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Biocrusts do not differentially influence emergence and early establishment of native and non-native grasses

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Abstract. Biological soil crusts (biocrusts) cover the soil surface of global drylands and interact with vascular plants. Biocrusts may influence the availability and nature of safe sites for plant recruitment and the susceptibility of an area to invasion by non-native species. Therefore, to investigate the potential role of biocrusts in invasive species management, we sought to determine whether native and non-native grass recruitments in two North American deserts were differentially affected by biocrusts. We conducted a series of coordinated experiments in field, semi-controlled, and controlled environment settings in the Colorado Plateau and Sonoran Desert using contrasting biocrust and grass functional types. Experiments in field environments focused on early establishment of grass seedlings whereas controlled environment experiments focused on seedling emergence. Within each experiment, we compared responses (frequency, magnitude, and timing of emergence/establishment) both across species (biocrust types pooled) and across species and levels of biocrust development. Native grasses varied by experiment and included *Aristida purpurea*, *A. purpurea* var. *longiseta*, *Bouteloua gracilis*, and *Vulpia octoflora*. Emergence of non-native *Bromus tectorum* was similar to that of native grasses on the Colorado Plateau. Differences in emergence of native vs. non-native grasses in the Sonoran Desert were species- and response-specific. Emergence of the non-native *Bromus rubens* was comparable to that of native grasses whereas emergence frequency and magnitude of the non-native *Pennisetum ciliare* was lower compared with two of four native species. Within a grass species, emergence was higher and faster on bare soil compared with biocrusts in the Sonoran Desert semi-controlled and greenhouse environment experiments. However, the pattern was not consistent across other experiments. When comparing across Colorado Plateau and Sonoran Desert biocrusts in greenhouse experiments, we found that emergence of native grasses was higher on Colorado Plateau biocrusts. Based on the lack of consistent results across our experiments, grass recruitment on biocrusts appears to be driven more by species-specific traits than species provenance. Our greenhouse experiments suggest that biocrust topographic relief is an important safe site trait influencing plant recruitment.

Key words: biological soil crusts; *Bromus rubens*; *Bromus tectorum*; buffelgrass; cheatgrass; germination; *Pennisetum ciliare*; red brome.

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INTRODUCTION

Semi-arid, arid, and hyper-arid lands (hereafter “drylands”) encompass roughly one-third

of the world’s land mass and contain ~20% of the world’s population (Safriel et al. 2005). Within North America, ~25% of the land is arid or semi-arid and supports ~18% of the continent’s

population (Reynolds et al. 2007). Biological soil crusts (biocrusts), communities of cyanobacteria, eukaryotic algae, fungi, bryophytes, and lichens on and in the soil surface are an important component of these drylands (Belnap 2003) where they play a variety of roles: soil surface stabilization (Belnap and Gardner 1993), wind and water erosion mitigation (Mucher et al. 1988, Belnap and Gillette 1998), nutrient capture (Williams et al. 2012), and soil nitrogen and organic matter enrichment (Harper and Marble 1988). Biocrusts also affect infiltration, runoff, and evaporation (Belnap 2006) and interact with vascular plants in a variety of positive, negative, or variable ways across a broad range of spatiotemporal scales to potentially influence species abundance and vegetation composition (Bowker 2007, Havrilla et al. 2019). Germination, emergence, and early establishment are typically “bottlenecks” in the plant lifecycle (Leck et al. 2008). Accordingly, our focus here is on how biocrusts influence these early, critical stages in the plant life cycle.

