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RESEARCH NOTE

Seasonal Fires, Bison Grazing, and the Tallgrass Prairie Forb *Arnoglossum plantagineum* Raf.

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ABSTRACT: Fire and grazing can interact to affect the structure and composition of vegetation communities in a manner that may differ from the effects of fire or grazing that occurs in isolation of the other. In order to better understand the effects of a fire-grazing interaction at the level of an individual plant species, we studied the response of a perennial tallgrass prairie forb, *Arnoglossum plantagineum* Raf., to the interaction of spring and summer fires with grazing by bison (*Bison bison* L.). During one field season (2006), we collected data in areas that had been treated with summer fires while in a subsequent field season (2007) we collected data in areas that had been treated with spring fires. Many measures of plant growth (plant height, vegetative biomass, and total biomass) and reproductive effort (reproductive biomass, indices of flowering plant density) suggested greater resource availability for individuals of *A. plantagineum* growing in areas that had been recently burned and were being heavily grazed by bison. However, the response of these variables to the fire-grazing interaction often varied among differing topographical positions. Our results demonstrate that the interaction of fire and bison grazing can further interact with topographical position in tallgrass prairie to affect the growth and reproductive effort of the perennial forb *A. plantagineum*.

Index terms: heterogeneity, patch burn grazing, pyric herbivory, shifting mosaic

INTRODUCTION

A variety of management tools and techniques are available to natural area managers tasked with the preservation, maintenance, and restoration of tallgrass prairie ecosystems. Prescribed fire has a long history of application in the restoration and management of tallgrass prairies (Kollmorgen and Simonett 1965; Hoy 1989), particularly in the context of natural area management and restoration where its use is widespread (Curtis and Partch 1948; Helzer 2010; Rowe 2010). The use of grazing as a restoration and management tool in tallgrass prairies has not been as ubiquitous as the use of fire. Certainly, in western portions of the tallgrass prairie, there is a long history of cattle (*Bos taurus* L.) grazing as an economic activity that has shaped the ecosystem in areas where it has occurred (Malin 1942; Kollmorgen and Simonett 1965). In other areas, perhaps especially in the eastern portion of this ecosystem's range, there has been debate over the value of large herbivore grazing as a conservation tool (Williams 1997; Harrington 1998; Henderson 1998; Davison and Kindscher 1999; Howe 1999; Knapp et al. 1999; Leach et al. 1999).

Management of tallgrass prairies is often focused on manipulating the richness, diversity, and composition of vegetation communities (Brudvig et al. 2007). While vegetation productivity of tallgrass prairies is driven largely by a few species of warm season grasses (Knapp et al. 1998), forbs make the greatest contribution to species richness of this ecosystem (Freeman 1998; Palmer 2007). Fire may affect the diversity of tallgrass prairies by altering competitive relationships between dominant grasses and subdominant forbs; spring fires enhance the growth of dominant warm-season grasses, which may then preempt resources available to subdominant forbs, resulting in reduced forb growth or reproductive effort (Knapp 1984; Hartnett 1990; Hartnett 1991). Frequent spring fires can contribute to greater dominance of grasses with concomitant declines in the abundance of forbs (Kucera and Koelling 1964; Collins and Steinauer 1998).

Grazing in tallgrass prairie can modulate community diversity by reducing the competitive ability of dominant grasses when they are grazed and by altering the environmental conditions at the microsite occupied by an individual forb (Collins et al. 1998). Selective grazing of grasses can create a favorable growing environment around a prairie forb as a result of greater levels of light and higher soil temperatures (Fahnestock and Knapp 1993, 1994). Prairie forbs growing among grazed grasses can be characterized by greater biomass than conspecifics in ungrazed areas, exemplifying the relationship between resource availability and biomass accumulation (Fahnestock and Knapp 1993, 1994; Damhoureyeh and Hartnett 1997). Somewhat counterintuitively, prairie forbs growing in grazed areas can be shorter than conspecifics growing in ungrazed areas (Fahnestock and Knapp 1993, 1994; Damhoureyeh and Hartnett 1997), suggesting that forbs

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growing among ungrazed grasses need to be taller to obtain sufficient light resources. When prairie forbs are able to capitalize on increased resource availability as a result of altered competitive interactions with neighboring grasses, they may allocate biomass in a manner that differs among species: forbs that are primarily asexual may increase total biomass while forbs that are primarily sexual may increase reproductive biomass, number of florets, or number of seeds (Fahnestock and Knapp 1993, 1994; Damhoureyeh and Hartnett 1997).

A management practice gaining increased attention in the last decade is known variously as patch burn grazing, heterogeneity management, the fire grazing interaction, or pyric herbivory (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2006; Fuhlendorf et al. 2009). This practice capitalizes on the profound influence of fire on the distribution and behavior of grazing animals to alter vegetation heterogeneity across landscapes (Fuhlendorf et al. 2004; Vermeire et al. 2004; Fuhlendorf et al. 2006; Coppedge et al. 2008; Allred et al. 2011; McGranahan et al. 2012; Winter et al. 2012). Because application of the fire grazing interaction has been the subject of focused research for a relatively short time, land managers accustomed to using fire alone or grazing alone may have uncertainty regarding its use.

Fire and grazing can interact in landscapes to create heterogeneity when fire concentrates grazing activity within a burned patch of a landscape, thereby reducing grazing activity in other landscape patches that haven't burned for an extended period of time; a subsequent fire that occurs in another patch of the same landscape causes grazing activity to shift to the newly burned patch (Fuhlendorf and Engle 2004; Allred et al. 2011). The resulting dynamics of disturbance and rest through space and time create a patchwork of contrasting vegetation structure and composition (Fuhlendorf and Engle 2004; Vermeire et al. 2004; Coppedge et al. 2008; McGranahan et al. 2012; Winter et al. 2012). The compositional changes that characterize this shifting mosaic are presumed to arise from the altered competitive dynamics between grasses and forbs driven by the selective grazing of grasses within recently burned patches, contrasting with the limited grazing of grasses within patches that have not burned recently (Coppedge et al. 1998; Winter et al. 2012).

