

Research Article

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Relationship between local-scale topography and vegetation on the invasive *C₄* perennial bunchgrass buffelgrass (*Pennisetum ciliare*) size and reproduction

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Abstract

Buffelgrass [*Pennisetum ciliare* (L.) Link] is an invasive *C₄* perennial bunchgrass that is a threat to biodiversity in aridlands in the Americas and Australia. Topography influences *P. ciliare* occurrence at large spatial scales, but further investigation into the relationship between local-scale topography and *P. ciliare* growth and reproduction would be beneficial. Further, density-dependent effects on *P. ciliare* growth and reproduction have been demonstrated in greenhouse experiments, but the extent to which density dependence influences *P. ciliare* in natural populations warrants further investigation. Here we present a study on the relationships between local-scale topography (aspect and slope gradient) and vegetation characteristics (shrub cover, *P. ciliare* cover, and *P. ciliare* density) and their interactions on individual *P. ciliare* plant size and reproduction. We measured slope gradient, aspect, shrub cover, *P. ciliare* cover, *P. ciliare* density, and the total number of live culms and reproductive culms of 10 *P. ciliare* plants in 33 4 by 4 m plots located in 11 transects at the Desert Laboratory at Tumamoc Hill, Tucson, AZ, USA. We modeled the relationships at the local scale of (1) *P. ciliare* cover and density with aspect and slope gradient and (2) *P. ciliare* size and reproduction with abiotic (slope gradient and aspect) and biotic (*P. ciliare* cover and density and native shrub and cacti cover) characteristics. Aspect and slope gradient were poor predictors of *P. ciliare* cover and density in already invaded sites at the scale of our plots. However, aspect had a significant relationship with *P. ciliare* plant size and reproduction. *Pennisetum ciliare* plants on south-facing aspects were larger and produced more reproductive culms than plants on other aspects. Further, we found no relationship between *P. ciliare* density and *P. ciliare* plant size and reproduction. Shrub cover was positively correlated with *P. ciliare* reproduction. South-facing aspects are likely most vulnerable to fast spread and infilling by new *P. ciliare* introductions.

Introduction

Buffelgrass [*Pennisetum ciliare* (L.) Link; syn.: *Cenchrus ciliaris* L.] is a perennial, *C₄*, warm-season bunchgrass native to Africa, India, and the Middle East (Ibarra et al. 1995). In the 1940s, *P. ciliare* strain T-4464 collected from Kenya was introduced to the southwestern United States as forage for cattle and for soil erosion control (Ibarra et al. 1995; Marshall et al. 2012; Rodríguez-Rodríguez et al. 2017). Due to its drought tolerance and rapid establishment, *P. ciliare* has since been used to enhance livestock production by converting desert scrub vegetation to grassland throughout the Sonoran Desert (Brenner 2011; Jernigan et al. 2016; Williams and Baruch 2000). By 1985, this strain of *P. ciliare* (T-4464) had unintentionally expanded to more than 4 million ha (Cox et al. 1988), and today *P. ciliare* has invaded 8 to 10 million ha of Sonoran Desert ecosystem in the United States and Mexico (Burquez et al. 1996; Williams and Baruch 2000).

Invasion by *P. ciliare* poses a significant threat to Sonoran Desert plant communities, both directly via competition and indirectly via ecosystem modification. In upland Sonoran Desert habitats, *P. ciliare* reduces the species richness and diversity of native vegetation through competition for water and space (Jernigan et al. 2016; Olsson et al. 2012a). *Pennisetum ciliare* outcompetes ecologically similar native perennial bunchgrasses such as Arizona cottontop [*Digitaria californica* (Benth.) Henr.] by reducing both their aboveground biomass and reproductive output (Stevens and Fehmi 2011). Spread of *P. ciliare* also has the potential to increase the frequency and intensity of fire, leading to a shift from native desert scrub to nonnative grassland vegetation (McDonald and McPherson 2011; Rodríguez-Rodríguez et al. 2017; Stevens and

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Management Implications

Our results suggest that south-facing aspects are especially vulnerable to high rates of *Pennisetum ciliare* (buffelgrass) spread. Increased reproduction of *P. ciliare* on south-facing aspects results in high propagule pressure, which promotes successful establishment of exotic species in newly invaded areas. Invasive plants often have higher spread rates in newly established patches. Furthermore, larger *P. ciliare* plant size on south-facing aspects likely results in greater abundance of fine fuel, which increases the risk of wildfire on south-facing aspects invaded by *P. ciliare*. Therefore, early detection and control of *P. ciliare* on south-facing aspects is imperative for efficient management of *P. ciliare* invasion.

We recommend enhanced *P. ciliare* monitoring on south-facing aspects to increase early detection of *P. ciliare*. It is also imperative for managers to monitor previously treated areas to detect regrowth of *P. ciliare* from the seedbank. Remote sensing may be a viable tool for early detection *P. ciliare* invasion and regrowth following treatment where managers need to monitor large or inaccessible areas. We also recommend treating *P. ciliare* on south-facing aspects early in the growing season (before it sets seed) to reduce *P. ciliare* spread rates. Manual removal and herbicide application have been shown to be effective at reducing *P. ciliare* abundance, although soil disturbance from manual removal may enhance *P. ciliare* germination and establishment of new seedlings. Combining treatment methods (i.e., herbicide application followed by seeding native plants) is most effective for reducing *P. ciliare* abundance.

