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RESEARCH ARTICLE

Aeolian erosion increases drought susceptibility of grass seedlings relative to that of shrub invaders in a Chihuahuan Desert grassland

Furong Niu · Nathan A. Pierce · Yafei Shi · Steven R. Archer · Gregory S. Okin

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Abstract

Background and aims Shrub encroachment is a widespread ecological state change in global arid grasslands, often driven by changes in disturbance regimes (e.g., livestock grazing). While various direct and indirect effects of grazing may promote grassland-to-shrubland transitions, the relative importance of these mechanisms remains unclear. A well-documented consequence of grazing and other disturbances is aeolian erosion, which reduces soil water and nutrient availability. We conducted a greenhouse experiment to ascertain whether such changes might favor shrubs establishment over that of grasses under drought conditions, potentially promoting shrub encroachment.

Methods We quantified seedling establishment and growth of an aggressive grassland invader (*Prosopis glandulosa*) to that of two grass species (*Bouteloua eriopoda* and *Sporobolus airoides*) on wind-eroded (winnowed) and intact (non-winnowed) soils under contrasting watering regimes: control (FC, field capacity), medium drought (MD, 80% of FC), and severe drought (SD, 50% of FC).

Results The combination of soil winnowing and drought negatively impacted growth of grass seedlings more than that of shrub seedlings. In well-watered (FC) conditions, seedling biomass was comparable ($p > 0.05$) between soil types for all species. Under MD and SD, above- and belowground biomass declined, with the greatest reductions observed for seedlings on winnowed soils, particularly for the two grass species. Additionally, grass leaf production was reduced on winnowed soils, while that of the *P. glandulosa* shrub seedlings was unaffected.

Conclusion These disparities in drought susceptibility on wind-eroded soils should give shrub seedlings a survival advantage in drought periods, thereby setting the stage for grassland-to-shrubland transitions.

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Keywords Desert grassland · Shrub encroachment · Wind erosion · *Prosopis glandulosa* · Seedling establishment · Water stress

Introduction

Arid and semiarid grasslands are among the most widespread biomes on Earth (Schimel 2010), contributing substantially to provision of key ecosystem services associated with carbon sequestration, biodiversity, and livestock production (Briske et al. 2023; Gross et al. 2024; Maestre et al. 2022). However, grasslands are increasingly facing pressures from natural and anthropogenic disturbances (Bestelmeyer et al. 2015; Reynolds et al. 2007). These combined pressures often lead to the transition from grass-dominated ecosystems to shrub-dominated landscapes, a state change commonly referred to as “shrub encroachment” (Archer et al. 2017). This ecological transformation drastically alters the physical structure of arid grasslands, with far-reaching effects on ecosystem functions, e.g., disrupting water and carbon cycles, impacting biodiversity and vital ecosystem services that underpin human well-being (Archer and Predick 2014; Eldridge et al. 2011; Sala and Maestre 2014).

Shrub encroachment poses a significant challenge to the sustainable management of drylands, particularly in regions where livelihoods depend on grassland productivity (Jones et al. 2024). Changes in disturbance regimes centered around livestock grazing have been identified as a primary driver of shrub encroachment (Archer et al. 2017; D’Odorico et al. 2012). Other factors, including climate variability, soil properties, and plant-plant interactions, also mediate grass-shrub interactions, favoring shrub persistence in arid grasslands (Archer et al. 1995; Jones et al. 2023; Pierce et al. 2019). However, evidence from long-term grazing exclosures that have undergone shrub expansion in the absence of grazing pressure (Browning and Archer 2011; Browning et al. 2014; Riedel et al. 2013) suggests other drivers, such as altered fire regimes, aeolian processes, and hydrology, may be at play.

Drylands are characterized by low and highly variable rainfall, with episodic precipitation events triggering cascading biological processes such as seed germination, seedling establishment, and eventually recruitment to adult life history stages (Davis et al. 2022; Pyle et al. 2021). As climate variability increases drought severity, grasses may become more vulnerable to mortality than drought-tolerant shrubs (Báez et al. 2013; Winkler et al. 2019). While soil moisture is considered a broad driver of shrub encroachment, its effects are mediated by local factors like soil texture (Yao et al. 2006). For instance, higher clay content can enhance soil water retention, supporting greater grass cover under drought conditions (McAuliffe 1994; Yao et al. 2006). Aeolian erosion, on the other hand, has increasingly been recognized as a driver of vegetation dynamics in drylands, particularly in arid environments, where its effects can surpass those of water erosion (Okin et al. 2018; Payne et al. 2023; Ravi et al. 2010). Through the aeolian feedback loop, vegetation loss promotes further wind erosion, exacerbating land degradation and fostering conditions conducive to shrub expansion (Okin et al. 2006). Grasses are disproportionately affected by this process, as windblown sand damages their exposed tissues, whereas shrubs, with more protected structures and more growth above the height where most aeolian transport occurs, experience less harm (Niu et al. 2023). Moreover, wind erosion strips away nutrient-rich topsoil layers, leaving behind coarser, nutrient-poor soils (Li et al. 2007). These soil changes may further disadvantage grasses, which rely on fine-textured soils for moisture and nutrient retention, while shrubs, equipped with deeper root systems and greater drought tolerance, may persist under degraded conditions (Báez et al. 2013; Liu et al. 2021).

