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Demographic evaluation of a herbivory-sensitive perennial bunchgrass: does it possess an Achilles heel?

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Plant and tiller demography of a C_4 perennial bunchgrass, *Eriochloa sericea*, were evaluated to define specific traits that contribute to its sensitivity to herbivory by domestic grazers. We tested three hypotheses: (1) defoliation adversely impacts tiller recruitment to a greater extent than mortality, (2) tiller recruitment and/or mortality are particularly sensitive to defoliation at the time of culm elongation, and (3) synchronous tiller recruitment contributes to a meristematic limitation which constrains growth following defoliation. Demographic variables were monitored on permanently marked plants and tillers that were defoliated at various frequencies and stages of phenological development for two successive years. Hypotheses one and three were rejected because defoliation adversely impacted per capita tiller mortality to a greater extent than per capita tiller recruitment and tiller recruitment occurred throughout the spring and summer, rather than synchronously. Apical meristem elevation in vegetative tillers did not extend beyond 5 mm above the soil surface and the proportion of reproductive tillers did not exceed 10% of the total number of tillers. Low values for both morphological attributes indicate that they did not contribute to a meristematic limitation constraining leaf growth. Hypothesis two was not rejected because cumulative, but not per capita, tiller recruitment was reduced to a greater extent by defoliation during culm elongation than during the pre-culm or post-culm stage. Plants that received multiple defoliations exhibited the greatest decline in basal area and tiller number compared to undefoliated plants, and only the undefoliated plants and plants defoliated during the pre-culm stage recruited a sufficient number of tillers to offset tiller mortality. In spite of the adverse effects of two of the four defoliation regimes, we were unable to identify a specific trait (i.e., Achilles heel) within this species that contributed to a meristematic limitation and herbivory-sensitivity. An alternative interpretation of herbivory-sensitivity is proposed which emphasizes the involvement of more subtle extrinsic mechanisms, including herbivore-mediated competitive interactions and drought-herbivory interactions. Assessment of herbivory resistance based on the 'specific trait approach' fails to recognize and address the importance of extrinsic mechanisms associated with herbivore-induced processes at higher ecological scales.

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Grass–grazer interactions have been intensively investigated since the 1970's and experimental evaluations of grass responses to defoliation have been conducted in North America since the turn of the century (Briske and Richards 1994, 1995). Yet, in spite of intensive research activity, a thorough understanding of the mechanisms and/or attributes that convey herbivory sensitivity or tolerance have not been clearly established. Consequently, herbivory tolerance is often applied on a comparative, rather than a mechanistic basis

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(Briske 1996, Briske et al. 1996). Herbivory resistance is established by the qualitative and/or quantitative expression of attributes conferring resistance (e.g., specific trait approach) and/or the extent of biomass removal or damage associated with herbivory (e.g., bioassay approach) (Simms 1992). Limited insight into the mechanisms conferring herbivory-sensitivity to individual species populations further constrains our ability to extrapolate this important concept to higher ecological scales (e.g., Brown and Allen 1989, Brown and Stuth 1993).

A current assessment of herbivory tolerance in grasses indicates that demographic processes and architectural attributes are of greater importance than physiological processes. A thorough comparative investigation of a herbivory-tolerant and herbivory-sensitive C_3 perennial bunchgrass by Caldwell et al. (1981) demonstrated that the ability to replace leaf area by rapid tiller initiation and development of leaves with low specific mass were more important than compensatory photosynthesis (Nowak and Caldwell 1984) or size of reserve carbon pools (Richards and Caldwell 1985). Similar conclusions have been drawn from investigations of species populations with contrasting histories of grazing (i.e., grazing morphs). Decumbent canopy architectures comprised of a larger number of smaller tillers with lower leaf areas make a greater contribution to herbivory resistance than physiological processes including photosynthetic rate, transpiration rate or water-use efficiency (Detling and Painter 1983; but see Polley and Detling 1988). Architectural attributes limiting the amount and photosynthetic efficiency of remaining leaf area following defoliation also have been emphasized as an explanation for herbivory-sensitivity of *Themeda triandra* (Coughenour et al. 1985, Hodgkinson et al. 1989, Mott et al. 1992). This information collectively identifies meristematic availability, including leaf differentiation from apical meristems and tiller initiation from axillary buds, as a critical variable determining herbivory resistance in perennial grasses.