However, grassland landscapes are characterized by topoedaphic variability that also affects vegetation communities (Barnes and Harrison 1982; Knapp et al. 1993; Dodd et al. 2002; Winter et al. 2011). Slope and aspect are topoedaphic features that influence the microsite conditions experienced by individual plants. Contrasting slope and aspect features can be characterized by contrasting levels of soil temperature and soil moisture content (Ayyad and Dix 1964), contrasting plant leaf temperatures (Smith et al. 1983), and contrasting level of response by grasses and forbs to altered levels of nutrient availability (Benning and Seastedt 1995). Thus, any shifting mosaic of altered competitive dynamics between dominant grasses and subdominant forbs arising from a fire-grazing interaction may be constrained or modulated by a pre-existing template of heterogeneity imposed by topoedaphic variability (Winter et al. 2011).

To better understand the effect of a fire-grazing interaction on individual prairie forbs, we collected data on a common perennial forb of tallgrass prairies, *Arnoglossum plantagineum* Raf. Furthermore, we quantified the topographical setting of individual plants that were sampled to determine if there was an influence of slope and aspect on the plant variables that were measured. Our research was conducted at The Nature Conservancy's Tallgrass Prairie Preserve in northeast Oklahoma, a natural area where the interacting processes of fire and bison (*Bison bison* L.) grazing are used to restore historic patterns of disturbance and rest (Hamilton 2007). We selected *A. plantagineum* as a study species because its level of abundance at the study site was sufficient to permit sampling, it had an architecture that permitted differentiation of vegetative and reproductive biomass, it did not appear to be palatable to bison, and it has not been the subject of previous autecological research in tallgrass prairie. We acknowledge that more information would have been generated by an examination of multiple species of tallgrass prairie forbs, but we were constrained by limitations on the time available for field activities.

We conducted our study to gain insight into whether a prairie forb experiences different levels of resource availability in the different patches characterizing the shifting mosaic of a fire-grazing interaction. While we did not explicitly measure resource availability (e.g., levels of light, water, or nutrients) in patches with different burn histories, we assume our measures of plant growth and reproductive effort infer resource availability. Specific null hypotheses that we tested in our research were: (1) measures of plant growth (height, vegetative biomass, and total biomass) does not differ between plants growing in patches that were recently burned and were being heavily grazed and plants growing in patches that were not recently burned and were being minimally grazed; and (2) measures of reproductive effort (number of floral structures, reproductive biomass, and density of flowering individuals) does not differ between plants growing in patches that were recently burned and were being heavily grazed and plants growing in patches that were not recently burned and were being minimally grazed.

METHODS

Species Description

Arnoglossum plantagineum (Indian plantain) is a perennial herb arising from a weakly rhizomatous caudex with fleshy-fibrous roots (Barkley 1986; Anderson 2006). Spring growth at our study site was initiated with the production of a basal rosette of long-petioled leaves. Anthesis is realized with the production of a stem terminating in a broad, corymbiform cyme, and 50–100 cm in height. The cyme consists of numerous capitula, each containing five florets. Flowering individuals of *A. plantagineum* at our study site were typically single-stemmed. Non-flowering individuals (i.e., presence of only a basal rosette) were present at our study site into July but anemochory of seeds from individuals that did flower appeared to be well-synchronized, occurring in mid-

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July. In the northern part of its range, *A. plantagineum* occurs from South Dakota to Ontario, while in the south it ranges from Texas through Alabama (Anderson 2006). Typical habitats of *A. plantagineum* are prairies and pastures where it can be a common species (Smeins and Diamond 1983; Foti 1989; Leidolf and McDaniel 1998; Hickman and Derner 2007; Polley et al. 2007).

Study Site

The study site was The Nature Conservancy's 15,700-ha Tallgrass Prairie Preserve in Osage County, Oklahoma (36°50'N, 96°25'W). Long-term (1945 – 2007) average annual precipitation at the nearby Foraker weather station in Osage County was 89.21 cm (www.ncdc.noaa.gov; www.mesonet.org). In 2005, 2006, and 2007, the annual total precipitation and percent deviation from the long-term average were 77.75 cm (87%), 61.09 cm (68%), and 133.25 cm (149%), respectively. Soils are derived from sandstone, shale, limestone, and chert of Permian and Pennsylvanian age (USDA-NRCS 2009). Specific areas sampled during this study were characterized by soils in the Ustoll (very shallow to very deep; moderately well-drained to well-drained; slopes of 0–30% slope), Udert (deep; moderately well-drained; 0–5% slopes), and Ustalf (moderately deep; moderately to well-drained; 0–30% slopes) suborders (USDA-NRCS 2009). The majority of the Preserve is characterized by tallgrass prairie vegetation with the dominant grass species being *Andropogon gerardii* Vitman., *Sorghastrum nutans* (L.) Nash, *Sporobolus compositus* (Poir.) Merr., *Panicum virgatum* L., and *Schizachyrium scoparius* (Michx.) Nash (Palmer 2007).

Beginning in 1993, management of the Preserve has included the restoration of historic cycles of rest and disturbance driven by the interaction between fire and bison grazing. Within the Preserve's bison pasture, seasonal fires are applied in a spatially-random manner such that approximately 40% of the area burned in a single year is burned during March – April, 20% during July – September, and 40% during November – December, resulting in an approximately three-year fire return interval for most areas of the pasture (Hamilton 2007). In 2006, the bison pasture was 8517 ha and contained approximately 2400 animals during the summer. In 2007, the pasture was expanded to 9532 ha and contained approximately 2600 animals during the summer. With the exception of an annual fall roundup in which surplus animals are culled and remaining animals receive veterinary maintenance treatments, bison are free to move throughout the pasture during the year and receive no supplemental feed. Salt and trace minerals are provided to bison on a free-choice basis at multiple locations, and streams and stock ponds provide water at scattered locations throughout the pasture (Hamilton 2007). Bison distribution within the pasture is strongly correlated with the location of burned patches with the most recently-burned patches being areas characterized by the highest level of bison activity (Coppedge and Shaw 1998; Schuler et al. 2006; Allred et al. 2011).