Differences in the extent of wind erosion may help explain why some grasslands have been more susceptible to shrub encroachment than others. Our previous study found that germination and early seedling growth of grasses and shrubs on wind-eroded soils was comparable to that of seedlings on intact soils under well-watered conditions (Niu et al. 2021). However, interactions between wind erosion and drought remain less understood, despite their likely role in shaping shrub-grass competition through soil texture-mediated effects on plant available water (McAuliffe 1994; Yao et al. 2006). In this study, we hypothesized that shrubs would exhibit superior early establishment compared to grasses on coarser, nutrient-depleted, wind-eroded soils under drought conditions, thus facilitating their expansion in arid grasslands. Here, we present the results of a greenhouse experiment designed to test this hypothesis and explore its implications for shrub-grass dynamics in dryland ecosystems.

Materials and methods

Soil collection and targeted species

Winnowed (wind-eroded) and non-winnowed (intact) soils were collected from the Jornada Experimental Range (JER)/Jornada Basin Long-Term Ecological Research site in New Mexico, U.S. (see Niu et al. 2021 for sampling details). Briefly, winnowed soils were obtained from near-surface layers (~ 2 cm depth) at a location downwind of a long-term vegetation removal ("scrape") site that has been heavily affected by intensified aeolian processes (Gillette and Chen 2001). Non-winnowed soils were collected (~ 5 cm depth) from an adjacent intact site located perpendicular to the prevailing wind direction where aeolian erosion would be minimized. All soils were air-dried, sieved (5 mm mesh), and homogenized prior to use.

The grass species used in the study were *Bouteloua eriopoda* (Torr.) Torr., a perennial stoloniferous grass historically dominant in the Chihuahuan Desert grassland (Gibbens et al. 2005), and *Sporobolus airoides* (Torr.) Torr., a perennial bunchgrass also prominent in the region. The shrub species was the N_2-fixing *Prosopis glandulosa* Torr., the primary encroaching woody plant species on the sandy basin floor of the JER (Gibbens et al. 2005) and a common invader of grasslands in the Southern Great Plains and southwestern deserts of North America.

B. eriopoda seeds were sourced from the Los Lunas Plant Materials Center, Natural Resources Conservation Service, USDA (https://www.nrcs.usda.gov/plant-materials/nmpmc; accessed 3 March 2025). *S. airoides* seeds were purchased from a local supplier (Plants of the Southwest, Albuquerque, NM, USA). *P. glandulosa* seeds were collected at the JER in 2010 and stored in sealed jars in darkness. Prior to the experiment, seed viability was assessed through a germination trial, yielding germination rates of 77% for *B. eriopoda*, 67% for *S. airoides*, and 72% for *P. glandulosa* (Shereen Nadoum, unpublished data). To overcome dormancy and enhance water imbibition, *P. glandulosa* seeds were scarified by scratching the seed coat before sowing. Grass seeds were sown without any pre-treatment.

Greenhouse seedling establishment experiment

A 90-day pot experiment was conducted from 21 April to 20 July 2021 in a greenhouse at the University of Arizona campus to assess seedling growth on non-winnowed vs. winnowed soils under different soil moisture conditions. The greenhouse provided full sunlight, with temperatures maintained between 24 °C and 32 °C. Plastic pots (15 cm in diameter, 14.5 cm in height) were filled with a base layer of fine-grain washed sand and topped with a 5 cm layer of either non-winnowed or winnowed soil. This stratification was designed to mimic field conditions, where aeolian winnowing primarily alters the surface soil layer, affecting its texture and nutrient retention, while deeper layers remain relatively unchanged (Li et al. 2007). The washed sand served as a homogenized base layer to standardize conditions across treatments and isolate the effects of surface soil differences. Three watering regimes were applied: (1) a well-watered control (FC), in which soil moisture was maintained at field capacity by watering every other day; (2) a mild drought treatment (MD), receiving 80% of the FC watering volume every other day; and (3) a severe drought treatment (SD), receiving 50% of the FC watering volume every other day. Drought treatments were developed based on a pilot experiment to ensure sufficient seedling survival for growth analysis, while still imposing controlled water stress. Each combination of soil type, watering regime, and species had 10 replicates, resulting in a total of 180 pots. Pots were randomly placed on greenhouse benches and re-randomized every two weeks to minimize potential microclimatic effects.

Ten seeds were sown per pot at a depth of 1 cm. Following sowing, all pots were watered daily to field capacity to promote germination. After three weeks, when germination was mostly complete, all seedlings were of comparable size and vigor; these were then randomly thinned to three plants per pot. The different watering regimes (FC, MD, and SD) were then randomly assigned. Sensors (EC5, Meter Environment, Pullman, WA, USA) gravimetrically calibrated for each soil type were installed in two pots per treatment per soil type for *B. eriopoda* and *P. glandulosa*, to quantify volumetric soil water content in the top

5 cm. Plant height and number of leaves per plant were recorded at the end of the trial. Aboveground biomass was harvested and soil was washed from roots. Plant materials were oven-dried at 65 °C for 48 h and weighed. Leaf area was measured on fresh leaves using WinFOLIA software (Regent Instruments Inc., Quebec, QC, Canada). Specific leaf area was calculated as the ratio of fresh leaf area to leaf dry mass.

