ECOLOGICAL IMPLICATIONS OF GENETIC VARIATION IN

BOUTELOUA CURTIPENDULA (MICHX.) TORR.

A Dissertation

by

MARIA ANDREA LUJAN TOMAS DE PISANI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2004

Major Subject: Rangeland Ecology and Management

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ABSTRACT

Ecological Implications of Genetic Variation in *Bouteloua curtipendula* (Michx.) Torr.

(December 2004)

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The two most common varieties of the grass *Bouteloua curtipendula* (Michx.)Torr. in North America use different strategies of clonal growth and have contrasting continental distributions. Variety *caespitosa* (phalanx form) ranges from central Texas westward to Arizona and California and var. *curtipendula* (guerrilla form) occurs in a more mesic region over the North American Great Plains. This study sought to determine whether the strategies had an ecological significance and investigated the possible relationship between changes in environmental factors and characteristics of each clonal growth strategy.

Varieties showed to be morphologically variable, but the variability did not follow the pattern of the precipitational gradient. The abundance of var. *curtipendula* was related to soil depth and parent material (limestone types). Abundance of var. *caespitosa* could not be explained by any environmental factor separately. The performance of clones of the two growth forms in response to changes in resource availability (light and nutrients) and defoliation suggested similarities between the varieties in photosynthetic rate and only showed differences in water potential under extreme conditions. The major differences were related to the proportion of biomass allocated to structures related with seed production versus propagation by rhizomes. Intra-variety genetic variation for several life history traits was detected even with a very small sample size. The caespitose growth form showed more biomass and rate of tiller recruitment after defoliation on average, but responses between genotypes were

dissimilar. Varieties also showed levels of plasticity in the allocation to reproductive structures in response to environmental factors.

Responses to fire were compared between varieties by experimental burnings with increasing load of artificial fuel. Plants of the two varieties reached similar maximum temperatures although var. *caespitosa* suffered temperatures considered to be lethal for longer periods of time. Results from this study suggested that, although characteristic of the pattern of clonal growth were not distinctly associated to resource availability or defoliation, distribution of the varieties may be related to a combination of biotic and abiotic factors beyond the factors studied here.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Clonal growth, common among plants, is characterized by the production of potentially independent ramets. A large proportion of plant species exhibit some kind of clonal growth; and aspects of the morphology, regulation and function of clonal plants have been widely studied (Cheplick 1997, Derner and Briske 1999, 2001, Humphrey and Pyke 1998, Lovett Doust 1981, Schmid 1985, Schmid and Harper 1985, Winkler et al. 1999) According to the relative position of the ramets, two broad categories of growth strategies have been delimited: the phalanx strategy which involves the production of a compact structure of closely spaced ramets; and the guerrilla strategy which involves the production of a loosely arranged group of more widely spaced ramets (Harper 1977, Lovett Doust and Lovett Doust 1982). The spatial arrangement of ramets determines the way the plants relate to their environment and determine their performance and persistence within a community. Differences in the competitive ability of the phalanx and guerrilla growth strategies have been simulated in models and experimentally evaluated (Humphrey and Pyke 1998, Slade and Hutchings 1987, Sutherland and Stillman 1990). From such studies, it is generally accepted that the phalanx growth form should dominate in competitive situations because its clones perform the best when they interact with ramets of the same genet. Alternatively, the guerrilla strategy would avoid competitive environments by spreading into unoccupied spaces via long radiating structures (e.g., rhizomes, stolons) (Lovett Doust and Lovett Doust 1982, Slade and Hutchings 1987, Sutherland and Stillman 1988).

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This dissertation follows the style and format of Plant Ecology.

Depending on the mechanisms the plants use to acquire resources, three strategies of clonal growth have been proposed: 1) foraging (how plants explore homogeneous and patchy habitats), 2) conservation (efficiency of resource utilization) and 3) consolidation (monopolization of resources in space and time) (de Kroon and Hutchings 1995, de Kroon and Schieving 1990). It has been suggested that guerrilla clones will better exploit patchy resources by elongation of spacers and activation of buds for placing absorbing structures where resources are available or, in resource-rich environments, consolidate space occupation by the formation of short spacing organs. On the other end of the spectrum, phalanx clones are considered as having a conservative use of resources (de Kroon and Schieving 1990). In grasses, rhizomatous and caespitose forms have been reported to have differences in functional characteristics such as resistance to herbivory (Briske 1996), light interception (Caldwell et al. 1983) or accumulation of nutrients (Derner and Briske 2001, Vinton and Burke 1995). However, little is known about the distribution of clonal attributes in relation to environmental variables or their functional significance in certain habitats (de Kroon and van Groenendael 1990).

Bouteloua curtipendula (Michx.)Torr. is a warm season, perennial grass widely distributed in North America. It is primarily represented by two contrasting growth forms that have been categorized as varieties (Gould 1979, Gould and Kapadia 1964). *Bouteloua curtipendula* var. *caespitosa* is a tussock forming bunchgrass that is predominantly distributed in the western part of the United States, from central Texas westward to Arizona and southwestern California (Kapadia and Gould 1964). The var. *curtipendula* continental distribution extends over the eastern zone of the country, from Texas through the Great Plains of the United States and part of Canada. The distribution of the two varieties overlaps in the central part of Texas, particularly on the Edwards Plateau Region (Gould and Kapadia 1962). The species is common in North American grasslands and has been extensively used as forage and in restoration of

abandoned farmlands (Voigt and Sharp 1995). However, the ecological significance of the differentiation between the two growth forms of *B. curtipendula* has been scarcely evaluated.

At a continental scale the distribution of the varieties of *B. curtipendula* can be contrasted with patterns of variation of key environmental factors such as resource availability and response to disturbance. Comparing the pattern of distribution of the varieties with the range of precipitation in the United States suggests that the differentiation between growth forms may be related to variation in characters involved in the adaptation to particular habitats. In Figure 1, the distribution of var. *caespitosa* in general overlaps with regions having mean annual precipitation of < 500 mm while var. *curtipendula* is mostly distributed in a region with predominantly mean annual precipitation > 500 mm.

Continental distributions of the two varieties also correspond to soil orders in North America (Figure 2). The caespitose variety occurs in regions characterized by Aridisols and Entisols, typically soils with a relative poor nutrient content; the rhizomatous variety occurs on Mollisols and Alfisols which are characterized by relatively high nutrient availability.
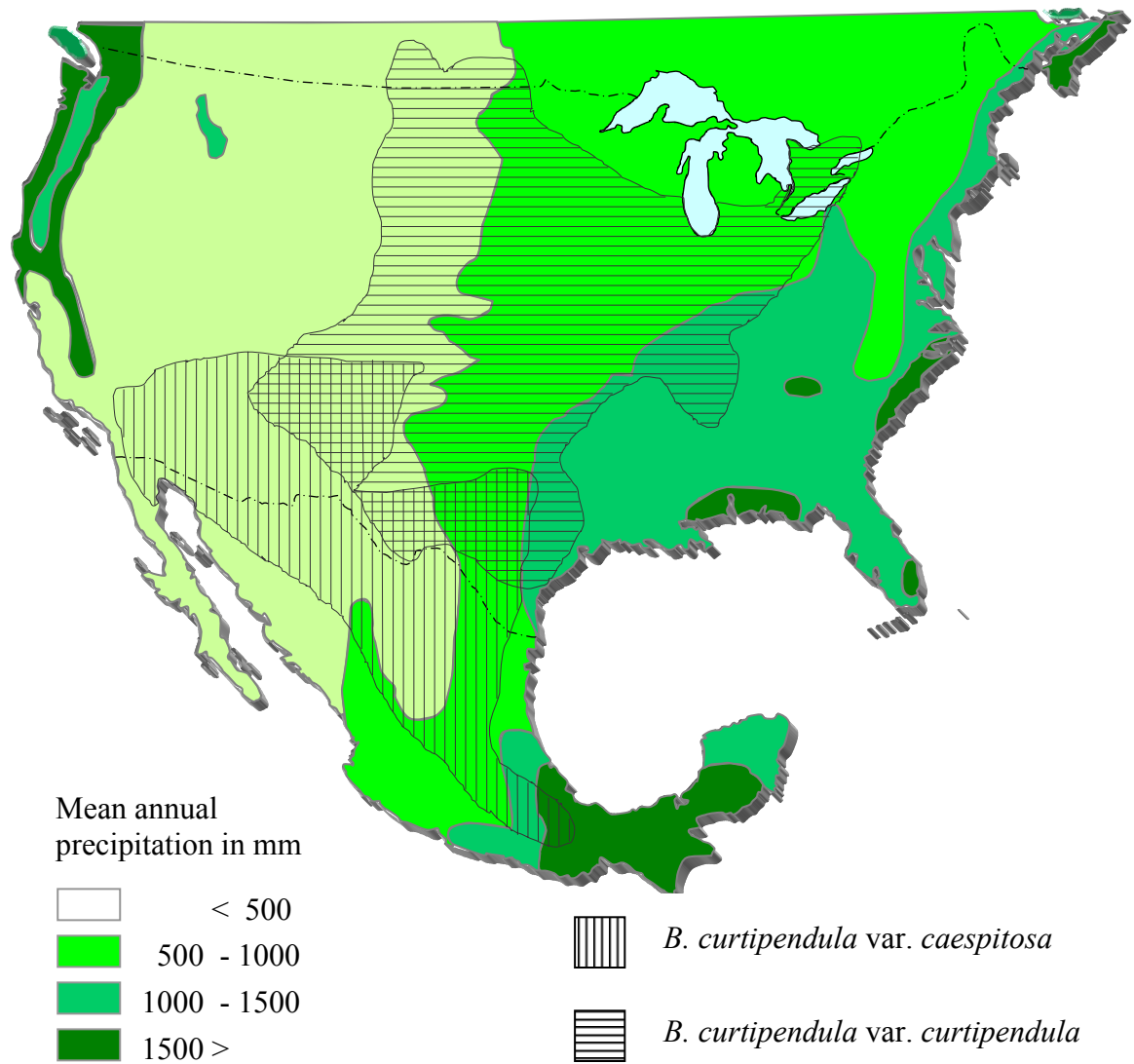
Figure 1. Regional distribution of the two varieties of *B. curtipendula:* comparison in relation to mean annual precipitation in North America (Gould and Kapadia 1964).

5
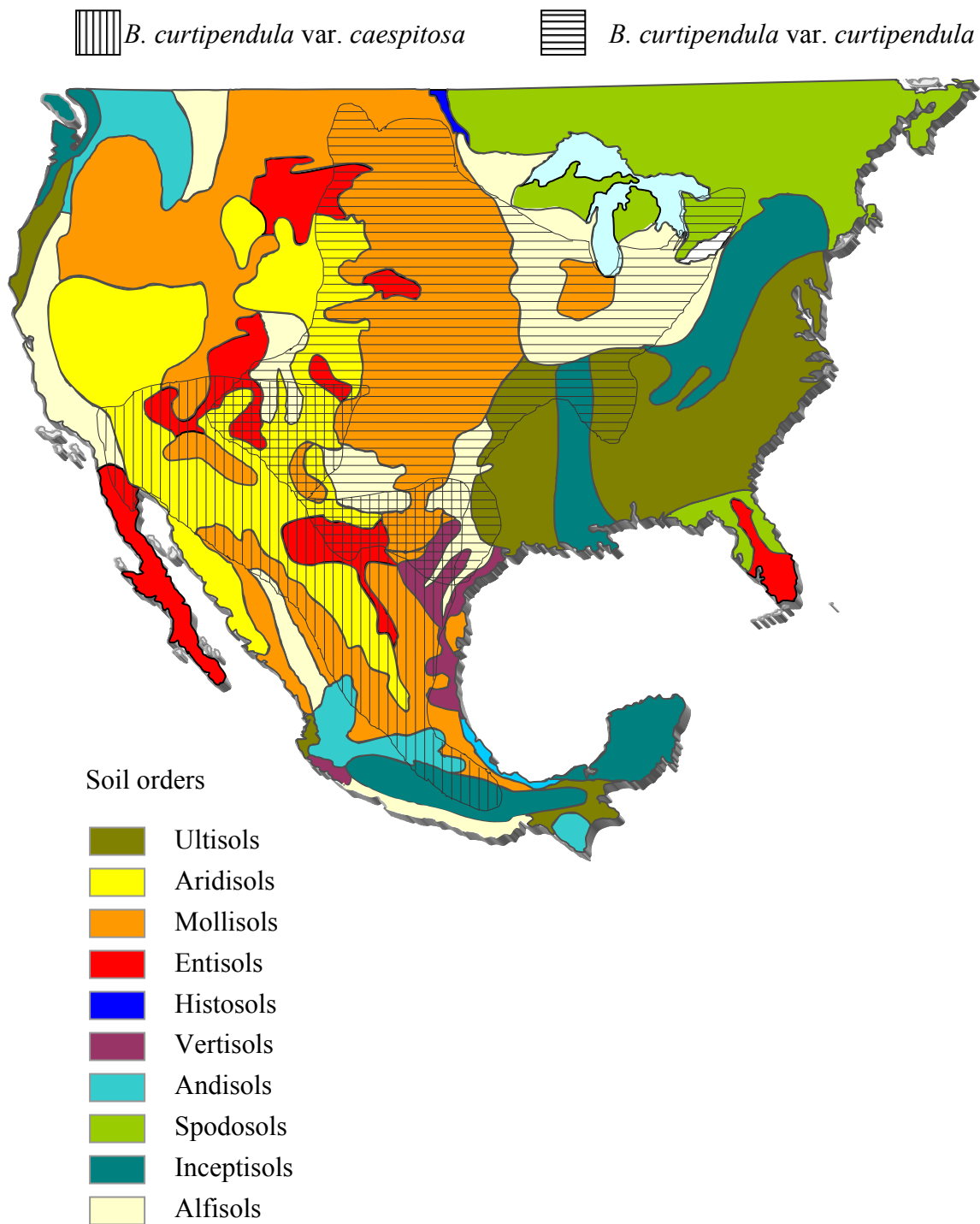
Figure 2. Regional distribution of the varieties of *B. curtipendula* in relation to soil orders in North America (Brady and Weil 2001, Gould and Kapadia 1964).

This study sought to determine the ecological significance of the differentiation between the two varieties (growth forms) of *B. curtipendula* given their contrasting distribution. If explanations for the continental-scale distribution of the varieties are a reflection of differences in the adaptation of the two growth forms to resource availability (water and nutrient), then it stands to reason that plants of var. *curtipendula* and var. *caespitosa* will exhibit predictable and consistent differences in their local distributions and response to environmental factors or disturbance in their zone of sympatry. The goal of this study was thus to determine if this is in fact the case. Specific objectives of the study were to:

1) assess the potential role of selected environmental factors in determining the distribution of *B. curtipendula* varieties in a portion of their zone of sympatry.

2) evaluate if the local distributions of the two varieties in their zone of sympatry can be predicted from their continental distributions.

3) quantify the role of disturbances (defoliation and fire) in determining the local pattern of distribution of the two growth forms.

4) determine whether or not there is a niche separation that allows coexistence of the two varieties so that their local distribution could be predicted by local differences in resource availability within and among sites.

The subsequent chapters summarize the results of two experiments and two surveys conducted to address these objectives. Chapter II presents the results of surveys intended to correlate the local distribution of the two growth forms with environmental characteristics of particular sites. Chapter III summarizes an experiment conducted to determine the extent to which resource (light and nutrient) availability and defoliation might differentially affect the relative distribution of the two varieties. Chapter IV then explores how fire might affect the distribution of the two varieties.

Description of the species of interest: **Bouteloua curtipendula *(Michx.) Torr.***

The "*Bouteloua curtipendula* complex" consists of 12 related species (Gould and Kapadia 1964) that occur throughout the New World. One of them, the species *B. curtipendula* (Michx.) Torr. proper, occurs in a broad belt through the central United States and Mexico (Gould and Kapadia 1964). Commonly known as 'sideoats grama', this grass is an important livestock forage species (Voigt and Sharp 1995) that has been extensively used in the restoration of rangelands, abandoned farmlands and in establishing pastures for livestock (Harlan 1949). The complex consists of sexual polyploids at the tetraploid level and an agamic complex (5x to the 10x level) with an extensive and nearly continuous series of aneuploids (Grant 1981).

B. curtipendula consists of three varieties (Gould and Kapadia 1964; Voigt and Sharp 1995):

(1) var. *caespitosa* Gould and Kapadia has a bunchgrass growth-form lacking rhizomes and has high aneuploid chromosome numbers ($2n$ = 69 to ca. 103). It exhibits a wide range of variation both between and within populations with respect to plant size, leaf blade width, spikelets per branch, number of spikelets, and the color of glumes, lemmas, anthers and herbage (Gould and Kapadia 1962). It probably has evolved through hybridization of a number of diploid and the tetraploid taxa. Most plants of var. *caespitosa* are facultative or obligate apomicts but sexual reproduction has brought new combinations of characters that are then stabilized by apomixis (Kapadia and Gould 1964). Reproduction by seed probably is sexual and apomictic (Gould and Kapadia 1964). Pollination appears necessary for the initiation of endosperm development (Mohamed and Gould 1966). The var. *caespitosa* is regarded as frequent in loose, sandy or rocky soils, well-drained limey soils at elevations from 200 – 2,500 m. It occurs from central Texas westward through New Mexico and Arizona, to southern California and southward into South America (Venezuela, Bolivia, Uruguay, Peru and Argentina) (Gould 1979).

(2) var. *curtipendula* reproduces sexually and from spreading rhizomes and is widely distributed in the U.S. and includes tetraploids ($2n = 40$) and aneuploids ($2n = 41$ to 64). The distribution of plants with high chromosome numbers is centered in the region of overlap between the ranges of the bunch-type and rhizomatous tetraploid plants. The rhizomatous plants with high aneuploid chromosome numbers appear to have arisen from the hybridization of caespitose plants and rhizomatous tetraploids (Gould and Kapadia 1962). It is a characteristic prairie grass, growing best on rich loamy, well drained soils at elevations from near sea level in southern Texas to >2,500 m in the northwestern USA (Gould 1979).

(3) var. *tenuis* Gould and Kapadia, initially thought to be diploid ($2n = 20$), but subsequently known to be tetraploid and aneuploid with $2n = 41$ or 42 (Gould 1979). Its distribution is primarily in Mexico and thus was not included in this study.

CHAPTER II

ENVIRONMENTAL VARIATION AND THE DISTRIBUTION OF

PHALANX AND GUERRILLA GROWTH-FORMS IN *BOUTELOUA*

CURTIPENDULA

Introduction

The geographical distribution of plant species generally corresponds to variation in environmental factors determining their direction of evolution and pattern of developmental growth (Silvertown and Lovett Doust 1993, Stanton et al. 2000). As sessile organisms, plants are confronted with highly variable environmental conditions, both temporally and spatially and the amplitude of a species' distribution depends on its ability to tolerate abiotic limiting factors (Parker et al. 2003, Roy et al. 1999, Stanton et al. 1994). In the past ecologists considered that species distributions were dependent on the factor that was most critically in demand (in Barbour et al. 1998, Liebig 1840). Later they realized that it was almost impossible to isolate any one factor because all their interdependence and synergistism (Billings 1952). The optimum in the range of tolerance of a species to its limiting factors is a major determinant of the species distribution. Because of that, species distribution are not clearly defined (Barbour et al. 1998). In gradients where closely related species have overlapping distributions, limits could also be confounded if the species interbreed (Stebbins 1959).

The fact that some species are distributed across broad climatic gradients suggests the existence of within-species variation in the ability to tolerate constraints in different environments (HilleRisLambers et al. 2001, Linhart and Grant 1996). By means of local adaptation groups can be recognized at the extremes of the gradient (Joshi et al. 2001, Volis et al. 2002). However, even if morphological differences are apparent between groups, elucidation of the factor responsible for differentiation may be uncertain (Bazzaz 1996, Rice and Nagy 2000). Understanding the processes and mechanisms determining the pattern of distribution of organisms along gradients is

important to specification of the boundary of a species (Stanton et al. 1994, Sultan 1995).

Clonal growth affords a mechanism for sessile plants to respond to the changes in their environment and to exploit resource heterogeneity (Harper 1977). By means of clonal growth, plants can abandon low resource patches and situate resource-acquiring ramets in high resource patches (Silvertown and Lovett Doust 1993). Evolutionary theory predicts that plant investments in spacing structures that allow them to vegetatively expand into new patches (e.g. stolones or rhizomes) should occur when benefits outweigh the costs (de Kroon and Hutchings 1995). Accordingly, plants in nutrient-poor environments might be expected to allocate little to spacing structures and hence have a compact growth form, whereas plants in resource-rich environments would be expected to invest in spacing structures such as rhizomes because these would increase the likelihood that new ramets would exploit favorable patches (de Kroon and Schieving 1990). A variety of clonal growth strategies have been proposed based on simulation models relating plant growth to environmental parameters (Sutherland and Stillman 1988). However, inconsistencies in the morphological response of species to experimentally induced changes in resource availability suggest our understanding of the evolutionary and ecological significance of clonal growth is incomplete (de Kroon and Hutchings 1995). Depending upon the length of the rhizomes and their frequency of branching, clonal growth can produce a variety of plant architectures, including what has been defined as a phalanx-guerrilla growth form continuum (Cheplick, Gregory P 1997). Phalanx growth forms invest little in spacing structures and are relatively compact, while guerrilla growth form invests substantially in spacing structure, giving the plants a spreading, spatially extensive growth form.

Taxonomists recognize three varieties of the warm season perennial grass *Bouteloua curtipendula* in North America. Two of these are widely distributed in the United States (Gould 1979, Gould and Kapadia 1964): var. *caespitosa*, a caespitose, bunchgrass (phalanx) growth-form lacking rhizomes that reproduces apomictically; and var. *curtipendula* that reproduces sexually and from spreading rhizomes (guerrilla

growth-form). The ecological significance of these taxonomic distinctions is subject to speculation. At a regional scale, the rhizomatous growth form occurs in the relatively mesic portions of the Great Plains, whereas the caespitose growth form occupies the more xeric southwestern region (Gould and Kapadia 1964). The regional distribution patterns are consistent with what might be predicted from plant foraging and clonal growth theory: the compact form inhabits the more xeric and stressful region and the spreading form the region where soil resource availability would tend to be consistently higher. By extension, it might be predicted that in their zone of sympatry, the two growth forms should be differentially distributed, such that var. *curtipendula* (guerrilla growth form) would dominated relatively resource rich landscape elements (deep soils, run-on, shallow water table sites, or slightly shaded sites where evaporative losses of soil moisture are spatially variable) and var. *caespitosa* (phalanx growth form) would dominate relatively xeric microsites (shallow soils, run-off, deep water table sites of full sun sites where soils are uniformly dry).

The overall objective of this chapter was to assess the potential role of environmental factors in determining the distribution of the two varieties of *B. curtipendula* in a portion of their zone of sympatry. Specifically,

1) To quantify morphological attributes of *B. curtipendula* plants across a precipitation gradient.

H1) plants of var. *caespitosa* will have comparatively more tillers and reproductive culms per area than those of var. *curtipendula.*

Rationale: because its abundance in western and poorer nutrient sites var. *caespitosa* will have a conservative strategy and a compacted form; var. *curtipendula* will have a looser arranged structure that will allow searching and placing the ramets in favorable sites.

H2) plants of var. *caespitosa* will have smaller leaves than the plants of var. *curtipendula*.

Rationale: if phalanx growth-forms (var. *caespitosa*) are better adapted to resource poor sites than guerrilla forms (var. *curtipendula*), they will have

attributes which confer resource conservation. One such attribute will be a reduction in transpirational leaf area.

2) To determine if the two *B. curtipendula* growth-forms (guerrilla vs. phalanx) were differentially distributed with respect to habitats or disturbance regimes within a portion of their zone of sympatry (Edwards Plateau Region ,Texas).

> H3) within their zone of sympatry, var. *curtipendula* will be more frequent under the canopy of trees than var. *caespitosa* and more abundant on deep soils of run-on sites. Conversely, var. *caespitosa* will predominate on drier habitats (open sun, shallow uplands).

Rationale: the guerrilla growth-form (var. *curtipendul*a) should be better adapted to mesic sites; the phalanx growth-form (var. *caespitosa*) should be better adapted to more xeric sites.

> H4) within their zone of sympatry var. *caespitosa* will be more frequent on rocky sites than var. *curtipendula*.

Rationale: large rocks will hinder spreading by rhizomes; phalanx growth-form will be better adapted to utilize resources (e.g. water) that are locally concentrated by large rocks.

> H5) within their zone of sympatry the relative abundance of var. *caespitosa* will be lowest on areas that have been burned.

Rationale: the bunch growth form accumulates more fuel in its crown than the rhizomatous type; hence, it is more likely to experience lethal temperatures.

> H6) for a given habitat, var. *caespitosa* will be less frequent than var. *curtipendula* on sites grazed by livestock.

Rationale: the concentration of foliage in the caespitose growth form makes it more preferred and hence more heavily utilized than the rhizomatous type.

To pursue these objectives and hypotheses a preliminary survey was conducted along a precipitational gradient in and near the zone of sympatry of the two varieties; and the role of environmental factors in determining the local pattern of distribution of

the varieties was evaluated in one point of the gradient (Texas Agriculture Experiment Station (TAES) at Sonora, TX).

Methods

Plant collection and study sites

Plant materials were collected at each of the sites described below. The collection sites were distributed across a mean annual precipitation gradient from ranging from 400 to 840 mm / year. Detailed descriptions of the climate, soils and vegetation of the ecoregions represented by the various sites can be found in (Correll and Johnston 1970, Diggs et al. 1999). Field studies quantifying the local distribution of the two *B. curtipendula* growth forms with respect to habitats and disturbance regimes were conducted at the TAES-Sonora site.

Chaparral Wildlife Management Area (CWMA)

Located in the South Texas Plains Ecological Region (28º 29' N; 99º 52' W). Mean annual precipitation (MAP) is 600 mm and periodic droughts are common. Average monthly rainfall is lowest during January and February and highest in May or June (Figure 3a). Mean monthly temperature ranges from 11° C in January to 29° C in July. Elevation is ca.190 m above sea level. Soils are alkaline to slightly acidic clays and clay loams. Woody plants in the area include *Prosopis glandulosa* Torr. var. *glandulosa*, *Quercus virginiana* Mill., *Acacia berlandieri* Benth., *A. constricta* Gray, *A. greggii* Gray, *Celtis pallida* Torr., and *C. lindheimeri* Engelm. *ex* K. Koch (Davis and Spicer 1965, Everitt and Drawe 1993). The area was used as a cattle ranch until purchased by Texas Parks and Wildlife in the 1960s.

Davis Mountains State Park (DMSP)

Located near Fort Davis, Texas (30º 40' N; 103º 53' W) in the Trans-Pecos Ecological region of western Texas. MAP is 400 mm. Peak rainfall months are July and August (monthly mean ca. 75 mm) (Figure 3b) (Griffiths and Orton 1968). Mean annual temperature is 16° C, ranging from 7° C in January to 24° C in July and August. Temperature in winters is often below freezing. Humidity is relatively low and summers

are characterized by hot days and cool nights. Elevation is 1600 to 1900 m. Soils have developed from mountain outwash materials and are varied in texture and profile characteristics. In general, soil reaction is calcareous. Vegetation includes both plains grasslands and woodlands (Hatch et al. 1990). Common species are *Pinus ponderosa* P. & C. Laws*., P. cembroides* Zucc., *P. strobiformis* Engelm*., Quercus grisea* Liebm., *Q. gravesii* Sudw., and several species of *Juniperus* L.

TAES

Located 56 km south of Sonora Texas USA (30º 35' N; 100º 39' W) on the southwestern portion of the Edwards Plateau at an elevation of ca. 730 m. The climate is sub-tropical, semiarid with no distinct dry season (Smeins and Merril 1988). MAP (600 mm) is bimodal, with peaks in spring and fall (Figure 3c). Mean monthly temperatures range from 30° C in July to 9° C in January. Landscapes are characterized by gentle (3-4 %) slopes and a heterogeneous mixture of soil depths and rock outcrops. Dominant soils are Tarrant stony clays of the thermic family of Lithic Haplustolls formed over fractured Edwards and Buda Cretaceous limestones. Valera clay, Abilene silty clay loam, Irion clay and Frio gravelly clay soils occur only occasionally on the station.

