50°42'N, 107°43'W, elev. 685 m). The site is located within a glacial lake plain near the northern edge of the mixed prairie in the northern Great Plains (Coupland 1950). Soils are Rego Brown and Calcareous Brown Series in the Sceptre Association of the Chernozemic Brown Subgroup (Aridic Borolls) (Coupland et al. 1974).

The study area is a clayey range site with northern and western wheatgrass potentially producing about 75% of the total phytomass (Coupland et al. 1974). Northern wheatgrass is clone-forming, with short slender rhizomes and clustered tillers. It is generally loosely to densely tufted, has intra- and extra-vaginal shoots, giving a tussock-like growth form. Several shoots may originate from one node.

Annual precipitation data were obtained from Beechy, Saskatchewan (50°46'N, 107°19'W, elev. 670 m) about 40 km northeast of the study site. Annual precipitation in 1988 was only

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70% of the 50-year mean of 373 mm, while precipitation in 1989 and 1990 was 106% and 113% of the long-term average.

Experimental Design and Sampling Methods

The experiment was conducted from 1988 to 1990 in a pasture that had been heavily grazed during the summer in several previous years; ecological range condition was estimated as fair in 1986 and 1987 (J.T. Romo unpub. data) according to Abouguendia's (1990) classification. A 50 × 50-m exclosure was established and 8-clipping treatments with 4-initiation dates and 2 intervals, and an undefoliated control were replicated 4 times in a randomized-complete-block design. Plots were 5 × 6 m and a 1-m buffer was maintained on all sides. Plots were initially defoliated in early May, June, July, or August, and again at 2- or 6-week intervals until mid-September of each year. In the text May+2 implies the first defoliation was in May and again every 2 weeks through the summer, and so on. A Jari sickle-mower was used to mow plots to a 5-cm stubble, and all harvested plant material was removed. Treatments were repeated on the same plots each year.

A 10 × 10-cm permanent quadrat was randomly established in each plot in mid-May 1988 to monitor tiller demographics. All live tillers were counted in May 1988 when the study was begun, marked with a colored wire at their base and grouped as the mixed-age tillers because their ages were unknown. These permanent quadrats were revisited at 2 to 4-week intervals from May or June through September each year, and survival of previously marked tillers was recorded and new ones were tagged with wires of different colors. Tillers that emerged on the 2 observation dates in each month were grouped. The recruitment observations were terminated in July 1990, but survival was determined until June 1991.

Soil water was determined biweekly from May through September each year. Soils were collected in 2.5-cm cores at the 0-15-cm depth, weighed and dried at 80°C for 48 hours. Dry weights were determined and gravimetric water content was then calculated.

A test of homogeneity was used to analyze the recruitment of tillers in each month among treatments,'and if Chi-square values were significant at $P\leq0.05$, each treatment was tested against the control. Because the number of tillers varied among plots and treatments, survival was expressed as the ratio of living tillers at a given time to the initial number of tillers. Each year survival of tillers over the growing season and through the winter was compared among treatments in September and the following May or June. Hypotheses were tested by using Chi-square assuming equal survival among treatments for tillers emerging within a month. Survival in the control and all defoliation treatments were set equal to test defoliation effects. Survival in the 2- and 6-week intervals of defoliation were set equal and survival in the initial defoliation in May, June, July, and August were equalized. All possible, pairwise Chi-square comparisons were made at $P\leq0.05$.

Results

Tiller Recruitment

With the exception of August and September 1988 (data not shown) when no tillers were produced, they were recruited throughout the study with most in June and September 1989 (Table 1). On average, defoliation increased tillering 71% more than the undefoliated control. Tiller recruitment in 1988 and 1990 was similar among treatments. In 1989, treatments of July+6 and August+6 produced 3- to 6-fold more tillers in May than the control, while in June every defoliation treatment except those initiated in June had twice as many new tillers as control. Greater than 2-fold more tillers were recruited in the July+2 and August+2 treatments than the control in September 1989.

Recruitment of tillers was positively correlated with soil water at 0-15 cm (Y=-25.7+1.62X, r=0.77, Y=tillers $0.04m^{-2}$). Tiller recruitment was negatively correlated with mean daily air temperature (Y=43.9-1.71X, r=-0.43).