Although both initiation and longevity of tillers of numerous bunchgrasses are known to be adversely affected by defoliation, tiller initiation is frequently the most sensitive (Butler and Briske 1988, Bullock et al. 1994; but see Olson and Richards 1988a). Differential tiller initiation among grasses following defoliation appears to be a function of axillary bud activation, rather than a reduction in the number and/or viability of axillary buds (Mueller and Richards 1986, Busso et al. 1989). Unfortunately, variable axillary bud growth among species following defoliation is difficult to interpret because our understanding of the physiological processes and environmental signals regulating tiller initiation is inconclusive (Cline 1991, Murphy and Briske 1992).

The magnitude of tiller recruitment can be influenced by the phenological stage of plant development at the time of defoliation, but the documented responses are inconsistent (Briske and Richards 1995). Defoliation at the time of culm elongation, just before inflorescence emergence, has been demonstrated to increase tiller initiation in several perennial grasses (e.g., Jameson and Huss 1959, Olson and Richards 1988b), but suppress it in others (Vogel and Bjugstad 1968, Culvenor 1994). Similarly, the periodicity of tiller initiation also may influence the capacity for growth by affecting meristematic availability (Mott et al. 1992, Culvenor 1994). Synchronous tiller initiation may exhaust the pool of axillary buds to the extent that minimal meristematic potential remains, if the current tiller cohort experiences mortality in response to defoliation, drought, or a combination of stresses.

We evaluated the C_4 perennial grass, *Eriochloa sericea* (Scheele) Munro, because of its recognized sensitivity to herbivory by domestic grazers. This species has shown a drastic decrease in abundance on the Edwards Plateau of Texas since high concentrations of domestic herbivores (cattle, sheep and goats) were introduced in the 1870's (Youngblood and Cox 1922). Viable populations of *E. sericea* currently exist in communities where grazing by domestic herbivores has been minimal or absent for long periods (≥ 50 yr; Smeins et al. 1976). We reasoned that an especially herbivory-sensitive species would provide an excellent opportunity to identify the specific trait(s) (i.e., Achilles heel) that contributed to the herbivore-induced decline in plant and tiller populations. We emphasized a demographic assessment because previous investigations have indicated that tiller replacement is among the most critical processes associated with herbivory tolerance in bunchgrasses (Caldwell et al. 1981, Mott et al. 1992). Annual tiller replacement is necessary to offset mortality associated with short tiller longevity (≤ 2 yr) to maintain both plant and population persistence (Olson and Richards 1988a, b, Briske and Butler 1989).

Three specific hypotheses were tested: (1) defoliation adversely impacts tiller recruitment to a greater extent than tiller mortality, (2) tiller recruitment and/or mortality are particularly sensitive to defoliation at the time of culm elongation, and (3) synchronous tiller recruitment contributes to a meristematic limitation which constrains growth. Research protocol involved identification of established *E. sericea* plants in a community that had been protected from domestic herbivores for approximately 50 yr. Demographic variables were monitored on permanently marked plants and tillers that were defoliated at various frequencies and stages of phenological development for two successive years.

Methods

Study site

Research was conducted at the Texas A&M University Agricultural Experiment Station located 56 km south of

Sonora, Texas, USA. The station lies in the southwestern portion of the Edwards Plateau Land Resource Area (30 18′N, 100 28′W; 735 m a.s.l.). Stony, clay soils of the Tarrant series (Lithic Haplustolls) dominate the area. Soil depth typically ranges between 15 and 30 cm and slopes are generally less than 5%. Soils contain limestone fragments, stones and gravel and are underlain by a limestone substratum (Wiedenfeld and McAndrew 1968). The area is potentially a midgrass grassland with individual and clustered trees including *Quercus virginiana* Mill, *Q. pungens* var. *vaseyana* Buckl., *Juniperus ashei* Buckl. and *J. pinchotii* Sudw. Late-seral midgrasses have decreased in abundance in response to intensive livestock grazing, but in areas excluded from grazing *E. sericea* and *Bouteloua curtipendula* (Michx.) Torr have retained or increased their relative abundance (Smeins and Merrill 1988). Median annual precipitation is 439 mm, but seasonal and annual droughts, as well as above normal rainfall events, are common. Annual precipitation was 98 and 93% of the long-term mean during the first and second year of the investigation, respectively. However, a distinct dry period occurred between June and August 1994 when precipitation was 56% less than the long-term mean for that interval. The study site was located in a 16-ha pasture excluded from livestock herbivory since 1948.