The vegetation is savanna/parkland with individuals or clusters of woody species interspersed in a matrix of mid- and short-grasses. Common woody species include *Quercus virginiana* Mill. var. *virginiana*, *Q. pungens* Liebm. var. *vaseyana* (Buckl.) Muller, *Juniperus ashei* Buckl., and *J. pinchotti* Sudw. Dominant herbaceous species include *Bouteloua curtipendula* (Michx.) Torr., *Eriochloa sericea* (Scheele) Munro *ex* Vasey, *Hilaria belangeri* (Steud.) Nash, *Aristida spp*. *Stipa leucotricha* Trin. & Rupr., *Bouteloua trifida* Thurb. and *Bouteloua hirsuta* Lag.

The station was originally established in 1916 to study animal diseases. In 1948 the primary emphasis was shifted to range management and the station was fenced into several pastures in order to study stocking rates, kinds and mixtures of animals and grazing systems. In 1948 an attempt was made to remove all juniper plants on the station by hand cutting. Several pasture-scale livestock grazing and prescribed burning experiments were in progress on the station during this study.

CWMA, Texas Elev: 187m 21.6°C 513 mm
30 years

DMSP, Texas Elev: 1487m 15.9°C 403 mm
30 years
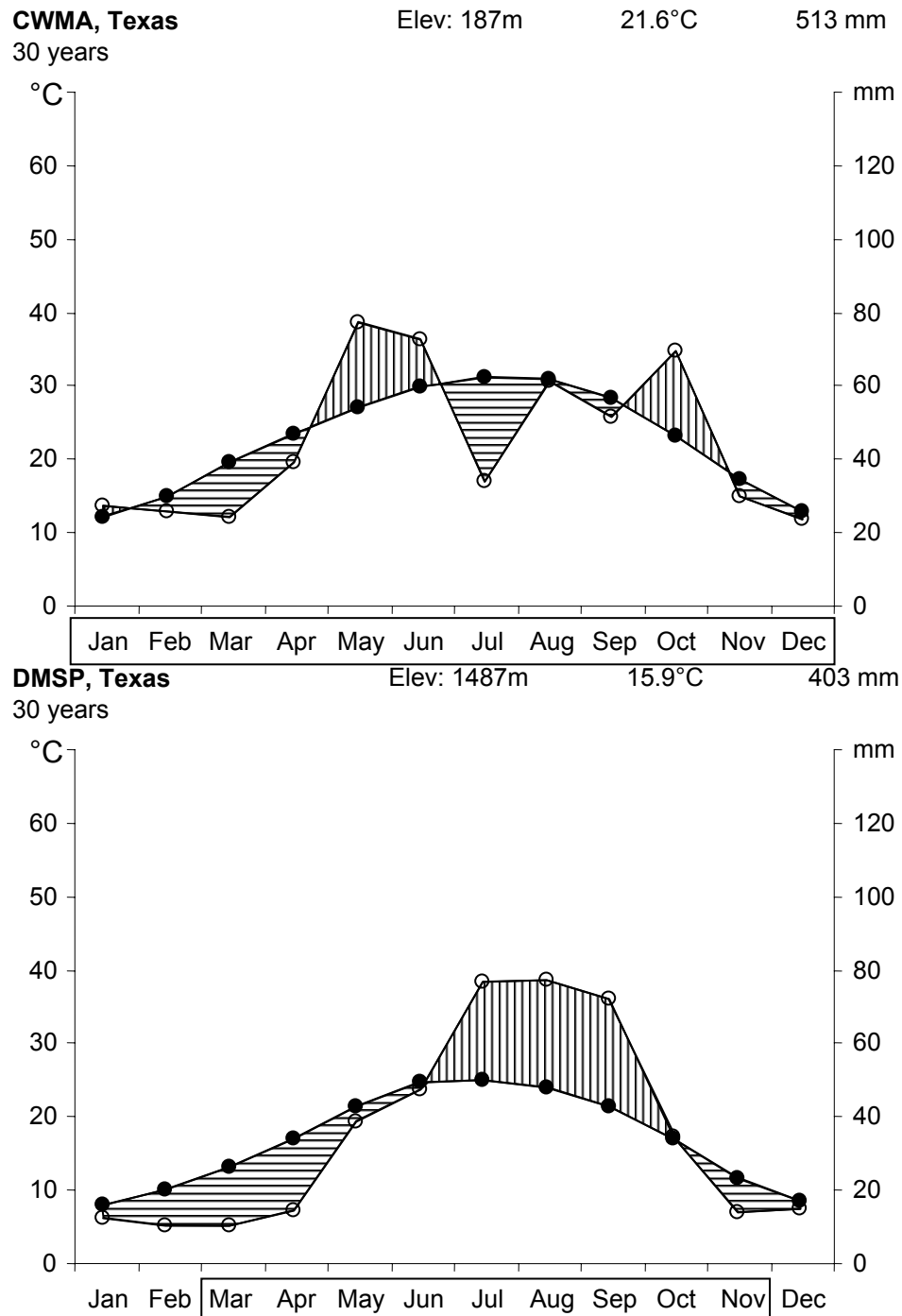
Figure 3. Climatic diagrams for the four collection sites along a precipitational gradient in the zone of sympatry of the two varieties of *B. curtipendula.* a) Chaparral Wildlife Management Area, b) Davis Mountains State Park, c) TAES-Sonora d) Pedernales Falls State Park. ▤ moist, ▥ dry, ☐ period when minimum temperature >0°C. open circle: precipitation, solid circle: temperature

TAES - Sonora, Texas   Elev: 640 m   18.3°C   568 mm
30 years

PFSP, Texas   Elev: 376 m   17.4°C   843 mm
30 years
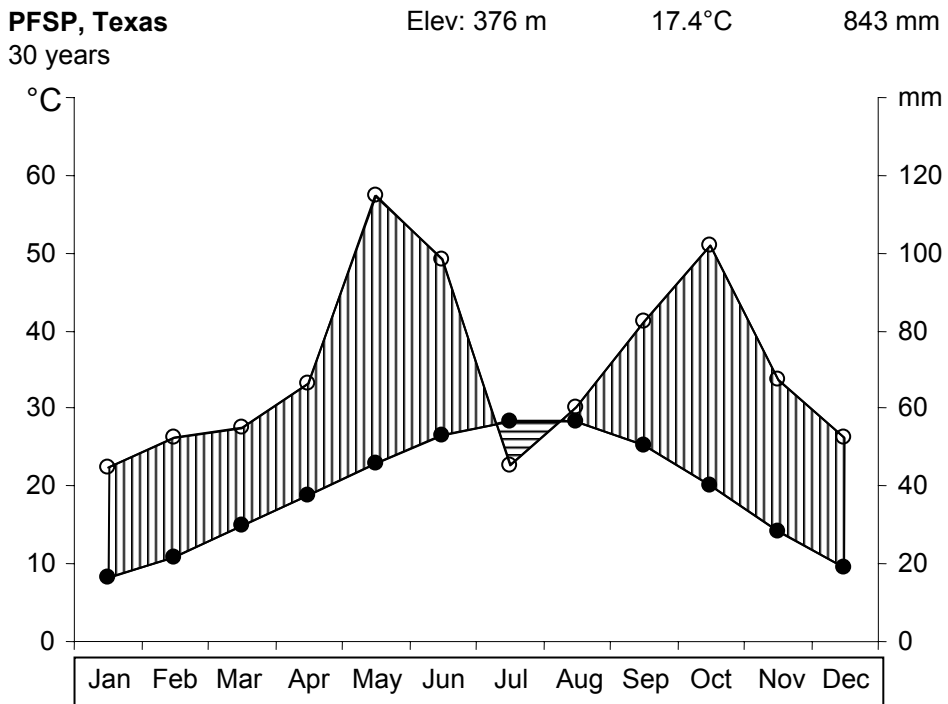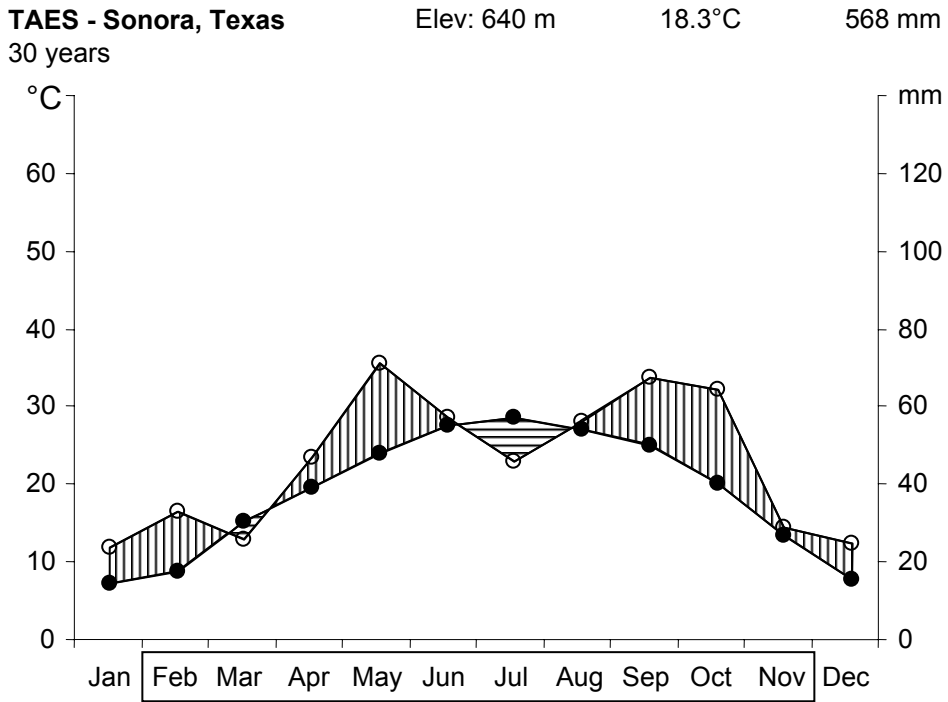
Figure 3. continued

Pedernales Falls State Park (PFSP)

Located approximately 90 km west of Austin, TX, USA (30º 17' N; 98º 25' W) in the Llano Uplift ecoregion in Texas. MAP is 840 mm with peaks in spring and fall (Figure 3d). Mean monthly temperatures range from 8 to 28º C, with an annual mean of 19º C. The elevation is 250 to 600 m above sea level. Geologically, the region is a large dome with rolling to hilly topography. Soils are predominately sandy. The vegetation consists of oak-woodlands to savanna and grassland. Common woody species include *Quercus virginiana* and *Juniperus ashei*. Herbaceous vegetation consists of *Stipa leucotricha*, *Sporobolus asper* (Michx.) Kunth, *Hilaria belangeri* (Steud.) Nash., *Bouteloua rigidiseta* (Steud.) A.S. Hitchc. and *B. hirsuta* Lag. (Diamond and Smeins 1985, Diggs et al. 1999, Fowler, N. L. and Dunlap 1985). The park was a working ranch until 1970; since then cattle have been excluded.

Morphological attributes of B. curtipendula *along a precipitation gradient*

The sites described above were visited in July 2001 and plants were selected following this scheme: ten plants of *B. curtipendula* var. *caespitosa* from what was considered a relict population in CWMA, ten plants of *B. curtipendula* var. *caespitosa* from each of three different settings in DMSP (a west facing slope, east facing slope and near an old river bed in the valley), 10 plants from each of the two varieties of *B. curtipendula* from burned (1999) and unburned portions of an ungrazed pasture at the TAES at Sonora and ten plants of each variety from PFSP. Ten morphological variables were measured in each plant collected: height, number of tillers and reproductive culms within a 10 cm radius of the center of the plant; length of the central axis (rachis) of the longest reproductive culm, length and number of inflorescences in the tallest reproductive culm; length and width of the blade and percentage of blade with hairs on the second leaf from the top in the tallest reproductive culm. Mean values for each variety were compared with Mann-Whitney U non-parametric test to determine inter- and intra-variety differences. Morphometric measurements on plants were evaluated using redundancy analysis (RDA) in CANOCO 4.5 (ter Braak and Šmilauer 2002). RDA is a constrained linear method of analysis that allows environmental variables with

different units (Lepš and Šmilauer 2003). Species matrices consisted of population/varieties at each collection site; morphometric variables constituted the environmental matrix.

Local distribution* B. curtipendula *varieties in their zone of sympatry

To determine if the growth form differences between *B. curtipendula* varieties have functional consequences in the zone where their continental distributions overlap, transects (20 m long) were inventoried on the Sonora Experiment Station. Transects were established in pastures with contrasting soil parent material and disturbance regimes. Disturbances included: burning in winter (March 1999), summer (August 1999); or not burned (control); livestock grazing (grazed and protected from grazing by big animals (=excloure). Transects were situated to include Edwards and Buda limestone parent material types within the grazing and fire treatments. Some transects were established on shallow soils with frequent rock outcrops; others were on deeper soils (Valera clays). See Table 1 for summary of transect sampling regime.

Twenty 1 x 0.5-m plots were placed at 1-m intervals along each transect. Within each plot, canopy cover of each *B. curtipendula* variety was visually estimated and assigned to a cover classes: 0 (= absent), 1 (< 5 %), 2 (5 to25 %), 3 (26 - 50 %), and 4 (>51 %). A total of 1280 plots were read (64 transects x 20 plots/transect). Eleven explanatory variables characterizing the biotic and abiotic environment and the disturbance history were rated in each plot (Table 2). Mean percent cover per transect of each variety for the factors limestone, fire and grazing treatment were assessed using ANOVA in a factorial analysis (N=64). Mean percent cover per plot of each variety relative to the position and size of the nearest tree were compared using ANOVA (SPSS 11.0) (N=1280). Data were also evaluated using canonical correspondence analysis (CCA) in CANOCO 4.5 (ter Braak and Šmilauer 2002). The recorded variables were analyzed as 46 nominal dummy variables. For the ordination, only those plots where either one or both of the *B. curtipendula* varieties were present were used (N = 321). CVA was performed by choosing CCA (direct constrained unimodal analysis) and Hill's scaling with focus on inter-species distances (Lepš and Šmilauer 2003). Forward

selection was used to rank explanatory variables in order of their importance in describing the distribution of *B. curtipendula* varieties. The significance of each variable was tested with the Monte Carlo permutation test (Legendre and Legendre 1998).

Table 1. Number of 20 m transects inventoried for *B. curtipendula* canopy cover.

	BUDA LIMESTONE		EDWARDS LIMESTONE	
	Deep soil	Shallow soil	Deep soil	Shallow soil
Protected from grazing (20 total)				
Control	2	2	5	3
Winter burn	4			
Summer burn	4			
Currently grazed (44 total)				
Control	4		5	7
Winter burn	7	1	4	
Summer burn	1	3	7	5
Total	22	6	21	15

Table 2. Description of the 46 nominal explanatory variables grouped into three groups: disturbance, abiotic and biotic environment.

Type	Variable		Definition
Disturbance	Grazing history	Protected from grazing	not grazed since 1949
			not grazed since 1999
		Grazed	moderately grazed, 15 au[1]
	Fire history	Control	not burned
		Winter burn	Burned in winter (2 pastures in Mar 1996, 1 in 1999)
		Summer burn	Burned in summer (in Aug 1996, 1997 and 1999)
Abiotic environment	Limestone type	Buda limestone	deep, rock below 15 cm
			shallow, rock above 15 cm
		Edwards limestone	deep, rock below 15 cm
			shallow, rock above15 cm
	Soil Depth[2]	Shallow	<9.9 cm
		Intermediate	10 -19.9 cm
		Deep	>20 cm
	Rock Cover	Rock_cv1	< 25 %
		Rock_cv2	25 -50 %
		Rock_cv3	50 - 75%
		Rock_cv4	>75%
	Rock Size	Rock_sz1	all rocks < 2 cm diameter
		Rock_sz2A	>50% rocks < 2cm;largest rock < 10 cm diameter
		Rock_sz2B	> 50% rocks < 2cm; largest rock > 10 cm diameter
		Rock_sz3A	< 50% rocks < 2cm; largest rock< 20 cm diameter
		Rock_sz3B	< 50 % rocks <2cm; largest rock > 20 cm diameter
		Rock-sz4	all rocks > 20 cm diameter

Table 2. continued

Type	Variable		Definition
Biotic environment	Soil Cover	Soil_cv1	> 75 % of surface is bare soil
		Soil_cv2	> 75% of area is covered with soil crust
		Soil_cv3A	> 50 % of standing cover is dead
		Soil_cv3B	> 50 %cover by live monocots
		Soil_cv3C	> 50 % cover by live dicots
	Distance to nearest oak tree[3]	Oak_dist1	plot is under oak tree
		Oak_dist2	plot is at drip line of oak tree
		Oak_dist3	plot < 2 m beyond tree drip line
		Oak_dist4	plot > 2 m beyond tree drip line
	Height of nearest oak tree[3]	Oak_hgt1	no oak tree nearby
		Oak_hgt2	< 50 cm
		Oak_hgt3	0.5 to 1 m
		Oak_hgt4	1 to 2 m height
		Oak_hgt5	> 2 m height
	Distance to nearest juniper tree[4]	Juni_dist1	plot under tree canopy
		Juni_dist2	plot at juniper canopy drip line
		Juni_dist3	plot < 2m beyond drip line
		Juni_dist4	plot > 2 m beyond tree drip line
	Height of nearest juniper tree[4]	Juni_hgt1	no juniper nearby
		Juni_hgt2	< 50 cm
		Juni_hgt3	0.5 to 1 m
		Juni_hgt4	1 to 2 m
		Juni_hgt5	> 2 m

[1] animal unit
[2] 10 mm diameter metal rod inserted into ground
[3] *Quercus virginiana*
[4] either *Junisperus ashei* or *J. pinchotii*.

Results

Morphometric variation in* B. curtipendula *along a precipitation gradient

Survey results suggested high levels of morphological variability among *B. curtipendula* plants from sites along a precipitation gradient in the zone of sympatry of the two varieties. With the exception of proportion of blade margins with hairs metrics differed significantly ($p < 0.05$) among the four location groups (Figure 4). Comparing varieties of *B. curtipendula,* they differed in six of the traits measured: tiller number, number of reproductive culms, culm axis length, blade width and area per leaf. Variation among plants within the same group in DMSP and TAES were not evident.

Plants in the mesic part of the gradient tended to be taller while plants in the more xeric part of the gradient had more reproductive culms with more branches per culm than the plants from the eastern part. However, the observed morphological extremes were not at the ends of the gradient considered in this study. Leaf width, length and area did not exhibit consistent differences along the precipitation gradient.

Morphological variables accounted for 34.3% of the total variation in a redundancy analysis. First axis distinguished the two growth forms but there was no indication of a consistent change in morphology in *B. curtipendula* along a precipitation gradient in the ordination diagram (Figure 5). Inter-set correlations of the morphological variables with the first two axes of the RDA are presented in Table 3; regression coefficients of these same axes with their respective t-values are in the same table.

Table 3. Inter-set correlations and canonical coefficients (t-values) of morphological variables with the first two axes of RDA in two varieties of *B. curtipendula* in four sites along a precipitational gradient in their zone of sympatry.

	Inter set Correlation		Correlation coefficients (t-values)	
	Axis I	Axis II	Axis I	Axis II
Fraction extracted	0.10	0.08		
Tiller number	-0.27	0.45	-0.06 (-0.49)	0.50 (2.01)
Plant height	-0.29	0.43	-0.07 (-0.52)	0.25 (4.6)
Number of culms	-0.55	-0.11	-0.34 (-2.9)	-0.30 (-2.62)
Culm height	-0.38	0.18	-0.36 (-2.46)	0.20 (1.4)
Culm raquis length	0.008	-0.04	0.52 (4.1)	0.17 (1.4)
Inflorescences / culm	-0.40	-0.46	-0.44 (-3.88)	-0.57 (-5.26)
Blade length	-0.13	0.14	-0.45 (-1.16)	0.57 (1.54)
Blade width	0.6	-0.38	0.02 (0.07)	0.03 (0.14)
Blade area	0.03	-0.10	0.32 (0.66)	-0.68 (-1.48)
Proportion of leaf margins with hairs	0.46	0.005	0.38 (4.11)	-0.05 (-0.52)
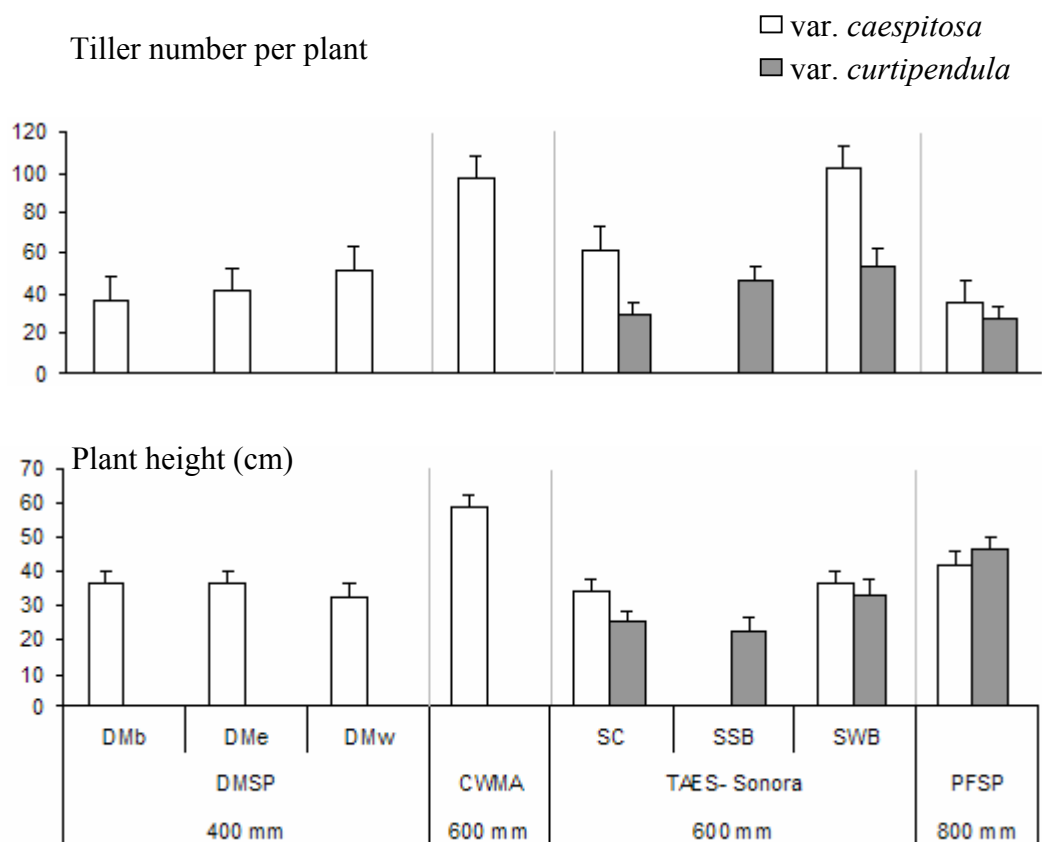
Figure 4. Morphological variation in two varieties of *B. curtipendula* along a precipitational gradient. Bars are mean values + S.E ☐ var. *caespitosa*; ■ var. *curtipendula*. DMSP**:** Davis Mountain State Park; DMb**:** plants from river bed; DMe**:** east facing slope; DMw**:** west facing slope; CWMA: Chaparral Wildlife Management Area; TAES: Texas Agriculture Experiment Station at Sonora; SC**:** not burned (control); SSB**:** summer burn (Aug 1999); SWB**:** winter burn (Mar 1999); PFSP: Pedernales Falls State Park.
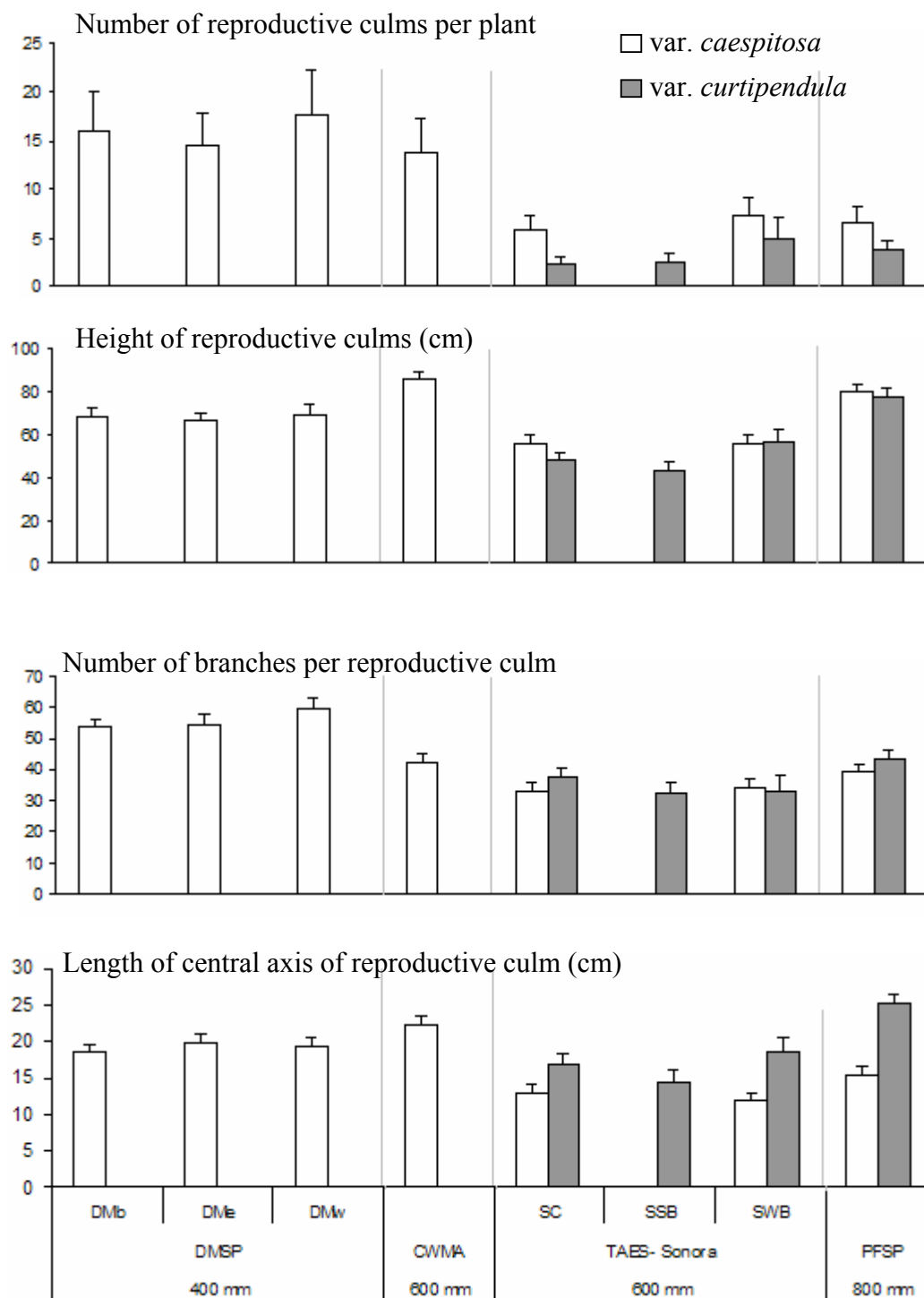
Figure 4. Continued
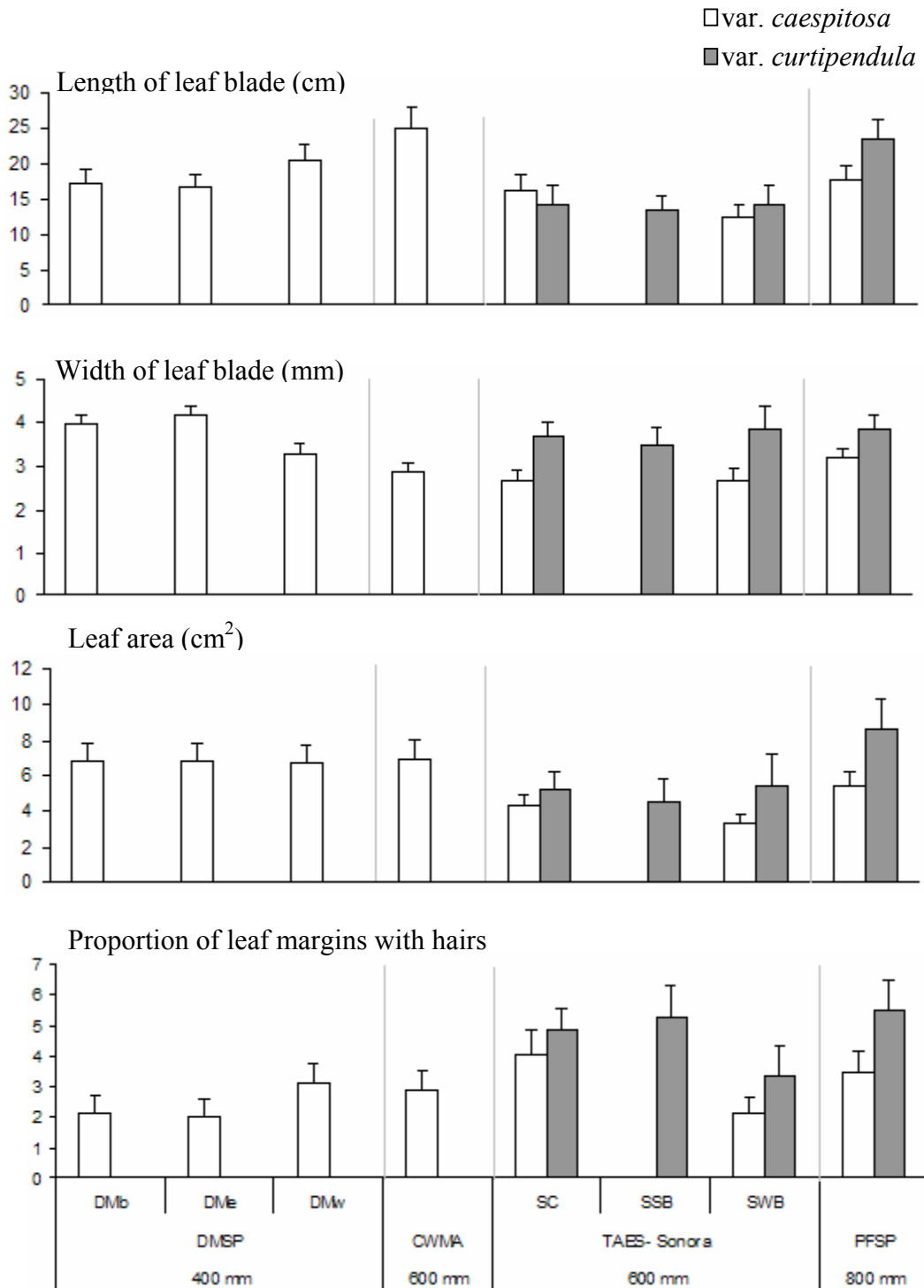
Figure 4. Continued
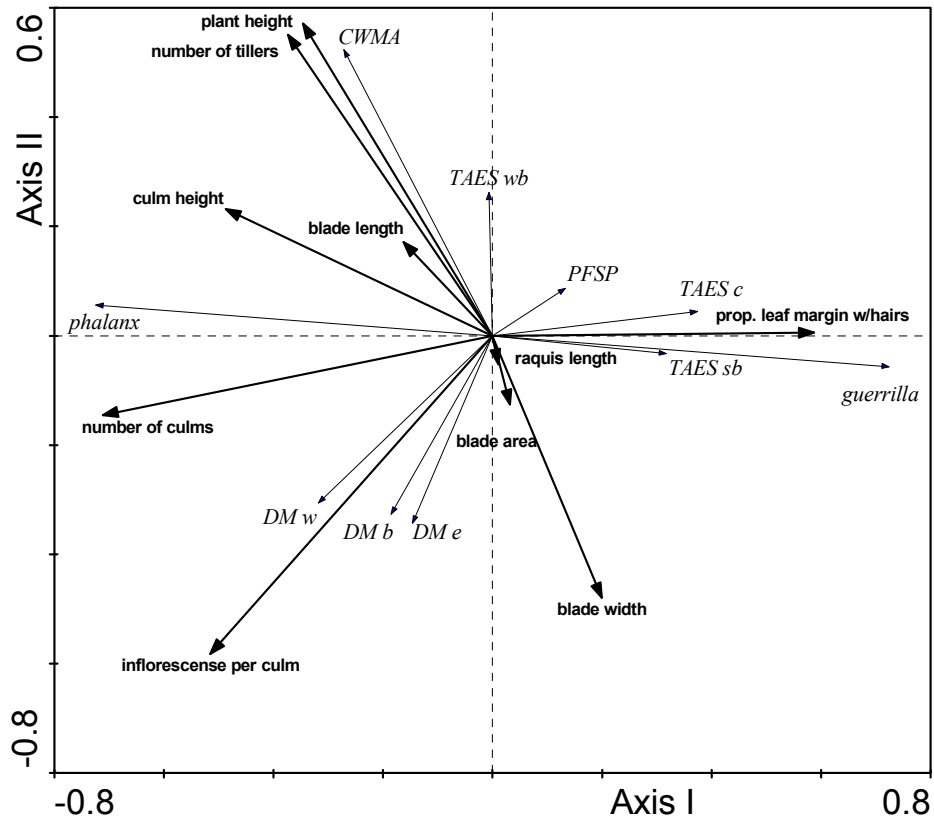
Figure 5. Species-environment biplot from redundancy analysis relating the morphological variation among plants of two varieties of *B. curtipendula* in four locations along a precipitational gradient in their zone of sympatry