2006 Field Sampling

There has been minimal work examining the response of prairie vegetation to prescribed fires conducted during seasons other than spring (Engle and Bidwell 2001; Towne and Kemp 2008; Howe 2011), and we elected to conduct our study in a manner that would contribute to this limited body of knowledge. Thus, we compared plants in recent summer-burned patches to plants in older summer burn patches within the Preserve's bison pasture. Three sites of paired patches were chosen in 2006 where a patch that was burned during the late growing season (July – September) in 2005 was adjacent to another patch that had been burned during the same season in 2003 or earlier. Recent summer burn patches (burned in 2005) were 85–114 ha (mean = 114 ha), and older summer burned patches (burned in 2001, 2002 or 2003) were 81–206 ha (mean = 161 ha).

At each site of paired patches, a population of *A. plantagineum* was located in which the population was subdivided by the boundary between the burn patches. Non-flowering individuals (i.e., basal rosettes) were readily obscured by other vegetation and difficult to locate, and we restricted our sampling to flowering individuals. We further restricted our sampling to individuals that were single-stemmed, the typical condition for this species at this study site. Additionally, we never observed evidence of herbivory on this species by bison, but we did occasionally observe, and did not sample, plants that appeared to have been trampled. Finally, to reduce the confounding effect of intra-specific competition, we did not sample individuals that were rooted within 5 cm of a neighboring *A. plantagineum*. Within each sub-population, plants suitable for sampling were located visually until a total of 30 plants had been sampled. The geographic coordinates of each sampled individual were recorded using a Garmin GPS Map60CSX. The Map60CSX was used with the Wide Area Augmentation System enabled, and accuracy of each sampled plant location was enhanced through use of the averaging function; estimated accuracy, as indicated by the unit during averaging, was consistently < 10 m. Sampled individuals were harvested at the ground surface and all tissues (basal leaves, stem, and inflorescence) were individually-bagged and labeled for further processing in an enclosed, climate-controlled laboratory. All sampling in 2006 occurred during June 21–26.

2007 Field Sampling

Because a statewide burn ban was in effect during the summer and fall of 2006, no burns occurred within the bison pasture during the period of July – September 2006. Consequently, it was not possible in 2007 to replicate the manner in which summer burns were sampled in 2006. Instead, in 2007 we located three sites of paired patches where a patch that was burned during the spring (March – April) in 2007 was adjacent to another patch that had been burned during the same season in 2005 or earlier. Thus, we compared plants in recent spring-burned patches to plants in older spring-burned patches within the bison pasture. Recent spring-burned patches (burned in 2007) were 88–366 ha (mean = 194 ha) and older burned patches (burned in 2004 or 2005) were 113–293 ha (mean = 184 ha). At each site of paired patches, a population of *A. plantagineum* was located in which the population was

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subdivided by the boundary between the burn patches. The methods used to locate, determine the sampling suitability, and eventually sample individual plants was identical to the methods utilized in 2006 except that 40 individuals were sampled within each sub-population of each patch-pair during 2007. All sampling in 2007 occurred during June 17–24.

Laboratory Procedures

During both years, immediately after field sampling, all plants were transported to a climate-controlled laboratory where plant height was measured from the cut portion of the stem to the farthest point that an individual's inflorescence tissues could be extended along a flat surface. The number of capitula on each individual was counted. Vegetative tissue (basal leaves, stem, and stem leaves) of each individual was separated from reproductive tissue (inflorescence consisting of stem, pedicels, and capitula) by cutting the stem at the base of the lowest stem leaf that had a pedicel with at least one capitula originating from its axis. Reproductive and vegetative tissue of each individual were bagged and labeled separately and oven dried at 60 °C for 48 hours. Following drying, samples were weighed to obtain measurements of reproductive biomass, vegetative biomass, and total (reproductive + vegetative) biomass.

GIS Procedures

A Geographic Information System (GIS) was constructed using the software package ArcMap 9.3 (www.esri.com). A 30-m grid Digital Elevation Model (DEM) was obtained from the National Elevation Dataset (Gesch 2007) and combined with the GPS coordinates of each sampled plant from each year of sampling within the GIS. Within the Spatial Analyst toolbox of ArcMap, the DEM was used as an input raster in the Aspect and Slope tools, creating aspect and slope datasets. Aspect and slope datasets were subsequently converted to polygon layers using the Raster to Polygon tool in the Conversion toolbox. In order to associate each sampled plant with an aspect and slope value, the aspect, slope, and plant location data layers were used as input features in the Intersect tool of the Analysis toolbox.

Aspect and slope values, originally expressed as degrees, were transformed using trigonometric functions (Guisan et al. 1999) and the product of the transformed values resulted in values of "northness" and "eastness" (Kariuki et al. 2006) that could be associated with each sampled plant:

northness = [sine(slope)]*[cosine(aspect)]

eastness = [sine(slope)]*[sine(aspect)]

Thus, each sampled plant was associated with a value of northness, ranging from -1 through 1, indicating if it was on a southern (northness = -1) or northern (northness = 1) aspect (northness = 0 indicated no orientation with regard to south or north). Likewise, each sampled plant was associated with a value of eastness, ranging from -1 through 1, indicating if it was on a western (eastness = -1) or eastern (eastness = 1) aspect (eastness = 0 indicated no orientation with regard to east or west). Subsequent analyses were done using eight of the possible combinations of northness and eastness values (north, northeast, east, southeast, south, southwest, west, and northwest) as well as the condition of no aspect (slope = 0).