Species description

Eriochloa sericea (Scheele) Munro, Texas cupgrass, is a C_4 perennial bunchgrass (Shaw and Smeins 1983). *E. sericea* is classified in the tribe Paniceae and subfamily Panicoideae within the family Poaceae. It has erect to ascending culms that can attain heights of 50–90 cm. Growth frequently begins in February and reproductive development occurs in May; however, flowering can occur as early as April and continue until November when environmental conditions are favorable. The geographic distribution of this species is limited to Texas, Oklahoma and Coahuila, Mexico. *E. sericea* has been described as a late-seral dominant for several grasslands in Texas (Dyksterhuis 1946, Allred 1956, Collins et al. 1975). This species has declined in abundance throughout its range following long-term intensive livestock grazing and land conversion (Shaw and Smeins 1983).

Experimental design

Sixty *E. sericea* plants with a mean basal area of 20.2 (s.e. 3.3) cm^2 and mean tiller number of 53 (s.e. 7.4) were identified in April 1994. Twelve plants were randomly assigned to each of four defoliation treatments and a control group along four line transects. Defoliation was imposed at three phenological stages of plant development to assess plant and tiller responses. A portion of the plants were defoliated in the (1) pre-culm elongation stage (mid-April), (2) culm elongation stage (mid-May), (3) post-culm elongation stage (mid-June), and (4) at all three phenological stages. Defoliation was implemented by hand clipping plants to a height of 6 cm above the soil surface which removed approximately 75% of the canopy volume. Neighboring plants within a 30-cm radius of the permanently marked plants also were defoliated, in the same manner as the target plants within a treatment, to a height of 6 cm to minimize confounding influences of neighborhood competition (e.g. Mueggler 1972, Belsky 1986). Neighborhoods were comprised of three or four conspecific neighbors of comparable size to the target plants.

Plant variables monitored were basal area, live tiller number, and the proportion of culmed and vegetative tillers. If plants showed signs of fragmentation (i.e, separation of the plant basal circumference), separate basal area measurements were made for each fragment. Plant variables were analyzed as the absolute change at each census from the initial census (April 1994). Plants that died during the investigation were included in the analysis to represent an absolute loss of basal area and tiller number.

Four tillers with three or four leaves and no visible juvenile tillers were permanently marked on the periphery of each plant with wire loops to monitor tiller demography. Tiller variables were juvenile tiller recruitment, height of apical meristem, phenology (vegetative and reproductive including those with culms) and survivorship by cohort. Tillers emerging between successive census intervals were analyzed as individual cohorts. Cumulative tiller recruitment and mortality were calculated as the summation of tillers that emerged or died from the initially marked tillers. Per capita tiller recruitment and mortality were calculated for each interval as the number of tillers emerging or dying during a census interval relative to the number of live marked tillers $plant^{-1}$ at the previous census (Bullock et al. 1994). Per capita tiller dynamics were analyzed as mean tiller $tiller^{-1}$ $plant^{-1}$ $month^{-1}$. Response variables for both plant and tillers were monitored in mid-April, mid-May, mid-June and in mid-October of both years.

The experiment was arranged as a split-plot design with defoliation the main plot factor and time the subplot factor. Data were analyzed using GLM procedures (SAS Institute Inc. 1988). Means were separated using Bonferroni T-tests when a factor was significant. Significance was determined at $P < 0.05$ unless otherwise indicated. A LIFETEST logrank procedure was used to determine if defoliation treatment altered tiller survivorship within individual cohorts (Pyke and Thompson 1986, SAS Institute Inc. 1988).

Results

Plant variables

The generalized pattern of plant response to defoliation over the 2-yr investigation was characterized by an increase in mean basal area plant^{-1}, with the exception of plants receiving multiple defoliations, and a decrease in mean tiller number plant^{-1} (Fig. 1a and b). Defoliation was significant for both variables; a significant defoliation × time interaction was not observed. Time was significant for mean tiller number plant^{-1}, but not for mean basal area plant^{-1}. Tiller number plant^{-1} after October 1994 was significantly lower compared to tiller number plant^{-1} before October 1994 which may have been a result of below average precipitation (56% less than the long-term mean) during July and August 1994.

Multiple defoliation was the only treatment that induced a significant decrease in mean basal area plant^{-1} (Fig. 1a). Undefoliated plants and plants defoliated at the pre-culm stage exhibited 55 and 24% increases in basal area plant^{-1}, respectively. Plants defoliated during the pre-culm stage showed a significantly greater ($P < 0.10$) increase in basal area plant^{-1} compared to plants defoliated during the culm stage or post-culm stage (−5 and +17% change, respectively).