Falk 2009). Conversion of desert scrub to grassland causes ecophysiological changes and alters the microclimate near the soil surface, reducing germination and establishment of native plant species (Bracamonte et al. 2017; Castellanos et al. 2016). Presence of *P. ciliare* also elevates the risk of wildfires spreading from higher-elevation biomes such as grassland and oak (*Quercus* spp.) woodland into lower-elevation desert habitat and “wildland–urban interfaces” by providing a continuous fine fuel source (Brenner and Franklin 2017; Olsson et al. 2012b).

In large-scale studies of its distribution in the Sonoran Desert region, *P. ciliare* is mainly found on steep south, southeast, and southwest aspects and is less commonly found on north and east aspects (Elkind et al. 2019; Van Devender and Dimmitt 2006). Abella et al. (2012) found that there was no difference in aspect or slope gradient in patches occupied or unoccupied by *P. ciliare* in Saguaro National Park but concluded that *P. ciliare* had likely not yet invaded every vulnerable site. Given observed variation in *P. ciliare* distribution across differing aspects and slope gradients, it is likely that these factors contribute to *P. ciliare*’s ability to establish, grow, and spread, as has been found with other grasses (Shriver et al. 2021). However, to date, we are not aware of a study that examines the effects of the abiotic variables of aspect and slope gradient on *P. ciliare* density, cover, growth, and reproduction at the scale of plant neighborhoods in which plants experience specific microsite conditions and plant–plant interactions are likely to occur (i.e., local scale).

Interactions between the extant plant community and *P. ciliare* may also affect *P. ciliare* growth and reproduction, as has been observed with native Sonoran Desert plants. In highly stressful conditions (e.g., during drought), plants can facilitate their neighbors. The effect of ironwood trees (*Olneya tesota* A. Gray) on the

surrounding plant community shifted from positive to neutral/negative along a stress gradient in the Sonoran Desert (Tewksbury and Lloyd 2001). In dryer xeric sites, *O. tesota* had a positive effect on plant richness and abundance but little to no effect on plant richness and abundance in less-stressful mesic sites (Tewksbury and Lloyd 2001). Griffith (2010) demonstrated that native shrubs facilitated both seedling establishment and reproductive potential of the invasive grass cheatgrass (*Bromus tectorum* L.) by providing higher soil fertility and a less extreme microhabitat in the Great Basin Desert. Gray and Steidl (2015) found variable associations between native shrubs and *P. ciliare* cover. Farrell and Gornish (2019) found that seeding native species reduces *P. ciliare* abundance and enhances the effectiveness of other *P. ciliare* control measures (i.e., herbicide application or manual removal). It is possible that *P. ciliare* may be facilitated by shrub cover in physically stressful environments or inhibited by native grasses and forbs. The relationships between native vegetation and density, cover, growth, and reproduction of *P. ciliare* warrant further investigation, especially in local-scale plant neighborhoods.

Due to the significant ecological damage caused by *P. ciliare*, as well as the ongoing challenges of controlling the invasion, information about how *P. ciliare* responds to within-site abiotic and biotic characteristics would help land managers develop more targeted management strategies. Our aim was to determine the relationships between environmental factors and *P. ciliare* size and reproductive output during the primary growing season. We specifically chose easily identifiable site characteristics, as it is our goal to provide land managers—who often rely on technologically simple approaches to characterize invaded sites—with recommendations for control. We examined the local-scale relationships of (1) abiotic characteristics (slope gradient and aspect) with *P. ciliare* cover and density and (2) abiotic (slope gradient and aspect) and biotic (*P. ciliare* cover and density and cover of native shrubs and cacti) characteristics with *P. ciliare* size and reproduction in a heavily invaded site in Tucson, AZ, USA. We hypothesized that (1) *P. ciliare* cover and density would be higher on steeper slopes and on south- and west-facing aspects due to its drought and temperature tolerance; (2) *P. ciliare* size and reproduction would be higher on south- and west-facing aspects (i.e., more heat/sun); (3) there would be positive interaction between shrub cover and *P. ciliare* size and reproduction on south- and west-facing and steep slopes (i.e., nurse effect in more abiotically stressful conditions); and (4) *P. ciliare* size and reproduction would be lower in plots with higher *P. ciliare* density and cover due to intraspecific competition.

Materials and Methods

Study Area

This study was conducted at the Desert Laboratory on Tumamoc Hill, located west of downtown Tucson, AZ, USA (32.217°N, 111.000°W). Tumamoc Hill is approximately 25 km away from Saguaro National Park Rincon Mountain District and approximately 19 km away from Saguaro National Park Tucson Mountain District. The Desert Laboratory is a 352-ha research station and ecological preserve owned and managed by the University of Arizona. The 1981 to 2010 30-yr mean annual precipitation at the Desert Laboratory is 296 mm yr⁻¹, approximately half of which falls during the summer monsoon season (141 mm from July to September) and half of which falls during the winter months (129 mm from November to March) (PRISM Climate Group 2021). The 1981 to 2010 30-yr mean maximum and minimum