Analyzing the data with ArcMap, we obtained multiple indices of the density of flowering individuals. First, we used the Average Nearest Neighbor tool, within the Spatial Statistics toolset of ArcMap, to compute nearest neighbor distances (NND) for all sampled plants within each sub-population of each patch-pair during each year of sampling. Additionally, we used the Hawth's Tools extension (Beyer 2004) to construct minimum convex polygons (MCP) enclosing each sub-population of each patch-pair during each year, to obtain two additional indices of the density of flowering individuals: the area (ha) of each MCP and the density (flowering individuals/ha) of sampled plants contained within each MCP.

Statistical Analysis

Statistical analyses were conducted using the SAS/GLIMMIX procedure (version 9.2; SAS Institute 2007) with Kenward-Roger degrees of freedom adjustments. Plant variables (height, number of capitula, biomass) measured in 2006 and 2007 were analyzed using a linear mixed model where patch-pair identity, plant sub-population identity, and individual plant identity were treated as random effects, while burn history (recent burn, older burn) was treated as a fixed effect. Northness and eastness were included as covariates in the mixed model analyses. Density indices (NND, MCP, density of flowering individuals) were analyzed by sample year using a generalized linear mixed model with a fixed effect of burn history. For all analyses, statistical significance was set at $\alpha = 0.05$.

RESULTS

2006 Sampling of Summer Burns

Mixed model analyses identified a significant effect of burn history on vegetative biomass ($P = 0.04$). The aspect variables were adopted as covariates in the analysis of plant height ($P \leq 0.014$), total biomass ($P = 0.045$), and reproductive biomass ($P \leq 0.046$). After adopting the aspect variables as covariates, post-hoc analyses comparing the two burn histories at selected values of the covariates were performed. Height of plants within recent burns was lower ($P < 0.001$) than those in older burns on southwestern and western aspects while vegetative biomass of plants in recent summer burns was higher ($P \leq 0.04$) than those in older summer burns on northern, northeastern, eastern, southeastern, and southern aspects as well as on areas with no slope or aspect (Figure 1). In 2006, MCP values were higher ($P = 0.028$) in older summer burns and density of flowering individuals was higher ($P = 0.029$) in recent summer burns (Figure 2).

2007 Sampling of Spring Burns

The aspect variables were adopted as covariates in the analysis of plant height ($P = 0.026$), vegetative biomass ($P \leq 0.027$), total biomass ($P \leq 0.029$), reproductive

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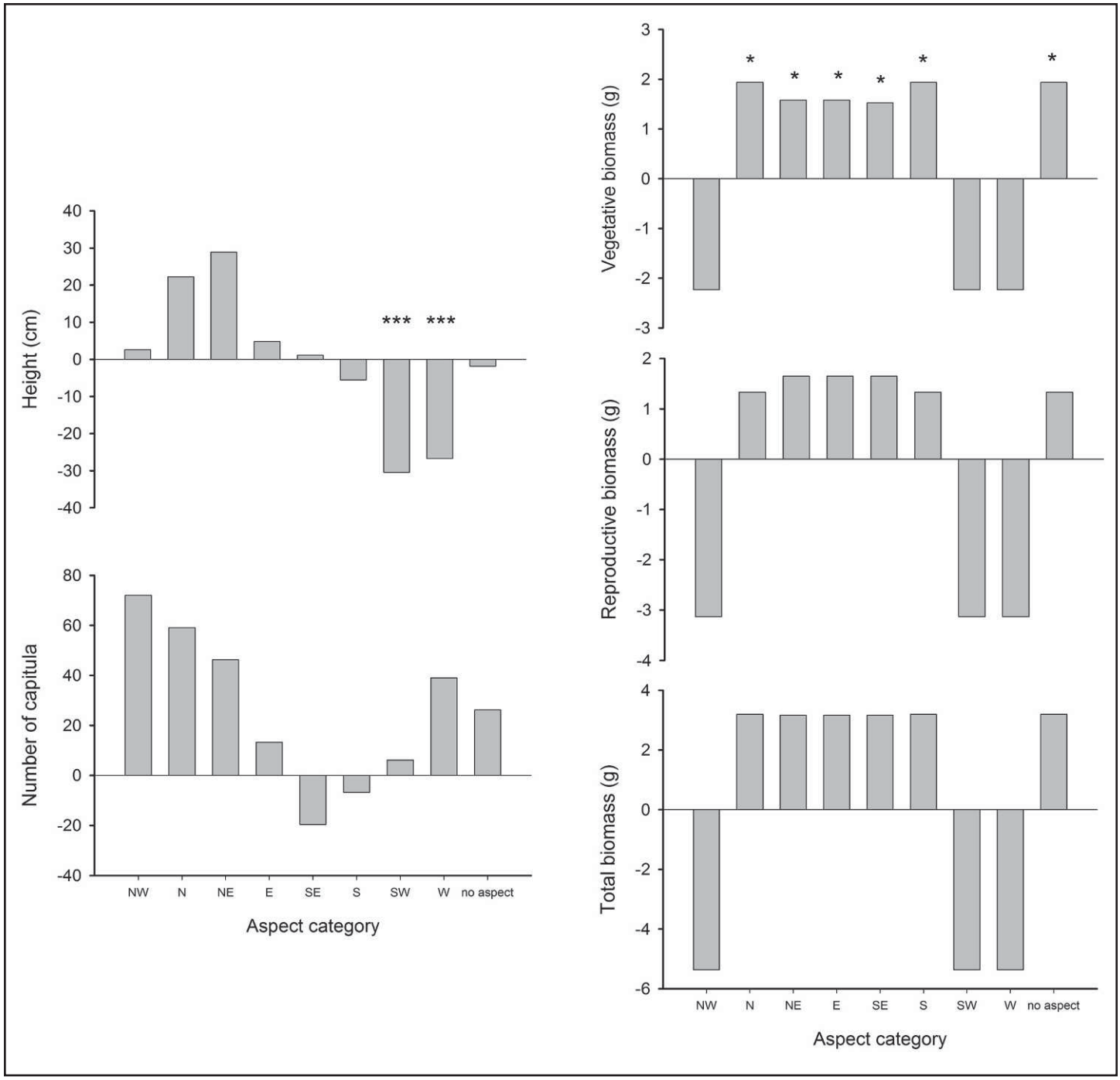