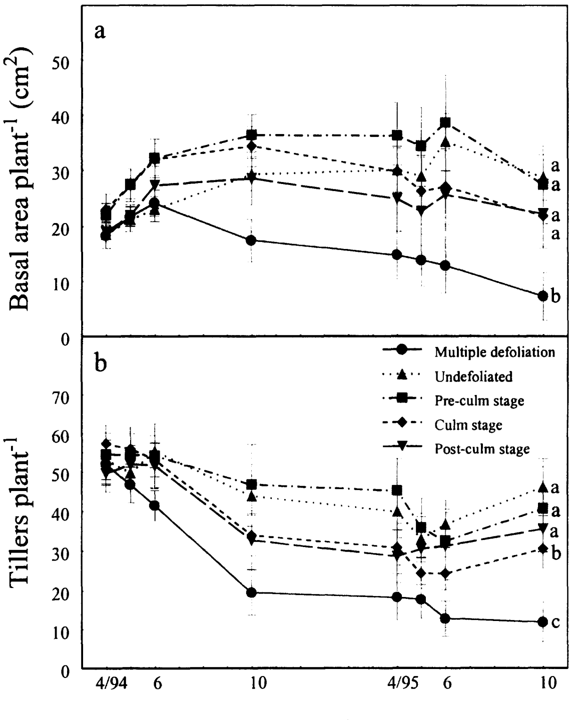

Fig. 1. Mean (±s.e.) basal area plant^{-1} (a) and tiller number plant^{-1} (b) for *Eriochloa sericea* plants subjected to defoliation to a height of 6 cm at pre-culm, culm, post-culm and at all three stages of phenological development compared to undefoliated plants on the Edwards Plateau, Texas. Different letters indicate significant ($P < 0.05$) differences between defoliation treatments. Census dates were pooled for analysis.

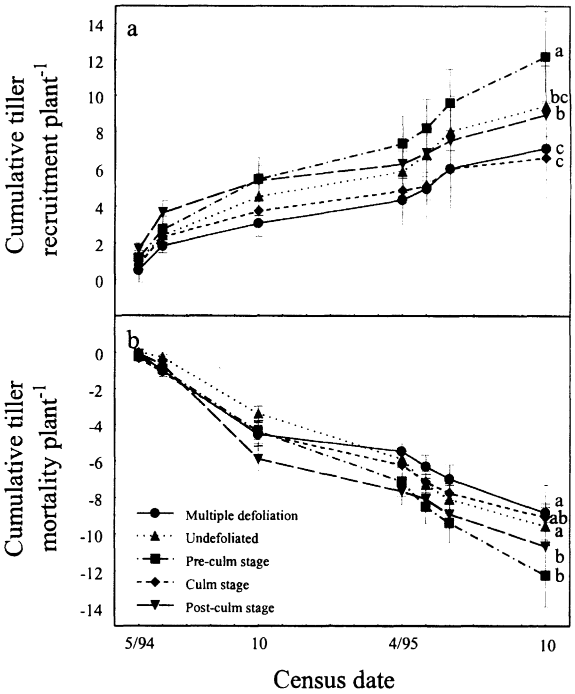

Fig. 2. Mean (±s.e.) cumulative tiller recruitment (a) and cumulative tiller mortality (b) for *Eriochloa sericea* plants subjected to defoliation to a height of 6 cm at pre-culm, culm, post-culm and at all three stages of phenological development compared to undefoliated plants on the Edwards Plateau, Texas. Cumulative values represent the accumulated sum of tillers throughout the 2-yr investigation. Different letters indicate significant ($P < 0.05$) differences between defoliation treatments. Census dates were pooled for analysis.

Plants receiving multiple defoliations showed the greatest decline (−77% relative to the initial census) in mean tiller number plant^{-1} and significantly differed from all other treatments (Fig. 1b). Plants defoliated during the culm stage exhibited an intermediate response (−47%) to plants receiving multiple defoliations and undefoliated plants (−13%) and those plants defoliated during the pre-culm (−25.6%) and post-culm stages (−28.5%).

Plant fragmentation and mortality occurred in the multiple defoliation and post-culm treatments in October 1994 (4 and 1 plant deaths, respectively). Plants in both of these treatments were defoliated in June at the beginning of a dry period which occurred between June and August 1994. Plant fragmentation occurred in all defoliation treatments while undefoliated plants showed little fragmentation throughout the investigation.

Tiller variables

Maximum tiller initiation occurred in spring and early summer of both years and continued throughout much of the growing season (Fig. 2a). Cumulative tiller recruitment and mortality showed significant responses to defoliation. Multiple defoliation and defoliation at the culm stage significantly reduced cumulative tiller recruitment compared to the other treatments. Plants that received multiple defoliations exhibited slightly greater (7%) recruitment than those plants defoliated during the culm stage. Plants defoliated during the post-culm stage showed the least reduction (−5%) in recruitment compared to undefoliated plants. Plants defoliated during the pre-culm stage exhibited significantly greater recruitment compared to all treatments.