daily temperatures are 19.05 and 4.11 °C in the coldest month (January) and 38.17 and 20.56 °C in the hottest month (June) (PRISM Climate Group 2021). In 2020, the Desert Laboratory received only 123.2 mm total rainfall (a 59% decrease compared with the 30-yr average), 50.8 mm during the monsoon season (July to September; a 63% decrease compared with the 30-yr average) and 61.5 mm from January to April (a 53% decrease compared with the 30-yr average) (PRISM Climate Group 2021). In 2020, the mean maximum and minimum daily temperatures were 19.05 and 4.5 °C in January and 41.0 and 26.39 °C during the hottest month, which was August (PRISM Climate Group 2021). The substrate of Tumamoc Hill is a rocky basaltic-andesitic soil (Bowers et al. 2006). *Pennisetum ciliare* was first recorded at Tumamoc Hill in 1968 and became naturalized after two periods of elevated monsoon season rainfall in 1970 to 1972 and 1982 to 1984 (Burgess et al. 1991). Between 1983 and 2005, the frequency of *P. ciliare* occurrence at Tumamoc Hill increased by nearly 8,000% (Bowers et al. 2006).

Study Design and Data Collection

In August and September of 2020, eleven 20 by 4 m transects were installed on Tumamoc Hill. Transect locations for each aspect were selected randomly within the mapped extent of *P. ciliare* on Tumamoc Hill using GIS. Three transects were installed on north-facing aspects, three on west-facing aspects, three on south-facing aspects, and two on east-facing aspects. Each transect contained three 4 by 4 m plots separated by a 4 by 4 m gap.

In each plot, we measured percent cover of the following plant classes: (1) shrubs and cacti; (2) native grasses; (3) forbs; and (4) *P. ciliare*. We counted individual *P. ciliare* plants in each plot to calculate *P. ciliare* density (*P. ciliare* plants m⁻²). In each plot, we threw 10 Trail Chasers® (brightly colored ground markers made of highly durable 15-cm plastic whiskers; Elusive Hunter, Norcross, GA 30092, USA) haphazardly into the plot from the plot edges and tagged the *P. ciliare* plants nearest to each Trail Chaser® to follow through time. For each tagged plant, we counted the number of live reproductive culms and total live culms. Previous years' growth that was still attached to the tagged plants (senesced, brown/gray, had no visible green) was not counted. Finally, we took five point measurements of ground-surface slope gradient (percent grade in degrees) in each plot using a clinometer and calculated the mean slope gradient for each plot.

Data Analysis

Pennisetum ciliare cover and density were log transformed to meet normality assumptions. To test the relationships between local-scale topography (slope gradient and aspect) and *P. ciliare* cover and density, we performed forward stepwise regression with linear mixed-effects models using transect as a random effect and the following candidate variables as fixed effects: slope gradient, aspect, and a slope gradient by aspect interaction. *Pennisetum ciliare* cover and density were the response variables. To test the relationships between plot-scale topography and vegetation characteristics (slope gradient, aspect, *P. ciliare* cover, *P. ciliare* density, and shrub cover) and individual *P. ciliare* size and reproduction, we performed forward stepwise regression with generalized linear mixed-effects models using transect as a random effect and the following candidate variables as fixed effects: slope gradient, aspect, *P. ciliare* density, *P. ciliare* cover, shrub cover, and all possible interactions between aspect and the other fixed-effects variables. The response variable for plant size was number of live culms per plant,

and the response variable for reproduction was number of reproductive culms per plant. We eliminated native grass cover and native forb cover as predictor variables, because the range of values was too low (mean ± SE native grass percent cover was 4.2 ± 1.75; mean ± SE forb percent cover was 1.79 ± 0.54). We used Poisson distribution for count data (number of live culms and number of reproductive culms). We refit all best-fit models, determined model significance by comparing best-fit models to intercept-only models, and calculated the Nagelkerke pseudo-R² for the refit models (Mbachu et al. 2012). All analyses were conducted in R Statistical Software v. 4.2.1 (R Core Team 2022).

Results and Discussion

Slope gradient ranged from 4.4° to 31.6° with a mean ± SD of 15.1° ± 6.1°. *Pennisetum ciliare* cover ranged from 12% to 90% with a mean ± SD of 38.9% ± 19.1% and density ranged from 1.7 to 9.1 plants m⁻² with a mean ± SD of 3.8 ± 1.5 plants m⁻². Shrub cover ranged from 0% to 40% with a mean ± SD of 18.5% ± 12.1%.

Aspect, slope gradient, and the aspect by slope gradient interaction were all included in the best model for *P. ciliare* cover ($F(7, 25) = 1.86$, $P < 0.119$, adjusted $R^2 = 0.159$). Transect was not included as a random effect in the best model for *P. ciliare* cover. Aspect, slope gradient, and the aspect by slope gradient interaction had no relationship with *P. ciliare* cover ($P = 0.25$, $P = 0.77$, and $P = 0.23$, respectively; Figure 1A and C; Table 1). Aspect, slope gradient, and the aspect by slope gradient interaction were not included in the best model for *P. ciliare* density, which included transect as a random effect ($P < 0.001$; Figure 1B and D). Transect accounted for 40% of the random-effects variance; the remaining 60% of the random-effects variance was accounted for by within-transect variation.