Figure 1. Differences between the estimated least square means for *Arnoglossum plantagineum* plant variables in recent (2005) and older (2001 – 2003) summer burns for each aspect category in 2006. A positive value indicates the least square means estimate for the recent burn was greater than the estimate for the older burn; a negative value indicates the estimate for the recent burn was less than the estimate for the older burn. Significance levels for tests of recent burn means versus older burn means are as follows: * indicates P < 0.05; ** indicates P < 0.01; * indicates P < 0.001).**

biomass (P = 0.027), and number of capitula ($P \leq 0.049$). After adopting the aspect variables as covariates, post-hoc analyses comparing the two burn histories at selected values of the covariates were performed. Height of plants within recent spring burns was lower (P = 0.010) than those in older spring burns on southern aspects (Figure 3). Vegetative biomass within recent spring burns was higher ($P \leq 0.026$) than within older spring burns on northwestern, northeastern, eastern, southeastern, southwestern, and western aspects. Likewise, total biomass within recent spring burns was higher ($P \leq 0.031$) than within older spring burns on northwestern, northeastern, eastern, southeastern, southwestern, and western aspects. The number of capitula per plant in recent spring burns was higher (P = 0.017) on northeastern aspects but this variable was lower ($P \leq 0.039$) than

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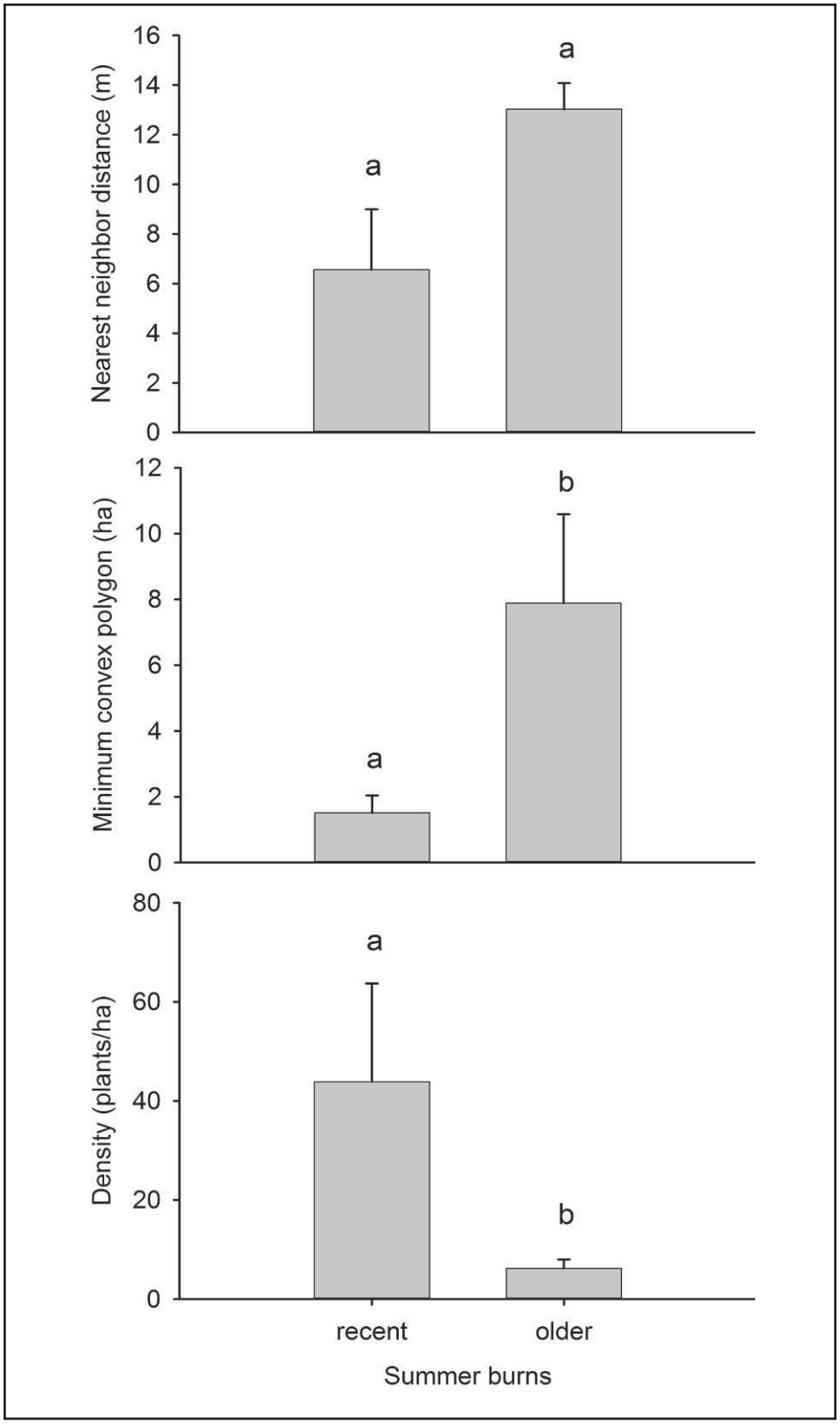


Figure 2. Estimates of least square means (± SE) for *Arnoglossum plantagineum* density indices in recent (2005) and older (2001 – 2003) summer burns measured in 2006. Different letters above bars indicate significant differences at the α = 0.05 level.

the number of capitula per plant in older spring burns on southern, southwestern, and western aspects. In 2007, NND and MCP values were higher (P = 0.038 and P = 0.032, respectively) in older spring burns while flowering plant density was higher (P = 0.033) in recent spring burns (Figure 4).