Plants defoliated during the pre-culm and post-culm stages displayed significantly greater cumulative tiller mortality (28% and 11%, respectively) compared to undefoliated plants and (39% and 21%, respectively) compared to plants receiving multiple defoliations during the year (Fig. 2b). Plants defoliated during the culm stage showed an intermediate response and did not significantly differ from any other treatment. The ratio of cumulative tiller recruitment to cumulative tiller mortality within a treatment corresponded closely with the number of live tillers plant^{-1}.

Tiller tiller^{-1} recruitment showed a significant time response based on greatest tiller recruitment during the spring and early summer. Although a significant defoliation response was not observed, a significant defoliation × time interaction occurred and was likely caused by high variation in recruitment in June 1995 for plants defoliated in the culm and pre-culm stages (Fig. 3a). Tiller tiller^{-1} mortality rates were similar in magnitude to recruitment rates; however, mortality rates did show a significant defoliation response because of lower treatment variability (Fig. 3b). Plants subjected to multiple defoliations had a significantly higher mortality rate than did undefoliated plants. The other three defoliation treatments did not differ significantly compared to undefoliated plants.

The majority of tillers within all cohorts survived only 1 yr regardless of defoliation treatment. Undefoliated plants exhibited greatest tiller survivorship with the exception of the October 1994 cohort (Fig. 4). Tillers in the October 1994 cohort had the greatest survivorship in those treatments showing the greatest decrease in tiller number and basal area plant^{-1} which is indicative of a density-dependent response. Defoliation treatments significantly affected tiller survivorship in the June 1994 and April 1995 cohorts. In both of these cohorts, tiller survivorship was significantly reduced by defoliation during the culm stage compared to undefoliated plants. Tiller survivorship was significantly reduced by post-culm and multiple defoliation treatments in only the June 1994 cohort. Tiller survivorship for the May 1995 and June 1995 cohorts was similar to the respective 1994 cohorts (data not shown).

Mean apical meristem heights for vegetative, culmed and reproductive tillers were 5.5 (s.e. 0.4), 64.5 (s.e. 8.3), and 197.4 (s.e. 16.9), mm, respectively in April 1995. The percentages of culmed and reproductive tillers relative to vegetative tillers for undefoliated plants in 1995 were 1, 10 and 6% in April, May and June, respectively.

Discussion

Our demographic evaluation of *E. sericea* failed to identify a specific trait that contributed to herbivory-sensitivity, but it did support the interpretation of a meristematic constraint on growth following defoliation. Two of the initial three hypotheses were rejected. Defoliation adversely impacted tiller tiller^{-1} mortality to a greater extent than tiller tiller^{-1} recruitment (hypothesis 1) and tiller recruitment was not synchronous (hypothesis 3), but occurred throughout the spring and early summer when growing conditions were most favorable. Tiller recruitment was reduced to a greater extent by defoliation during culm elongation than during the pre-culm stage or post-culm stage of phenologi-

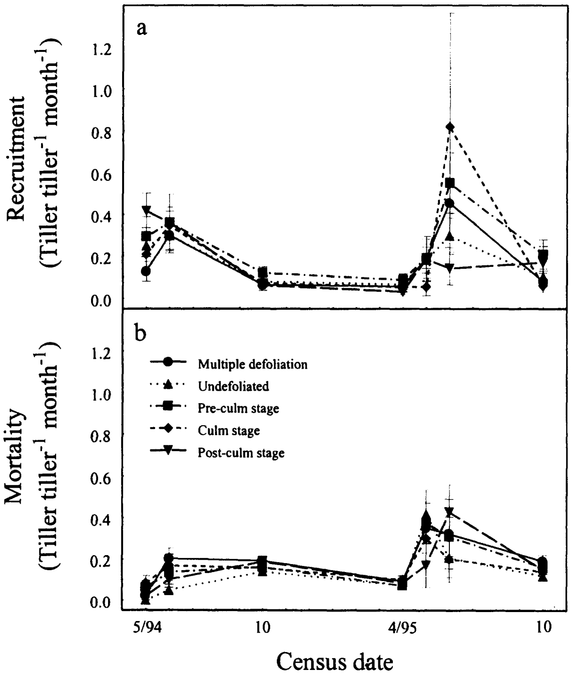

Fig. 3. Mean (±s.e.) tiller tiller^{-1} plant^{-1} month^{-1} recruitment (a) and mortality (b) for *Eriochloa sericea* plants subjected to defoliation to a height of 6 cm at pre-culm, culm, post-culm and at all three stages of phenological development compared to undefoliated plants on the Edwards Plateau, Texas. Rates calculated as the number of tillers recruited/died during a census interval relative to the number of live tillers present at the beginning of that interval. Rates were presented on a monthly basis to standardize for uneven census intervals. Census dates were pooled for analysis.