Data analysis

A generalized linear model (GLM) with a Gamma distribution and inverse link function was used to assess the effects of plant functional type (grass vs. shrub), soil type (non-winnowed vs. winnowed), watering regime (FC, MD, and SD), and their interactions on plant biomass and morphological traits of grass and shrub seedlings. Statistical significance of explanatory variables in the GLM was tested using Type II analysis of deviance in the car R package (Fox and Weisberg 2019). Estimated marginal means were calculated using the emmeans package (Lenth 2024) and used to explore interaction effects among soil type, watering regime, and functional type. Model residuals were evaluated using the DHARMa package (Hartig 2024) to validate model assumptions. A one-way analysis of variance (ANOVA) was conducted to compare volumetric soil water content, biomass, and morphological characteristics across watering regimes. Tukey's HSD test was used for post hoc multiple comparisons. All analyses were performed in R version 4.4.1 (R Core Team 2024).

Results

Soil moisture conditions across watering regimes

Volumetric soil moisture condition experienced by *B. eriopoda* seedlings was highest under well-watered conditions (FC), moderate under mild drought (MD), and lowest under severe drought (SD) in both non-winnowed and winnowed soils ($p < 0.05$; Fig. 1). Soil water content in FC and MD treatments was higher in non-winnowed soils compared to winnowed soils ($p < 0.05$; Fig. 1), but comparably low in the SD treatment. Among *P. glandulosa* seedlings, soil water content was highest in the FC on non-winnowed soils, and lower, but statistically comparable on both soils in the MD and SD treatments ($p > 0.05$; Fig. 1).

Biomass on winnowed vs. non-winnowed soils across watering regimes

A significant two-way interaction between soil type and watering regime ("Soil × Water") was evident for aboveground biomass, belowground biomass, total biomass, number of leaves, and plant height ($p < 0.05$; Table 1). Furthermore, a significant three-way

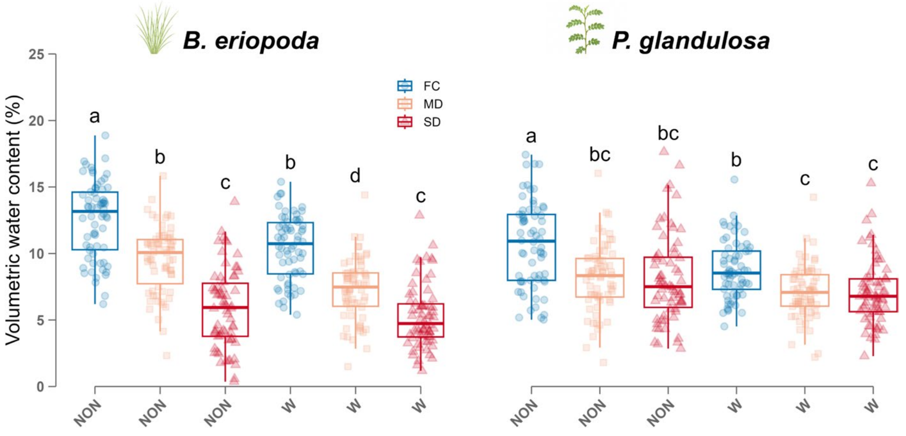


Fig. 1 Soil volumetric water content for *B. eriopoda* (grass) and *P. glandulosa* (shrub) seedlings on non-winnowed (NON) and winnowed (W) soils subjected to different watering regimes [FC (Field Capacity), MD (Moderate Drought), and SD (Severe Drought)]. Daily mean values are represented by points (circles for FC, squares for MD, and triangles for SD). Different letters denote significant differences among watering regimes within each species ($p < 0.05$)

Table 1 Results (chi-square values) of GLM examining the effects of the plant functional type (PFT; grass vs. shrub), soil type (Soil; non-winnowed vs. winnowed), watering regime (Water; field capacity vs. moderate or severe drought), and their interactions on aboveground biomass, belowground biomass, total biomass, root:shoot ratio, number of leaves, height, and specific leaf area

Factor	df	Aboveground biomass	Belowground biomass	Total biomass	Root:shoot ratio	Number of leaves	Height	Specific leaf area
PFT	1	27.75***	9.28**	1.80	100.02***	25.44***	438.11***	53.52***
Soil	1	4.29*	4.63*	5.98*	0.31	0.94	8.85**	1.86
Water	2	64.19***	20.92***	55.26***	0.43	59.16***	30.99***	1.46
PFT × Soil	1	2.44	8.71**	5.56*	1.77	1.14	0.00	0.95
PFT × Water	2	2.89	8.79*	6.61*	0.071	8.56*	0.79	18.99***
Soil × Water	2	23.48***	10.89**	23.07***	0.36	12.12**	14.38***	1.04
PFT × Soil × Water	2	2.77	15.24***	7.56*	2.85	4.09	0.51	4.26

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; *df* degree of freedom

interaction among plant functional type, soil type, and watering regime ("PFT × Soil × Water") was observed for belowground biomass ($p < 0.001$) and total biomass ($p < 0.05$). Interaction plots revealed that the two grasses were more sensitive to drought than the shrub, particularly on winnowed soils, where aboveground, belowground, and total biomass of grasses declined substantially from FC to SD. In contrast, biomass declines for the shrub were more moderate across watering regimes regardless of soil type (Fig. 2).