Aspect, slope gradient, *P. ciliare* cover, *P. ciliare* density, shrub cover, aspect by slope gradient, aspect by *P. ciliare* cover, aspect by *P. ciliare* density, and aspect by shrub cover were included in the best model for number of live culms per plant ($P < 0.001$, pseudo- $R^2 = 0.75$). Transect was not included as a random effect in the best-fit model for number of live culms per plant. *Pennisetum ciliare* plants on south-facing aspects had the highest number of live culms ($P < 0.001$; Figure 2A; Table 1). *Pennisetum ciliare* plants on north- and west-facing aspects had fewer live culms than those on east-facing aspects ($P = 0.003$ and $P < 0.001$, respectively; Figure 2A; Table 1). Slope gradient alone had a slightly negative relationship with number of live culms per plant ($P = 0.001$; Figure 2D). There were significant slope gradient by aspect interactions. Slope gradient had a significant negative relationship with number of live culms per plant on north-, south-, and west-facing aspects when compared with east-facing aspects ($P < 0.001$; Figure 2B). *Pennisetum ciliare* cover had a positive relationship with number of live culms per plant on north-, south-, and west-facing aspects, but a negative relationship with number of live culms per plant on east-facing aspects ($P < 0.001$; Figure 2C). *Pennisetum ciliare* density had an overall negative relationship with number of live culms per plant ($P < 0.01$; Figure 2D). It had a positive relationship with number of live culms per plant on south-facing aspects, but a negative relationship with number of live culms per plant on north-, east-, and west-facing aspects ($P < 0.01$ and $P < 0.01$, respectively; Figure 2D). Neither shrub cover nor aspect by shrub cover interactions had a significant relationship with total live culms per plant ($P = 0.61$ and $P = 0.20$, respectively; Figure 2E).

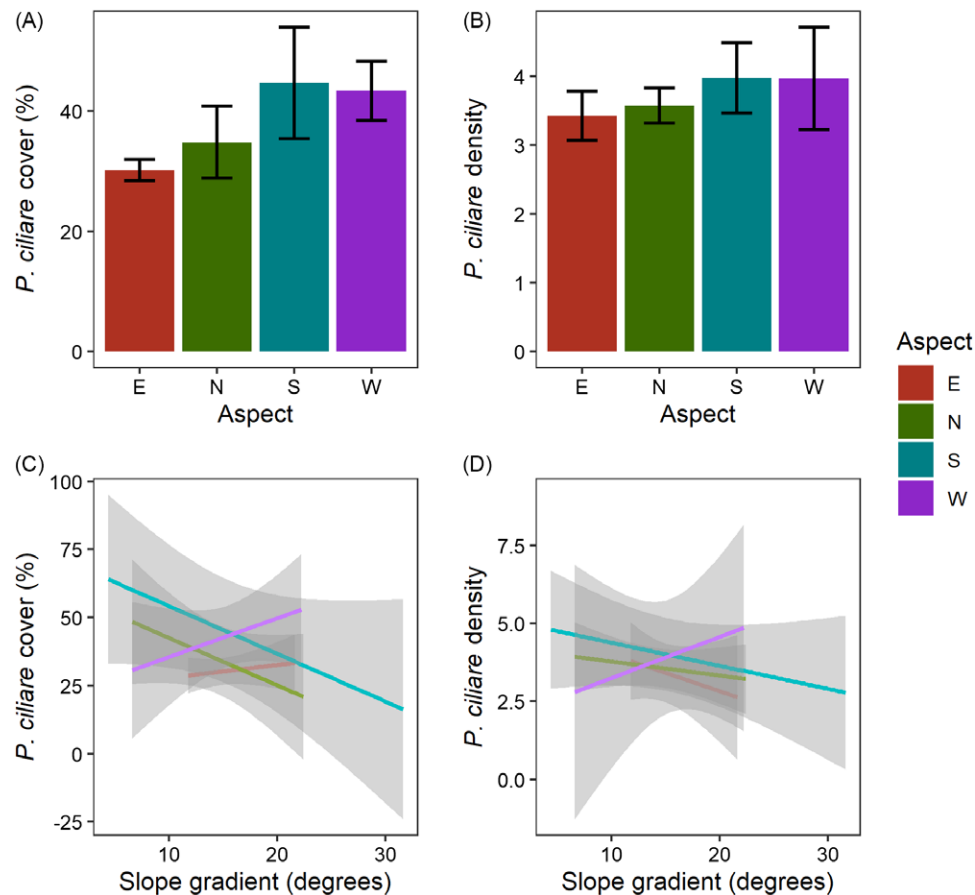


Figure 1. Mean *Pennisetum ciliare* percent cover by aspect (A) and in response to slope gradient (C). *Pennisetum ciliare* density (plants m⁻²) by aspect (B) and in response to slope gradient (D). Error bars represent SE. Gray shading represents the 95% confidence interval of the best-fit regression line.