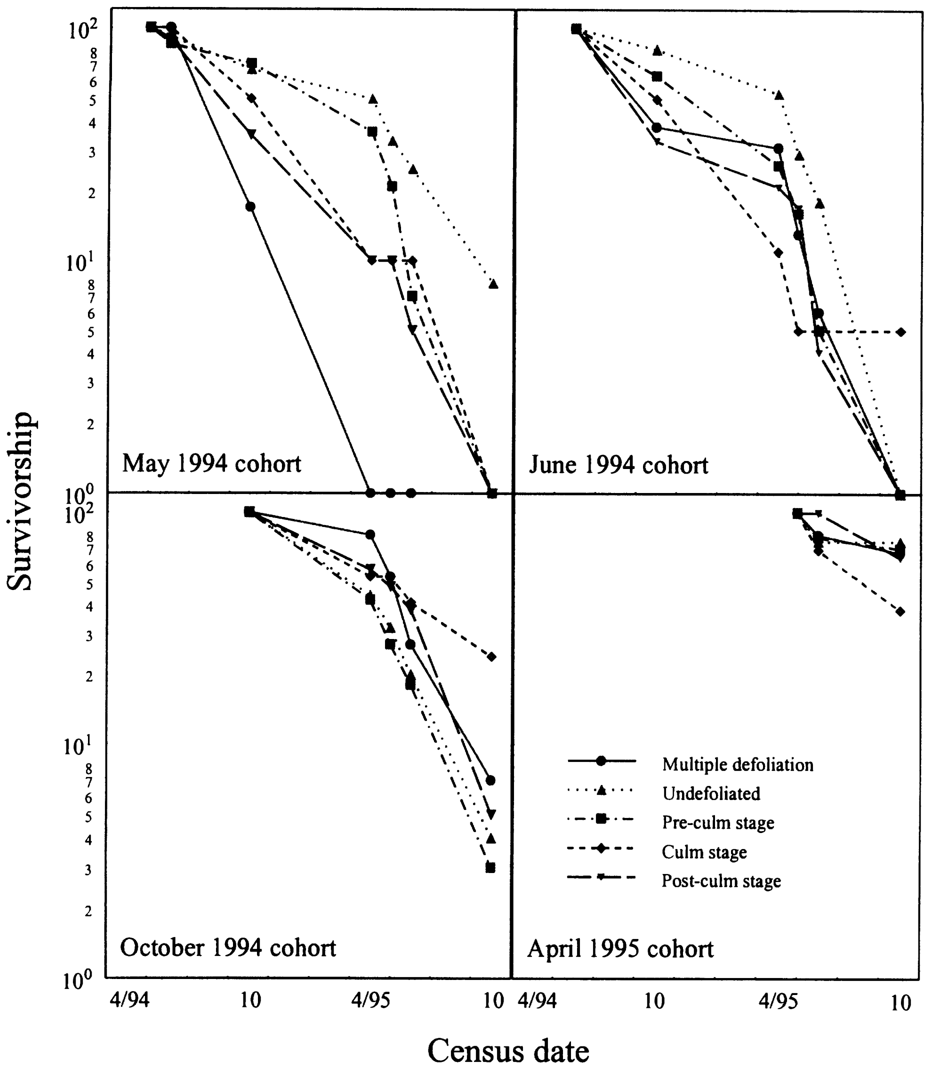

Fig. 4. Survivorship for April, May, June, and October 1994 tiller cohorts for *Eriochloa sericea* plants subjected to defoliation to a height of 6 cm at pre-culm, culm, post-culm and at all three stages of phenological development compared to undefoliated plants on the Edwards Plateau, Texas.

cal development (hypothesis 2). Plants receiving multiple defoliations during the growing season exhibited the greatest decline in basal area and tiller number compared to undefoliated plants. Plant fragmentation and death became evident in these plants by the end of the first growing season. Plants defoliated once a year during the culm elongation stage exhibited only slightly less adverse responses than plants receiving multiple defoliations. At the end of the 2-yr investigation, sufficient tiller recruitment had occurred to compensate for tiller mortality in only undefoliated plants and those plants defoliated during the pre-culm stage. The adverse responses of *E. sericea* to defoliation were not proportionately greater than those observed for its remaining codominant, *Bouteloua curtipendula*, (Hendrickson and Briske unpubl.) and an extremely herbivory-tolerant bunchgrass, *Agropyron desertorum* (Caldwell et al. 1981).