Local distribution of **B. curtipendula** *varieties in their zone of sympatry*

ANOVAs showed *var. curtipendula* to be significantly affected by limestone (p<0.05) but it was not affected by grazing or fire (interactions were not significant and are not shown) (Figure 6a). *B. curtipendula var. caespitosa* showed significant interactions among these three environmental and disturbance factors (GxL, FxL) (Table 4a), but no pattern was evident for response of this variety to grazing regime, fire history or limestone type (Figure 6b). There was no significant association between size and distance to the nearest oak (*Quercus virginiana*) and cover of two varieties of *B. curtipendula,* nor were associations between var. *caespitosa* and size and distance to the nearest juniper tree (*Junisperus*) (Table 4b,c, Figure 7a). However, cover of var. *curtipendula* was significantly associated with height of the nearest juniper (p<0.05); the highest mean percent cover per plot of var. *curtipendula* was 2.6 ± 0.5 and was related to juniper < 0.5 m height (Table 4c, Figure 7b).

Environmental and disturbance variables accounted for 26.5 % of the total variance in the distribution of the two varieties of *B. curtipendula* at the Sonora site. Twelve of the initial 46 variables used in the full model were significant based on Monte Carlo Permutation Test results. A reduced model based on this subset accounted for 20.1% of the variance. CCA eigenvalues for the first four axes were 0.451, 0.121, 0.064 and 0.043 respectively. These four axes accounted for 96.6 % of the variance in the species-environment relationships, with 81 % accounted for by axes I and II. A Monte Carlo test indicated that the first canonical axis (CA) was significant ($F = 48.01$, $P < 0.01$), as were all CA combined ($F = 2.68$ $P < 0.01$). The distribution of cover classes and environmental variables in relation to CA I and CA II in the reduced model are shown in Figure 8. Inter-set correlations of environmental variables with the first two canonical axes and canonical coefficients of the same axes with their t-values are given in Table 5.

Table 4. Results from the analysis of variance of the effect of environmental, biotic and disturbance factors on the local distribution of two varieties of *B. curtipendula*. Values are Type III *F*-test and respective degrees of freedom. Transformation did not improve normality; results are shown on untransformed data. *$P<0.05$; **$P<0.01$; ***$P<0.001$
a) grazing and fire history and limestone type, b) distance and size of the nearest oak (*Quercus virginiana*) c) distance and size of the nearest juniper (*Junisperus*).
a) grazing and fire history and limestone type

	var. *curtipendula*		var. *caespitosa*	
	df	F	df	F
Grazing treatment (G)	2	0.6	2	8.7**
Limestone type (L)	3	3.4*	3	4.7*
Fire history (F)	2	0.65	2	2.3
F x G	2	0.4	2	11.6***
F x L	4	0.4	4	5.8**
G x L	1	0.99	1	1.8
F x G x L	1	0.5	1	1.8
Error	48		48	

b) distance and size of the nearest oak (*Quercus virginiana*)

	var. *curtipendula*		var. *caespitosa*	
	df	F	df	F
Distance to oak	3	0.5	3	1.2
Oak height	3	1.2	3	0.7
Distance oak * Height oak	9	1.4	9	1.3
Error	738		738	

c) distance and size of the nearest juniper (*Junisperus spp.*)

	var. *curtipendula*		var. *caespitosa*	
	df	F	df	F
Distance to juniper	3	1.4	3	1.4
Juniper height	3	2.9*	3	0.4
Distance juniper * Height juniper	9	1.5	9	0.8
Error	758		758	

a)

B. c. curtipendula
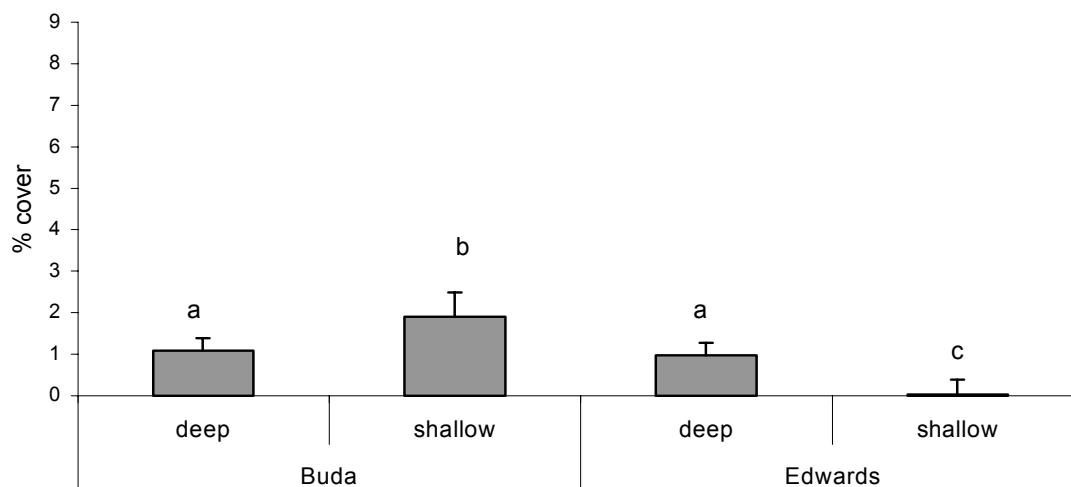
b)

B. c. caespitosa
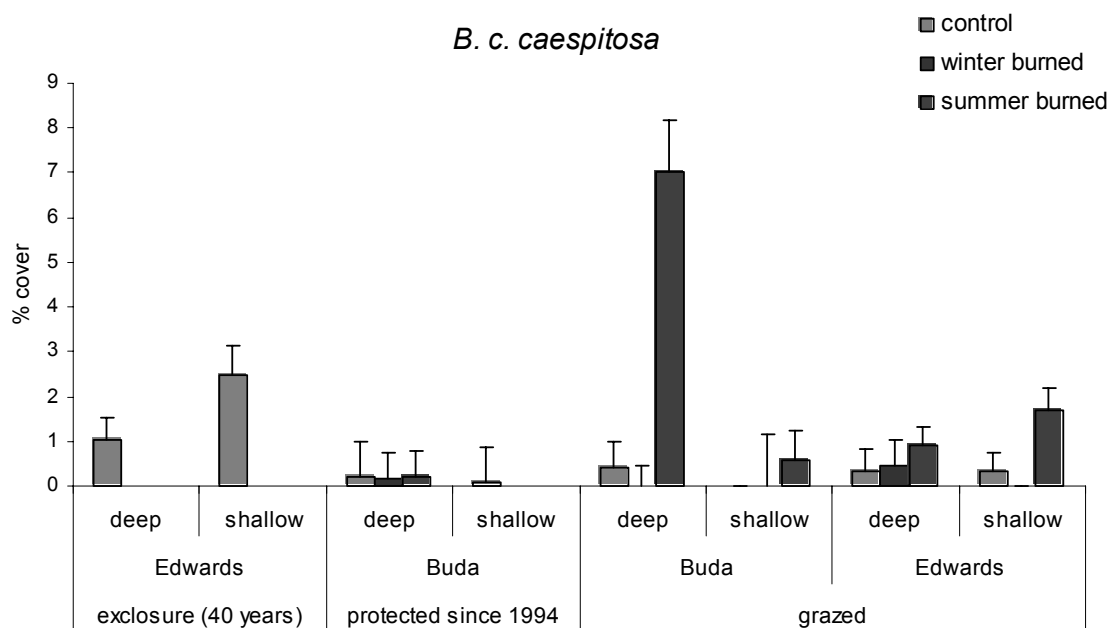
Figure 6. Distribution of var. *caespitosa* and var. *curtipendula* with respect to environmental and disturbance factors. Bars are the mean + S.E. percent cover of the varieties of all transects (N=64). Environmental factors are: a) Limestone type, b) fire history, grazing history and limestone type.

31

a) *Quercus virginiana*

B. c. caespitosa
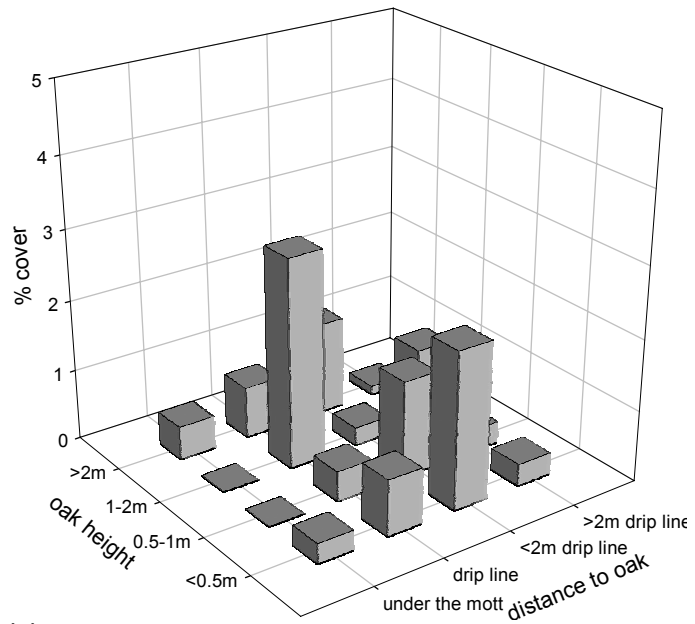
B. c. curtipendula
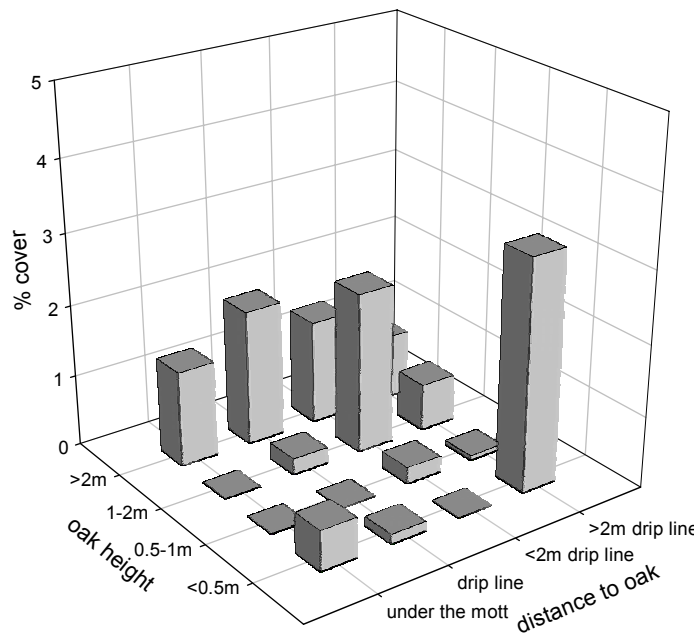
Figure 7. Distribution of *B. curtipendula* var. *caespitosa* and var. *curtipendula* with respect to distance and size of the nearest tree. a) oak trees (*Quercus virginiana*) b) juniper trees (*Junisperus spp*). Bars are the mean of percent cover of the varieties of all plots (N=1280).

b) Juniper

B. c. caespitosa
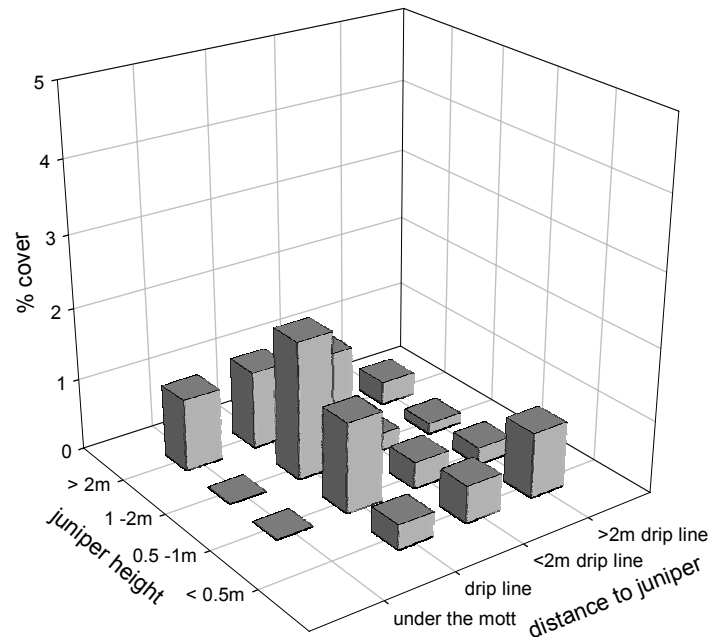
B. c. curtipendula
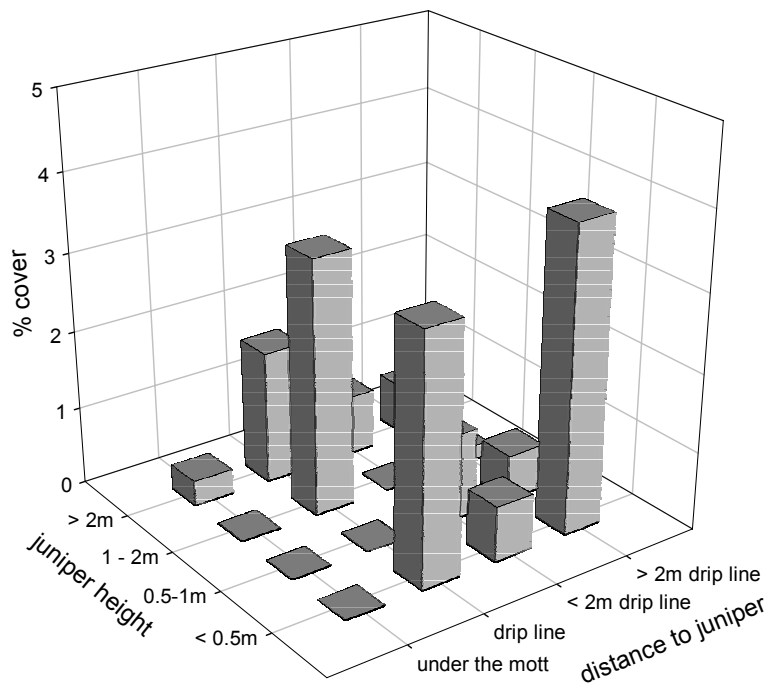
Figure 7. Continued

CA I was correlated to parent material: positively correlated to shallow (r = 0.47) and deep soils (r = 0.17) as well on Edwards limestone and negatively correlated with both deep (r = -0.4) and shallow soils on Buda limestone (r = -0.27). CA II was positively correlated with monocot cover (r = 0.33). Both varieties of *B. curtipendula* were associated with microsites having high overall grass cover (Figure 8).

Table 5. Inter-set correlations and canonical coefficients (t-values) of environmental variables with the first two axes of CCA in the abundance of varieties of *B. curtipendula* in their zone of sympatry. See Table 2 for descriptions of environmental variables.

	Correlations		Canonical coefficients (t-values)	
	Axis I	Axis II	Axis I	Axis II
Fraction extracted	0.05	0.02		
Exclosure	0.20	0.09	0.1 (1.24)	0.35 (2.66)
Summer burn	0.15	0.15	-0.27 (3.69)	0.37 (3.06)
Buda deep	-0.39	0.01	-0.95 (-11.11)	-0.09 (-0.61)
Buda shallow	-0.27	-0.01	-0.8 (-9.95)	-0.36 (-2.64)
Edwards deep	0.17	-0.05	-0.4 (-4.75)	-0.25 (-1.73)
Edwards shallow	0.47	0.05	0	0
>50% graminoid cover	-0.15	0.33	-0.15 (-2.48)	0.7 (6.81)
< 2m drip line oak tree	-0.03	0.17	0.001 (-0.02)	0.31 (2.89)
Oak <0.5m height	-0.02	0.17	0.11 (1.74)	0.39 (3.48)
Juniper 2m beyond drip line	-0.08	-0.01	-0.2 (-2.35)	0.23 (1.61)
Juniper <0.5m height	-0.20	0.10	-0.28 (-4.01)	0.31 (2.67)
Juniper > 2m height	-0.04	0.02	-0.31 (-3.64)	0.24 (1.67)
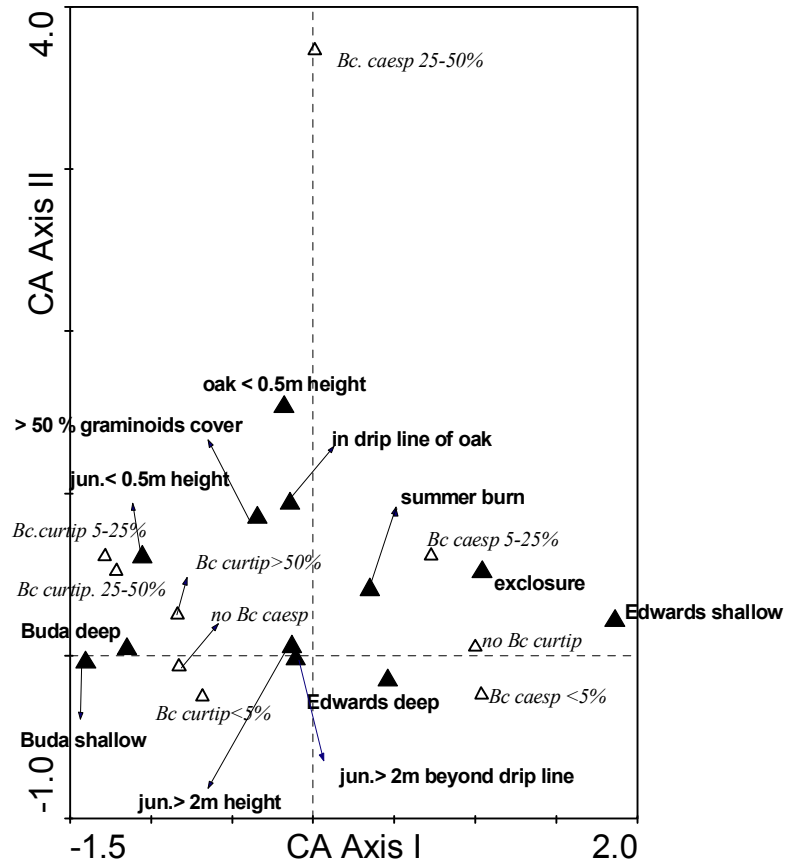
Figure 8. Results of canonical variate analysis: open triangles are centroids for species distribution of each cover class of two varieties of *B. curtipendula:* var. *caespitosa* and var. *curtipendula*. Solid triangles are centroids for distribution of sites for environmental explanatory variables (as defined in Table 2). The plot shows the association with variables that were significant ($p < 0.05$) as indicated by a Monte Carlo permutation test.

Discussion

Morphological attributes of **B. curtipendula** *along a precipitation gradient*

Survey results showed evidence of substantial morphological variation in *B. curtipendula*, but variation in the characters measured did not appear to be associated with a precipitation gradient per se. This study constituted an exploratory survey of the morphological variation between and within varieties. Although the sample size was quite small (only 10 plants per site) growth forms of *B. curtipendula* showed differentiation for some of the morphological variables measured. It cannot be determined from this survey if the observed differences in morphology are the result of adaptations to local microhabitats or the phenotypic expression of generalist genotypes (Alpert and Simms 2002, Joshi et al. 2001, Kittelson and Maron 2002, Linhart and Grant 1996, Tienderen 1997).

Populations of *B. curtipendula* were sampled in a precipitational gradient within the zone where the distribution of the two varieties overlapped. In this study, var. *curtipendula* was difficult to find at sites with lower annual precipitation, suggesting this form could be less adapted to xeric conditions than the caespitose form. The caespitose variety was found in all the sites sampled. Less tillering and no rhizomes, like in the caespitose growth form, have been thought as conservative strategies enabling a better use of resources in less favorable conditions (de Kroon and Schieving 1990). However, the expected reduction in leaf area in the caespitose form (H2) was not consistent along the precipitation gradient and did not support any trend in the distribution of this variety suggesting that other factors besides amount of precipitation might be involved in the distribution of these growth-forms.

The caespitose growth form was not encountered in the summer burn pasture at TAES-Sonora site; the small sample size and the fact that this variety was found in the winter burned section revokes the hypothesis that var. *caespitosa* was more sensitive to fire (H5). Other factors as drought, previous status of the plant before the burning treatment, micro-heterogeneities in the concentration of resources in the pasture, etc,

could have been involved in the differences reported here (Aerts and van der Peijil 1993, Bond and van Wilgen 1996, Busso et al. 1989, Fernandez et al. 2002).

Local distribution of* B. curtipendula *varieties in their zone of sympatry

The pattern of distribution of the varieties at the regional scale suggested that the local abundance of the two growth forms of *B. curtipendula* within the zone of sympatry should reflect different adaptations to resource availability, stress and disturbance. Results showed that var. *curtipendula* was associated with Buda limestone particularly on shallow soils but was almost never found on shallow soils on Edwards limestone (Figure 6a). Multiple depositions of limestone occurred in warm, shallow, epicontinental seas in Cretaceous times around 100 million years ago (Loomis and Gabriel 1991). As Edwards limestone was deposited first, it is more weathered than the relatively recent Buda limestone. Currently, blocks of Edwards limestone crop out along the plateau margins and form resistant base levels for streams draining the outcrop while Buda occurs on the divides between the major drainage systems (Eckhardt 2004, Loomis and Gabriel 1991). One possible reason for the differential distribution of the varieties in the limestone types could be related to the differences in rock size and penetrability inherent to the parent materials. Soils on Buda limestone are generally level and although depth could be variable parent material is younger and perhaps more continuous with fewer fractures and hence is harder to penetrate. In addition, soils on Buda limestone are commonly shallow then, it could be speculated that rhizomatous plants are better adapted to explore laterally and be in a position to capture water made available in small rainfall events common in semi-arid lands. Alternatively, soils on Edwards limestone are apparent on slopes and rock outcrops, form uneven surfaces frequently associated to big size rocks (Eckhardt 2004) that might hinder the expansion of rhizomes (Sutherland and Stillman 1988, 1990). A similar difference in plant distribution with respect to limestone types has been observed in two species of *Juniperus* in the Edwards Plateau Region: *J. pinchotii* is most abundant on Buda limestone, whereas *J. ashei* is most abundant on Edwards limestone (C.A. Taylor, Jr., personal communication).

The environmental variables measured account for 26.5% of the variability in the local distribution of the two growth forms in the ordination analysis. High correlation of CA I to soil depth and limestone type suggest primary separation was related to soil and parent material. However, the highest correlations between environmental variables with the first axis were never higher than 0.5 (Table 5), and even though the majority of the cover classes of the two varieties were distributed along the first axis, the existence of an explanatory variable not considered in this study can be speculated. The second axis was not correlated with any of the variable measured, nor were the third and fourth (data not shown). The position of var. *caespitosa* 25-50% plots separated in the second axis suggests a possible relation with the missing variable (Figure 8). Measured variables considered variation at a spatial scale related to size and were relevant to grazing history, limestone type and fire history while others were relative to the plants as position of plants respect to trees, soil depth, rock cover and ground cover. However, there might be micro-scale variation that was not accounted for in this study. For example, micro-scale heterogeneity in the nutrient availability related to accumulation in island of fertility or subsequent changes related to the rate of decomposition of neighboring species (Aerts and van der Peijil 1993, Vinton and Burke 1995); or even through the result of asymmetric competition with other species (Aguilera and Lauenroth 1995, Bliss et al. 2002, Fowler, Norma 1986).