The significant interaction terms reflected the fact that grass aboveground, belowground, and total biomass responded differently to soil moisture availability treatments. These metrics were comparable between soil types across all species in the FC treatment ($p > 0.05$; Fig. 3). However, biomass declines in seedlings grown on winnowed soils were greater than those of seedlings growing on non-winnowed soils, with this effect being more pronounced in the grasses than in the shrub ($p < 0.05$; Figs. 2, 3; Table 1). For *B. eriopoda* and *S. airoides* grasses on winnowed soils, aboveground and total biomass were significantly reduced ($p < 0.05$) under MD and SD compared to FC (Fig. 3). In contrast, biomass of grasses growing on non-winnowed was unaffected ($p > 0.05$) by the imposed reductions in soil moisture. Additionally, belowground biomass of *S. airoides* significantly declined ($p < 0.05$) under MD and SD on winnowed soils. Conversely, the shrub exhibited similar biomass trends across varying watering regimes when grown on two soil types, with significant biomass reductions only occurred in the SD treatment ($p < 0.05$). Root-to-shoot ratios remained consistent across soil types and watering regimes for all three species ($p > 0.05$; Fig. 3).

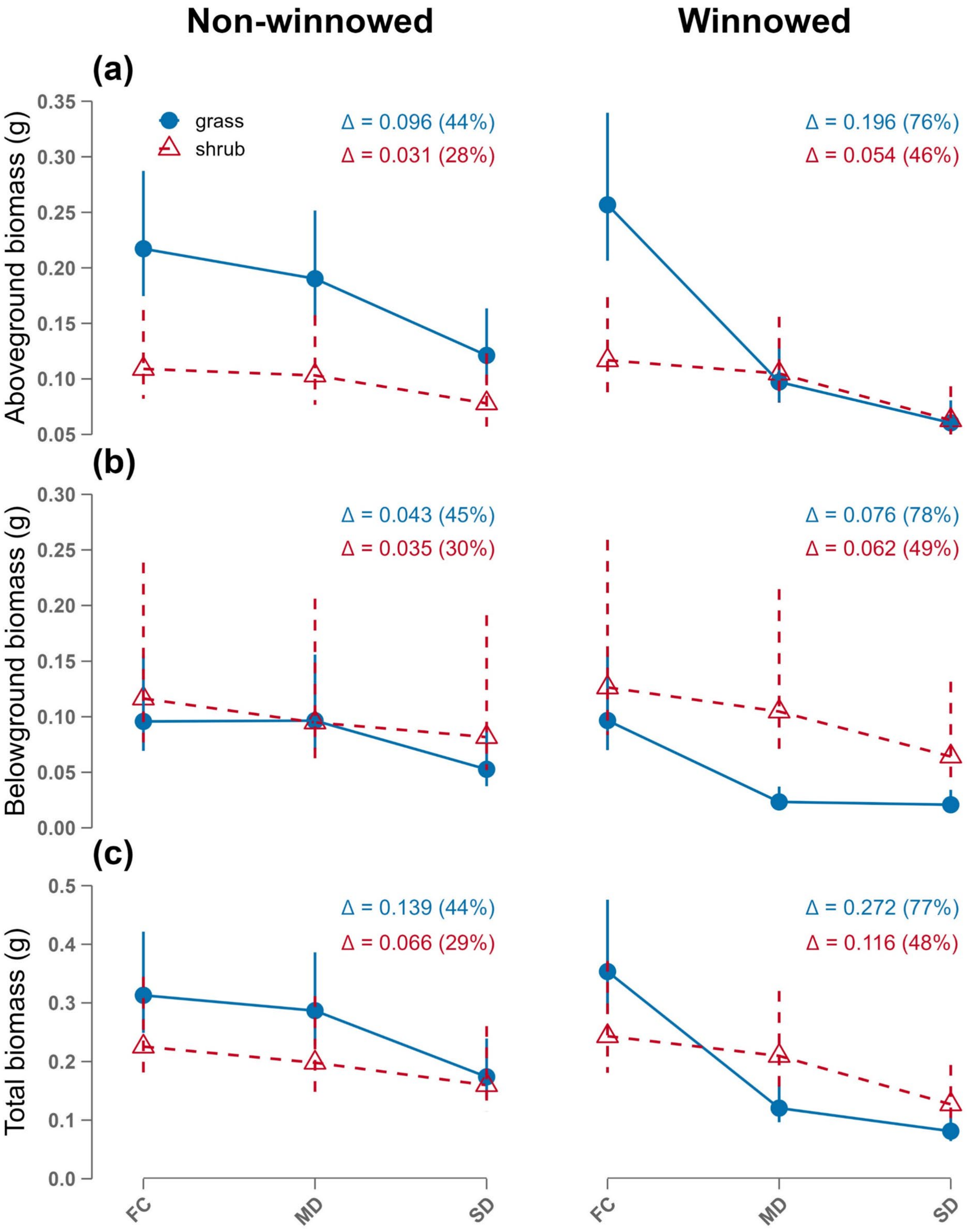
Seedling morphology on winnowed vs. non-winnowed soils across watering regimes