Tiller recruitment is generally considered to be more responsive to defoliation than mortality in perennial grasses (Butler and Briske 1988, Bullock et al. 1994; but see Olson and Richards 1988a). However, per capita tiller mortality increased significantly in plants subjected to multiple defoliations compared to undefoliated plants, while per capita tiller recruitment showed greater variability and less response to defoliation. A comparable response has been documented for *A. desertorum*, a perennial herbivory-tolerant bunchgrass introduced into North America from Eurasia (Olson and Richards 1988a). Responses of per capita tiller recruitment and mortality to defoliation significantly modified both cumulative tiller recruitment and mortality in *E. sericea* plants throughout the 2-yr investigation. However, live tiller number plant^{-1} appears to have resulted primarily from differential per capita tiller mortality, rather than from differential per capita tiller recruitment. Cumulative tiller recruitment varied in response to live tiller number plant^{-1} as opposed to per capita tiller recruitment which was not significantly influenced by defoliation.

Tiller recruitment in *E. sericea* occurred throughout the spring and early summer regardless of the phenological stage at which defoliation was imposed. Perennial forage grasses frequently exhibit a marked decline in tiller recruitment during the culm elongation stage (e.g., Langer et al. 1964, Laude et al. 1968, Culvenor 1994). However, this response is not consistently observed in native perennial grasses (Jameson and Huss 1959, Olson and Richards 1988b). Suppression of tiller initiation at this stage of phenological development is often interpreted on the basis of hormonal regulation (Jewiss 1972, Murphy and Briske 1992) and/or resource diversion from juvenile tillers to support culm elongation at the time of flowering (Ryle and Powell 1972, Smith and Leinweber 1973, Ong et al. 1978). Resource diversion from juvenile tillers to reproductive culms is not a plausible explanation for reduced tiller initiation in *E. sericea* because of the low percentage (10% maximum) of reproductive tillers observed. Tiller recruitment over a several month period demonstrates that synchronous tiller recruitment was not an important component of herbivory-sensitivity.

E. sericea does not possess morphological attributes traditionally associated with herbivory-sensitive grasses. The reproductive:vegetative tiller ratio did not exceed 10% and apical meristem elevation above the soil surface did not exceed 5 mm in vegetative tillers. A high reproductive:vegetative tiller ratio determines that a greater portion of canopy replacement must originate by tiller initiation from axillary buds, rather than from leaf differentiation from existing apical meristems, because apical meristems have been committed to inflorescence development (Branson 1953, Briske and Richards 1995). Elevation of apical meristems in vegetative tillers increases susceptibility to removal by grazers which also determines that canopy replacement must occur by tiller growth from axillary buds (Branson 1953, Booysen et al. 1963). In both instances, canopy replacement by tiller initiation from axillary buds is a slower process than continuation of leaf growth from intercalary meristems or leaf differentiation from apical meristems (Olson and Richards 1988b, Briske and Richards 1995). Herbivory-sensitivity without the occurrence of elevated apical meristems and a high proportion of reproductive tillers supports the conclusion of Caldwell (1984) indicating that care must be taken to avoid unwarranted generalizations concerning herbivory tolerance in relation to plant architecture. For example, both *A. desertorum* and *A. spicatum* display early elevation of apical meristems and possess a relatively high proportion of reproductive tillers, but *A. desertorum* is much more tolerant of herbivory than is *A. spicatum* (Caldwell et al. 1981, Caldwell 1984).

The absence of a specific trait contributing to the defoliation-induced meristematic limitation in *E. sericea* makes it difficult to explain the significant reduction in cumulative tiller recruitment and basal area and increased rate of tiller mortality in plants subjected to multiple defoliations and defoliation at the culm stage of phenological development. Perhaps these plants encountered a carbon limitation imposed by minimal leaf area and low photosynthetic efficiency of the remaining canopy following defoliation as has been observed in *Themeda triandra* (Coughenour et al. 1985, Hodgkinson et al. 1989, Mott et al. 1992). However, neither leaf area nor photosynthetic rate was measured in this investigation based on the evidence indicating that herbivory-sensitivity in North American bunchgrasses is a function of meristematic limitations, rather than physiological constraints (e.g., Caldwell et al. 1981, Detling and Painter 1983, Busso et al. 1989).