Aspect, slope gradient, *P. ciliare* cover, *P. ciliare* density, shrub cover, aspect by slope gradient, aspect by *P. ciliare* cover, aspect by *P. ciliare* density, and aspect by shrub cover were included in the best-fit model for number of reproductive culms per plant ($P < 0.001$, pseudo- $R^2 = 0.67$). Transect was not included as a random effect in the best-fit model for number of reproductive culms per plant. *Pennisetum ciliare* plants on south-facing aspects had the highest number of reproductive culms ($P < 0.02$; Figure 3A; Table 1). On north-facing aspects, the number of reproductive culms per plant was lower than on south- and west-facing aspects ($P < 0.001$; Figure 3A; Table 1). Slope gradient alone did not have a significant relationship with number of reproductive culms per plant ($P = 0.10$; Figure 3B). However, on north-facing aspects, slope gradient had a negative relationship with number of reproductive culms per plant ($P < 0.016$; Figure 3D). Overall, *P. ciliare* cover had a positive relationship with number of reproductive culms per plant ($P < 0.01$; Figure 3C). On east-facing aspects, *P. ciliare* cover had a significant negative relationship with number of reproductive culms per plant ($P < 0.01$; Fig 3C). *Pennisetum ciliare* density alone did not have a significant relationship with number of reproductive culms per plant ($P = 0.35$), but on north-facing aspects, *P. ciliare* density had a significant negative relationship with number of reproductive culms per plant ($P < 0.01$; Figure 3D). Neither shrub cover nor shrub cover by aspect

interaction had a significant relationship with number of reproductive culms per plant ($P = 0.19$ and $P = 0.16$, respectively; Figure 3E).

Plot-Wide Patterns of Density and Cover

Aspect and slope gradient were poor predictors of *P. ciliare* cover and density in invaded areas at Tumamoc Hill at the scale of our 4 by 4 m plots. Although other studies have shown *P. ciliare* generally occurs more frequently on south-facing aspects, Jarnevich et al. (2018) found no evidence that environmental conditions such as summer and winter temperatures and precipitation limit the occurrence of *P. ciliare* within regionally suitable habitat. The observed distribution favoring south-facing aspects in other studies may simply indicate that *P. ciliare* has not yet invaded all suitable habitat available (Elkind et al. 2019; Jarnevich et al. 2018). Alternatively, although north-facing aspects may fall within the environmental tolerance thresholds of *P. ciliare*, their comparatively lower habitat suitability could slow per capita population growth rates of *P. ciliare*, resulting in slower colonization and lower observed occurrence rates in large-scale studies (Elkind et al. 2019; Jarnevich et al. 2018).

Slope gradient was also a poor predictor of *P. ciliare* distribution in Saguaro National Park (Jarnevich et al. 2018). Because our transects were located in invaded areas that are suitable habitat for *P.*

Table 1. *Pennisetum ciliare* percent cover, density (plants m⁻²), live culms per plant, and reproductive culms per plant (mean ± SE) for each aspect.

Aspect	<i>P. ciliare</i> % cover	<i>P. ciliare</i> density	<i>P. ciliare</i> live culms	<i>P. ciliare</i> reproductive culms
North	34.8 ± 5.96	3.58 ± 0.26	18.3 ± 1.34	6.58 ± 0.77
South	44.7 ± 9.27	3.98 ± 0.51	26.3 ± 1.74	12.2 ± 0.87
East	30.2 ± 1.76	3.43 ± 0.36	10.5 ± 1.99	9.75 ± 1.03
West	43.3 ± 4.93	3.97 ± 0.75	17.6 ± 1.25	9.90 ± 0.87