Survival of the Mixed-age Tillers

Tiller survival in the control was significantly lower (60 to 67%) than the mean of defoliation treatments except in June 1991 when it was 63%, a difference that was not significant (Table 2). When defoliation was initiated in May, survival in September 1988 and May 1989 was lower than if defoliated later. Survival

Table 1. The number of northern wheatgrass tillers recruited in 1988, 1989, and 1990. An initial defoliation was imposed in early May, June, July, or August and repeated at 2- or 6-week intervals in 1988, 1989, and 1990. Values for control are also presented.

	Defoliation Treatments								
Month of Observation	May +2	May +6	Jun. +2	Jun. +6	Jul. +2	Jul. +6	Aug. +2	Aug. +6	Control
	Tillers $0.4m^{-2}$								
1988									
Jun.	7	2	3	2	7	9	6	6	0
Jul.	12	11	2	11	14	11	8	13	7
1989									
May	10	8	8	7	8	13*	8	23*	4
Jun	44*	40*	37	30	59*	45*	46*	43*	23
Jul.	7	0	7	6	5	6	3	3	3
Aug.	6	2	3	6	1	1	5	3	4
Sep.	20	14	22	14	30*	25	29*	23	13
1990									
May	9	2	6	5	2	5	6	7	4
Jun.	8	4	8	6	2	4	6	3	6
Jul.	2	5	3	8	2	2	2	0	1
Total	125*	88	99*	95*	130*	121*	119*	124*	66

* Numbers within an observation data are significantly ($P\leq0.05$) different from control.

Table 2. Mean survival of mixed aged tillers for northern wheatgrass marked in May 1988 and observed through 3 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1988	May 1989	Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)					
Control	54a[1]	43a	31a	31a	24a	19a
Defoliation mean	81b	68b	49b	45b	40b	30a
May	65a[2]	46a	38a	37a	33a	26a
Jun.	82ba[3]	72ba	46aa	39aa	37aa	26aa
Jul.	83baa[4]	69baa	47aaa	43aaa	36aaa	28aaa
Aug.	92bba	84bbb	65bbb	61bbb	55bbb	40bba
2-weeks	83a[5]	70a	52a	48a	41a	28a
6-weeks	80a	66a	47a	42a	40a	32a

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July, and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

of tillers was similar when first defoliated in June or July, and delaying defoliation until August generally improved survival. With the exception of September 1988 and June 1991 tiller survival was greater in the August than the July defoliation treatment. Tiller survival was similar when defoliated at 2- or 6-week intervals, decreasing from 82% in September 1988 to 30% in June 1991.

Survival of Tillers Produced in 1988

Since no tillers emerged in the control plots in June 1988, comparisons of survival were made only among the defoliation treatments on all dates. Survival was highest when initially defoliated in May (Table 3). None of the tillers produced in June 1988 and defoliated in June were living after September 1988. All tillers produced in June 1988 died by June 1991 if defoliated during July. Tillers defoliated in August had higher survival rates than those defoliated either in June or July. On average 39% of the tillers were living in the May and August defoliation treatments in June 1991. Survival of tillers was 33 to 50% less when defoliated every 6 weeks than biweekly except in September 1988 and June 1991 when it was similar.

With the exception of September 1989, May 1990, and June 1991 survival in control was 42 to 64% of the mean of defoliation treatments for tillers produced in July (Table 4). Survival of tillers was lowest in the May and June defoliation treatments after May 1989. Tiller survival was generally greatest when defoliation was delayed until August. Except in May 1989 survival was greater when first defoliated in August than July. After 3 years, survival was lowest when first defoliated in May or June and highest in August. Generally there were no differences between 2- or 6-week intervals of defoliation.