Why were we unable to identify an "Achilles heel" in a bunchgrass species recognized as being remarkably sensitive to herbivory? The explanation may lie beyond the inherent ability of individual species to replace leaf area following defoliation (i.e., intrinsic mechanisms; sensu McNaughton 1983). The specific trait approach (Simms 1992) for evaluating and interpreting herbivory resistance is based on the assumption that a relatively small number of traits, or even a single trait, associated with the developmental morphology or physiological function of individual species is responsible for herbivory-sensitivity. An alternative interpretation of herbivory-sensitivity, within comparable grass growth forms, is based on the involvement of more subtle extrinsic mechanisms (sensu McNaughton 1983) and their interaction with intrinsic mechanisms, rather than on the exclusive contribution of intrinsic mechanisms (e.g., Barnes 1972, Brown and Stuth 1993). Extrinsic mechanisms involve both biotic and abiotic processes external to plants that potentially influence their response to defoliation (McNaughton 1983). Important extrinsic mechanisms include selective herbivory among species (Brown and Stuth 1993, Anderson and Briske 1995), herbivore-mediated competitive interactions (Mueggler 1972, Caldwell et al. 1987) and drought-herbivory interactions (Mott et al. 1992, O'Connor 1995). A significant decrease in tiller number plant^{-1}, reduced survivorship of the June 1994 tiller cohort, and the occurrence of plant mortality during the dry summer of 1994 indicate that a drought-defoliation interaction contributed to the decline in tiller and plant populations of *E. sericea*. Extrinsic mechansims may be of equal or greater importance than intrinsic mechanisms in determining species responses to herbivory in grazed systems (Archer and Smeins 1991). Unfortunately, extrinsic mechanisms are often excluded from investigations designed to assess herbivory-sensitivity or tolerance based on the specific trait approach.

We speculate that herbivory-sensitivity of *E. sericea* may partially result from the possession of a competitor life-history strategy (Grime 1979: 9). This strategy is characterized by early growth initiation, several weeks before that of associated C_4 species, a high nitrogen content and a low proportion of structural materials (Shaw and Smeins 1983). These attributes are frequently associated with rapid growth rates as described in the resource availability hypothesis of plant defense (Coley et al. 1985). These attributes may have contributed to the competitive ability of *E. sericea* by effectively preempting resources early in the season in the absence of severe herbivory. However, early growth initiation and rapid growth may have predisposed this species to selective herbivory, which may have in turn compromised its competitive advantage relative to other perennial grasses within the community following the introduction of large numbers of domestic herbivores. Herbivory early in the growing season would likely predispose this species to multiple defoliations which we have shown to adversely affect tiller populations.

This species has historically been subjected to more severe defoliation than imposed in this experiment based on estimates of livestock numbers in the region during the late 1800's (Youngblood and Cox 1922). Sheep were the initial domestic herbivore introduced into the region and are capable of grazing closer to the soil surface than horses or cattle based on their prehensile abilities (Hofmann 1989). The herbivory tolerance of even the most tolerant species could have been suppressed by this severe grazing regime. In addition, *E. sericea* may have shown a greater decrease in abundance than an associated late-seral species, *B. curtipendula*, because *E. sericea* appears unable to shift from a tolerance to an avoidance strategy (Anderson and Briske 1995, Briske et al. 1996). *E. sericea* expresses minimal morphological plasticity because juvenile tiller development occurs within the subtending leaf sheaths preventing the angle of tiller exertion from approaching the soil surface (e.g., Hodgkinson et al. 1989, Painter et al. 1993). Consequently, *E. sericea* may have been unable to retain sufficient photosynthetic and meristematic tissues below grazing height to maintain a positive carbon balance.

The specific trait approach was initially adopted as the predominant paradigm for investigating and evaluating herbivory resistance in North American grassland ecology and management during the middle of the 20th century (e.g., Branson 1953, Cook and Stoddart 1953, Neiland and Curtis 1956, Rechenthin 1956). An interpretation of herbivory-sensitivity based on the partial involvement of extrinsic mechanisms, rather than solely on intrinsic mechanisms, challenges this paradigm. Species do not necessarily have to possess obvious physiological or morphological traits for herbivory to induce a decrease in tiller and plant density and potentially contribute to species replacement. While we did not investigate all potential intrinsic variables that may have contributed to the herbivory-sensitivity of *E. sericea*, these results do represent a case where herbivory-sensitivity could not be explicitly attributed to a specific trait inherent to a species population. The alternative interpretation indicates that herbivory-sensitivity also can result from more subtle extrinsic mechanisms within a community. Assessment of herbivory resistance based on the specific trait approach fails to recognize and address the importance of extrinsic mechanisms associated with herbivore-induced processes at higher ecological scales.

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