CA II explained a very small part of the variation in species distribution and showed low correlation with all variables (Table 5). The highest correlations with CA II involved > 50% graminoid ground cover and the distance and relative position of the plot with respect to the oak trees. No significant effects of the size and distance to the nearest oak and the weak relation of the abundance of the two varieties with the second axis contrasts with previous results and suggests an improved microenvironment for grasses establishment in the drip line of woody plants (increased water by through fall from the tree, reduced temperatures by shading and accumulation of nutrients) (Fuhlendorf 1992, Marshall 1995, Thurow et al. 1986).

Presence of juniper trees of less than 0.5 m height showed a negative but low correlation to CA II (r =0.2, Table 5); the association of relatively high cover of var. *curtipendula*, the guerrilla growth form with small juniper trees was sustained by a significant positive effect of the variable <0.5 m juniper height on var. *curtipendula* cover. These observations concur with previous studies at the site reporting high percentage of herbaceous cover related to small juniper trees although only in sites with no grazing (Fuhlendorf 1992).

Data from defoliation studies suggest guerrilla growth forms are more grazing resistant than the phalanx type (Briske 1996). Thus, it was hypothesized that var. *curtipendula* would be more abundant on grazed sites and var. *caespitosa* would be more abundant on sites protected from grazing. Contrary to expectations, cover of the rhizomatous growth form was not affected by grazing (Table 4a). Significant interactions between grazing and fire history and grazing and limestone type in var. *caespitosa* confirmed that these factors were inter-related. *Bouteloua curtipendula* var. *caespitosa* showed different responses to grazing depending on the fire and limestone conditions. Ordination analysis also showed a distinct pattern in this variety (Figure 8): plots with relative high cover (25-50%) seemed to be related to a factor that was not considered in this study. It can be speculated that this factor could in fact be the result of the interactions of several factors all together. The fact that the interactions were only evident in var. *caespitosa* while var. *curtipendula* was only affected by the limestone type suggested a level of dissimilarity between growth forms. However, these dissimilarities could be effects of the scale at which growth forms responded to the heterogeneity. For example, clones of *Glechoma hederacea* L. showed different response in environments that were coarse-grained with large patches of nutrients compared to environments that were fine-grained with small scale patches (Wijesinghe and Hutchings 1997). Applied to the particular case of *B. curtipendula*, the two varieties might have responded to the same pattern of heterogeneity but, at different scales. Thus, rhizomes in var. *curtipendula* might extend over bigger areas and it might perceive the heterogeneity in soil nutrients, water, etc as coarse grained. Alternatively, the compact

form of var. *caespitosa*, not able to extend laterally to escape poor patches might sense the heterogeneity in the environment as fine-grained. It can be speculated that interactions between environmental factors could only be detected at this fine-grained heterogeneity scale.

The fact that the caespitose growth form was not found on the summer burn treatment in the preliminary survey (Figure 4) prompted the hypothesis that var. *curtipendula* would be more abundant on burned sites and var. *caespitosa* would be more abundant on sites that were not burned. Correlation coefficients relating summer burn and the CA were both 0.15. Then, although the variable tested to be significant in the ordination, it did not give information about the relative abundance of the varieties respect to seasonal fire treatments. Additionally, local distribution of var. *curtipendula* was not significantly affected by fire treatments. Studies on fire resistance in *B. curtipendula* (referring only to var. *curtipendula*, the variety present on the their site) proposed this variety would be sensitive to fire (Wink and Wright 1973); and later reports mentioned var. *caespitosa* as capable "to thrive after fire" (Wright 1974). Results of this study did not show an increase or a decrease with respect to the burning treatments in var. *curtipendula* (Figure 6a). Alternatively, significant interactions between fire and grazing histories and fire and limestone types mediate interpretation of the singular results of these factors on var. *caespitosa.*

Conclusions

The preliminary survey of the two varieties of *B. curtipendula* in part of their zone of sympatry suggested that although the species is morphologically variable, this variation could not be related to a precipitational gradient. Local distribution of *B. curtipendula* var. *curtipendula* on the Sonora Experiment Station was related to soil depth and parent material. Results suggested that local distributions of *B. curtipendula* var. *caespitosa* might be determined by the interaction of environmental factors. Morphological variation between and within varieties and their low explanatory power to distinguish between the varieties used in this study implied that the distinction

between growth forms (in morphology and broad regional distribution) may involve other factors than those ones considered here.

CHAPTER III

RESOURCE AVAILABILITY, DISTURBANCE AND PATTERNS OF

DISTRIBUTION OF *BOUTELOUA CURTIPENDULA* VARIETIES

Introduction

Plant species are not homogeneous groups of individuals; their members vary in several attributes as a response to environmental conditions, resource availability, competition and disturbance. Although it is impossible to isolate the importance of one single factor on the distribution of a species, subspecies or varieties, certain factors may have overriding importance in determining pattern of distribution in a particular system (Barbour et al. 1998, Billings 1952). In determining the causes underlying patterns of plant community structure, emphasis has been placed on resource availability, in particular light, water and nutrients (Olff et al. 1990).

Wide-ranging species are frequently made up of populations specifically adapted to the conditions that prevail in a given area. The distinctiveness between groups of individuals can be morphological, physiological or phenological, and frequently makes the most adapted group the predominant one in the environment (Silvertown and Lovett Doust 1993). These groups of individuals may be identified as into taxonomic categories below the species level but the criteria used for discriminating among groups are often not formally quantified. Plant architecture has been used as one of the criteria to characterize groups of the same species with difference in their growth form commonly associated with the type of habitat where they live. Plant architecture is associated with physiological and morphological characteristics that give the plants the ability to cope with heterogeneities in the environment. It has been suggested that plants with a compact architecture (phalanx), are associated with resource-poor environments as they can reduce evapotranspiration by self-shading making an economic use of the resources. Alternatively, plants with a expanded architecture with lateral extensions or runners (guerrilla) have been related to sites with more resources as their growth is less limited

and they can expand to occupy gaps when resources are available (de Kroon and Schieving 1990).

Bouteloua curtipendula (Michx.) Torr consists of three varieties: (1) var. *curtipendula* reproduces sexually and from spreading rhizomes and occurs in a broad belt from southeastern Canada to southwestern the U.S. (2) var. *caespitosa* Gould and Kapadia has a bunchgrass growth-form lacking rhizomes and reproduces apomictically and occurs from central Texas westward through New Mexico and Arizona, to southern California and southward to South America; and (3) var. *tenuis* Gould and Kapadia, is only found primarily in central Mexico (Gould and Kapadia 1964). At the regional scale, the rhizomatous growth forms of *B. curtipendula* dominate the relatively mesic portions of the Great Plains, with caespitose growth forms occupying western semi-arid to arid habitats (Gould & Kapadia 1962). The Edwards Plateau of Texas is a region where the ranges of the caespitose and rhizomatous varieties overlap substantially. The functional ecology of these taxonomic varieties has not been systematically investigated; hence the potential ecological significance of differences in their morphology and phylogeny is based on qualitative observation and conjecture.

The goal of this study was to (a) assess whether or not there is a niche separation that allows the coexistence of *B. curtipendula* var. *curtipendula* and var. *caespitosa* within their zone of sympatry; (b) determine if local distributions of the two varieties correspond to environmental conditions as might be predicted from their continental scale distributions; and (c) ascertain how resource availability (nutrients and light) and disturbance (defoliation) affect the local distribution of *B. curtipendula* varieties. Specific objectives and hypotheses of the study were as follows:

Objective 1: Determine whether the varieties of *B. curtipendula* differ in their ecophysiological response to resource availability.

H1) Plants of var. *caespitosa* maintain higher water potential than plants of var. *curtipendula* under similar conditions.

Rationale: clustered tillers in var. *caespitosa* result in self-shading of the foliage (Caldwell et al. 1983). Shading reduces leaf temperature and vapor pressure

difference between leaf and air so that water losses through transpiration are reduced. By contrast, var. *curtipendula* tillers are loosely arranged and amelioration of microclimate is less likely.

> H2) Plants of var. *caespitosa* will have higher photosynthetic rates in low nutrient conditions than var. *curtipendula* while in shaded environments var. *curtipendula* will exhibit higher rates than var. *caespitosa*.

Rationale: if plants of var. *caespitosa* are better adapted to poor nutrient environments, they will be able to maintain the photosynthesis rate per area even under low nutrient availability. If plants of var. *curtipendula* are better adapted to high nutrient environments with high overall productivity (high nutrients availability but limiting light because of interspecific competition) they will have mechanisms to keep the rate of photosynthesis per area in shaded conditions (Olff et al. 1990).

Objective 2: To compare vegetative and reproductive growth of plants of the two varieties growing at different combinations of light and nutrient supply.

> H3) var. *caespitosa* and var. *curtipendula* will respond differently to low and high resource availability levels.

Rationale: if var. *caespitosa* (phalanx growth forms) is better adapted to resource poor sites than var. *curtipendula* (guerrilla growth forms), it will allocate more biomass to roots and will be less impacted by low resource availability than var. *curtipendula.* Conversely, if var. *curtipendula* will perform better than var. *caespitosa* on sites with high resource availability it will expand and cover more area through an increase in the allocation to rhizomes (Dong and de Kroon 1994).

> H4) Patterns of biomass allocation in response to increases in resource availability will differ in the two varieties. Plants of var. *caespitosa* will increase biomass allocation to reproductive culms whereas plants of var. *curtipendula* will increase allocation to rhizomes.

Rationale: If var. *caespitosa* is better adapted to nutrient-poor habitats, it will allocate biomass to seed which can be potentially dispersed to more favorable distant habitats; if plants of var. *curtipendula* are better adapted to sites with higher nutrient availability, they will allocate biomass to rhizomes so that new tillers can locally exploit high resource patches in the vicinity of the parent (Bell and Tomlinson 1980).

Objective 3: Contrast the response of *B. curtipendula* varieties to defoliation.

> H5) Plants of var. *curtipendula* are more tolerant to defoliation than the plants of var. *caespitosa.*

Rationale: If var. *curtipendula* is better adapted to sites with high resource availability it will tolerate defoliation by active tiller recruitment after defoliation, if var. *caespitosa* is better adapted to nutrient-poor sites it will rely on avoidance mechanisms and will have less tiller recruitment after defoliation than var. *curtipendula*.

Objective 4: To contrast levels of genetic variability in *B. curtipendula* varieties.

> H6) Plants of var. caespitosa have a higher degree of genotypic variability than plants of var. curtipendula.

Rationale: if var. *curtipendula* plants are better adapted to sites with good nutrient availability they will grow fast enough to turn over modules rapidly and thus track environmental fluctuation via phenotypic variation. Conversely, if plants of var. *caespitosa* are better adapted to poor nutrient sites they will have slow tiller turnover rates and cope with environmental heterogeneity via genetic variation between genotypes.

To test these hypotheses, clones of eight genotypes of each of the two varieties of *B. curtipendula* were grown in a common garden. The plants were subjected to different levels of defoliation and resource (light and nutrient) availability and their growth and physiological performance monitored.

Methods

Study site

The study was conducted at the *Texas Agricultural Experiment Station* (TAES) near Sonora, Texas, (31º 18'N; 100 º 28'W). The station is located on the southwestern portion of the Edwards Plateau Area at an elevation of ca. 730 m above sea level. The climate is sub-tropical, semiarid with no distinct dry season (Smeins and Merril 1988). Mean annual precipitation (600 mm) is bimodal, with peaks in spring and fall. Seasonal and annual droughts are common. Mean monthly temperatures range from 34 °C in July to 16 °C in January (Station records). Landscapes are characterized by gentle (3-4 %) slopes and a heterogeneous mixture of soil depths and rock outcrops. Dominant soils are Tarrant stony clays of the thermic family of Lithic Haplustolls formed over fractured Edwards and Buda Cretaceous limestones. Valera clay, Abilene silty clay loam, Irion clay and Frio gravelly clay soils occur only occasionally on the station.

The vegetation is savanna/parkland with individuals or clusters of woody species interspersed within a matrix of mid- and short-grasses. Common woody species include *Quercus virginiana* Mill. var. *virginiana*, *Q. pungens* Liebm. var. *vaseyana* (Buckl.) Mull., *Juniperus ashei* Buckholz, and *J. pinchotti* Sudw.. Dominant herbaceous species include *Bouteloua curtipendula* (Michx.) Torr., *Eriochloa sericea* (Scheele) Munro *ex* Vasey, *Hilaria belangeri* (Steud.) Nash, *Aristida, Stipa leucotricha* Trin. & Rupr., *Bouteloua trifida* Thurb. and *Bouteloua hirsuta* Lag.

The station was established in 1916 to study animal diseases and the management and breeding of cattle, sheep and goats. Landscape-scale livestock grazing management trials were initiated in 1948, when 25 pastures were established and assigned various stocking rates and rotational grazing management regimes.

Plant sampling and propagation

Eight plants of *B. curtipendula* var. *curtipendula* and eight plants of *B. curtipendula* var. *caespitosa* were collected from different pastures in March 2002, separated more than 500 m so that they could be considered different genotypes.

Individual plants were separated by 100 m to ensure they represented unique genets. The plants chosen exhibited the extremes in the phalanx-guerrilla growth-form continuum, i.e. the presence or absence of rhizomes could be clearly recognized. Ramets from the collected plants were vegetatively propagated to generate more than 50 clones per genet. The clones were reared in cone-tainers (Stuewe & Sons, Inc., Corvalis, OR, USA) filled with the soil from the study area. Racks of cone-tainers were maintained in a greenhouse at the Sonora Experiment Station for two months and watered every two days.

Experimental design

Growth and physiological performance of the two growth forms of *B. curtipendula* were assessed in the field under two levels of solar radiation and nutrient availability and two levels of defoliation (Figure 9). The experiment was conducted using a series of 3 m x 1.5 m garden beds situated in an oak parklands on a Tarrant silty-clay soil (Clayey-skeletal, smectitic, thermic Lithic Calciustolls), in an area protected from grazing since 1994 but containing sectors subjected to different prescribed fire treatments. Eight garden beds were established on oak-induced 'islands of fertility' soils. Four of these gardens were in oak (*Quercus virginiana)* mottes on sectors not previously burned (= high nutrient, low light treatment). The other four gardens were established in an area where oak canopies had been eliminated by fire in August 1999 (= high nutrient, high light treatment). An additional eight gardens were established in a grass-dominated sites paired with the sites where oaks had influenced soil nutrient pools. Soils in these grassland gardens had lower C and N levels than those associated with oaks (54.4 ± 3.3 mg C m^2 and 3.5 ± 0.1 mg N m^2 in the open vs. 96.7 ± 9.3 mg C m^2 and 6.1 ± 0.6 mg N m^2 under the oak mottes; Marshall 1995). Four of the grassland gardens were under full sunlight (= low nutrient, high light treatment) and four gardens were artificially shaded to generate photosynthetically active radiation levels approximating those in oak mottes (ca. 500 μmol m^{-2} s^{-1}). In total, sixteen garden beds were prepared for transplanting. Soils were lightly tilled by hand and periodically weeded to minimize intraspecific herbaceous competition. Roots of oak trees and other woody species were abundant and densely packed in soils under the motts; oak resprouts from tree roots were cut

periodically. Artificial light attenuation was achieved by draping a 2.15 x 3.95 m neutral density shade cloth over a metal frame at a height of 1.4 m (giving 0.7 m side walls). Photosynthetic photon flux density (PPDF) determined with a line quantum sensor at solar noon was ca. 1,800 and 500 µmol m^{-2} s^{-1} on the open and artificially shaded plots, respectively. Within oak mottes, PPDF was more (400 to 700 µmol m^{-2} s^{-1}) owing to sunflecks.

Gardens were planted May 15-18 2002. One ramet of each of the eight genotypes of each variety was planted in each garden. Thus, each genet was exposed to all the levels of the experimental treatments. Two clones from each genotype were randomly assigned to one of the treatment combinations that were repeated four times, totaling 512 plants (2 light levels x 2 nutrient levels x 2 defoliation levels x 2 varieties x 8 genotypes x 4 replicates). Clones were planted in gardens in arrays of 4 rows with 10 plants per row with. 30 cm spacings. Additional 'sacrifice' tillers were planted for use in water potential and gas exchange measurements and to make a surrounding border line (no measurements were taken in border plants).

Senescent biomass was removed from transplants in late May, 2002 and the numbers of tillers were recorded for each plant. Tiller recruitment and mortality were quantified by marking four vegetative tillers on the periphery of each plant with fine gauge color-coded wire on June 15, 2002. Plants in each light/nutrient treatment combination were randomly assigned one of two defoliation treatments: not defoliated (control) or defoliated.
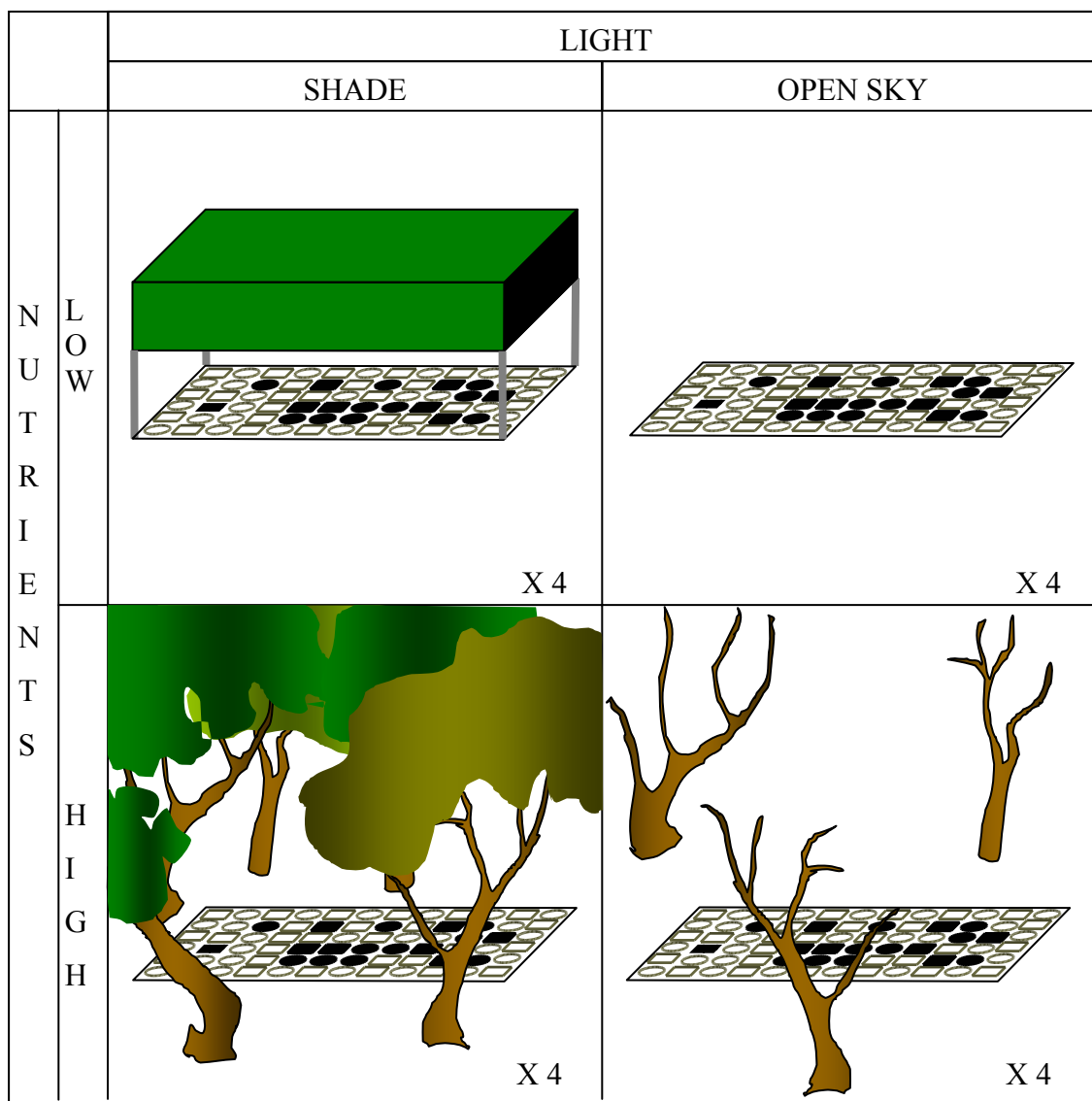
Figure 9. Design of experimental gardens. Four environmental settings were created with the combination of light (normal, attenuated) and nutrient availability (relatively low, relatively high). Eight genotypes of each *B. curtipendula* variety were replicated four times in each treatment. Data was not collected from border plants. Plants of different genotypes were used for water potential (Ψ) and photosynthesis (A) measurements. Extra plants were used for borders.

▦ var. *curtipendula* control	● var. *caespitosa* control
☐ var. *curtipendula* defoliation	○ var. *caespitosa* defoliation
▦ var.. *curtipendula* border	◌ var. *caespitosa* border
■ var. *curtipendula* (Ψ and A measurements)	● var. *caespitosa* (Ψ and A)

Physiological and morphological measurements

Plants in the defoliation treatment were clipped to 5 cm on June 11 and again on July 18, 2002. The shoot biomass removed was dried and weighed. Marked tillers were censused on July 18 and August 5, 2002. Tiller recruitment and mortality were calculated as the number of new or dead tillers associated with each tiller marked with colored-wire at time t minus the number of tillers in the wire at time, t-1. Tiller replacement rate was calculated by subtracting the number of dead tillers from the cumulative number of tillers (initial number plus all the tillers recruited) and dividing this difference by the initial number of tillers.

Net photosynthesis (A) was measured on the most recently fully expanded leaves using a portable gas analyzer (LI-6200, LI-COR, Inc.), between 10 AM and 2:00 PM, on July 20 and on August 6/7, 2002. Leaf xylem water potential (Ψ) was measured diurnally (pre-dawn, noon (12:00), mid-afternoon (15:00) and evening (19:00), with a pressure chamber [Plant Soil Moisture Systems, Inc.] in June 12/16, July 19/20 and August 7/8, 2002. A and Ψ were determined in two tillers per variety per treatments.

Plants were harvested on October 19-25, 2002. Reproductive culms were cut above the second node from the base and weighed. Soils were washed from the roots and plants dried at 60ºC. Biomass of roots, shoots and rhizomes in were recorded for each plant in each treatment and root to shoot ratios (roots and vegetative shoots) and below to aboveground biomass ratios (belowground = roots + rhizomes; aboveground = shoots and reproductive culm biomass) were calculated.

Statistical analyses of data

Initial tiller number was used as covariate in a factorial analysis of covariance (ANCOVA) to determine the effects of light and nutrient availability and defoliation on genotypes of *B. curtipendula*, var. *caespitosa* and var. *curtipendula* (GLM; SPSS 11.0). Genotypes were treated as a fixed factor because the plants used in the study were not picked randomly but rather, were clear representatives of the opposite ends of the phalanx-guerrilla growth form continuum (see plant sampling and propagation). A Kolmogorov-Smirnov test was used to assess normality; variables were ln transformed

before analysis as necessary to meet normality assumptions. For some variables, transformation did not improve normality. Those instances are noted in the results and the outcomes of untransformed analyses are reported.

Genetic differentiation between varieties was indicated by a significant variety effect. Evidence of genetic variation between genotypes within varieties was shown by significant genotype effect. Variation within genotypes denoted phenotypic plasticity. Variation in reaction norms (the continuous morphological variation within genotypes (Silvertown and Lovett Doust 1993)) was compared among genotypes in each variety. Traits were considered plastic if there was a significant response to the treatments (light and nutrient availability and defoliation) or if there was significant interaction between variety or genotype and treatments. Significant interactions between varieties and treatments (light, nutrient or defoliation) would indicate significant variation in phenotypic plasticity between varieties (Miller and Fowler 1994). A significant interaction term (genotype x treatment) would indicate that genotypes differ in their plastic response to treatments (Schlichting and Levin 1988).

Results

Differences between varieties

Ecophysiology

Diurnal patterns of leaf Ψ looked similar in the two *B. curtipendula* varieties (Figure 10). However, a significant (*P*< 0.01) interaction Nutrient (N) x Variety (V) x Time of day (TOD) suggested that the response to changes in nutrient availabilities in Ψ differed between varieties and the response to these changes was different across the day (Table 6). Time of day (TOD) significant interactions with Light (L) and Nutrient (N) indicated a difference of the effects of these factors on Ψ between dawn and the afternoon. Significant interactions L x TOD x M and N x TOD x M suggested that effects of limiting resources (light and nutrient availability) on plant Ψ were different not only along the day but also between months with progressing of the growing season.

Table 6. Analysis of variance results for leaf water potential (Ψ) measurements in June, July and August, 2002 on two varieties of *B. curtipendula* grown under contrasting light and soil nutrient treatments. All values were the mean of measurements of two consecutive days. Values are Type III *F*-test. Only significant (P < 0.05) are shown. **P<0.05; **P<0.01; ***P<0.001*

	Df	*F III*- value and significance
Light (L)	1	63.3***
Nutrient (N)	1	7.7***
Variety (V)	1	6.2*
Time of Day (TOD)	1	872.9***
Month (M)	2	81.5***
L x TOD	1	42.8***
N x TOD	1	5.7*
N x V x TOD	1	7.5**
L x M	2	11.1***
TOD x M	2	36.2***
L x TOD x M	2	15.9***
N x TOD x M	2	6.5**
Error	144	

a)
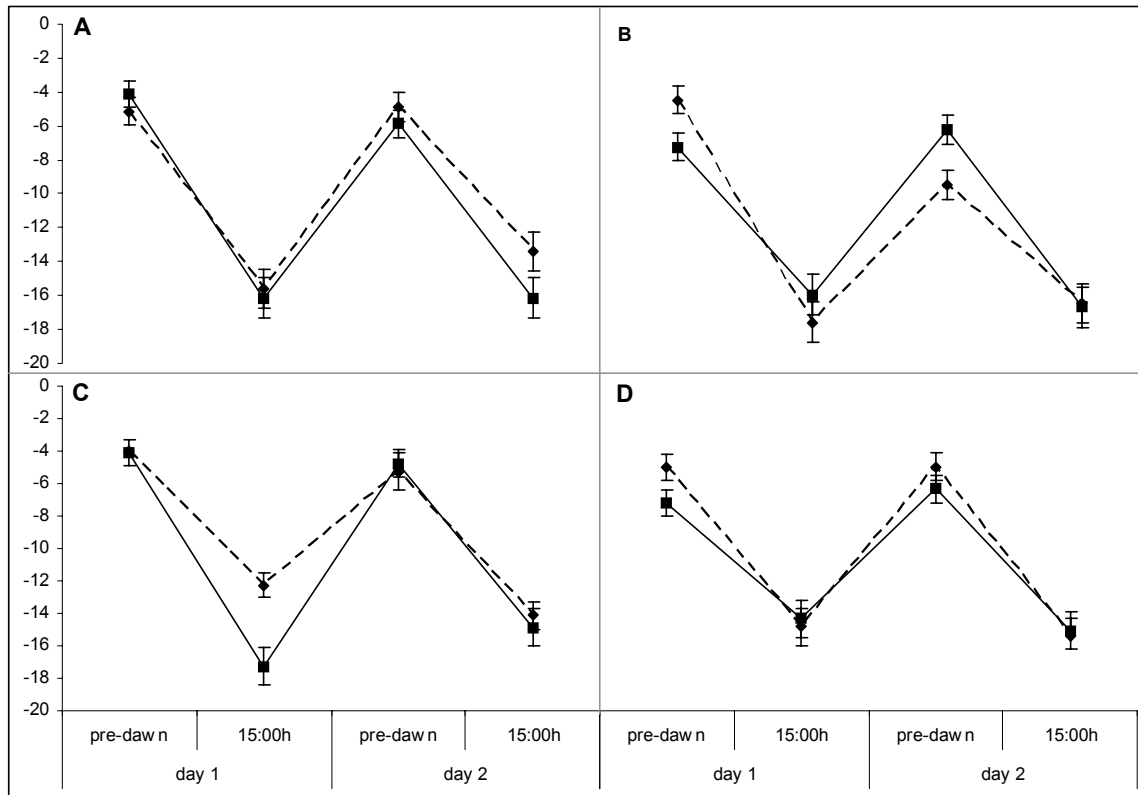
Figure 10. Diurnal variation in leaf water potential in two varieties of *B. curtipendula* growing in contrasting light and nutrient availability settings in a) July and b) August 2002. Values are means ± SE (*N*=4). A) light / high nutrient; B) light / low nutrient; C) shade / high nutrient; D) shade / low nutrient

- - - - - - - - - - - - **v**ar. *caespitosa*   _____var. *curtipendula*

b)
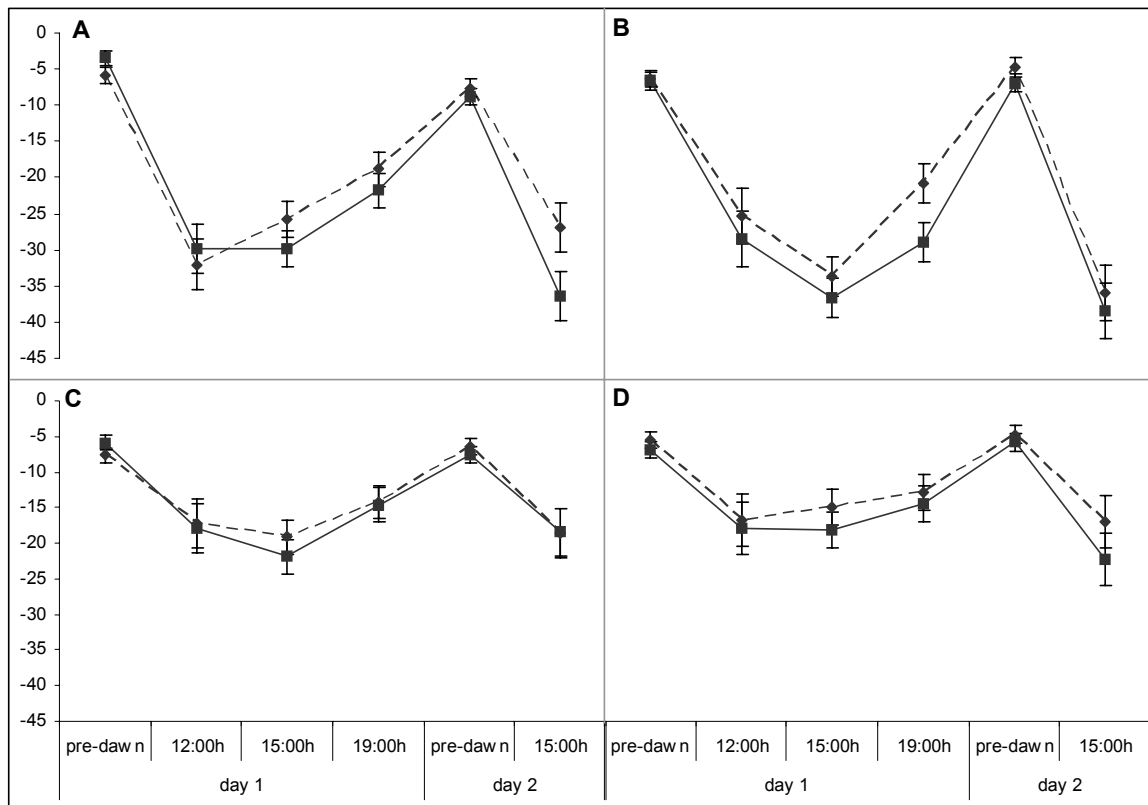
Figure 10. Continued

Bouteloua curtipendula varieties exhibited comparable levels of carbon fixation in July and August 2002 (Tables 7 and 8). Photosynthesis rate responded only to light availability ($P < 0.001$); no effect of nutrient availability was detected.