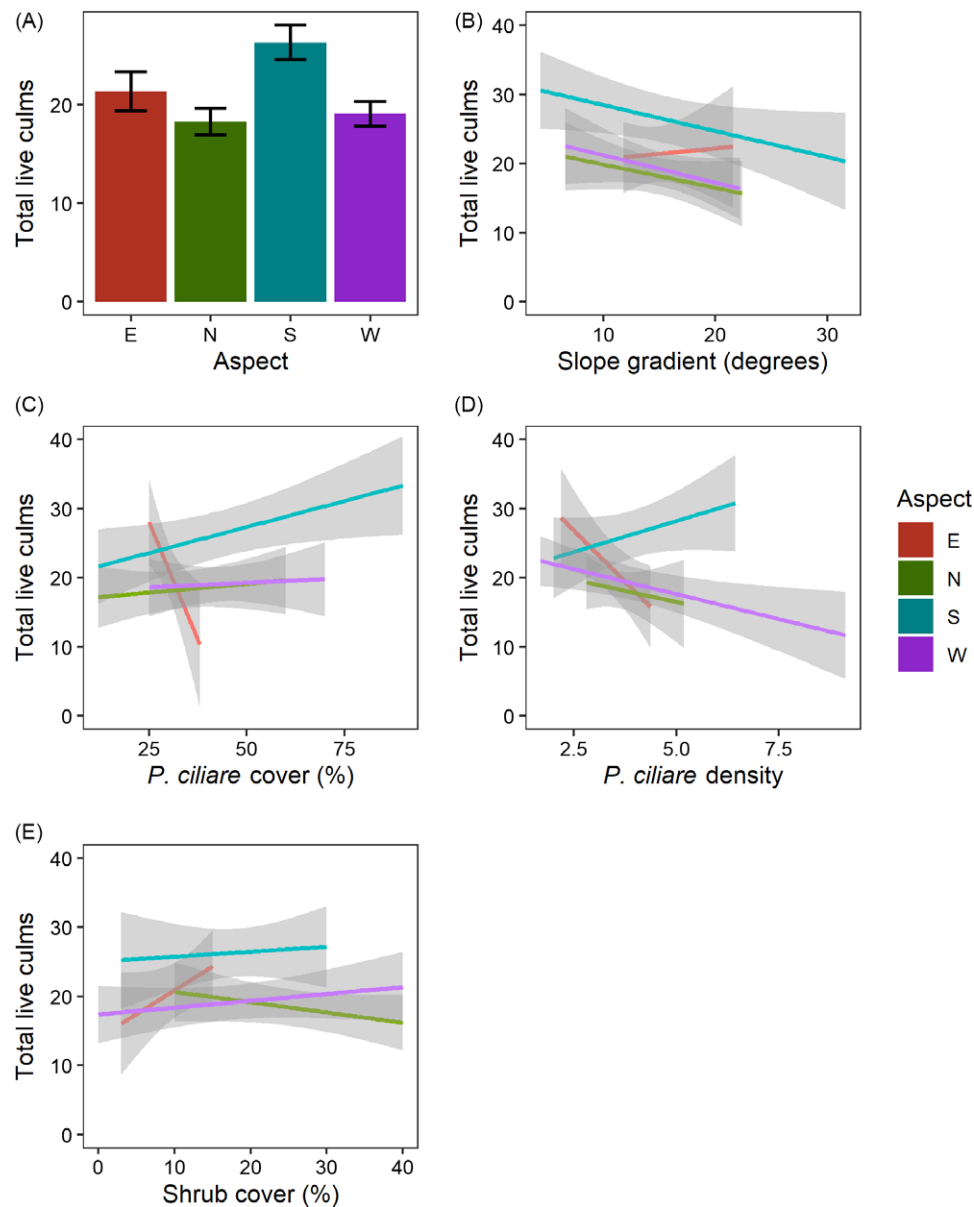


Figure 2. Total live culms of *Pennisetum ciliare* plants in response to aspect (A), slope gradient (B), *P. ciliare* cover (C), *P. ciliare* density (plants m⁻²) (D), and shrub cover (E). Error bars represent SE. Gray shading represents the 95% confidence interval of the best-fit regression line.

ciliare and because *P. ciliare* had been present at the site for >50 yr at the time of data collection, we conclude that *P. ciliare* has saturated areas where plots were located. Although we did not detect any effect of aspect or slope gradient on *P. ciliare* cover or density at

the scale of our 4 by 4 m plots, topographic variation can still affect microclimate conditions and individual plant growth and reproductive rates, resulting in greater frequency of *P. ciliare* on south-facing aspects at large scales (Elkind et al. 2019).