DISCUSSION

Our results demonstrate that fire, bison grazing, and topographic position interact to influence the growth and reproductive effort of *A. plantagineum*. In most instances where *A. plantagineum* responded to this interaction, the response suggested greater resource availability in recently burned patches that were being heavily grazed relative to patches where a longer period of time had elapsed since burning and where minimal grazing was occurring. Furthermore, this response occurred when the fire-grazing interaction was driven by both summer fires and spring fires. During both years of our study, plant height was usually similar between patches with differing burn histories for most aspect categories, but there were instances where plant height was significantly lower in recently burned patches that were being heavily grazed compared to plants that were in patches that weren't recently burned and were being minimally grazed. This suggests that, on some topographical aspects, grazing in a recently burned patch allowed sufficient light to reach *A. plantagineum* plants such that this forb could allocate carbon resources to life history attributes other than height, such as leaves or reproductive structures. A similar response of plant height in areas grazed by bison compared to ungrazed areas was reported for the prairie forbs *Ambrosia psilostachya* DC., *Symphyotrichum ericoides* (L.) G.L. Nesom var. *ericoides*, and *Vernonia baldwinii* Torr. (Fahnestock and Knapp 1993, 1994). A caveat of the research done by Fahnestock and Knapp (1993, 1994) is that their use of the term grazed implied that sampling occurred in areas where the vegetation matrix surrounding a sampled forb was primarily grasses that had been recently grazed. Conversely, their use of the term ungrazed implied that sampling occurred in an area

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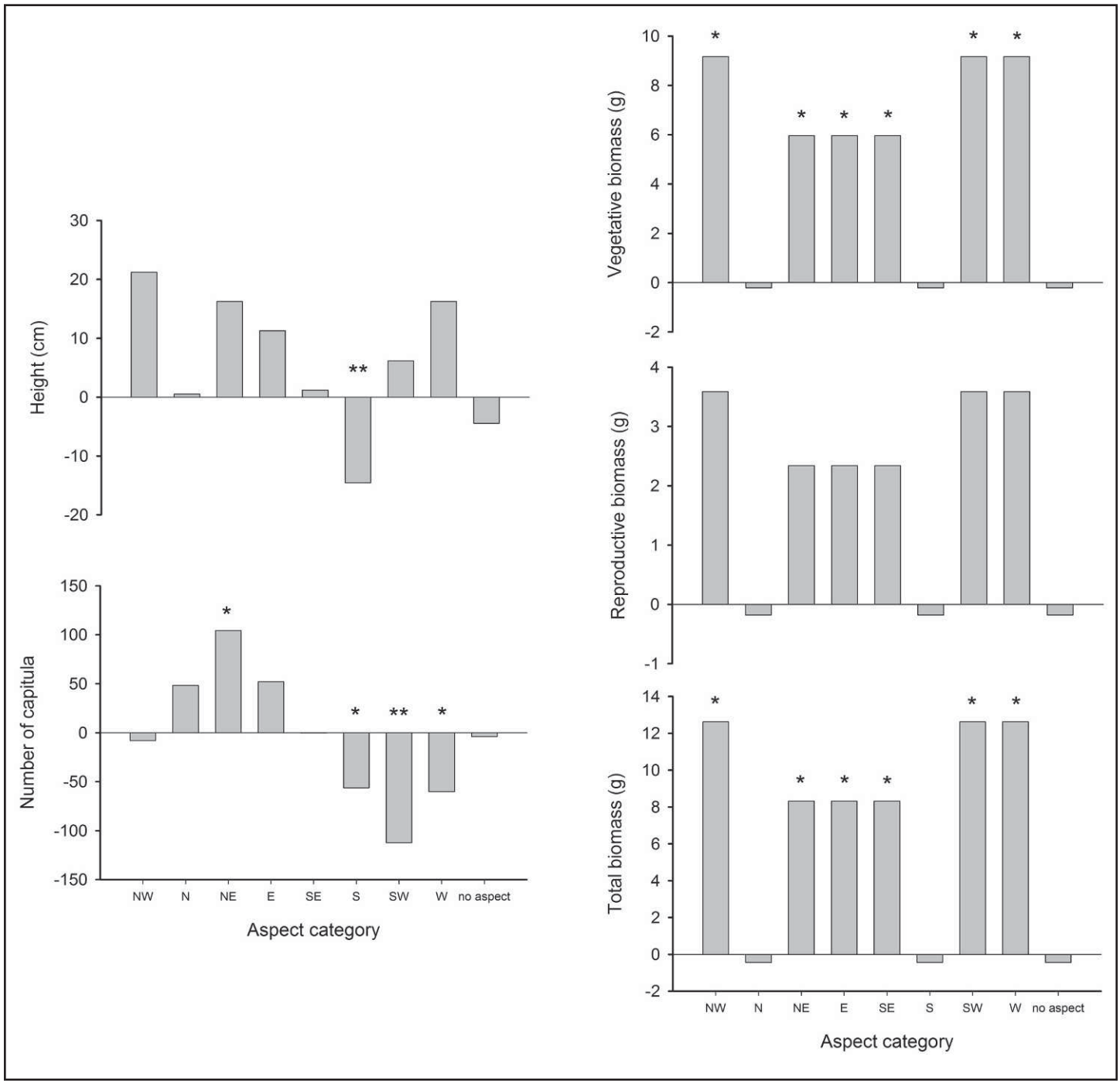


Figure 3. Differences between the estimated least square means for *Arnoglossum plantagineum* plant variables in recent (2007) and older (2004 – 2005) spring burns for each aspect category in 2007. A positive value indicates the least square means estimate for the recent burn was greater than the estimate for the older burn; a negative value indicates the estimate for the recent burn was less than the estimate for the older burn. Significance levels for tests of recent burn means versus older burn means are as follows: * indicates P < 0.05; ** indicates P < 0.01; * indicates P < 0.001).**

where the vegetation matrix surrounding a sampled forb was primarily grasses that had not been grazed recently, even though that area was actually in a pasture where grazing animals were present and grazing may have occurred earlier in the season or in previous seasons.