Table 7. Type III *F*-ratios from the analysis of variance of measurements of photosynthetic rate in two varieties of *B. curtipendula* under contrasting light and nutrient treatments. Measurements were performed between 10:00h and 14:00 h once in July and on two consecutive days in August (the values were averaged before the analysis). *$P<0.05$; **$P<0.01$; ***$P<0.001$

	Df	July 2002	August 2002
Light (L)	1	45.2***	39.9***
Nutrient (N)	1	2.05	0.03
Variety (V)	1	0.29	0.49
L x N	1	0.28	0.73
L x V	1	0.61	0.12
N x V	1	1.95	0.83
L x N x V	1	0.57	0.00
Error	24		

Table 8. Photosynthesis rate [μ CO_2 m^{-2} s^{-1}] (mean $\pm$ se; n=16) in two varieties of *B. curtipendula* under treatments with contrasting levels of light and nutrient availability.

	Photosynthesis rate [μmol CO_2 m^{-2} s^{-1}]	
	July 2002	August 2002
Full sun	33.7 $\pm$ 1.7	29.8 $\pm$ 1.6
Shade	17.1 $\pm$ 1.8	15.3 $\pm$ 1.6
P	*0.001*	*0.001*
Nutrient availability		
High	27.2 $\pm$ 1.8	22.4 $\pm$ 1.6
Low	23.6 $\pm$ 1.7	22.8 $\pm$ 1.6
P	*0.2*	*0.9*
Variety		
B.c. var. *caespitosa*	26.1 $\pm$ 1.8	21.8 $\pm$ 1.6
B.c. var. *curtipendula*	24.8 $\pm$ 1.7	23.4 $\pm$ 1.6
P	*0.6*	*0.5*

Biomass production

Root biomass production was comparable in the two *B. curtipendula* varieties (*P*= 0.218) and both varieties responded similarly to variation in light and nutrient availability (Table 9 and 10). The varieties did, however, differ with respect to shoot and total biomass production. Plants of *Var.* var. *caespitosa* produced significantly greater shoot biomass (*P*=0.001) and more tillers (*P*=0.06) than var. *curtipendula*.

In general, plant performance was best in the high light / high nutrient combination and poorest in the low light / high nutrient setting. In low nutrient environment, plant performance was similar regardless of light levels (Figure 11). No significant interactions between varieties and light and nutrient availability or defoliation

factors in final tiller number, shoot, root and total biomass suggested the two varieties have the same type of response to any of the treatments applied. However, interactions variety x treatment were all significant for reproductive biomass implying that light and nutrient availability and defoliation have different impact in the reproductive output in the two varieties (Table 10, Figure 11d).

Significant interactions ($P<0.05$) suggested that varieties responded to treatments (light and nutrient availability and defoliation) changing the root to shoot ratio but in a different rate. When growing in full sun, the root to shoot ratio of the two varieties increased in low nutrient setting. When growing in the shade, the var. *curtipendula* had similar root to shoot ratio when in low or high nutrient conditions but contrary to expectations, the var. *caespitosa* increased the root to shoot ratio with high nutrient availability (Figure 11f). Rhizomes were produced only in var. *curtipendula*, regardless of treatment. Interactions between factors were significant. Defoliation differently reduced rhizome production whether in high or low nutrient availability treatments. Opposite response were observed in the shade: while rhizome production decreased with low nutrients in plants growing in full sun, it increased with low nutrient in the shade. Total belowground biomass production (roots for var. *caespitosa* and roots plus rhizomes for var. *curtipendula*) was then higher in var. *curtipendula* given that the two varieties produced comparable root biomass (Figure 11 c).

Bouteloua curtipendula var. *curtipendula* had a smaller amount of biomass allocated to reproductive structures than var. *caespitosa* in all treatments (Figure 11d). A complete set of significant interactions between factors suggested different changes in the pattern of allocation to reproductive structures related to changes in the environmental conditions. Both var. *caespitosa* and var. *curtipendula* showed a decrease in reproductive biomass when reducing light or nutrients and when plants were defoliated; although to a greater extent in the caespitose variety. The rhizomatous variety showed a small decrease in reproductive biomass with lowering resource availability or when plants were defoliated.

Considering the entire below and above biomass production in the two varieties, var. *curtipendula* had a higher investment in underground structures (root and rhizome biomass) while var. *caespitosa* allocated more to aerial parts (shoot and reproductive biomass). The below to aboveground biomass ratio showed minor changes in var. *caespitosa*. However, in var. *curtipendula* the ratio was greater in low nutrient settings and showed a reduction with defoliation in all conditions (Figure 11 g). Plants growing in high or low nutrient conditions had a different response to changes in light availability in both varieties: they decreased the reproductive biomass in the shade only in high nutrient conditions.

Table 9. Shoot, root, rhizome and total biomass and final tiller number of *B. curtipendula* varieties (mean ± SE) in response to light and nutrient availability and defoliation.

	Biomass (g / plant)				Final tiller number
	Shoot	Root	Rhizome	Total	
Var. *caespitosa*	6.6 ± 0.4	0.8 ± 0.03	0	9.1 ± 0.5	35.0 ± 1.7
Var. *curtipendula*	5.0 ± 0.3	0.8 ± 0.03	1.1 ± 0.2	7.2 ± 0.5	30.8 ± 1.5
P	0.001	0.218		0.018	0.063

Table 10. Results from the analysis of covariance of two varieties of *B. curtipendula* in response to light, nutrient and defoliation treatments. Values are Type III *F*-test. The covariate was initial tiller number. The degrees of freedom of the error term are included. Transformation did not improve normality; results are shown on untransformed data. *$P<0.05$; **$P<0.01$; ***$P<0.001$

	Final tiller #	Shoot biomass	Root biomass	Rhizome biomass	Reprod. biomass	Total biomass	R/S ratio	B/A ratio
Covariate	92.3***	65***	95***		27.4***	66.9***		
Light (L)	157***	102***	168***	46.8***	61.5***	90.7***	0.6	0.02
Nutrient (N)	23.7***	23***	22***	6.2*	21.6***	21.8***	0.3	7.**
Defoliation (D)	20.3***	26***	53***	20***	33.2***	26***	5.5*	9.6**
Variety (V)	3.5	11**	1.5		43.9***	5.6*	1.2	203***
L x N	146***	127***	97***	48.4***	76***	102***	43***	8.0**
L x D	3.4	8.8**	15***	5.7*	18.2***	10.8**	1.9	0.6
N x D	5.7*	9.7**	9.8**	6.7*	13***	10.8**	0.3	0.1
L x N x D	6.2*	12.3**	10.5*	2.4	17.7***	12.5***	0.2	0.3
L x V	0.04	1.3	0.7		7.5**	0.6	8.2**	3.9*
N x V	1.6	0.04	0.8		2.3	0.01	6.4*	13.6***
D x V	0.01	0.9	0.6		8.0**	0.4	0.06	1.8
L x N x V	1.1	3.7	0.3		9.0**	2.8	2.6	4.1*
L x D x V	0.6	0.09	0.2		1.1	0.3	1.8	0.4
N x D x V	0.05	0.5	0.2		2.4	1.1	0.2	0.1
L x N x D x V	0.3	2.3	0.3		5.1*	3.1	0.2	0.3
Df error	430	444	430	232	476	476	443	443
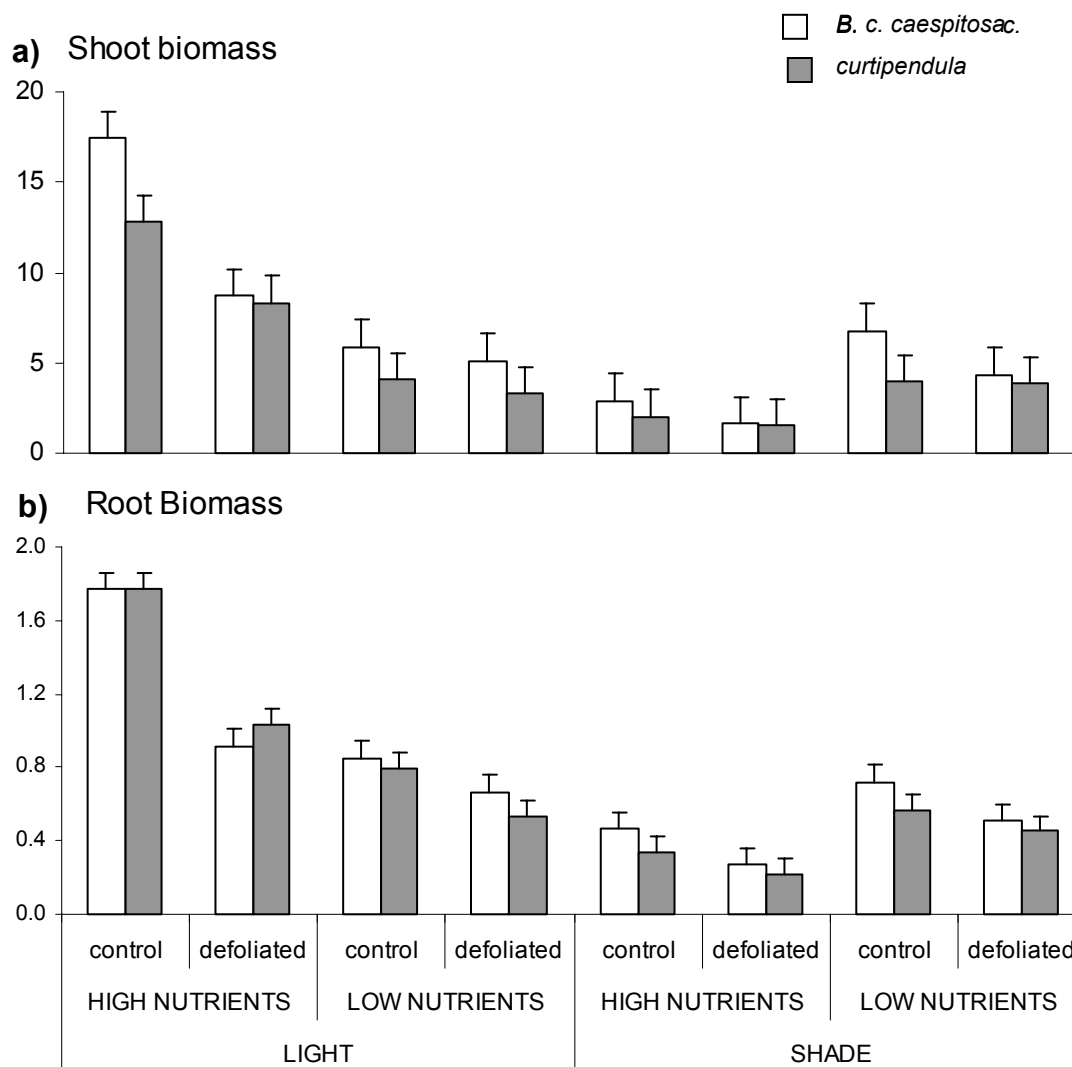
Figure 11. Biomass allocation in two varieties of *B. curtipendula* in response to a combination of light and nutrient availability and defoliation. Values are estimated marginal means + SE (n=32) evaluated at covariate initial tiller number=3.86. a) shoot biomass, b) root biomass, c) final tiller number, d) reproductive biomass, e) total biomass, f) root to shoot ratio, g) total belowground biomass and h) below to aboveground biomass ratio. ☐ var. *caespitosa*, ■ var. *curtipendula.*

Figure 11. Continued

f) Root to shoot ratio

g) Total belowground biomass

h) Belowground to aboveground biomass ratio

B. c. caespitosa
B. c. curtipendula

control   defoliated   control   defoliated   control   defoliated   control   defoliated
HIGH NUTRIENTS   LOW NUTRIENTS   HIGH NUTRIENTS   LOW NUTRIENTS
LIGHT   SHADE
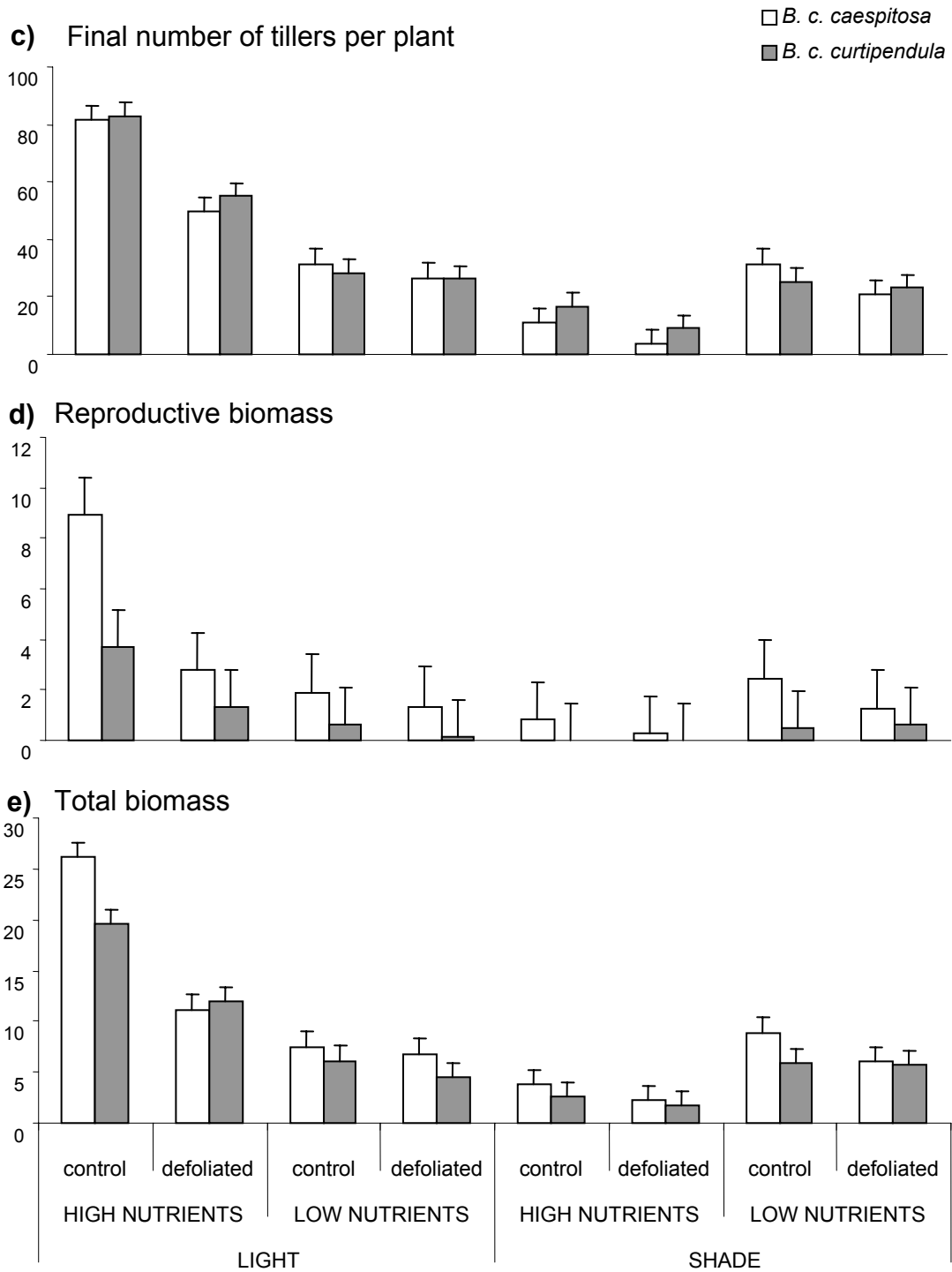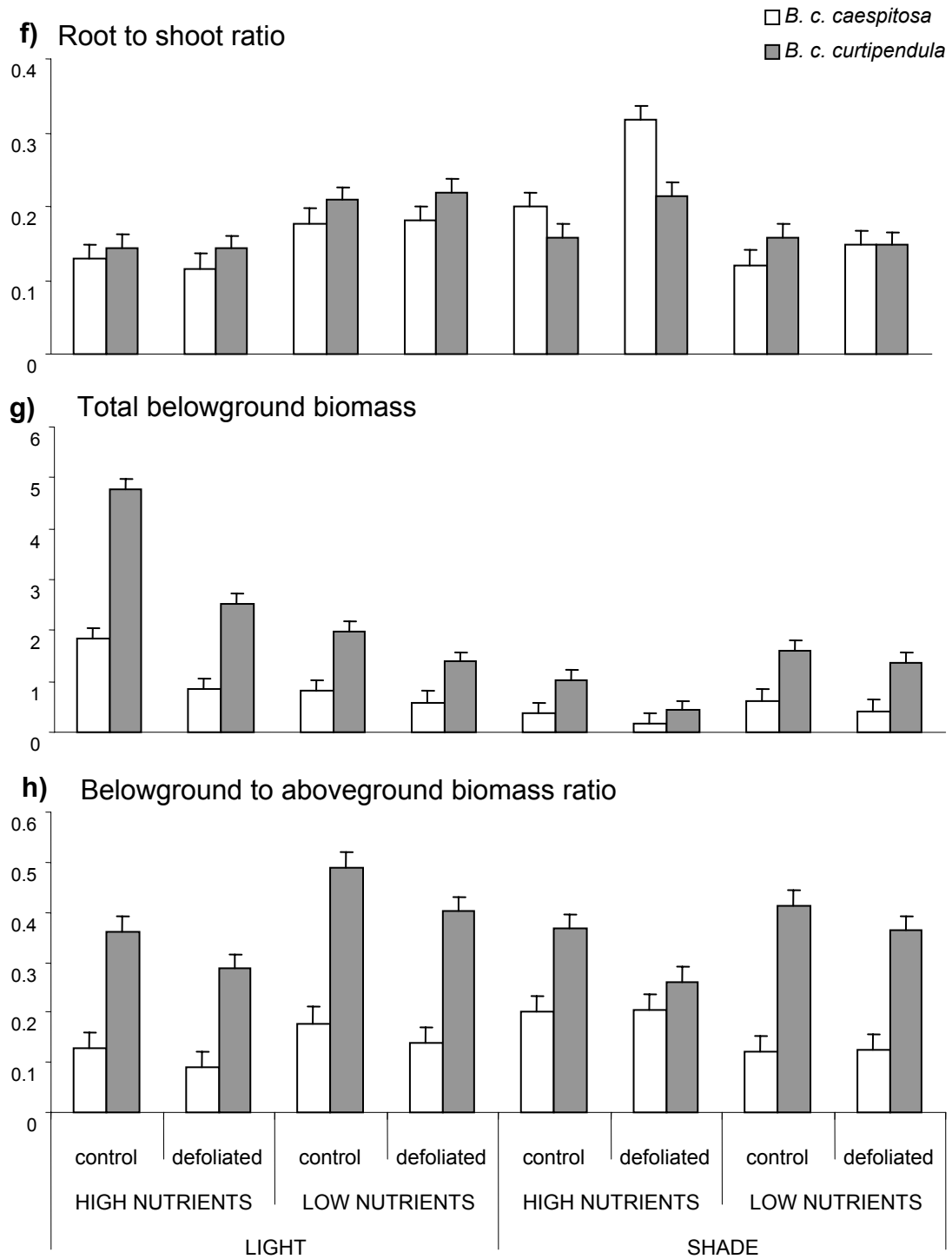
Figure 11. Continued

Tiller demography

Tiller recruitment and mortality was significantly different for the two growth-forms of *B. curtipendula*, but the two varieties responded similarly to alterations in light and nutrient levels and to defoliation, as indicated by general lack of significant interactions among these terms (Table 11). *Bouteloua curtipendula* var. *caespitosa* produced more tillers var. *curtipendula* in August ($P= 0.003$). Defoliation had no significant effect on tiller recruitment. A three-way interaction (L x N x V) was significant in July. More tillers were recruited in light-high nutrient conditions, although var. *curtipendul*a produced comparatively few in this setting (Figure 12 a). In July, var. *caespitosa* had more tillers recruited in shade- low nutrient than var. *curtipendula,* but a similar number in August (Figure 12 a, b).

B. curtipendula var. *caespitosa* produced more tillers in August than var. *curtipendula* but also had higher tiller mortality the same month (Figure 12 b, c). Fewer tillers were recruited in defoliated plants of the two varieties in August. The rate of tiller replacement showed significant V x L and V x D interactions. Variety *caespitosa* tiller replacement rate was relatively higher in light-low nutrient conditions, particularly when defoliated; var. *curtipendula* had relatively higher replacement in shade-low nutrient in the absence of defoliation (Figure 12 d).

Table 11. Results of the factorial analysis of variance of tiller recruitment, mortality and replacement rate of two varieties of *Bouteloua curtipendula* under contrasting light and nutrient availability and defoliation treatments. * $P<0.05$; **$P<0.01$; ***$P<0.001$