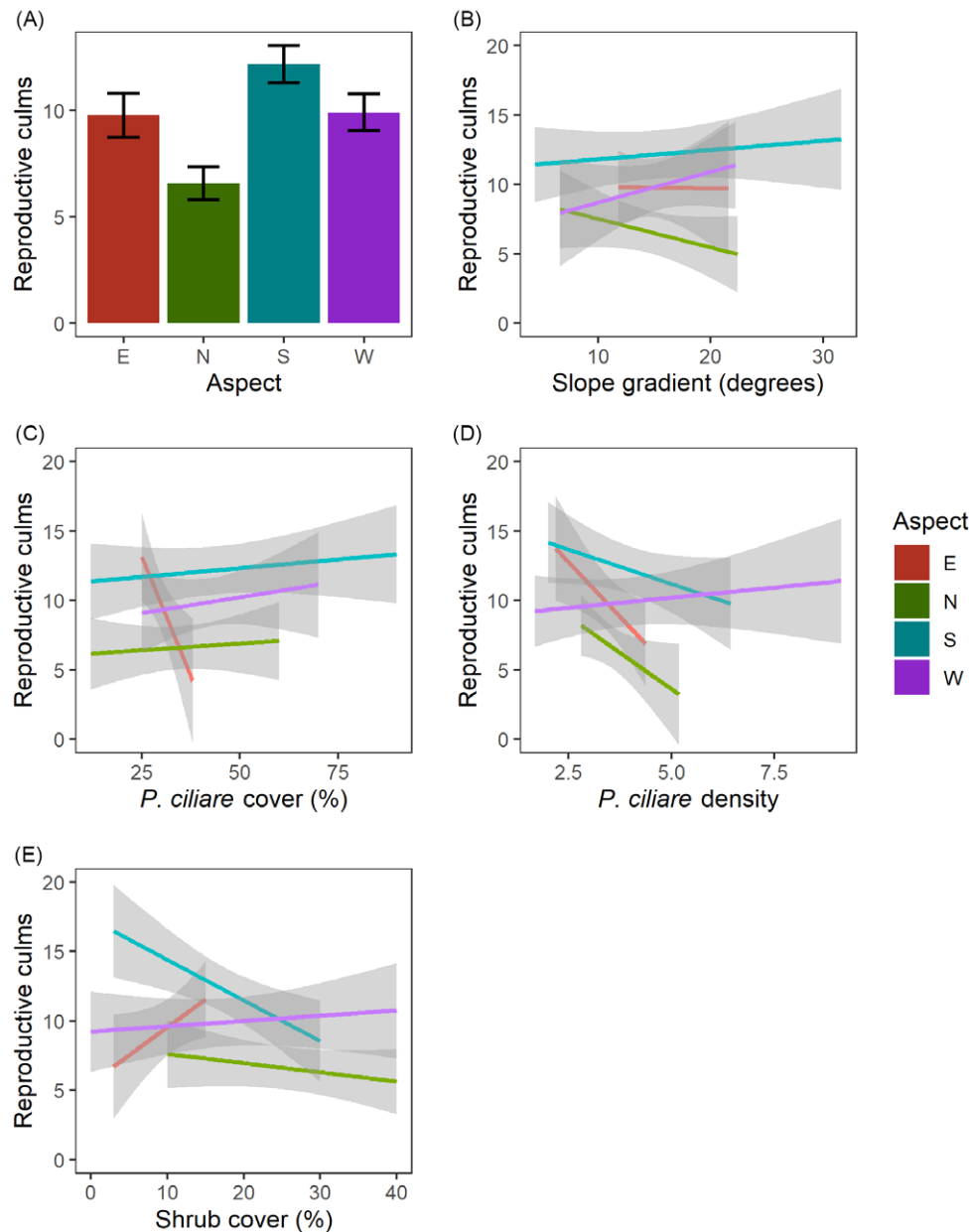


Figure 3. Number of reproductive culms per *Pennisetum ciliare* plant in response to aspect (A), slope gradient (B), *P. ciliare* cover (C), *P. ciliare* density (plants m^{-2}) (D), and shrub cover (E). Error bars represent SE. Gray shading represents the 95% confidence interval of the best-fit regression line.

Individual Plant Patterns

Total Live Culms

Individual *P. ciliare* plants were largest on south-facing aspects, as expected; however, *P. ciliare* plants on east-facing aspects had more live culms than those on north- and west-facing aspects, contrary to our predictions. The larger plants on south-facing aspects may be explained by higher photosynthetic rates on south-facing aspects. South-facing aspects experience higher ground-surface temperatures and increased solar radiation in the Northern Hemisphere (Bennie et al. 2008; Moeslund et al. 2013; Parker 1988). *Pennisetum ciliare* has maximum photosynthetic efficiency at 35 C (Marshall et al. 2012). Increased solar radiation and temperatures on south-facing aspects may increase the photosynthetic

efficiency of *P. ciliare* on those aspects during the active growing season. The microclimate on north-facing aspects is less suitable for *P. ciliare* (Jarnevich et al. 2018), which may explain why *P. ciliare* plants were smaller on north-facing aspects.

The effects of aspect on ground-surface temperature and solar radiation lead to effects of aspect on soil moisture, which is typically lower on southwest-facing aspects than on northeast-facing aspects (Moeslund et al. 2013). Although *P. ciliare* is drought tolerant, annual precipitation in 2020 was less than half of the 30-yr average and was below the lower tolerance limit for *P. ciliare* (Cox et al. 1988). *Pennisetum ciliare* plants may have been smaller than expected on west-facing aspects due to the combined stresses of topography (generally drier soils on west aspects) and low growing season precipitation in 2020, while water stress from the exceptionally dry conditions

may have been mitigated by topography on east-facing aspects (generally wetter soils on east-facing aspects).

Pennisetum ciliare plant size decreased as slope gradients increased on north-, west-, and south-facing aspects. Steeper slopes typically have shallower soils and reduced rainfall infiltration into soils, leading to lower soil moisture retention (Austin et al. 1984; Bishop et al. 2019; Parker 1988). Nicole et al. (2011) found that steeper slopes amplified the negative effects of other environmental stressors on plant performance. *Pennisetum ciliare* plants on steeper slopes likely experienced increased drought stress from low growing-season rainfall in 2020, which would explain their smaller size. Slope gradient did not affect *Pennisetum ciliare* plant size on east-facing aspects. This may be explained by slightly higher soil moisture on east-facing aspects generally mitigating drought stress (Moeslund et al. 2013).

Overall, as *P. ciliare* density increased, size of individual *P. ciliare* plants decreased. This is the expected result of negative density dependence, which has been demonstrated in greenhouse experiments with *P. ciliare* (Vera et al. 2006) and in the field with many other grasses (e.g., Aguilera and Lauenroth 1993; Fowler 1986, 1995). Experimental increase of *P. ciliare* density resulted in reduced height, number of leaves, and biomass of individual plants after 15 and 30 d (Vera et al. 2006). However, on south-facing aspects, *P. ciliare* plant size increased with increasing density. Greater habitat suitability on south-facing aspects may reduce negative density dependence, giving *P. ciliare* plants a fitness advantage on south-facing aspects (Jarnevich et al. 2018). Negative density dependence may not be detected from observation of individual plant life-history traits alone (Fowler et al. 2006). Furthermore, individual plants respond to small-scale plant neighborhood density more strongly than overall population density (Aguilera and Lauenroth 1993). The scale at which we measured density (total density in a 16-m² plot) is more representative of overall population density than of plant neighborhood-scale density (e.g., the scale at which direct interactions between individual neighboring plants occur).

Pennisetum ciliare plant size increased with increasing *P. ciliare* cover on all aspects except for east-facing aspects. Plant size and cover are expected to be positively correlated, because larger plants necessarily cover more area. We measured *P. ciliare* cover as the percentage of the plot occupied by the *P. ciliare* canopy, which is affected by both the number of live culms and the orientation of the culms (more vertical or more horizontal). Bunchgrasses with culms oriented more vertically experience less self-shading (Tomlinson et al. 2007). Shading by bunchgrass canopies reduces soil moisture evaporation, which may mitigate soil moisture stress in drought conditions (Greenlee and Callaway 1996). It is possible that due to reduced soil moisture stress on east-facing aspects generally, culms of *P. ciliare* plants on east-facing aspects were oriented more vertically than culms of *P. ciliare* plants on the other aspects, resulting in plants with similar number of live culms covering a smaller area on east-facing aspects.