Height of *S. airoides* and *P. glandulosa* was significantly reduced under SD compared to FC on winnowed soils ($p < 0.05$; Fig. 4), whereas height in *B. eriopoda* was comparable across soil types and watering regimes ($p > 0.05$). The number of leaves per plant was also significantly reduced under MD and SD in two grass species on winnowed soils ($p < 0.05$), but was similar across watering regimes in *P. glandulosa* shrub seedlings (Fig. 4). Specific leaf area was generally unaffected by watering regime and soil type. The exception was *P. glandulosa*, which exhibited significantly greater specific leaf area under SD on winnowed soils compared to that of seedlings in the FC treatment on non-winnowed soils ($p < 0.05$; Fig. 4).

Discussion

Impacts of wind erosion and drought on shrub-grass dynamics

Shrub encroachment is a transformative process in dryland ecosystems, driven by the complex interaction of abiotic and biotic factors that favor woody plants over grasses (Archer et al. 2017). This phenomenon is prominent in arid and semi-arid landscapes, where soil texture and its influence on


Non-winnowed
Winnowed
(a)
grass
shrub
Δ = 0.096 (44%)
Δ = 0.031 (28%)
Δ = 0.196 (76%)
Δ = 0.054 (46%)
Aboveground biomass (g)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
(b)
Δ = 0.043 (45%)
Δ = 0.035 (30%)
Δ = 0.076 (78%)
Δ = 0.062 (49%)
Belowground biomass (g)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
(c)
Δ = 0.139 (44%)
Δ = 0.066 (29%)
Δ = 0.272 (77%)
Δ = 0.116 (48%)
Total biomass (g)
0.5
0.4
0.3
0.2
0.1
0.0
FC
MD
SD
FC
MD
SD

◂**Fig. 2** Interaction plots showing estimated marginal means (±95% CI) of aboveground biomass (**a**), belowground biomass (**b**), and total biomass (**c**) for two plant functional types (grass and shrub) across soil types (non-winnowed and winnowed) and watering regimes [FC (Field Capacity), MD (Moderate Drought), and SD (Severe Drought)]. Values are derived from a Gamma generalized linear model (GLM) with soil type, watering regime, and their interactions as predictor variables. Δ values indicate the absolute difference between FC and SD treatments (FC minus SD), while percentages in parentheses represent the corresponding relative change from FC

moisture and nutrient availability play pivotal roles in regulating plant recruitment. Our greenhouse trial revealed that, under drought conditions, grasses experienced significantly greater reductions in aboveground, belowground, and total biomass, as well as reduced leaf production, on wind-eroded (winnowed) soils compared to shrubs (Figs. 2 and 3). Collectively, these results indicate that grasses are more negatively impacted by drought on degraded soils, whereas shrubs maintain higher performance across multiple growth parameters. This suggests that shrubs may have a competitive advantage over grasses on wind-eroded, water-limited sites during the critical plant recruitment phase, thereby promoting their proliferation in arid grasslands.

These results provide mechanistic insights into how soil properties and water availability interact to shape plant establishment dynamics in arid environments. Topoedaphic factors such as soil depth, restrictive layers (e.g., petrocalcic horizons), parent material, and soil texture are well-known to influence plant-available water and thereby shape vegetation dynamics (Duniway et al. 2010; Jones et al. 2023; Shepard et al. 2015). Alongside these factors, aeolian erosion plays a critical role, particularly in league with disturbances like drought, grazing, and land-use change (Okin et al. 2006). Wind erosion preferentially removes fine, nutrient-rich soil particles, leaving behind coarser sand particles, which thereby alter the surface soil texture and water retention and fertility (Li et al. 2007).

While the previous study found no significant differences in seed germination and seedling establishment of grass and shrub species on wind-eroded versus intact soils under well-watered conditions (Niu et al. 2021), the current study revealed a negative impact of wind-eroded soils on grass seedling growth under drought conditions. The combined effect of altered soil texture and drought suggests that shrubs, such as *P. glandulosa*, may gain a recruitment advantage on wind-eroded and water-limited environments, facilitating their establishment during dry years (Fig. 5). This pattern broadly aligns with field observations from the Jornada Basin, where *P. glandulosa* has been reported to occur more frequently on sandy soils and where encroachment has been observed to intensify during droughts (Archer et al. 2022; Browning et al. 2012; Ji et al. 2019). While our greenhouse results cannot directly replicate complex field dynamics, the similarities suggest that the mechanisms identified here may contribute to such patterns under natural conditions. Comparable interactions among woody–grass dynamics, precipitation, and soil characteristics have been reported across other North American drylands (Munson et al. 2016; Renne et al. 2019).