	Rate			
	Tiller recruitment		Tiller mortality	Tiller replacement
	July	August	August	July-August
Light (L)	58***	18***	8.6**	0.9
Nutrient (N)	4.4*	1.7	6.3*	1.0
Defoliation (D)	1.9	7.1**	1.2	1.8
Variety (V)	8.4*	9.2**	9.5**	0.08
L x N	50***	29***	0.3	0.8
L x D	0.47	2.5	0.3	0.2
N x D	1.7	0.1	0.04	1.6
L x N x D	2.7	0.04	0.9	0.6
L x V	1.5	2.8	0.7	5.3*
N x V	0.04	2.4	0.3	0.3
L x N x V	4.0*	0.2	0.1	2.7
D x V	3.2	1.01	1.3	4.3*
L x D x V	0.7	0.008	1.0	1.4
N x D x V	2.5	1.01	0.007	0.6
L x N x D x V	1.7	0.000	3.0	0.002
Df error	455	438	440	452
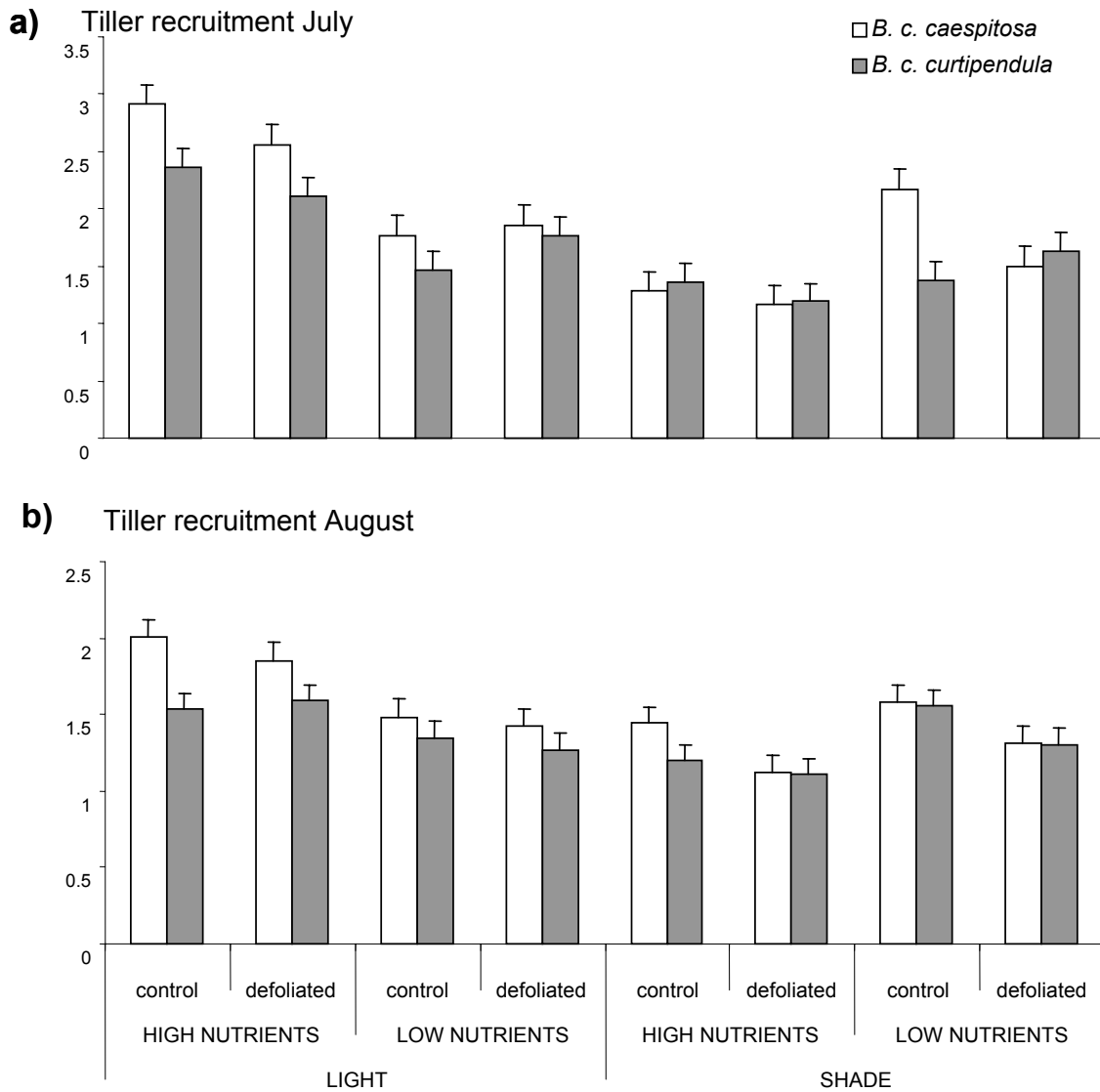
Figure 12. Tiller demography in two varieties of *Bouteloua curtipendula* under contrasting light and nutrient availability and defoliation treatments. Values are means + SE (N=32) [tiller / tiller / plant / month] a) tiller recruitment in July 2002, b) tiller recruitment in August 2002, c) tiller mortality and d) tiller replacement rate.
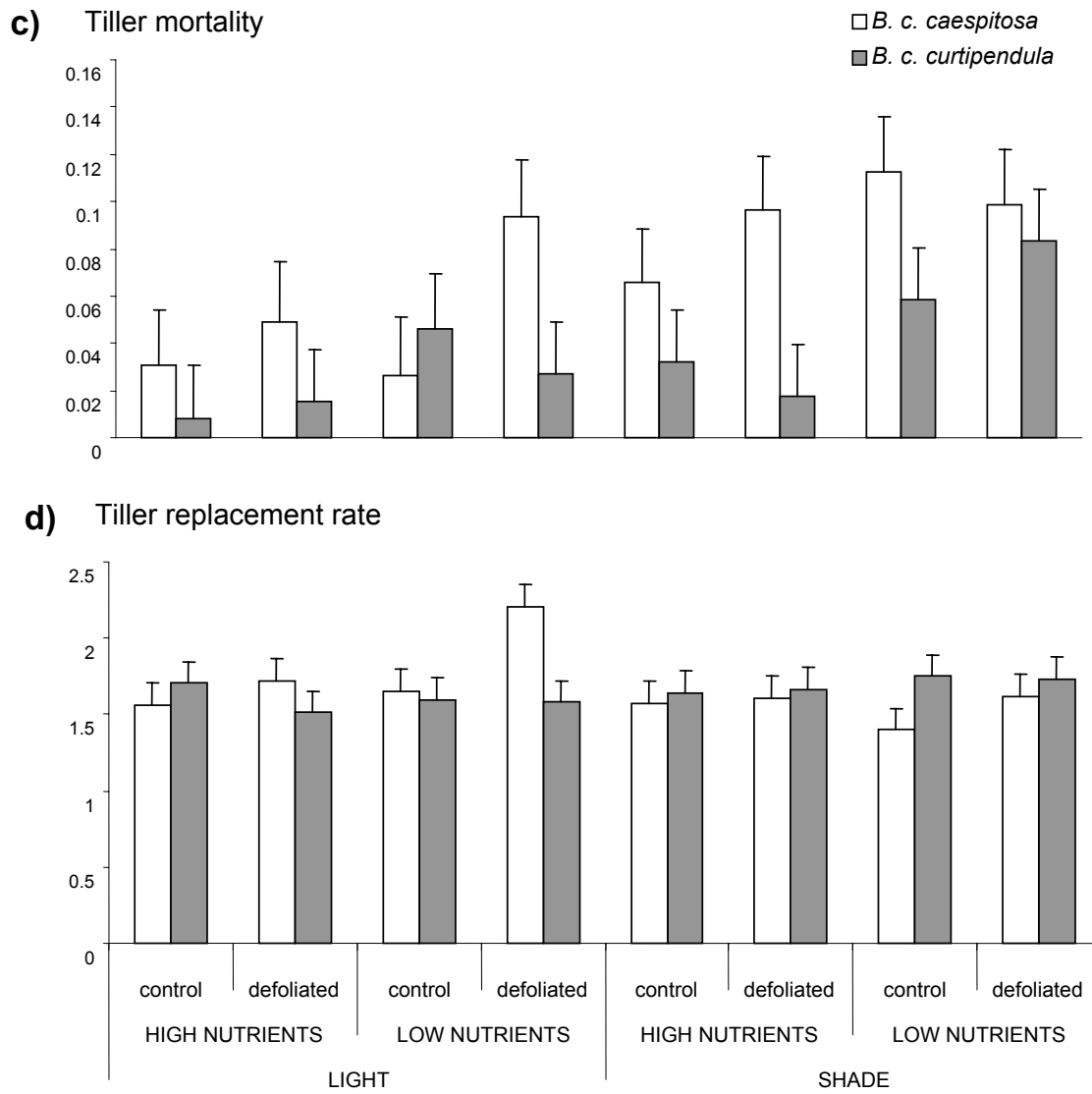
Figure 12. Continued.

Within variety genetic variation

Biomass production

Clones of *B. curtipendula* varieties exhibited significant genotypic variation when grown in contrasting light, nutrient and defoliation settings (Table 12). Clone performance was generally best in the high light-high nutrient-undefoliated settings and poorest in -low light-high nutrient-defoliation settings.

Genotype effects (G) were significant in var. *caespitosa* for all variables except root biomass. Significant light (L) x G and nutrient (N) x L x G interactions for reproductive biomass in *var. caespitosa* suggested genotypes of this variety differ in the way they allocate biomass to reproductive structures. Reaction norms of the eight genotypes of var. *caespitosa* are shown in Figure 13. Some genotypes were plastic (e.g., genotypes 4 and 6) and greatly increased their allocation to reproduction as the environmental conditions improved. Other genotypes (e.g., genotype 7) exhibited no changes in biomass allocated to reproduction with the variation in resource availability or defoliation. Variety *curtipendula* showed evidence of genotypic variation in shoot biomass, R/S and B/A biomass ratios but there was no evidence of differences in plasticity among genotypes for other morphometric variables (no significant genotype x treatment interactions).

Table 12. Factorial ANOVA results for final tiller number and biomass variables for clones (n=8) of *B. curtipendula* var. *caespitosa* and var. *curtipendula* genotypes in response to light and nutrient availability and defoliation.* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$

	Final tiller number				Shoot biomass				Root biomass			
	var. *caespitosa*		var. *curtipendula*		var. *caespitosa*		var. *curtipendula*		var. *caespitosa*		var. *curtipendula*	
	df	F	df	F	df	F	df	F	df	F	df	F
Covariate	1	26***	1	30***	1	26.5***	1	15***	1	47***	1	15***
Light (L)	1	49***	1	87***	1	289***	1	83***	1	44***	1	114***
Nutrient (N)	1	5.2*	1	18***	1	4.4*	1	25***	1	6.0*	1	18***
Defoliation (D)	1	6.7*	1	7.6**	1	11**	1	13***	1	13**	1	30***
Genotype (G)	7	2.1*	7	1.3	7	4.4***	7	2.1*	7	1.59	7	1.99
L x N	1	50***	1	75***	1	32***	1	83***	1	30***	1	62***
L x D	1	1.0	1	4.1	1	2.6	1	6.0*	1	1.2	1	10**
N x D	1	1.6	1	3.8	1	5.0*	1	5.4*	1	3.1	1	5.1*
L x N x D	1	2.1	1	3.0	1	5.9*	1	2.9	1	2.3	1	4.3
L x G	7	0.81	7	1.2	7	1.8	7	1.5	7	1.0	7	2.0
N x G	7	1.1	7	0.4	7	0.6	7	0.3	7	1.4	7	0.7
L x N x G	7	1.4	7	1.4	7	1.5	7	0.9	7	1.5	7	1.3
D x G	7	1.0	7	0.6	7	0.7	7	0.4	7	1.1	7	0.7
L x D x G	7	0.5	7	0.4	7	0.5	7	0.4	7	0.7	7	0.7
N x D x G	7	0.4	7	0.9	7	0.6	7	1.0	7	0.7	7	1.5
LxNxDxG	6	0.2	7	0.5	7	0.5	7	0.9	6	0.2	7	0.6
	139		179		149		182		139		179	

Table 12. Continued.

	Reproductive biomass				R / S ratio				B / A ratio			
	var. *caespitosa*		var. *curtipendula*		var. *caespitosa*		var. *curtipendula*		var. *caespitosa*		var. *curtipendula*	
	df	F	df	F	df	F	df	F	df	F	df	F
Covariate	1	16***	1	0.03								
Light (L)	1	37***	1	47***	1	6.1*	1	2.6	1	8.7**	1	0.1
Nutrients (N)	1	11**	1	22***	1	1.6	1	6.3*	1	2.4	1	16***
Defoliation (D)	1	24***	1	18***	1	2.8	1	3.8	1	0.2	1	5.1*
Genotype (D)	7	6.0***	7	1.7	7	2.8**	7	2.1*	7	2.7*	7	5.6***
L x N	1	45***	1	58***	1	19***	1	16***	1	22***	1	4.6*
L x D	1	8.5**	1	14***	1	2.2	1	0.02	1	2.5	1	0.4
N x D	1	8.6**	1	11**	1	0.04	1	0.6	1	0.06	1	0.1
L x N x D	1	14***	1	8.1**	1	0.1	1	0.6	1	0.7	1	0.4
L x G	7	2.4*	7	1.4	7	0.3	7	0.9	7	0.3	7	0.3
N x G	7	1.2	7	0.6	7	0.7	7	1.1	7	0.7	7	1.1
L x N x G	7	2.6*	7	0.9	7	1.4	7	1.4	7	1.4	7	1.5
D x G	7	1.9	7	0.7	7	1.4	7	0.6	7	1.3	7	0.7
L x D x G	7	1.2	7	1.0	7	0.6	7	0.7	7	0.8	7	0.3
N x D x G	7	0.7	7	0.6	7	0.2	7	1.1	7	0.3	7	0.6
LxNxDxG	7	0.6	7	0.5	7	0.6	7	0.8	7	0.5	7	0.9
	175		188		148		183		148		183	
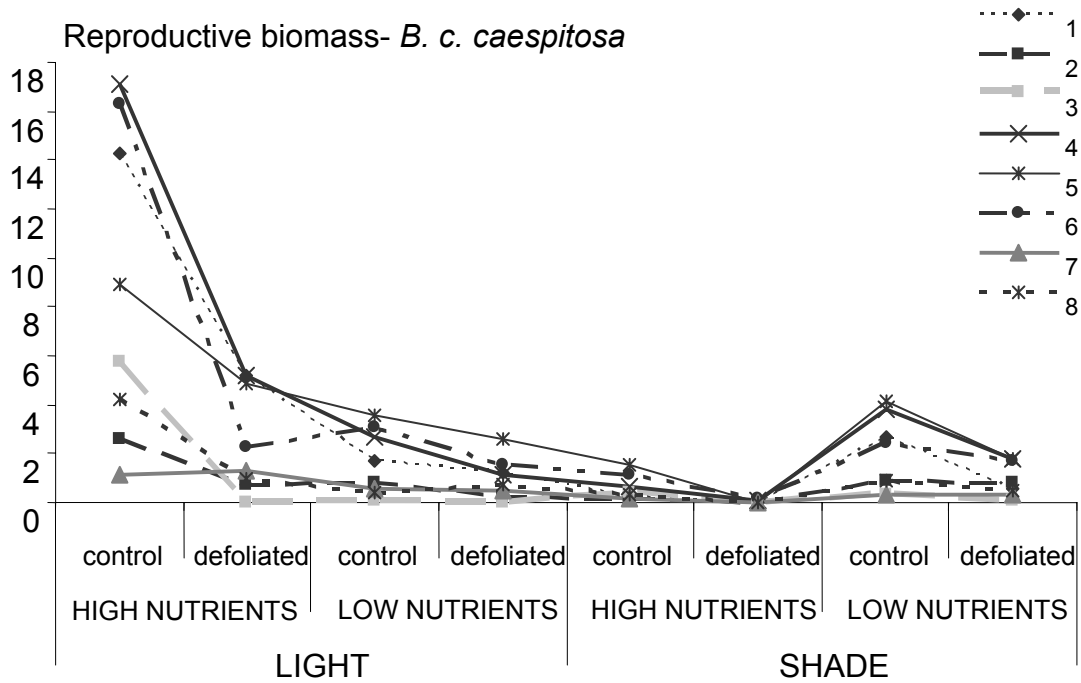
Figure 13. Reaction norms for reproductive biomass (g/plant) of eight genotypes of var. *caespitosa* illustrating significant genotype x treatment interactions (Table 12). Each line connects the mean (n=4) of a given genotype in a given treatment.

Tiller demography

   Bouteloua curtipendula varieties showed some evidence of genetic variation in the rate of tiller recruitment among genotypes (Table 13). Genotypes of var. *caespitosa* differed significantly with respect to tiller recruitment in July but not in August, whereas var. *curtipendula* genotypes differed significantly in August but not July. The varieties differed in the amplitude of tiller recruitment response to treatments in July and August: genotypes of var. *caespitosa* ranged from 0.8 (G3) to 2.6 (G7) tillers/tiller/plant/month, whereas genotypes of var. *curtipendula* had a narrower range (1.6 (G1) to 2.5 (G8)) (Table 14). Similar values were recorded in August. There was no significant genotype x treatment interaction. No genotype effect was detected for tiller mortality in either variety. The two varieties also exhibited significant genotypic differences in rates of tiller replacement (Table 13), ranging from a mean of 1.6 (G6) to 3.1 (G7) tiller/tiller/plant/month for var. *caespitosa* (not shown). The amplitude of the response in genotypes of var. *curtipendula* was narrower than for var. *caespitosa*. In addition, significant interactions (L x G; D x G and L x D x G) in var. *caespitosa* suggested genetic variation in the way the genotypes respond to light availability and defoliation (Figure 14a). For example, in var. *caespitosa* G7, tiller replacement following defoliation in a high light environment was ca. 3X higher than that of non-defoliated plants whereas when shaded, G7 did not change in replacement in response to defoliation. In contrast to G7, G3 was unresponsive to treatments. Genotype x treatment interactions (L x N x G; D x G; N x D x G and L x N x D x G) were also significant in var. *curtipendula* clones (Figure 14b). Genotypes differed in the plasticity in tiller replacement rate in response to light and nutrient availability and in response to defoliation, but the amplitude of the responses was dampened relative to var. *caespitosa.*

Table 13. Factorial ANOVA results for tiller demography variables in clones (n=8) of *B. curtipendula* var. *caespitosa* (caespit.)and. var *curtipendula* (curtipend.) genotypes in response to light and nutrient availability and defoliation. * = *P<0.05*; ** = *P<0.01*; *** = *P<0.001*

	Rate							
	Tiller recruitment				Tiller mortality		Tiller replacement	
	July		August		August		July-August	
	caespit.	*curtipend.*	*caespit.*	*curtipend.*	*caespit.*	*curtipend.*	*caespit.*	*curtipend.*
	F	*F*	*F*	*F*	*F*	*F*	*F*	*F*
Light	26***	40.8*	17***	8.7**	4.6*	3.6	0.7	1.99
Nutrient	1.7	5.3*	3.05	0.02	1.2	9.1**	0.3	0.8
Defoliation	2.4	0.2	3.9	3.9*	1.3	0.02	0.4	0.01
Genotype	4.9***	0.8	1.3	2.1*	0.5	0.8	9***	5.3***
L x N	23***	24***	11**	25***	1.3	0.6	1.5*	4.2*
L x D	0.5	0.005	0.4	1.7	0.6	0.24	12**	0.4
N x D	0.05	6.6*	0.1	1.7	0.09	0.03	1.7	0.2
L x N x D	3.3	0.03	0.04	0.09	0.3	1.8	0.5	0.02
L x G	1.6	1.02	1.2	0.7	0.6	1.3	2.5*	1.1
N x G	1.0	0.7	0.6	0.6	0.5	0.2	0.4	0.9
L x N x G	1.2	0.5	0.9	0.9	0.4	1.9	1.6	2.2*
D x G	0.7	1.2	1.3	1.3	1.4	0.8	4***	3**
L x D x G	0.8	1.1	1.1	1.6	0.6	2.5*	2.7*	1.3
N x D x G	0.7	1.9	1.2	1.3	0.3	1.9	0.7	3.1**
LxNxDxG	0.7	0.5	1.1	1.6	0.5	1.0	0.9	2.9**
df error	146				148		185	

Table 14. Mean ($\pm$ SE; n=4) tiller recruitment rate (tiller / tiller / plant / month) in genotypes of *B. curtipendula* var. *caespitosa* and var. *curtipendula* in July and August 2002 averaged across a combination of light and nutrient availability and defoliation treatments (none of the interactions genotype (G) x treatment was significant).

	B. curtipendula var. *caespitosa*							
	Genotype 1	Genotype 2	Genotype 3	Genotype 4	Genotype 5	Genotype 6	Genotype 7	Genotype 8
July	1.8 (0.78)	1.9 (0.66)	0.8 (0.39)	2.4 (0.91)	2.5 (0.58)	2.6 (0.57)	2.6 (1.37)	2.4 (0.60)
August	1.3 (0.51)	1.8 (0.43)	1.5 (0.28)	1.7 (0.38)	1.9 (0.30)	2.0 (0.27)	2.3 (0.77)	2.5 (0.81)

	B. curtipendula var. *curtipendula*							
	Genotype 1	Genotype 2	Genotype 3	Genotype 4	Genotype 5	Genotype 6	Genotype 7	Genotype 8
July	1.6 (0.74)	1.7 (0.47)	1.9 (0.63)	1.9 (0.36)	2.1 (0.52)	2.1 (0.52)	2.1 (0.34)	2.5 (0.50)
August	1.5 (0.49)	1.5 (0.20)	1.4 (0.16)	1.7 (0.30)	1.8 (0.21)	1.9 (0.34)	1.9 (0.21)	2.1 (0.16)
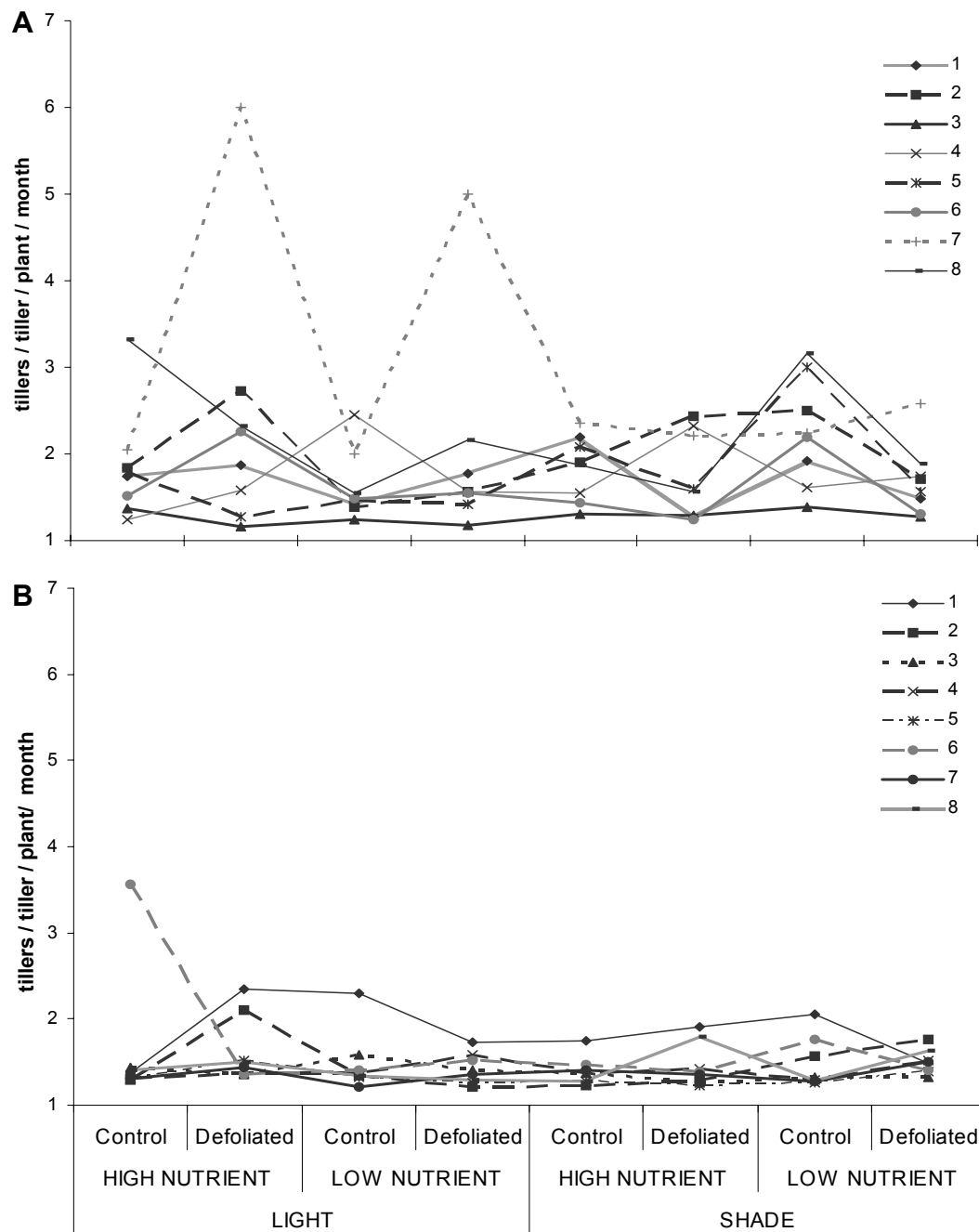
Figure 14. Tiller replacement ratio reaction norms for eight genotypes of two varieties of *B. curtipendula* (a) var. *caespitosa* and (b) var. *curtipendula*. Each line connects the means (n=4) of a given genotype across treatments.

Discussion

Ecophysiology

The two varieties of *B. curtipendula* exhibited difference in Ψ in different nutrient settings along the day (pre-dawn and mid-afternoon). However, the interactions of resource availability and time of the day had different effects depending on the month of the growing season. The difference could be related to the accumulated rainfall per month at the study site (54.3 mm in June, 135.3 mm in July compared to only 16.3 mm in August). A low amount of rainfall in August may have accentuated the conditions increasing the difference between settings (resulting from the combination of two levels of light and nutrient availability) shown in the significant Light x Time of Day x Month and Nutrient x Time of Day x Month interactions Table 8). This dissimilarity in conditions might have manifested the difference between varieties. When the amount of precipitation was higher (e.g., in July), relative differences between varieties may be consequence of the osmotic potential added to the soil by nutrient concentration (Lambers et al. 1998). No evidence was found to support H2 as the two varieties of *B. curtipendula* had comparable photosynthetic rates in all treatments.

Biomass production

Varieties of *B. curtipendula* differed with respect to shoot biomass production but had comparable root biomass. Differences in tiller number were marginally significant (P= 0.063). The significant Variety x Treatments interactions for root/shoot ratios gives partial support to H3 (Table 5). Since competition for nutrients may play a role in species arrangement in resource poor environments (Rebele 2000) it was expected that if var. *caespitosa* was better adapted to sites with low nutrient availability, it would produce more roots in order to acquire more resources, whereas var. *curtipendula* would rely on the nutrients accumulated in the rhizomes (Dong and de Kroon 1994). Results showed that ratios increase in the two varieties in low compared to high nutrient conditions in high light settings but contrary to the expectation the rhizomatous root to shoot ratio was comparatively higher than the caespitose one (Figure

11f). One possible explanation for the relatively lower root to shoot ratio observed in var. *caespitosa* that still agrees with the idea that this variety acquires more nutrients, might be an increase in nutrient absorbing surface without a proportional increase in root biomass by increasing the specific root length (Olff et al. 1990) but root length was not measured in this study.

The observed increment in the root to shoot ratio in var. *caespitosa* growing in soils with higher nutrient content and shaded environments was also contrary to the expectations. The relative increase in root production in high nutrient conditions might be explained by a failure in the experiment settings. The two varieties had the poorest overall performance in shaded/high nutrient (under the oak motts) compared to all others treatment setting combinations. The unexpected increase in root to shoot ratio in var. *caespitosa* may suggest that although the nutrient content in soils associated with oak motts was higher than in the surrounding grassy areas, nutrient availability was in fact reduced because of competition with oaks. The fact that the soil was cleared before the experiment was set up, made the appropriate conditions for seed germination and the basal resprout of the oak trees, accentuating overall competition for resources.

Plants of var. *curtipendula* significantly increased rhizome production under high nutrient settings relative to low nutrient settings. According to plant foraging theory, conditions have to be sufficiently good to allow high growth rate to pay for the resource investment in clonal structures (de Kroon and Schieving 1990). Although it seemed contrary to this prediction, rhizome biomass decreased with increasing in nutrients under the shade. This is consistent with the notion that nutrient availability in oak mott soils was in fact low due to competition.

Plants of the two varieties of *B. curtipendula* exhibited a dissimilar pattern of allocation to reproductive biomass (i.e. significant Variety x Light, Variety x Defoliation and Variety x Light x Nutrients interactions). Nonetheless, there were certain similarities. Reproductive biomass was highest in the light/ high nutrient environment and it was reduced by defoliation in both varieties but to a different extent (more pronounced in the caespitose variety). The effect of defoliation suppressing reproduction

has been previously reported (Damhoureyeh and Hartnett 2002). The two varieties showed comparable biomass allocation to reproductive structures in low nutrient environments. The reduction in allocation to reproduction in low nutrient settings would correspond with a proposed trade-off between resource acquisition and reproductive allocation (Sugiyama and Bazzaz 1998). This trade-off is more likely to occur under low resource conditions *(Biere 1995)* because increases in allocation to organs to acquire limiting resources may result in a proportional decrease in the investment to reproductive structures (Sugiyama and Bazzaz 1998). Although number of seeds per culm and viability of the seeds produced were not quantified in this study, *B. curtipendula* has been referred as producing a fair amount of rather low viability seeds (Weaver 1968); while seeds are transient and not stored in the seed-bank (Kinucan and Smeins 1992). It could be inferred that the effects of resource limitations and disturbance (defoliation) would decrease the seed output and a decline in the species cover could be expected if such conditions are sustained for several years.

Comparing the two growth forms or varieties, var. *caespitosa* allocated more biomass to producing reproductive culms and eventually more seeds than var. *curtipendula*. If the caespitose form is better adapted to nutrient poor habitats then the production of tall stems would elevate reproductive structures thus increasing potential propagule dispersal distance as wind can take seeds further away from the mother plant (Craine et al. 2001). Alternatively, if the rhizomatous form is better adapted to higher levels of nutrients, rhizomes will provide an effective means of short distance reproduction as ramets will emerge in the vicinity of the mother plant. Then, production of new clones could be facilitated via a carbon subsidy from older parts of the plant through clonal integration (de Kroon et al. 1996). Relatively resource rich sites are expected to have higher levels of competition for light as the vegetation cover that the environment can held is greater than in resource poor sites. As new ramets are connected to the mother plant they could be resource subsidized and that would allow new propagules to emerge through existing canopies or litter layers under which seedlings are likely to perish (Craine et al. 2001).

Foraging theory states that resource availability is related to the pattern of clonal growth. Results from this study agree with a proposed trade-off between vegetative and reproductive growth when resources are limiting or due to a disturbance. The two varieties of *B. curtipendula* showed a comparable reduction of biomass allocated to reproductive structures in response to reduce nutrient and defoliation. Results from this study suggest that resource availability on the site is not only related to the pattern of clonal growth but also to forms of reproduction (seed production or vegetative by rhizomes) and dispersal of propagules. It could be speculated that difference in resources between sites could contribute to the reproductive success of a growth form at a site.

Genetic variation within varieties

Variation among genotypes in response to light and nutrient availability and defoliation was detected in the two varieties of *B. curtipendula*. The eight clones of var. *caespitosa* used in this experiment varied significantly in final tiller number, shoot, reproductive and total biomass and the B/A ratio in their response to treatments. Although eight genotypes is a relatively small sample of the entire populations on the study site, the significant effect of genotype identity on these traits suggests a genetic basis for phenotypic variation in response to resources availability (light and nutrients) and disturbance (defoliation) (Smith 1998). Similarly, the eight clones of var. *curtipendula* showed significant variation among genotypes in shoot biomass, R/S and B/A ratios. Genetic variation have been widely reported in several grass species (Carino and Daehler 1999, Carman and Briske 1985, Cheplick 1995, Detling and Painter 1983, Huff et al. 1998, Kotanen and Bergelson 2000, Smith 1998, Steinger et al. 1997). The existence of genetic variation among genotypes within varieties in life history traits leaves open the possibility of microevolution in populations in response to selection factors (Cheplick 1995, Miller and Fowler 1994, Smith 1998).