Table 3. Mean survival of tillers for northern wheatgrass marked in June 1988 and observed through 3 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1988	May 1989	Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)					
Control	—[1]	—	—	—	—	—
Defoliation mean	85	54	40	39	33	19
May	100a[2]	100a	78a	78a	67a	44a
Jun.	80ba[3]	0ba	0ba	0ba	0ba	0ba
Jul.	69baa[4]	50bba	25bba	19bba	13bba	00baa
Aug.	92bbb	67bbb	58bbb	58bbb	50bbb	33bbb
2-weeks	87a[5]	70a	52a	52a	39a	17a
6-weeks	79a	47b	32b	26b	26b	21a

[1]No tillers were produced in the control
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 4. Mean survival of tillers for northern wheatgrass marked in July 1988 and observed through 3 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1988	May 1989	Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)					
Control	43a[1]	43a	43a	43a	14a	14a
Defoliation mean	74b	52b	38a	36a	33b	24a
May	59a[2]	41a	37a	33a	26a	11a
Jun.	69aa[3]	38aa	15ba	15ba	15aa	15aa
Jul.	80baa[4]	60bba	32aba	32aba	32aba	28bba
Aug.	90bbb	67bba	62bbb	57bbb	52bbb	43bbb
2-weeks	75a[5]	58a	44a	44a	39a	25a
6-weeks	76a	48a	34a	30b	28a	24a

[1]A similar letter within an observation data indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 5. Mean survival of tillers for northern wheatgrass marked in May 1989 and observed through 2 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)			
Control	100a[1]	75a	50a	25a
Defoliation mean	82b	76a	69b	58b
May	56a[2]	50a	50a	33a
Jun.	93ba[3]	87ba	67ba	60ba
Jul.	90baa[4]	86baa	81bba	67baa
Aug.	87baa	77baa	74baa	65baa
2-weeks	85a[5]	74a	62a	47a
6-weeks	80a	78a	75b	65b

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 6. Mean survival of tillers for northern wheatgrass marked in June 1989 and observed through 2 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)			
Control	61a[1]	57a	48a	43a
Defoliation mean	83b	75a	61a	46a
May	83a[2]	79a	68a	52a
Jun.	84aa[3]	76aa	60aa	42aa
Jul.	85aaa[4]	67aaa	60aaa	41aaa
Aug.	79aaa	61bba	57aaa	47aaa
2-weeks	83a[5]	66a	57a	41a
6-weeks	82a	75a	66a	51a

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 8. Mean survival of tillers for northern wheatgrass marked in August 1989 through 2 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)			
Control	100a[1]	100a	75a	25a
Defoliation mean	74b	48b	44b	26a
May	50a[2]	38a	38a	25a
Jun.	89ba[3]	67ba	56ba	22aa
Jul.	100bba[4]	50aba	50aaa	50bba
Aug.	75bbb	38aba	38aba	25aab
2-weeks	75a[5]	38a	38a	25a
6-weeks	92b	83b	75b	42b

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Survival of Tillers Produced in 1989

As of September 1989 defoliation decreased tillers first marked in May 1989, but increased survival during September 1990 and June 1991 (Table 5). When initially defoliated in May tiller survival was only 52 to 67% of those defoliated during either June, July, or August. In September 1990 and June 1991 tiller survival was 21 to 38% greater when defoliated every 6 weeks than biweekly.

Survival of tillers produced in June 1989 was generally similar in the defoliation regimes and control, except in September 1989 when it was 26% lower in the control (Table 6). The initial month tillers were defoliated had no significant affect on tiller survival. Throughout the study survival of tillers produced in June 1989 was not significantly different in the 2- and 6-week intervals of defoliation.

All tillers produced in July 1989 died in the control, but 59% were living in the defoliation treatments in September 1989 (Table 7). Delaying defoliation until July or August increased tiller survival in September 1989. Delaying defoliation until tiller survival by 47 to 73% compared to defoliation in May, June or July the first 2 years. In September 1990 tiller survival in the June and August defoliation treatments was simliar, but survival of tiller was lower in the August than the July treatment. Except in June 1991 survival of tillers was greater in the August than the May treatment. Tiller survival was not significantly different when defoliated at 2- or 6-week intervals.