Shrub advantages in wind-eroded and water-limited environments

Aeolian erosion not only impacts moisture retention but also depletes essential nutrients by preferentially removing fine, nutrient-rich particles (Li et al. 2007; Schlesinger et al. 1990). This depletion reduces the cation exchange capacity of soils, lowering the availability of nitrogen and carbon for seedling growth (Niu et al. 2021). Shrubs, with their relatively flexible rooting (Case et al. 2020; Jiang et al. 2022; Maestre and Reynolds 2006), leaf morphology (Fig. 4 and Wellstein et al. 2017) and water use (Throop et al. 2012), appear better-suited to adjust to erosion-induced changes in soil properties than grasses as evidenced by their relative stable performance in the conditions experienced in our experiment. Additionally, *P. glandulosa* requires fewer nutrients due to its biological nitrogen fixation potential (Van Auken & Bush 1989), a process supported by evident nodulation observed in our greenhouse experiment and at field sites invaded by *P. glandulosa* (Johnson and Mayeux 1990). Shrubs such as *P. glandulosa* can form “fertile islands” beneath their canopies by trapping fine sediments and nutrients via wind and water erosion, creating favorable microenvironments that promote shrub emergence and seedling establishment (Franco-Pizaña et al. 1996; Schlesinger et al. 1990). *P. glandulosa* seedling growth has been also reported to be less affected by vertical soil nutrient

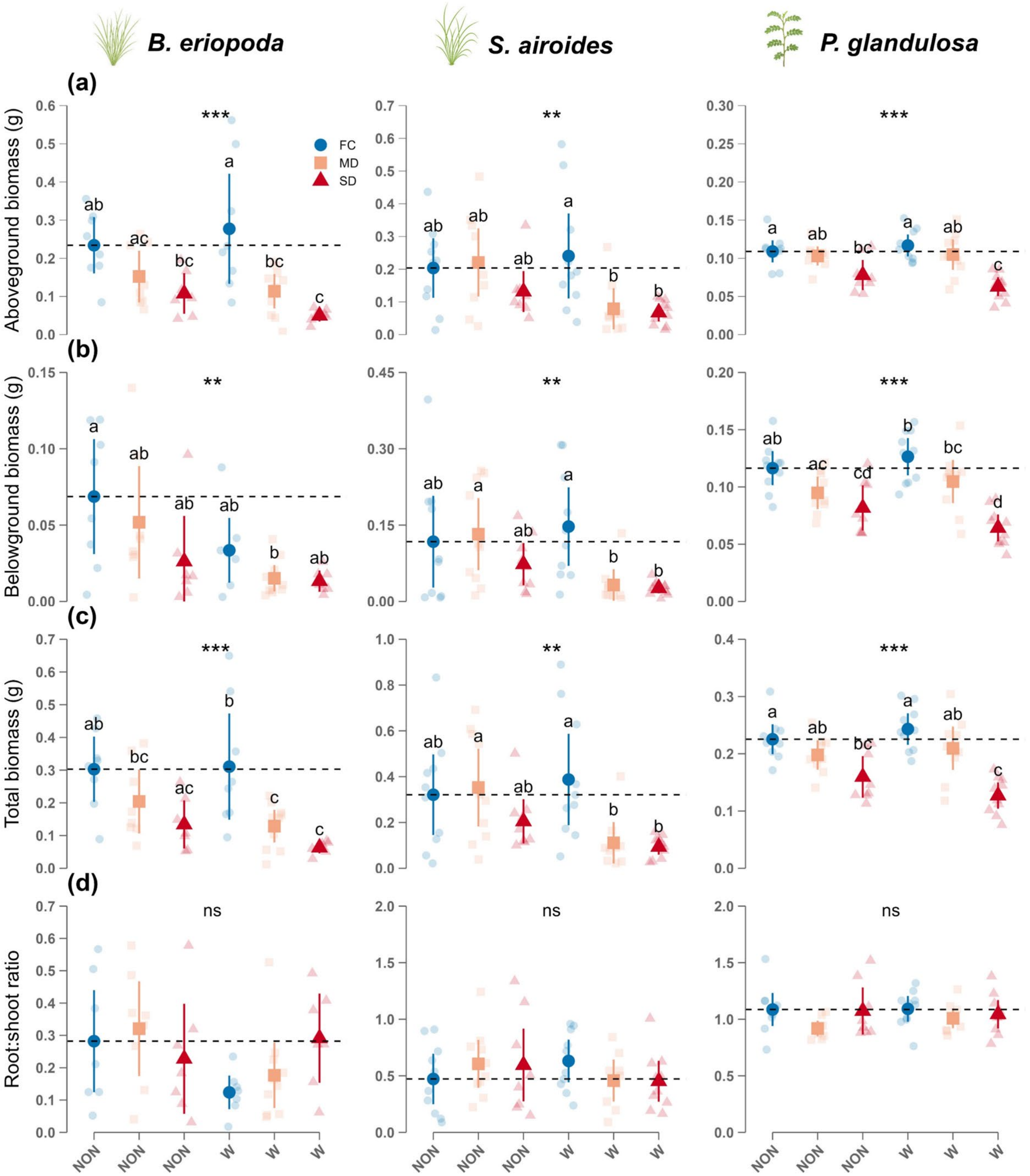


Fig. 3 Aboveground biomass [(**a**); mean ± 95% CI], belowground biomass (**b**), total biomass (**c**), and root:shoot ratio (**d**) of grass (*B. eriopoda* and *S. airoides*) and shrub (*P. glandulosa*) seedlings on non-winnowed (NON) and winnowed (W) soils subjecting to different watering regimes [FC (Field Capacity), MD (Moderate Drought), and SD (Severe Drought)]. Different letters denote significant differences among watering regimes within each species ($p < 0.05$). Dashed lines indicate FC values on non-winnowed soil; ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