B. curtipendula var. *caespitosa* also showed significant interactions between genotypes and treatments in reproductive biomass suggesting there are differences among plants (genotypes) in the way they allocate resources to reproduction in response to availability in resources (Schmid 1992). Other studies have reported variation in

reaction norms among populations in the allocation to reproduction (Biere 1995, Macdonald and Chinnappa 1989, Miller and Fowler 1994). The observed variation among genotypes represents potential for evolutionary change within var. *caespitosa* in response to two important factors: light and nutrient. The overall response was an increase in reproduction with optimal conditions (i.e. light and nutrients availability). It can be speculated that plasticity in reproduction confers the ability to be opportunistic and increase the allocation to reproductive structures when resource rich patches are encountered (Biere 1995, Schmid and Weiner 1993, Stratton 1994).

The two varieties of *B. curtipendula* showed genotype x environment interactions in response to all treatments in the tiller replacement rate suggesting that, within the varieties, genotypes differ in the tiller replacement rate in response to resources availability and defoliation. For example, genotype 7 in var. *caespitosa* (dashed line in figure 14a) compared to other genotypes expressed a much higher rate of replacement of tiller in defoliated conditions under light availability whereas genotype 6 (same figure) has a relatively higher rate under shaded settings. The variation among genotypes was less pronounced in var. *curtipendula* but still genotypes differed in tiller replacement rate response to changes in resource availability or defoliation. Although variations could be supposed to be common as they are the material for evolutionary change, some studies have failed to detect them for various reasons. For example: (Kotanen and Bergelson (2000) proposed that the morphological variation in response to defoliation in *Bouteloua gracilis* may be masked when compared to genotypic differences; (Steinger et al. (1997) claimed that genetic variation in response to CO_2 in grassland species was swamped by large environmental variation.

Conclusions

Results from this study showed that the two varieties of *B. curtipendula* have similar performance within their zone of sympatry. Differences between varieties only arose in particular combinations of treatments for some of the variables measured. The factors used in this study do not help explain the differences in the distributional range of the varieties. However, there was evidence of a different pattern of allocation of

resources between varieties, particularly related to the proportion of biomass that was allocated to reproduction by seeds. In this study, the distribution of the varieties of *B. curtipendula* could be related to the energy devoted to reproduction by seeds, although limiting resources or defoliation equally affected this proportion in each variety. Genetic variation among genotypes within varieties for several life history traits suggested the possibility of micro evolutionary changes in each variety in response to environmental or disturbance factors.

CHAPTER IV

THE ROLE OF FIRE IN DETERMINING THE PATTERN OF

DISTRIBUTION OF THE TWO VARIETIES OF *BOUTELOUA*

CURTIPENDULA

Introduction

Fire directly affects plant growth, survival and reproduction and patterns of species distribution (Bond and van Wilgen 1996, Cohn and Bradstock 2000, Hobbs et al. 1991, Howe 1994, Whelan 1995). For fires to occur, several conditions must be met (Bond and van Wilgen 1996, Taylor 2003). One of these conditions is the availability of combustible biomass. Ecosystems vary substantially in their primary productivity and hence in their capacity to generate fuels. As a result, fire frequencies in deserts are typically regarded as low, whereas grasslands and savannas of more mesic climates can accumulate fuel and burn at high frequencies if they are not subjected to heavy grazing (Hobbs et al. 1991).

The distributional range of *Bouteloua curtipendula* encompasses mesic regions where fire is regarded as a common disturbance and more xeric regions where fire is regarded as infrequent. Interestingly, the distributions of the two varieties of *B. curtipendula* (see Introduction) are distinctly associated with areas with different flammability (Figure 15). The distribution of var. *caespitosa* occurs primarily in regions mapped as "less flammable" whereas var. *curtipendula* is distributed over the region regarded as "flammable". If fire was an evolutionary force delimiting the distribution of these varieties, are there specific traits that can be considered adaptations to fire? If present, are these characters present in plants of the two varieties in their zone of sympatry?

The goal of this study was to investigate the potential role of fire in determining the local pattern of distribution of the two varieties of *B. curtipendula* in their zone of
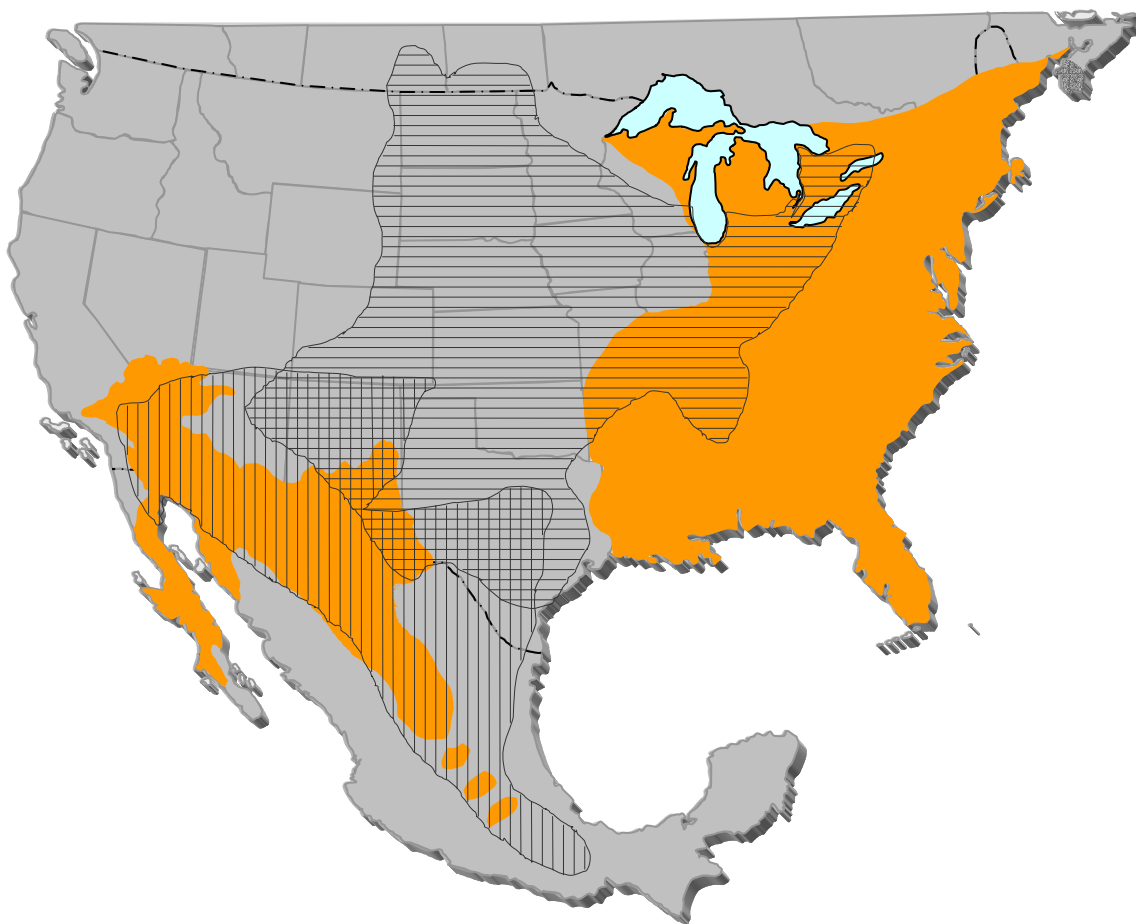
Figure 15. Distributions of *B. curtipendula* varieties in relation to vegetation flammability a in North America (from (Gould and Kapadia 1964) and (Bond and van Wilgen 1996).

sympatry and to ascertain the response of the two *B. curtipendula* growth forms to fire. In working towards this goal, the following objectives and hypotheses were addressed:

Objective 1: To determine whether the two varieties of *B. curtipendula* differ in their susceptibility to fire.

H1) *Bouteloua curtipendula* var. *caespitosa* plants will experience higher temperatures than the plants of var. *curtipendula* even if burning in the same conditions with equal fuel load. The compact architecture of var. *caespitosa* will develop higher temperatures than plants of var. *curtipendula* with a spreading architecture. As a result, var. *caespitosa* will experience lower regeneration and survival than var. *curtipendula* following fire.

Rationale: There is a positive correlation between fuel load per unit area and the maximum temperature achieved; plants with high surface area per volume have higher rates of moisture loss during burning, thus contributing to higher temperatures (Stinson and Wright 1969). Therefore, more leaves per unit volume in var. *caespitosa* (Chapter II) would be expected to increase both the surface area and the amount of fuel per unit volume. Consequently burning should generate higher temperatures and hence more adversely affect var. *caespitosa* than var. *curtipendula*.

H2) var. *caespitosa* plants will be more susceptible to fire than the plants of var. *curtipendula* under similar conditions.

Rationale: Among the properties that make plants susceptible to fire, the production and/or retention of dead material is one of the most important (Bond and van Wilgen 1996). If plants of var. *caespitosa* accumulate more dead material than plants of var. *curtipendula*, then, plants of var. *caespitosa* will burn at higher temperatures than plants of var. *curtipendula*.

H3) for a given fire intensity, plants of var. *caespitosa* will have a slower recovery and greater mortality s than plants of var. *curtipendula*.

Rationale: Buds in the rhizomes of plants of var. *curtipendula* that facilitate rapid re-growth following fire are insulated by soil and do not experience elevated temperatures. In contrast, a higher proportion of buds in var. *caespitosa* are nearer or above ground and hence more vulnerable to fire.

Objective 2- Compare the response to fire of plants of the two varieties of *B. curtipendula* on pastures with different prescribed burning histories (no fire, summer fire, winter fire).

> H4) Fires occurring in systems that have not recently been burned will generate higher temperatures than fires on sites which have recently burned. As a result, recovery of plants on frequently burned sites will exceed that of plants on sites where burnings are less frequent.

Rationale: As fire frequency decreases, fire intensity increases due to greater litter accumulation. Sites that have been recently burned should have less litter and hence burn at lower intensities. The intensity of the fire and the temperatures developed in sites with lower fire frequency are higher than the ones achieved in sites more frequently burned. Thus, high fire intensity can delay recover because it causes death of a higher proportion of plant tissue.

To pursue these objectives and hypotheses, an experiment was devised using plants of the two varieties of *B. curtipendula* from pastures having different fire histories. Plant response to fire intensity was simulated by applying different amounts of artificial fuels and monitoring post-fire recovery.

Methods

Study sites

Experiments were conducted on the Texas Agricultural Experiment Station (31° N; 100° W) located near Sonora, Texas in the Edwards Plateau. Elevation at the station is ca. 730 m. Topography is rugged, with slopes ranging from 0 to 8 %. Dominant soils are Tarrant stony clays of the thermic family of Lithic Haplustolls. Geologically, most of the Edwards Plateau is cretaceous limestone rock. Average annual precipitation (568 mm) is highly variable, ranging from 156 mm to 1,054 mm (Thurow et al. 1988). Annual rainfall is bimodally distributed with peaks in the spring and the autumn; seasonal and annual droughts are common. The growing season is about 240 days. Temperatures average 30°C in July and 9°C in January (Station records).

The area is a mixture of savanna grasslands and woodlands ((Smeins and Merril 1988). The primary woody plants include *Quercus virginiana* Mill. var. *virginiana*, *Q. pungens* Liebm. var. *vaseyana* (Buckl.) C. H. Mull., *Junisperus ashei* Buchh. and *J. pinchotti* Sudw. These trees often occur in discrete clusters or 'mottes' giving the site a savanna parkland physiognomy. Mid-height grasses include *Nassella leucotricha* (Trin. & Rupr.) R. W. Pohl, *Eriochloa sericea* (Scheele) Munro, *Aristida* and the two varieties of *Bouteloua curtipendula.* The most common short grass is *Hilaria belangeri* (Steud.) Nash. Natural plant communities have changed significantly under the impact of continuous grazing by livestock and elimination of fire (Fuhlendorf and Smeins 1997).

Plant response to fire intensity

Effects of fire intensity on the two *B. curtipendula* varieties were experimentally assessed on plants in three pastures differing in their fire histories: control (not previously burned), summer (August 1999) burn and winter (March 1999) burn. A range of fire intensities was achieved using shredded paper (density 70 g/m^2 cut in longitudinal strips 7 mm width) to generate different fuel loadings (45 g and 100 g for the mild and extreme burning treatments, respectively). Unburned plants of each variety at each site served as controls. To enable automated, simultaneous recording of temperatures, plants

were chosen such that at least 3 plants of each variety occurred within a 10 m radius. One week before burning, the number of tillers was recorded on each of the target plants. To standardize burning treatments, all other plants and litter within 1m of target plants were removed. Plants were protected from grazing with a cylindrical wire cages (70 cm tall; 35 cm diameter; 0.7 cm mesh) during the experiment.

Plants were individually burned in combustion chambers consisting of a perforated, open-ended 55-gal drum (Wright and Klemmedson 1965). Dried, shredded paper was placed uniformly around each plant just before the burning. Six barrels were used simultaneously and the process was repeated 10 times in each of the three pastures totalizing 180 plants. Paper was ignited with a lighter. Burning occurred between 10:00 and 17:30 h on August 10 to 12, 2002. Air temperature during the 3 days period averaged 36.2 ºC and relative humidity 30.6 %. The maximum wind speed recorded was 3 m/s. Material from other plants of each variety in the vicinity of the burning treatments were collected, dried and weighed to quantify relative moisture content at the time of the burning (Table 15).

Table 15. Mean (+ SE) relative moisture content in material of the varieties of *B. curtipendula* collected at the time of the burnings.

Site Fire Histories	var. *caespitosa*	var. *curtipendula*
Control	50.7 ±7.6	49.7 ± 7.5
Summer burned	82.3 ± 17.8	83.2 ± 4.0
Winter burned	59.9 ± 16.2	71.9 ± 5.5

Fire temperatures were monitored at 2 seconds intervals with type K thermocouples (chromel-alumel) attached to a datalogger (Model CR21X, Campbell Scientific Inc.). Thermocouples were paired, one at the base of the plant and the other 1.5 cm under the plant. After accounting for equipment malfunctions, temperature data was obtained for 120 plants (18 plants in the control pasture, 54 in the summer burn pasture; and 48 in the winter burn pasture).

In October 2003, 14 months after burning, plants were harvested and soil was washed from the roots. Plants were dried at 60° C, separated into shoots, roots, and rhizomes and weighed. Reproductive culms were counted, then cut below the second internode, and weighed. The number of vegetative tillers was recorded for each plant. From these measurements two additional variables were calculated: biomass per tiller and the proportion of culms per tiller (number of culms/number of final number of tillers). Root to vegetative shoot ratios and below (roots + rhizomes) to aboveground biomass ratios were also calculated.

Statistical analyses

Factorial analysis of variance (SPSS 11.0 for Windows) was used to determine the effects of fire intensity and fire history on the two varieties of *B. curtipendula.* To adjust for initial variation in plant size, the number of tillers on plants prior to burning was used as a covariate. Equality of variance was checked by studying residuals plots. A Kolmogorov-Smirnov test was used to test normality. To meet normality assumptions, final tiller number was ln-transformed; shoot biomass was log-transformed and root, rhizome and total biomass and culm number were square-root transformed prior analyses. Transformation did not improve normality for some variables. Those instances are noted in the results and the outcomes of untransformed analyses are reported. Estimated marginal means and their associated SEs were informed. When the covariate was significant, means were adjusted for the covariate. For transformed variables, non-transformed means and SEs are reported.

Results

Temperatures measured during burnings (H1)

Combustion of the two varieties of *B. curtipendula* generated statistically comparable maximum temperatures, both at the base of the plant (Table 16; P = 0.44) and at the 1.5 cm depth (P= 0.53). Average maximum temperatures at the base of the plants were also similar (P = 0.913) among pastures with different burning histories (Table 17). The temperatures were significantly different (P < 0.001) when using different amounts of fuel loads. Average maximum temperatures 1.5 cm belowground were comparable among burning treatments (P = 0.567) (Table 16). Belowground temperatures did not differ among pastures as well (P = 0.139). Interactions were never significant and are not reported.

According to (Wright 1970), temperatures between 68.3 and 73.9°C will kill grass plant tissue after 3.4 minutes of exposure at these temperatures. Experimental burnings in this study recorded temperatures for periods of 10 minutes on average. The length of time plants of var. *caespitosa* experienced temperatures beyond 70°C was significantly longer than the length time recorded in var. *curtipendula* in the same conditions (*P*<0.01) (Figure 16). Plants from pastures with different burning histories significantly differed in the length of time the temperature recordings were over 70°C (*P*<0.05). Plants from the control pasture experienced killing temperatures for periods of 180 ± 27 seconds on average while plants from the pastures that were burned previously in winter and summer experienced temperatures over 70°C during 87 ± 17 and 121 ± 16 seconds respectively (Figure 16). Length of time with temperatures over 70°C was not significantly different between fuel loading treatments (*P*=0.14). Second and third level interactions were not significant. Figure 17 compares the temperatures reached and the length of time they were registered between varieties at mild and extreme burnings in all three pastures studied.

Table 16. Mean ($\pm$ SE; n=120) maximum temperatures (º C) generated by varieties of *B. curtipendula* when burned with increasing fuel loads. Values did not differ significantly among pastures with different burning histories, so data were pooled.

	Average maximum temperature at base of plant (º C)[1]			Average maximum temperature at 1.5 cm depth(º C)[1]		
	var. *caespitosa*	var. *curtipendula*	*P*	var. *caespitosa*	var. *curtipendula*	*P*
Unburned	38.9 ±30.5	41.2 ± 30.5	0.4	31.5 ± 13.6	35.0 ± 9.6	0.2
Mild	241.6 ± 30.5	186.2 ± 30.5	0.3	36.8 ± 8.6	42.3 ± 8.6	0.2
Extreme	324 ± 30.5	277.9 ± 30.5	0.4	39.6 ± 8.6	57.0 ± 8.6	0.4

[1] transformation did not improve normality.
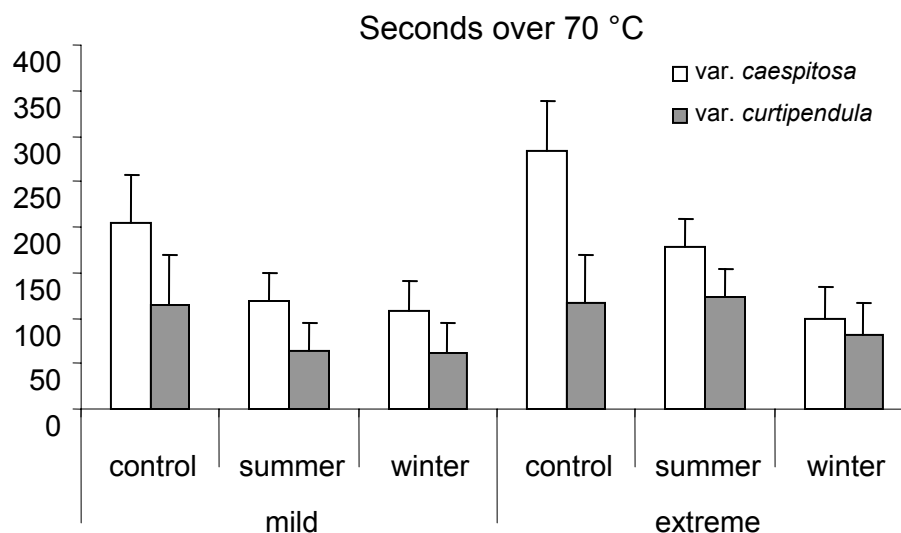
Figure 16. Mean ($\pm$ SE) length of time (seconds) plant basal temperatures exceeded 70ºC in *B. curtipendula* varieties from pastures with different prescribed burning histories (control, summer burned and winter burned) under two levels of artificial fuel loading (10g for mild; 25 g for extreme).
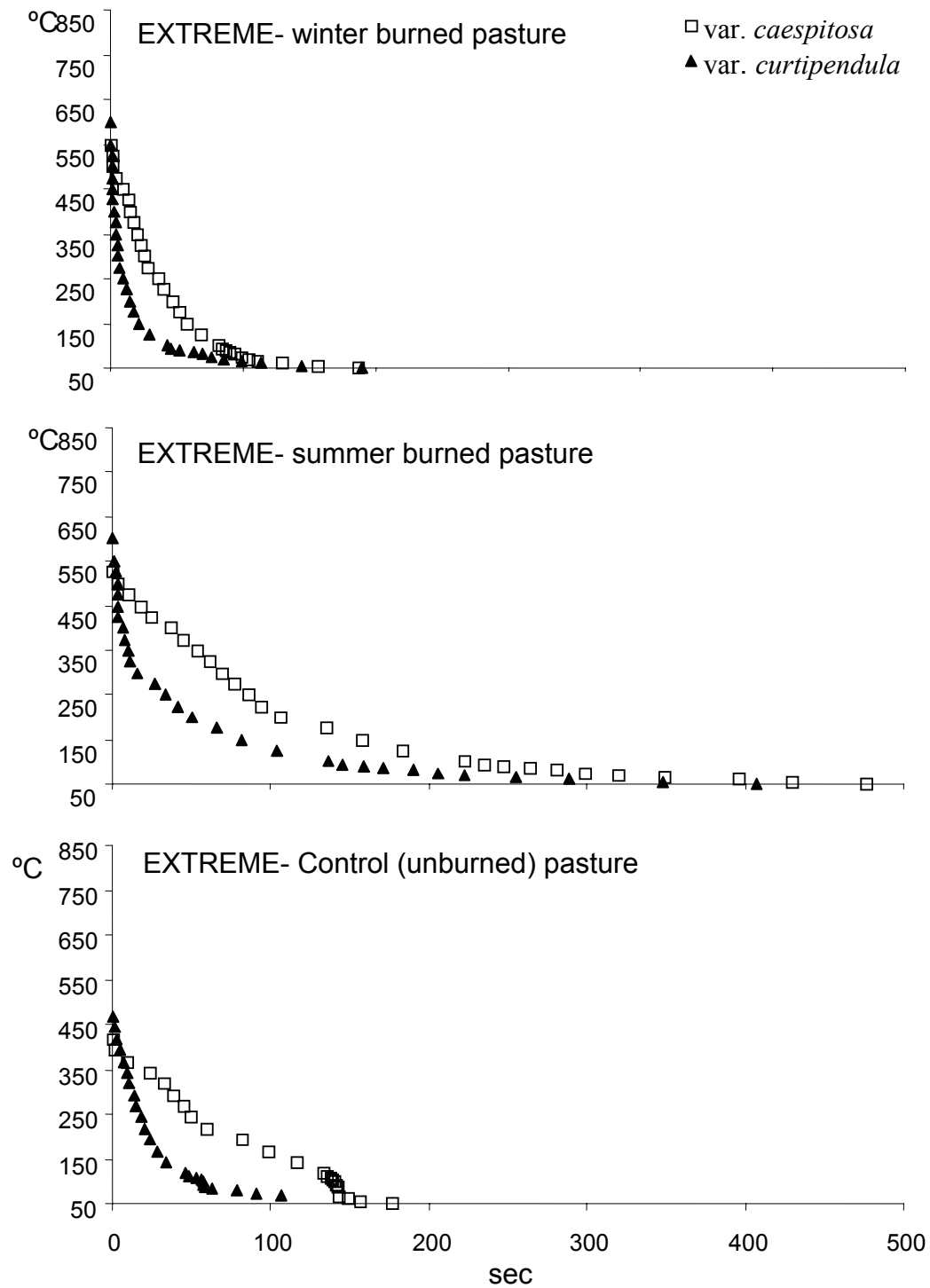
Figure 17. Temperature (°C)-duration (seconds) curves for *B. curtipendula* varieties on pastures with different prescribed fire histories (unburned, summer or winter burn) when loaded with different amounts of artificial fuels (mild = 10g; extreme = 25 g).
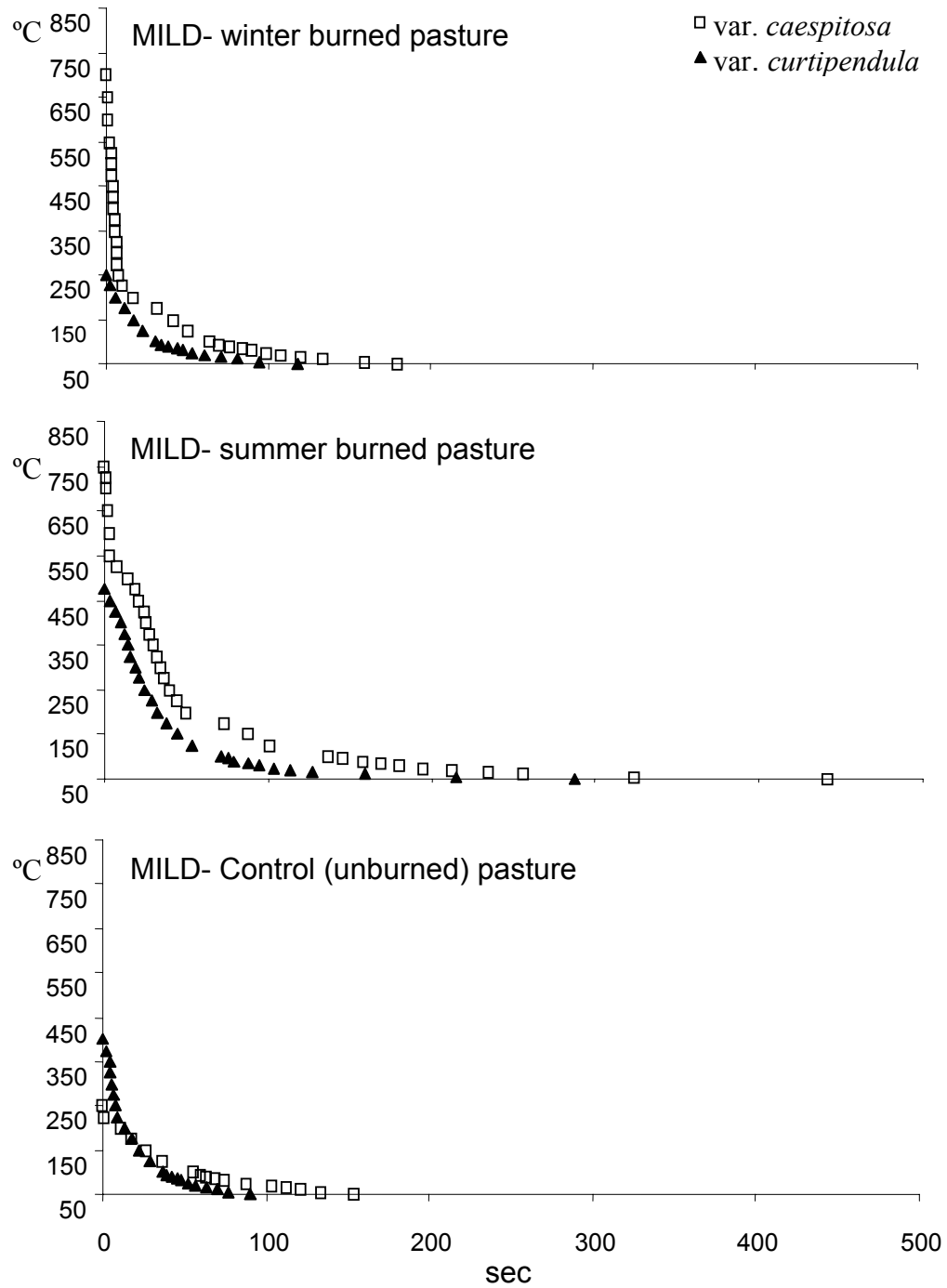
Figure 17. Continued

Plant response to burning treatments

Artificial fuel loading significantly elevated the temperatures experienced by plants (Table 16) but caused no detectable differences in any of the growth and reproduction variables measured (Table 17, Figures 18,19). Though not affected by fire *per se*, the two varieties exhibited some differences in growth allocation patterns. Both varieties produced similar root, shoot and total biomass (Table 18, Figure 19 a,b,c) and had comparable numbers of tillers (Figure 19d) after being burned. However, tillers of var. *caespitosa* (125 ± 6 mg) were larger than those of var. *curtipendula* (99 ± 6 mg) (Figure19e). *Bouteloua curtipendula* var. *caespitosa* allocated significantly more biomass to reproduction than var. *curtipendula* ($P < 0.001$) (Figure 19f). The var. *caespitosa* had also produced significantly more culms than the var. *curtipendula* (29.5 ± 3.5 and 5.7 ± 1.6 respectively) (Figure 19g). Consequently, var. *caespitosa* had more culms per tiller than the rhizomatous variety (0.28 vs. 0.08) (Figure 19h). The two varieties had comparable root to shoot ratios. However, the ratio of below (roots + rhizomes) to aboveground biomass (B/A ratio) was significantly different between varieties (Figure 19 i,j), reflecting the lack of rhizome production by var. *caespitosa* (Figure 18).