We observed no relationship between shrub cover and individual *P. ciliare* plant size. Shrubs neither facilitated nor did they limit *P. ciliare* size. Cover of some native shrubs has been found to be negatively correlated with *P. ciliare* cover, while others show no significant relationship with *P. ciliare* cover (Gray and Steidl 2015).

Reproductive Culms

Pennisetum ciliare plants on south-facing aspects had more reproductive culms than those on north-facing aspects. This may be explained by south-facing aspects being more favorable for *P.*

ciliare (Elkind et al. 2019; Jarnevich et al. 2018). Further, other perennial bunchgrasses in aridlands have been shown to have higher reproductive output on south-facing aspects than on north-facing aspects (Shriver et al. 2021). East- and west-facing aspects did not explain *P. ciliare* distribution in Saguaro National Park; therefore, microclimate differences between east- and west-facing aspects may not have a strong effect on *P. ciliare* reproduction (Jarnevich et al. 2018). The higher number of reproductive culms per *P. ciliare* plant on south-facing aspects likely results in more *P. ciliare* propagules on south-facing aspects, which could translate to more infilling in *P. ciliare* patches and faster spread of invasion on south-facing aspects (Wittmann et al. 2014). Conversely, the lower number of reproductive culms per *P. ciliare* plant on north-facing aspects may result in slower infilling and spread of *P. ciliare*. As a result, *P. ciliare* invasion may be easier to control on north-facing aspects. Early detection and control of *P. ciliare* invasion is critical to reduce invasion on south-facing aspects.

Although steeper slopes can lead to reduced reproduction in some plants, we observed no relationship between slope gradient and number of reproductive culms per *P. ciliare* plant (Nicole et al. 2011). Some plants allocate more resources to reproduction in stressful conditions to maintain reproductive output (Sultan 2003). It is possible that *P. ciliare* plants on steeper slopes increased resource allocation to reproduction due to stressful conditions on steeper slopes. This would also help explain why *P. ciliare* plants were smaller on steeper slopes and why distribution is invariant across slope gradients.

The number of reproductive culms per *P. ciliare* plant increased with increasing *P. ciliare* cover on all aspects except for east-facing aspects. Cheplick (2020) found that reproductive allocation positively correlated with vegetative mass in a warm-season perennial grass. Increasing the number of reproductive culms likely increases plant size, which is expected to be positively correlated with plant cover. As with *P. ciliare* size, there was an unexpected negative relationship between number of reproductive culms per *P. ciliare* plant and *P. ciliare* cover on east-facing aspects. We think this pattern may be explained by different canopy architecture of *P. ciliare* plants on east-facing aspects. Lower soil moisture stress on east-facing aspects may allow *P. ciliare* plants to grow with vertically oriented culms to reduce self-shading, whereas *P. ciliare* plants on other aspects may grow with more horizontally oriented culms to reduce soil moisture stress via shading (Greenlee and Callaway 1996; Moeslund et al. 2013; Tomlinson et al. 2007). Alternatively, there is a trade-off between vegetative and reproductive investment in many perennial bunchgrasses, and reproductive allocation can negatively correlate to plant height (Wilson and Thompson 1989).

Pennisetum ciliare plants had lower reproductive output on north-facing aspects as *P. ciliare* density increased, although we did not observe a relationship between *P. ciliare* density and reproductive output on all other aspects. Reduced reproductive output is an expected outcome of negative density dependence and intraspecific competition (Dyer and Rice 1999). Poor habitat suitability on north-facing aspects may enhance negative density dependence among *P. ciliare* plants on north-facing aspects (Jarnevich et al. 2018). Negative density dependence may be difficult to detect from individual life-history traits alone; detection of density dependence is more likely if the population growth rate (λ) is calculated (Fowler et al. 2006). Because our study spanned only one growing season, we could not calculate the per capita population growth rate of *P. ciliare*.

We found no relationship between shrub cover and the reproductive output of *P. ciliare*. In aridlands, shrubs may facilitate

neighboring plants by mitigating soil moisture stress and increasing nutrient availability (Cox et al. 1984; Griffith 2010; Tewksbury and Lloyd 2001). Abnormally low precipitation in 2020 likely increased water stress experienced by *P. ciliare* generally. We found no evidence that shrubs facilitated *P. ciliare* reproduction via the nurse plant phenomenon or that they limited *P. ciliare* reproduction via competition. Little is known about *P. ciliare* competition with shrubs, but *P. ciliare* is highly competitive against native grasses and forbs (Clarke et al. 2005; Jackson 2005; Stevens and Fehmi 2011).

Our findings that *P. ciliare* has larger plants and higher reproduction on south-facing aspects corroborate landscape-scale studies that have found associations between *P. ciliare* distribution and aspect (Elkind et al. 2019; Jarnevich et al. 2018; Van Devender and Dimmitt 2006). Furthermore, higher *P. ciliare* reproduction on south-facing aspects combined with no evidence of density dependence indicates that south-facing aspects are especially vulnerable to invasion by *P. ciliare* due to both high habitat suitability and potentially high propagule pressure. We recommend that managers focus *P. ciliare* monitoring and control efforts on south-facing aspects to most effectively mitigate *P. ciliare* invasion.

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