Damhoureyeh and Hartnett (1997) found that height of the prairie forb *Oenothera speciosa* Nutt. was less in bison-grazed areas relative to ungrazed areas (the ungrazed areas being pastures that were not being grazed by bison or cattle). However, Damhoureyeh and Hartnett (1997) found no differences in the height of three prairie forbs (*Baptisia bracteata* Muhl. ex Elliott, *Salvia azurea* Michx. ex Lam., and *V. baldwinii*) when bison-grazed areas were compared to ungrazed areas. Damhoureyeh and Hartnett (1997) also reported an effect of fire frequency on the response of height in the prairie forb *Solidago missouriensis* Nutt. to bison grazing; in annually burned

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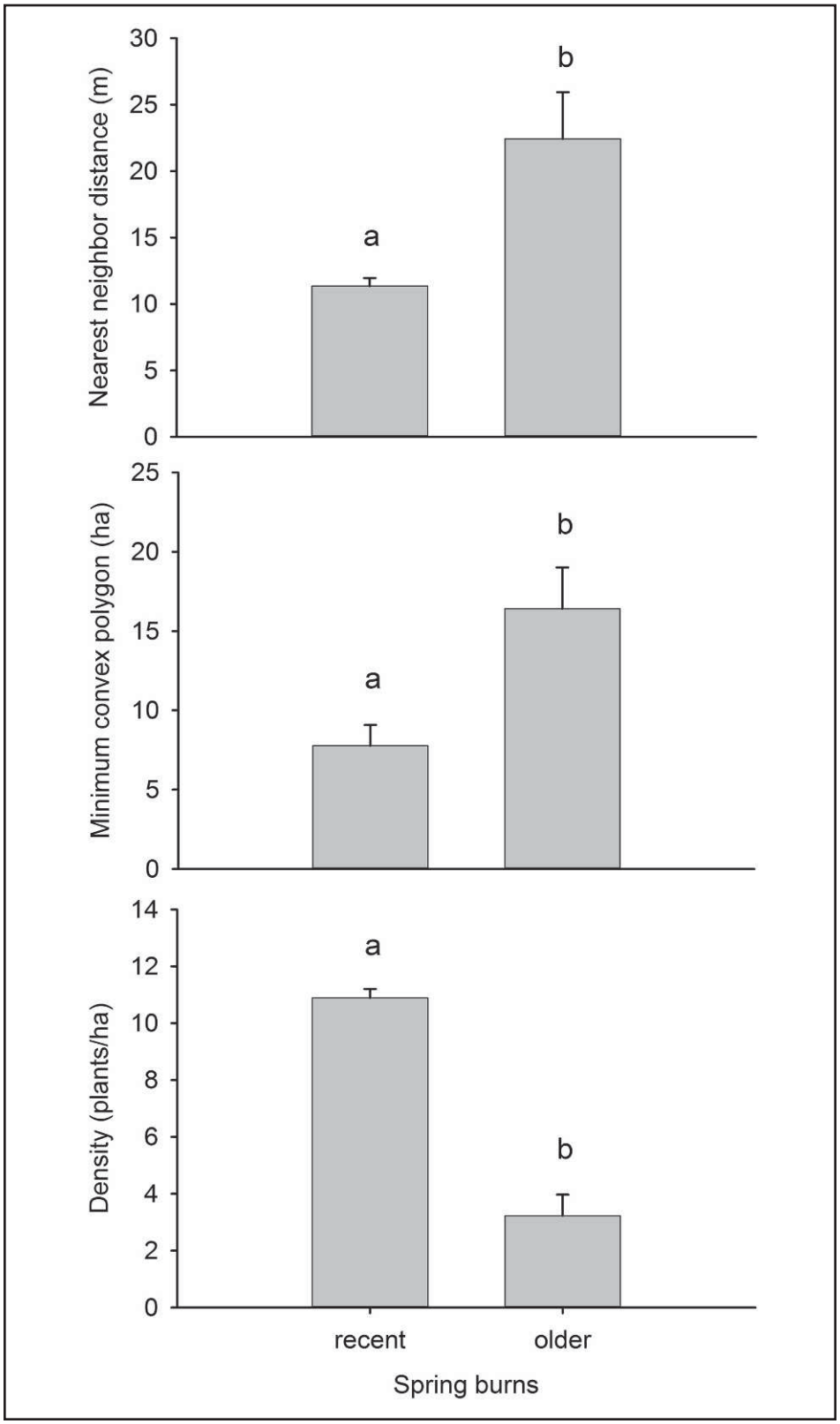


Figure 4. Estimates of least square means (± SE) for *Arnoglossum plantagineum* density indices in recent (2007) and older (2004 – 2005) spring burns measured in 2007. Different letters above bars indicate significant differences at the α = 0.05 level.

watersheds there was no difference in height, in watersheds burned every fourth year plants in ungrazed areas were taller than plants in grazed areas. When Damhoureyeh and Hartnett (1997) compared areas grazed by cattle to ungrazed areas, however, they found no differences in plant height for *B. bracteata*, *O. speciosa*, *S. missouriensis*, and *V. baldwinii*, regardless of fire frequency. Damhoureyeh and Hartnett (1997) did find that height of *S. azure* was greater in ungrazed areas than cattle grazed areas in watersheds that were annually burned, but there were no differences in height of *S. azure* in watersheds that were burned every fourth year.

During our study in 2006, total biomass did not differ between patches that had been recently burned and were heavily grazed compared to patches that had not recently burned and were minimally grazed, regardless of aspect category. In 2007, however, total biomass of plants in recently burned patches was higher for most aspect categories compared to total biomass of plants in patches that had not recently burned. During both years, vegetative biomass of plants in recently burned patches was higher for most aspect categories compared to total biomass of plants in patches that had not recently burned. Greater total biomass in areas grazed by bison compared to ungrazed areas was also reported for *A. psilostachya* (Fahnestock and Knapp 1993, 1994), while Damhoureyeh and Hartnett (1997) reported that *B. bracteata* had greater total biomass in bison-grazed areas compared to ungrazed areas within watersheds burned every fourth year, but not in watersheds that were burned annually. Total biomass of *V. baldwinii* was reported by Fahnestock and Knapp (1993, 1994) to not differ between areas grazed by bison compared to ungrazed areas; to not differ in annually burned watersheds grazed by bison compared to annually burned watersheds that were ungrazed (Damhoureyeh and Hartnett 1997); but to be greater in watersheds that were burned every fourth year and grazed by bison compared to watersheds that were burned every fourth year and were ungrazed (Damhoureyeh and Hartnett 1997).