Burning history effects

Bouteloua curtipendula varieties from pastures with different fire histories showed some significant differences in their response to burning (Table 17). Plants from the pasture experiencing a winter burn in 1999 had more tillers and produced more reproductive culms than plants from the unburned pastures and pastures burned in summer 1999. Plants from winter burned pastures also had more shoot, root, reproductive and overall biomass than plants on the unburned pasture and summer burned pastures. Plants from the summer burned pasture showed higher root/shoot ratio than the plants from the unburned and the winter burned pastures. No differences in rhizomes biomass, biomass per tiller and number of culms per tiller were detected.
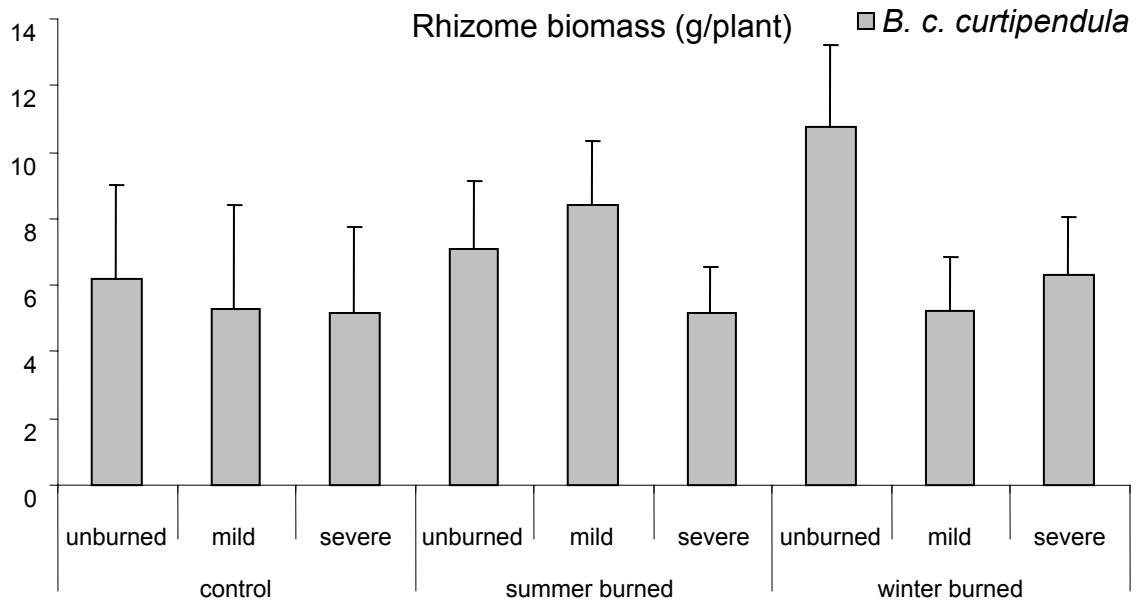
Figure 18. Mean (± SE) rhizome biomass of var. *curtipendula* plants 14 months after burning at different intensities (unburned, mild and extreme as defined in Table 15) in pastures with different prescribed fire histories (unburned and summer vs. winter burned). *Bouteloua curtipendula* var. *caespitosa* does not produce rhizomes, so data is not shown for it.
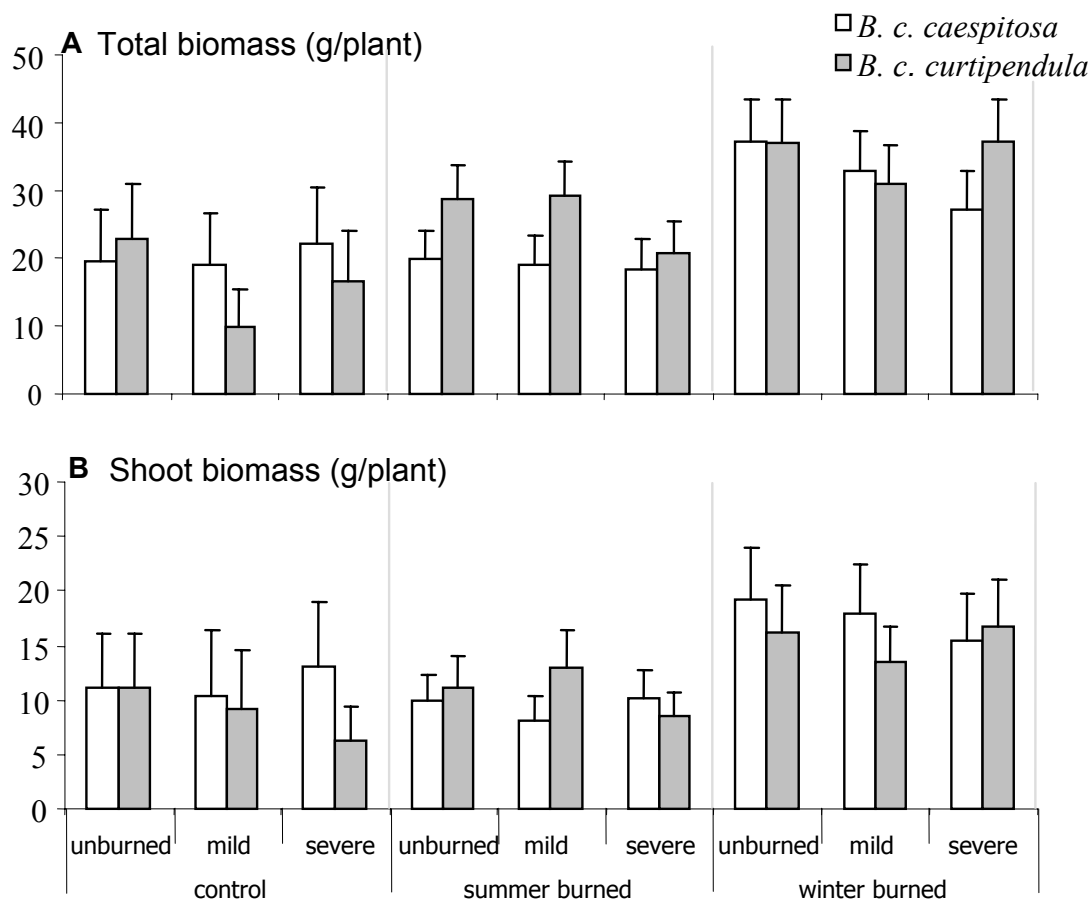
Figure 19. Characteristics (mean ±SE) of var. *caespitosa* and var. *curtipendula* plants 14 months after experimental burning. Plants were from pastures differing in their fire history and were subjected to different fire intensities (no fire, moderate and extreme; see Table 15 for details). A) total biomass, B) shoot biomass, C) root biomass, D) final tiller number, E) biomass per tiller per plant, F) reproductive biomass, G) number of reproductive culms, H) number of culms per tiller per plant, I) root to shoot ratio, J) below to aboveground biomass ratio.

Figure 19. Continued

F Reproductive biomass (g/plant)

□ *B. c. caespitosa*
■ *B. c. curtipendula*

G Number of reproductive culms

H Number of culms per tiller per plant

| unburned | mild | severe | unburned | mild | severe | unburned | mild | severe |
| control | | | summer burned | | | winter burned | | |
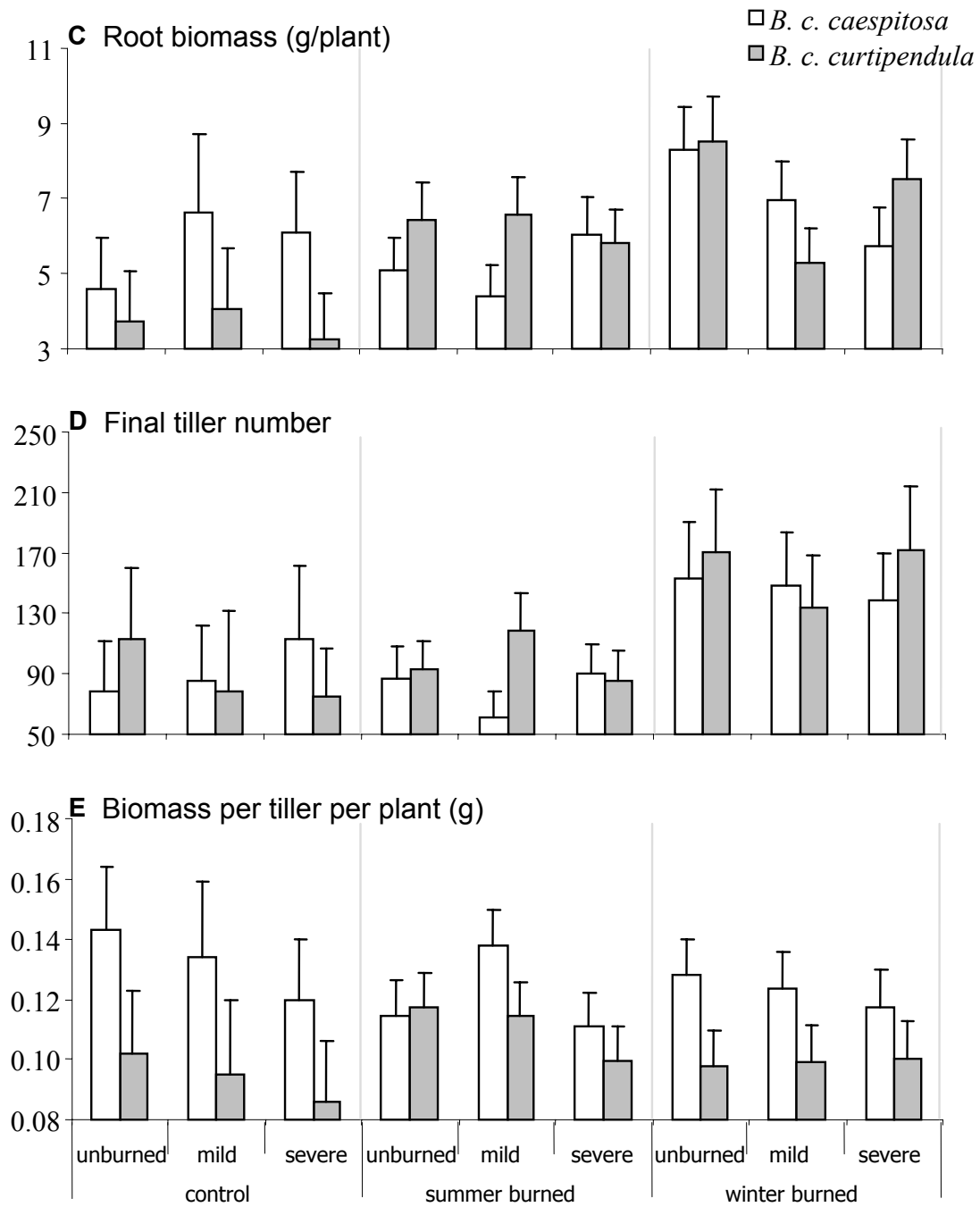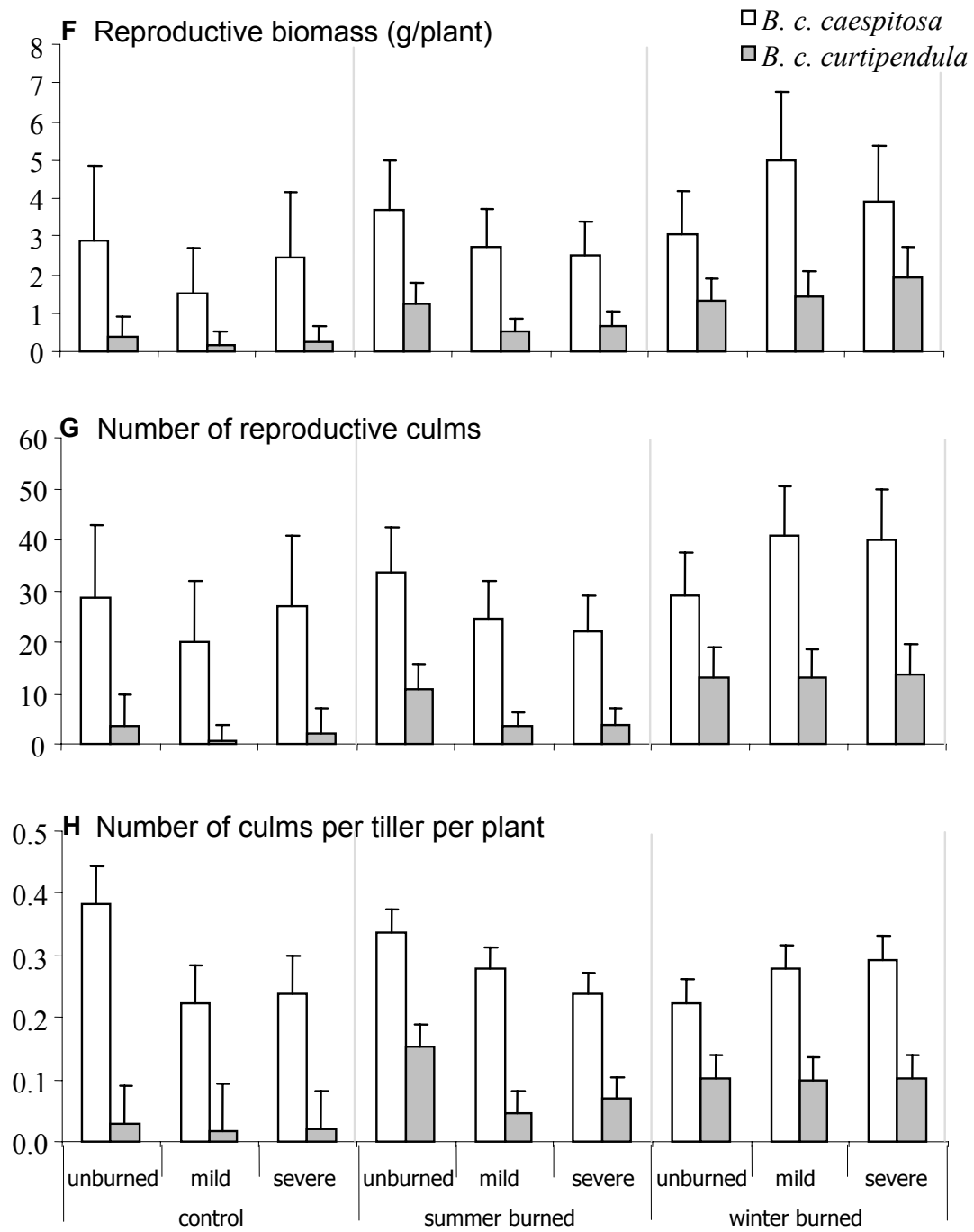
Figure 19 continued
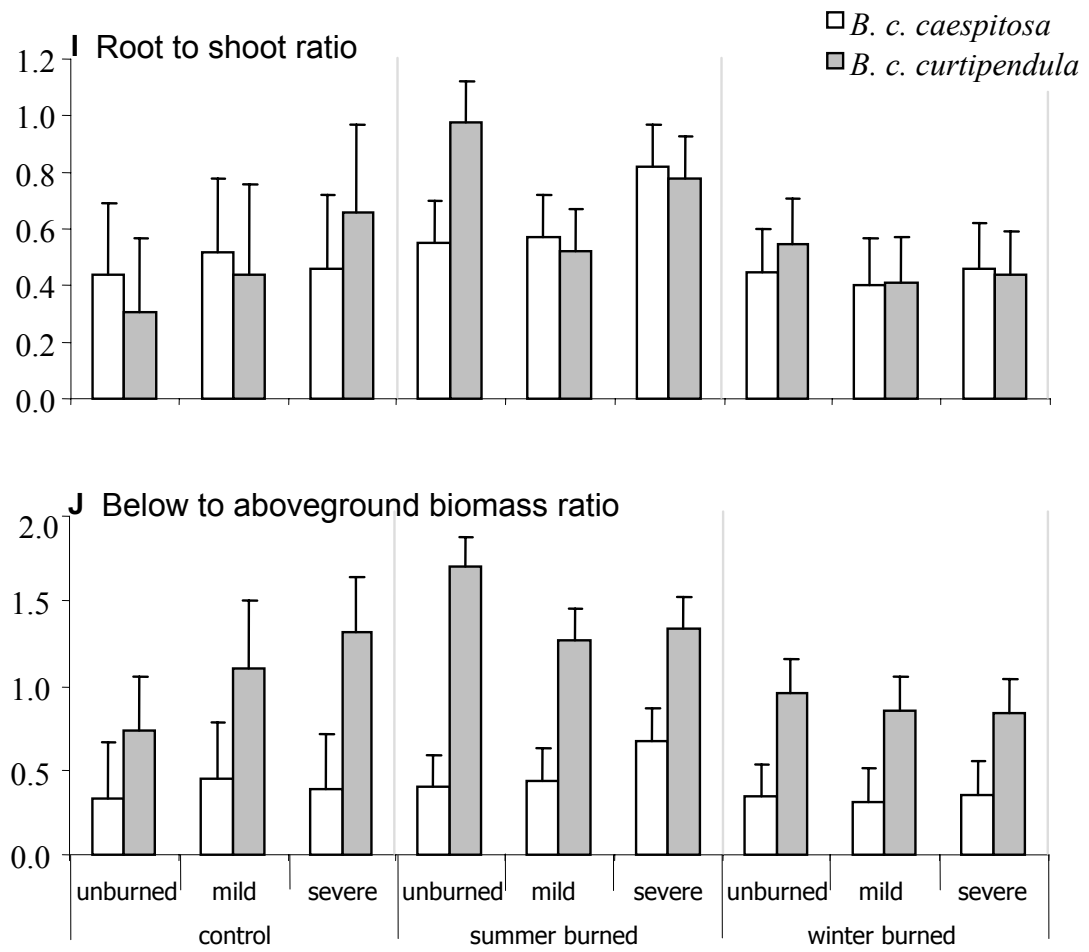
Figure 19. Continued

Table 17: Values for Type III *F*-test for the analysis of variance of *B. curtipendula* varieties (*B. curtipendula var. curtipendula* vs. *B. curtipendula var. caespitosa*) response to burning as a function of prescribed fire history (not burned, burned summer 1999, burned winter 1999) and fire intensity (no fire, moderate fire, extreme fire). Number of tiller/plant prior to burning was used as a covariate. The degrees of freedom of the error term are given in last row. Variables were transformed before the analysis as necessary with: [1] ln, [2] log and [3] square root. [4] transformations did not improve normality.

* P < 0.05, ** P < 0.01,   *** P < 0.001

	Final tiller number[1]	Shoot biomass[2]	Root biomass[3]	Rhizome biomass[3]	Reproductive biomass[1]	Culm number[3]
Covariate	25.3***	18***	55.3*	49.1*	3.3	8.5**
Fuel Load (L)	0.02	0.41	0.2	1.6	0.43	0.6
Fire history (H)	10.7***	7.1**	6.8***	0.5	46.3**	5.4**
Variety (V)	0.34	0.4	0.72		38***	47.5***
H x L	0.08	0.96	1.1	1.4	1.01	1.02
L x V	0.16	0.09	0.3		0.08	0.18
H x V	0.07	0.42	1.9		0.72	0.55
H x L x V	0.8	0.53	1.2		0.12	0.04
Df error	100	100	100	48	101	101

Table 17 continued.

* P < 0.05, *** P < 0.01, *** P < 0.001

	Total biomass[3]	Biomass per tilller[4]	Root to Shoot ratio[4]	Below to Above ground biomass ratio[4]	Culms per tiller[4]
Covariate	35.3***	-	-	-	-
Fuel Load (L)	0.9	1.14	0.5	0.2	1.9
Fire history (H)	11.3***	0.21	4.7*	5.4**	0.76
Variety (V)	0.28	10.8**	0.21	36.1***	86.3***
H x L	0.42	0.4	0.47	0.05	2.01
L x V	0.28	0.1	0.27	0.07	0.13
H x V	1.4	1.1	0.16	1.45	1.3
H x L x V	0.7	0.3	0.55	0.7	0.8
Df error	100	101	100	101	101

Discussion

Temperatures generated during plant combustion

Increasing fuel loads significantly elevated average maximum temperatures at the soil surface, but did not influence temperatures 1.5 cm below the surface. This poor heat penetration into soils is typical and related to the fact that convective heat is transferred upwards (Hobbs et al. 1991, Whelan 1995).

Plants of the two varieties of *B. curtipendula* experienced similar maximum temperatures on average in the experimental burnings. However, var. *caespitosa* burned at temperatures beyond 70°C for longer periods of time than the rhizomatous variety (2.75 min vs.1.55 min) even though the maximum temperatures registered were similar (Table 16). This result gave support to H1 suggesting that *B. curtipendula* var. *caespitosa*'s architecture has characteristics that enhance its flammability (higher density of tillers of phalanx growth form increasing the surface area to volume ratio of biomass). In addition, Figure 17 suggested the caespitose variety reached the highest temperatures between the two varieties in some of the treatments. Increasing the surface area may favor development of higher temperatures for two reasons: 1) the volume ratio will influence the amount of moisture (smaller parts loose water easily than larger ones) and 2) it attains an optimum proportion in the fuel:air mix (Bond and van Wilgen 1996). It can be speculated that sites dominated by caespitose plants would suffer greater mortality after a fire than sites with rhizomatous plants, since they will experience killing temperatures for longer periods of time.

Plant response to burning treatments

Vegetative regeneration after experimental burning at different intensities was comparable in the two *B. curtipendula* varieties, suggesting that although the caespitose growth form experienced killing temperatures for longer periods of time, it is not necessarily more sensitive to fire than the rhizomatous variety. The biomass allocated to reproductive structures (number of flowering culms and number of flowering culms per tiller), were two to fifteen times higher in the caespitose variety than in the rhizomatous

variety (Figure 19) regardless of the amount of fuel used in the burning treatments. The same difference in the pattern allocation to reproductive structures between the two varieties was observed in another experiment (Chapter III). Although fire-stimulated flowering has been reported as a rather common phenomenon in monocots (Bond and van Wilgen 1996), results from this experiment suggested this might not be the case for both varieties of *B. curtipendula* .

Bouteloua curtipendula have been specifically pointed out as an exception to the generalized idea of grasses as fire-resistant components of the community (Wright 1974, 1978) based on observed decreases in yield of $> 50\%$ after burning (Wink and Wright 1973). However, no adverse effects were observed in this study. These contrasting outcomes do not appear to be related to differences in the amount of the post-fire precipitation in the two studies (16.5 cm from November through May in their experiment; 17.6 cm for same period in this experiment). Possible reasons for the discrepancies may be related to the burning season. Wink and Wright (1973) burned their plots in March, whereas plants in this study were burned in August. Thus, data from the present experiment suggests that, at least summer burning (performed in August) is not harmful to *B. curtipendula*. It can be argued that this species is more susceptible to fire that take place early in the growing season. Grasses in general have been reported to be vulnerable after new shoots have emerged from the protective leaf bases and before they have replaced the energy and nutrient stores used for shoots elongation. Consequently, if the fire occurs when the roots switch from being a carbon source to a carbon sink, then recovery is poor (Bond and van Wilgen 1996).

Burning history effect on the response to fire

Burning history of the sites had a significant effect on the response of the plants to the fire treatments. Regeneration of plants on the pasture that had not been burned (control) was lower in terms of vegetative and reproductive biomass for both *B. curtipendula* varieties, whereas plants that had previously been burned either in summer or in winter of 1999 showed a better performance. The recovery of the plants seemed to be related to the length of time they experienced temperatures above 70°C (Figure 16).

As plants of the control pasture developed killing temperatures for longest periods of time (Wright 1970). Although litter around the plants was removed in this experiment, it can be argued that the interval between successive fires could affect the amount of fuel because of the increased rate of accumulation of dead material on the plant itself (Bond and van Wilgen 1996). In addition, the better recovery of the plants in the burned pastures might have been the result of factors that differed between pastures other than the fire history. To account for this variability, studies should consider burning plants from several pastures with the same fire history.

Conclusion

Although the distribution range of *B. curtipendula* var. *caespitosa* is largely within the less flammable region of southwestern North America and the distribution of var. *curtipendula* extends over the flammable zone, this study found no evidence of a difference in fire-resistance between varieties. Recovery from the range of experimental fire intensities imposed in this study was generally comparable for both varieties. However, there was evidence that the caespitose variety reached temperatures that can be considered lethal for longer periods of time than the rhizomatous growth form. Time between burnings also seemed to be related to the temperatures developed and to the recovery of the plants.

CHAPTER V

CONCLUSIONS

This study sought to determine the ecological significance of the differentiation between the two growth forms (varieties) of *B. curtipendula* given their contrasting distribution based on the premise that continental-scale distributions were a reflection of adaptations of each growth form to characteristics in the environment. The species of interest *B. curtipendula* is a warm perennial grass frequent in North American grasslands in arid and semiarid regions. Three varieties are described for the species and two of them were the focus of this study: var. *caespitosa* with phalanx architecture, apomictic reproduction that occupies the western, more xeric part of the range and var. *curtipendula*, guerrilla (rhizomatous) form, sexual reproduction and extends over the mesic part or the range. The zone of sympatry is quite extensive but this study was conducted on the Edwards Plateau region in Texas.

The varieties showed high morphological variability although it was not related to a precipitational gradient as expected. Looking at their local distribution on a particular site (TAES- Sonora), var. *curtipendula* abundance responded to limestone type while var. *caespitosa* could not be related to a single factor but to the interaction of fire and grazing treatments and limestone types. The guerrilla type local distribution was related to juniper size and cover but distribution for neither of the two varieties distribution was affected by oak cover. Although it is unlikely that the distribution of any organisms was determined by singular, detectable environmental factors, limestone type seemed to be overriding the effect of all others in the distribution of var. *curtipendula*. Morphological variation, such as the presence of rhizomes, could be hindered in sites with uneven and superficial rock cover such as the ones on the Edwards limestone. Then, the possibility of growing rhizomes on Buda soils may be directly involved in differences in local distribution of the guerrilla variety. Nonetheless, variability observed within and between varieties and the low explanatory power of the ordination analysis

performed here suggested that other factors or factor combinations may determine the local distribution of the varieties on the Edwards Plateau.

Clones were grown in a common garden to determine whether the varieties differ in physiology, pattern of biomass allocation and resistance to defoliation in response to variation in resource availability (light and nutrients) and disturbance (defoliation). The potential of differences in genetic variability was also evaluated. The growth forms showed similar photosynthetic rate along treatments; however, they did not follow the same pattern of response in Ψ at different nutrient levels and their response changed with the time of the day, so not a unique statement can be made for comparing their physiological response. A similar complex pattern of response was observed for changes in root to shoot ratio in response to varying resources. Although not to the same extent for all treatments, var. *curtipendula* produced fewer reproductive culms while allocating more biomass to rhizomes. For var. *caespitosa* allocation to reproductive structures changed in response to resource availability and defoliation. Thus, the two varieties were affected in a different manner.

The tiller recruitment and replacement rates changes in response to treatments showed a complex set of interactions between factors. The two varieties of *B. curtipendula* showed reduction in tiller demography at low resource levels or under defoliation but differed in extent of their responses. Both varieties showed a certain level of genetic variation, even with the small sample size used in this study. The var. *caespitosa* showed differences in the levels of plasticity expressed in reproductive biomass by the genotypes in response to environmental variation. Genetic variation between genotypes and variation in plasticity were also observed for changes in tiller demography in response to treatments.

The differences in flammability of the ranges of the varieties suggested that fire might have been a factor in determining their distribution. Plants of the two varieties developed comparable maximum temperatures when experimentally burned, although the caespitose form experienced temperatures above an injurious level for longer periods

of time. Longer exposure to lethal temperatures however, did not affect regrowth as the two varieties showed comparable biomass production after 14 months.

In summary, the two growth forms differed in pattern of response to environmental changes, although both varieties were affected or could recover from such changes to a certain extent. Coexistence did not necessarily imply niche separation of the forms. In fact, morphological and physiological variation within varieties plus a high level of genetic variability may offer flexibility to overcome abrupt changes in conditions common of semiarid regions.

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VITA

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