Relative to control survival of tillers produced in August 1989 was reduced 26% by defoliation in 1989 and 52 to 41% in May and September 1990, respectively (Table 8). With the exception of June 1991, tiller survival was less when first defoliated in May than in June. In September 1989 and June 1991 it was also greater when initially defoliated in July than in August. Survival averaged 26% among treatments in June 1991 with it being highest in the July defoliation. Nearly 50% fewer tillers lived when

Table 7. Mean survival of tillers for northern wheatgrass marked in July 1989 and observed through 2 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date Sep. 1989	May 1990	Sep. 1990	Jun. 1991
	(%)			
Control	00a[1]	00a	00a	00a
Defoliation mean	59b	46b	38b	30b
May	43a[2]	43a	29a	29a
Jun.	54aa[3]	46aa	38aa	23aa
Jul.	64baa[4]	36aaa	36aaa	36aba
Aug.	83bbb	67bbb	50bab	33aaa
2-weeks	59a[5]	50a	41a	32a
6-weeks	60a	40a	33a	27a

[1]A similar letter within an observation date indicates than means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

Table 9. Mean survival of tillers for northern wheatgrass marked in September 1989 and observed through 2 consecutive growing seasons and winters.

Defoliation Treatment	Observation Date May 1990	Sep. 1990	Jun. 1991
	(%)		
Control	92a[1]	69a	46a
Defoliation mean	91a	82b	55a
May	79a[2]	74a	47a
Jun.	94ba[3]	75aa	39aa
Jul.	87aaa[4]	84aaa	60aba
Aug.	100bbb	92bba	67bba
2-weeks	88a[5]	81a	51a
6-weeks	95a	84a	61a

[1]A similar letter within an observation date indicates that means aer not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6 week intervals of defoliation.

Table 10. Mean survival of tillers for northern wheatgrass produced in May, June or July 1990 and observed through 1 growing season and winter.

	Observation Date					
	May tillers		Jun. tillers		Jul. tillers	
Defoliation Treatment	Sep. 1990	Jun. 1991	Sep. 1990	Jun. 1991	Sep. 1990	Jun. 1991
	(%)					
Control	75a[1]	50a	67a	50a	67a	50a
Defoliation mean	90b	71b	80b	51a	96b	38a
May	82a[2]	73a	75a	42a	100a	57a
Jun.	82aa[3]	73aa	93ba	63ba	91ba	18ba
Jul.	100bba[4]	71aaa	100bba	33aba	100aba	50aba
Aug.	100bba	69aaa	100bba	44aba	100aba	50aba
2-weeks	87a[5]	74a	67a	50a	100a	22a
6-weeks	95b	68a	100b	53a	93b	47b

[1]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between control and the defoliation treatments.
[2]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) for all pairwise comparisons between months. First column of letters compares May to June, July and August defoliations.
[3]Second column of letters compares June to July and August defoliations.
[4]Third column of letters compares July and August defoliations.
[5]A similar letter within an observation date indicates that means are not significantly different ($P \geq 0.05$) between 2- and 6-week intervals of defoliation.

they received 2 rather than 6 weeks of rest between defoliation events.

Survival was similar in the defoliation treatments and control except in September 1990 when 16% fewer tillers were alive in the control (Table 9). More tillers survived when herbage was first removed in August than in May or June. Except for May 1990 tiller survival was equal in the July and August treatments. Rest periods between defoliation did not affect survival.

Survival of Tillers Produced in 1990

In September 1990 survival of tillers produced in all months during 1990 was greater when defoliated than in control (Table 10). Defoliation increased survival of May 1990 tillers during June 1991, but herbage removal had no effect on tillers initiated in either June or July. Deferring defoliation until July or August improved survival in September 1990 for May tillers while survival of June tillers was poorest when first defoliated in May. Fewer July tillers survived in the June-initiated defoliation than when defoliated earlier or later. Winter survival for May tillers was similar among treatments whereas winter survival of tillers produced in June and defoliated that month was greater than if defoliated in May, July, or August. Survival of tillers produced in July was lowest when defoliated in June. Two- or 6-week defoliation had no consistent effect on tillers initiated in 1990.

Discussion

Although a host of biotic and abiotic factors affect tiller production (Murphy and Briske 1992) recruitment of tillers in perennial grasses of temperate regions is most common in spring or fall (Butler and Briske 1988, Miller and Rose 1992). With the exception of August and September 1988, continuous recruitment of tillers was observed for northern wheatgrass, with most entering the population in June and September 1989. Maxwell (1977) also observed seasonal variation in northern wheatgrass tiller densities with most in May and least in August coinciding with peaks and minimums in precipitation and soil water. In the present study, tiller recruitment was also positively correlated with soil water. The absence of tillering in late summer and fall of 1988, and low recruitment in July and August of 1989 are attributed to dry conditions. Busso et al. (1989) also reported crested wheatgrass (*Agropyron desertorum* Fisch. ex Link) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love; Syn: *Agropyron spicatum* Pursh) did not produce tillers in a dry autumn.