Contrasting with much of the reported

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results for forb biomass in bison grazed and ungrazed areas, total biomass of *S. ericoides* was reported by Fahnestock and Knapp (1993) to be greater in ungrazed areas compared to areas grazed by bison. However, *S. ericoides* is a species known to be consumed by cattle, and a relationship between increasing cattle stocking rates and decreasing biomass of *S. ericoides* has been documented (Hickman and Hartnett 2002). Indeed, Fahnestock and Knapp (1993) indicated that some of the *S. ericoides* plants they sampled in grazed areas appeared to have had some of their plant parts removed by grazing bison. In areas grazed by cattle, Damhoureyeh and Hartnett (1997) reported that total biomass of *B. bracteata* and *O. speciosa* was greater when compared to ungrazed areas, while total biomass of *S. azurea*, *S. missouriensis*, and *V. baldwinii* did not differ between grazed and ungrazed areas, regardless of burn frequency.

In 2006, we found no differences in reproductive biomass or the number of capitula when recent summer burns were compared to older summer burns, regardless of topographic position. In 2007 when spring burns were sampled, there were no differences in reproductive biomass at any topographic position. There was variability, however, in the response of number of capitula that year. This variable was greater on some topographic positions, less on other topographic positions, and did not differ on the remaining topographic positions when recent spring burns were compared to older spring burns. *Vernonia baldwinii* was shown to have greater reproductive biomass in bison-grazed areas compared to ungrazed areas (Fahnestock and Knapp 1993, 1994). The number of florets and flowering heads of *V. baldwinii* were greater in bison-grazed areas compared to ungrazed areas (Fahnestock and Knapp 1993, 1994). Damhoureyeh and Hartnett (1997) measured multiple variables representing reproductive structures (flowers, flower heads, capsules, seeds, etc.); and in all instances when there were significant differences between grazed areas and ungrazed areas, those variables were greater in grazed areas, regardless of whether the grazing was done by bison or cattle.

During both years of our study, we found higher indices of flowering plant density in recent burns compared to older burns. We acknowledge these aren't indices of actual population density because we only recorded the presence of individuals that were flowering. Flowering individuals of *A. plantagineum*, which can have an inflorescence positioned up to 0.10 m above the ground, were readily visible during sampling while individuals that weren't flowering at the time of sampling were most often represented by only a basal rosette of leaves and were much less visible. This was especially the case within patches that hadn't been burned for multiple years and a rank canopy of grasses was present. Nonetheless, our density indices provide further evidence that *A. plantagineum* individuals within a recently burned patch were responding to greater resource availability. If there is an assumption that actual population density of this perennial plant was equal in all patches, the higher density of flowering individuals within recently burned patches implies that a greater proportion of individuals within recently burned patches had access to sufficient resources permitting sexual reproduction.

In the landscape we studied, where pyric herbivory and topography interacted to create a shifting mosaic of heterogeneity, *A. plantagineum* may have been responding to alterations of environmental conditions (light levels, soil temperature) experienced at the microsite of an individual plant as well as to altered competitive relationships with neighboring grasses. The occurrence of fire alone or grazing alone could potentially result in these alterations as well, but it is possible that the interaction of fire and grazing that arises from pyric herbivory facilitates an alteration of environmental conditions and community interactions that are unique, relative to the occurrence of either fire alone or grazing alone. This is supported by research on *V. baldwinii* and *Ratiba columnifera* (Nutt.) Woot. & Standl. in landscapes that were only burned and were not grazed, where multiple measures of plant growth and reproductive effort had their greatest values in unburned watersheds, or watersheds that had gone the longest time without being burned (Knapp 1984; Hartnett 1991).

The fire grazing interaction has been demonstrated to alter vegetation structure and composition (Fuhlendorf and Engle 2004; Vermeire et al. 2004; Coppedge et al. 2008; Winter et al. 2012). For natural area managers, application of the fire grazing interaction may be especially useful for the achievement of management objectives that seek to increase the heterogeneity or diversity of vegetation in prairies (Helzer and Steuter 2005; Fuhlendorf et al. 2006). Previous research has shown that forb communities or functional groups respond positively to the fire grazing interaction (Fuhlendorf and Engle 2004; Vermeire et al. 2004; Coppedge et al. 2008; Winter et al. 2012). Previous research on individual prairie forb species has highlighted the role of altered competitive dynamics between dominant grasses and subdominant forbs in driving the response of forbs at the level of an individual plant (Knapp 1984; Hartnett 1991; Fahnestock and Knapp 1993, 1994; Damhoureyeh and Hartnett 1997). Our results for a single prairie forb provide further evidence of the presumed mechanism for all of these responses – forbs growing in areas that have been recently burned, and where their neighboring grasses are being heavily grazed, can be characterized by enhanced growth and reproductive effort, regardless of fire season. This implies the fire grazing interaction provides prairie forbs with a period of enhanced resource availability.

The response of individual prairie forbs to altered competitive dynamics, as mediated by fire and grazing, has been shown to vary depending on the forb being studied, the plant variables being measured, fire frequency, and the species of herbivore; but the majority of results indicate that grazing of neighboring grasses around an individual forb has neutral to positive effects on the forb (Fahnestock and Knapp 1993, 1994; Damhoureyeh and Hartnett 1997). Our results provide evidence of another variable that influences the response of a prairie forb to altered competitive dynamics – the response of *A. plantagineum* to the fire grazing interaction varied depending on topographical position. This indicates that the effects of land management ac-

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tions, such as application of the fire grazing interaction, may vary among differing locations of a landscape.

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