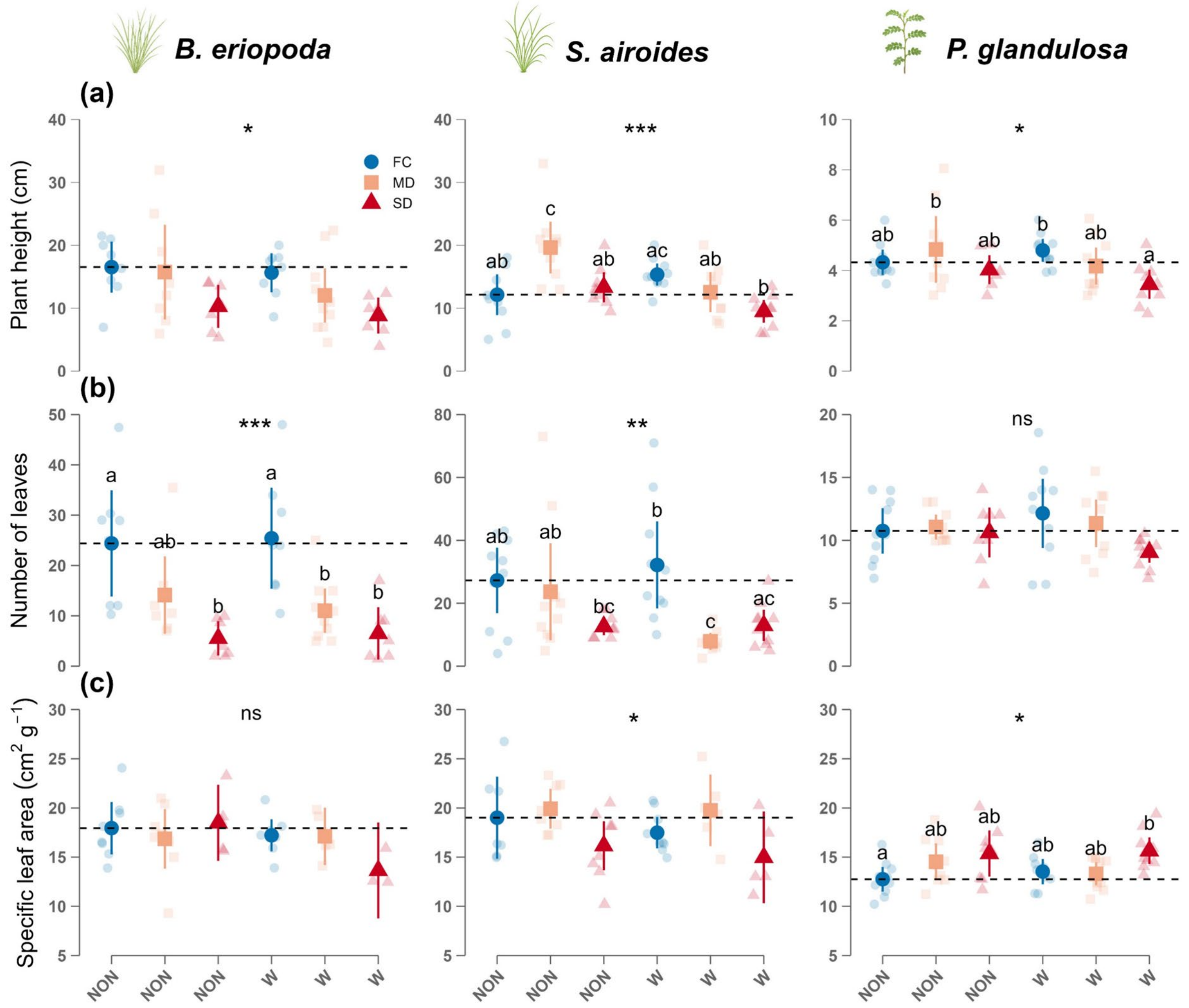


Fig. 4 Plant height [(**a**); mean ± 95% CI], the number of leaves (**b**), and specific leaf area (**c**) of the grass (*B. eriopoda* and *S. airoides*) and shrub (*P. glandulosa*) seedlings grown on non-winnowed (NON) and winnowed (W) soils subjecting to different watering regimes [FC (Field Capacity), MD (Moderate Drought), and SD (Severe Drought)]. Different letters denote significant differences among watering regimes within each species ($p < 0.05$). Dashed lines indicate FC values on non-winnowed soil. ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

heterogeneity (Maestre and Reynolds 2006), which may result from wind erosion that depletes surface nutrients and increases nutrient variability at depth.