Relatively low tiller recruitment in the control was attributed to the population adjusting to the removal of grazing, modification of the microenvironment, and apical dominance in tillers that were not defoliated. When defoliation pressure is removed, plant size may increase through larger tillers instead of more tillers being produced (Peterson 1962, Milchunas et al. 1988). Because phytomass production in the control equaled that in the defoliation treatments (Zhang and Romo 1994) and tiller number was less in the control, response of tillers must have been one of increased size with protection.

The accumulation of litter in the control compared to the defoliation treatments (Zhang and Romo 1994) probably reduced radiation, light, and temperature at the soil surface, inhibiting initiation of new tillers (Ong et al. 1978). On the other hand, tillering can be enhanced by opening the canopy, increasing surplus energy and the amount of red light at the base of the plant (Deregibus et al. 1985, Casal et al. 1985) as shown for plains rough fescue (*Festuca hallii* Vasey Piper) and rough fescue (*Festuca campestris* Rydb.) (Willms et al. 1986). Alternatively, apical dominance in tillers that were not defoliated may have limited initiation of new tillers (Murphy and Briske 1992).

Greater tillering by northern wheatgrass with defoliation represents overcompensation in response to defoliation (McNaughton 1983), however, shoot phytomass showed equal compensation while root and crown phytomass were undercompensated (Zhang and Romo 1994). This decline in roots may reduce resource acquisition, competitive ability and productivity (Caldwell 1984). Plants that have a greater potential for tillering tend to prevail under grazing (Carman 1985). Increased tillering may enable northern wheatgrass to tolerate defoliation by re-establishing lost photosynthetic area and maintaining or increasing basal area.

Generally, tiller survival was similar in the 2 defoliation intervals, suggesting that the frequencies were not temporally segregated enough to induce differences in responses. Defoliation during emergence tended to reduce survival of new tillers. Initiating defoliation after tillers emerged was less detrimental to their survival than herbage removal before or during tiller emergence. There was also a trend of decreasing tiller survival as the date of emergence in the growing season was delayed. New tillers rely on parent tillers for nutrients and energy during emergence (Welker et al. 1985, 1987) and if parent plants are defoliated, the resources for developing tillers may diminish and their survival reduced (Jónsdóttir and Callaghan 1989). Thus, delaying defoliation probably enabled uninterrupted development of tillers. In contrast tillers may escape defoliation at early stages, however, the removal of herbage on parent tillers may decrease their survival because of reduced assimilate transfer.

Assuming the initial mix-aged tillers all emerged in the previous season, tillers of northern wheatgrass can live more than 4 years because about 25% were alive at the end of the study. Zhang (unpub. data) noted that some of the mixed-age tillers were still living after 5 years. Coupland and Abouguendia (1974) reported that 29% of the tillers of northern and western wheatgrass lived 3 years while Maxwell (1977) noted that 21% lived at least 2 years. Tillers of western wheatgrass and several other mixed prairie grasses lived 2 to 3 years (White 1977).

Management Implications

Northern wheatgrass tillers have potentially long lifespans, and this perennial responded to repeated defoliation by increased tillering and longevity relative to the control. This enhanced production and survival of tillers may enable northern wheatgrass to increase phytomass production in a relatively short time when grazing pressure is relieved. Increased tillering with repeated defoliation can potentially be exploited to increase tiller densities and speed recovery of deteriorated range. This proposition must, however, be tested on a small scale before it is extensively applied because this range type can be damaged quickly by repeated defoliation (Zhang and Romo 1994).

Initiating defoliation before or during tiller emergence reduced tiller survival while delaying defoliation until August increased their survival. Tillers produced early in the season tended to have greater longevity and survival than those emerging later. It may be important to insure the recruitment and survival of these longer-lived tillers for they may add stability to populations when recruitment is limited. Delaying grazing until August will maximize potential phytomass harvest (Zhang and Romo 1994) and tiller production and survival in this grassland.

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