Aeolian feedback and shrub encroachment

The differential response of the grass and shrub seedlings to changes in near-surface soil properties suggests that wind erosion can set the stage for shrub encroachment. Under moderate to severe drought conditions, grasses are generally capable of establishing on intact, fine-textured soils. However, when wind-driven erosion removes fine particles and leaves behind coarser topsoil, the altered soil structure creates a harsher microenvironment that impedes grass establishment. In contrast, woody species such as *P. glandulosa* appear comparatively insensitive to these changes in soil texture. This differential response during early establishment may provide shrubs with a potential advantage, which could ostensibly initiate a positive feedback loop favoring shrub encroachment—a mechanism

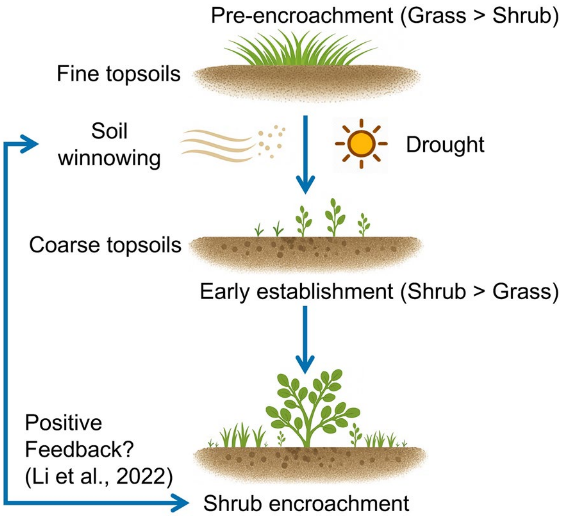


Fig. 5 Conceptual diagram illustrating an hypothesized mechanism of shrub encroachment in wind-erodible grasslands. Disturbance-induced aeolian erosion (e.g. by grazing; Okin et al. 2018) causes soil winnowing that leads to coarsened topsoils. This favors early shrub establishment over grasses (this study). This, in turn, may initiate positive feedbacks that promote shrub encroachment, further enhancing aeolian erosion and soil winnowing (Li et al. 2022). The diagram focuses on surface and aboveground processes; restricted rooting volumes in our pot study provided limited information on belowground dynamics. Field evaluations using a broader range of species/plant functional types and considering other mitigating factors (e.g., herbivory, soil crust, and soil microbial communities) are important next steps

not directly tested in this study but proposed as a possible outcome warranting further investigation under field conditions. Grass establishment failure on winnowed soils during drought reduces ground cover, which in turn promotes wind erosion that further amplifies soil degradation and diminishes habitat for grassland-dependent species (Fig. 5; Li et al. 2022; Winkler et al. 2019). These compounded impacts of wind erosion and drought are projected to intensify in the southwestern U.S. (Seager et al. 2007). This could eventually accelerate shrub encroachment, as observed in our study, where shrubs showed enhanced early growth under combined drought and soil degradation. Historical records from the Jornada Basin corroborate this pattern, linking multi-year droughts to declines in grass cover and subsequent woody plant expansion, with soil texture mediating the process (Ji et al. 2019; Yao et al. 2006). Notably, the belowground mechanisms highlighted here appear to operate independently of aboveground sandblasting effects previously described (Niu et al. 2023). These two processes—soil degradation belowground and physical damage aboveground—may act additively to accelerate shrub encroachment.

Implications for ecosystem management and restoration

Accordingly, ecosystem management should prioritize soil conservation and erosion mitigation with proactive interventions—such as managing grazing to maintain ground cover to reduce erosion and prioritizing susceptible soil types—to prevent degradation and avert crossing critical thresholds (Bestelmeyer et al. 2018; Li et al. 2022). Similarly, restoration activities on shrub-invaded grasslands (Archer and Predick 2014; Ding and Eldridge 2023) should seek to re-establish soil surface properties that would favor grass establishment. These measures are particularly important under predicted increases in climate variability, where more frequent and severe drought events will ostensibly exacerbate soil erosion and accelerate shrub encroachment. Although our greenhouse experiment isolated the effects of soil texture and short-term drought, field studies are needed to validate these dynamics in various topoedaphic and geomorphic settings and in the context of projected climate-induced increases in wind erosion and drought frequency (Naumann et al. 2018; Seager et al. 2007). In addition, field evaluations based on a broader range of species/plant functional types, in conjunction with consideration of other mitigating factors (e.g., root dynamics, herbivory, soil crust, and soil microbial communities), would provide a more comprehensive assessment of plant community responses to soil degradation and drought in drylands. Overall, our findings offer insights into the mechanisms underlying plant early establishment phase of shrub encroachment in dryland ecosystems, suggesting that once wind erosion occurs following ground cover loss, whether due to grazing, fire, or climate-induced drought, the resulting soil degradation may initiate a feedback loop that further suppresses grass recruitment while enhancing shrub establishment during drought years, promoting shrub dominance in wind-erodible grassland ecosystems.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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