Non-native invasive grass impacts on North American drylands have been profound (DiTomaso 2000). By 1930, annual cheatgrass (*Bromus tectorum*) had invaded ~40 M ha in the Intermountain West of the United States (Mack 1981). In the Sonoran Desert, the annual red brome (*Bromus rubens*; Esque and Schwalbe 2002) and the perennials Lehmann’s lovegrass (*Eragrostis lehmanniana*; Schussman et al. 2006) and buffelgrass (*Pennisetum ciliare* synonym *Cenchrus ciliaris*; Olsson et al. 2012) have increased in abundance. These exotic grasses reduce biodiversity and alter hydrological and fire regimes to promote further invasion (Ravi et al. 2009, Wilcox et al. 2012). From a co-evolutionary perspective, there is the potential for biocrusts to inhibit non-native grasses compared with native grasses (Warren and Eldridge 2003). For example, an inverse relationship between biocrust and *B. tectorum* cover has been observed in the Great Basin (Peterson 2013, Reisner et al. 2013) and Columbia Basin (Ponzetti et al. 2007). Furthermore, a recent global meta-analysis indicated that biocrusts reduce the germination/emergence of non-native species, while having a neutral effect on that of natives (Havrilla et al. 2019). However, while meta-analyses can be a powerful tool (Koricheva and Gurevitch 2013), studies of non-natives in United States have largely focused

on annual *Bromus* spp. in the Great Basin geographic region (Havrilla and Barger 2018) potentially biasing the meta-analyses when considering North American grasses. Additionally, the meta-analysis findings on the effect of biocrusts on non-native germination may also be an artifact of the longevity and unique seed morphology of the species comprising the study (Havrilla et al. 2019).

Assessments of biocrust influences on grass establishment and performance have been largely conducted in greenhouse settings (Havrilla et al. 2019). While such experiments provide insights into mechanisms under tightly controlled circumstances, they do not allow or account for important processes that may override, constrain, or amplify the outcome of those interactions under field conditions (Heinze et al. 2016, Forero et al. 2019). Therefore, complementary experiments in less controlled and field environments are needed to deepen our understanding of the influence of biocrusts on grass emergence. Here, we report on a coordinated series of controlled environment and field experiments conducted in contrasting bioclimatic regions to address whether biocrusts inhibit recruitment of non-native grasses relative native grasses (i.e., based on species provenance). If so, they could be an important component of prevention, mitigation, or restoration plans aimed at invasive species management.

Biocrust provision of “safe sites” (sensu Harper 1977) for grass recruitment depends on biocrust attributes. For example, biocrusts with rough and pronounced microtopography may provide more safe sites (Johansen 1986) and capture/retain more seeds (Belnap et al. 2003b) compared with smoother biocrusts. Biocrusts can be classified into four types based on surface morphology: smooth, rugose, pinnacled, and rolling (Belnap 2003). Here, we investigated native and non-native grass recruitments on biocrusts exemplifying two different morphologies in two North American deserts underrepresented in the biocrust influence on grass emergence/establishment literature—the Colorado Plateau and Sonoran Desert. Biocrusts on the Colorado Plateau, a cool desert, are pinnacled, with up to 15 cm relief (Rosentreter and Belnap 2003) and up to 40% lichen cover (Belnap 2003). Biocrusts in the Sonoran Desert, a warm desert, are dominated by

cyanobacteria and tend to have rugose morphology (Rosentreter and Belnap 2003), with typically <3 cm microrelief (Belnap 2003). Cyanobacteria-dominated biocrusts can also be classified by their “darkness” (Belnap et al. 2008). As darkness increases so too does the concentration of chlorophyll *a*, lichen and moss cover, soil aggregate stability (Belnap et al. 2008), and the presence of later successional species with higher N₂-fixation potential and photosynthetic capacity (Housman et al. 2006). Darker cyanobacteria biocrusts contain species with UV protective pigments and have the majority of their biomass above the surface, whereas lighter cyanobacteria biocrusts have the majority of their biomass below the surface (Pócs 2009, Colesie et al. 2016). Lichens and mosses have a large portion of their photosynthetic biomass above the soil surface (Belnap et al. 2003a). Globally, lichen biocrusts reduce plant germination/emergence, whereas cyanobacteria, moss, and lichen/moss biocrusts have a neutral effect (Havrilla et al. 2019). This supports the notion that biocrusts potentially differ with respect to the extent to which they provide “safe sites” for grass recruitment (Bowker 2007, Reisner et al. 2013). Accordingly, we sought to determine whether native/non-native grass emergence/early establishment varied among light and dark biocrusts from pinnacled Colorado Plateau and rugose Sonoran Desert biocrusts.

Here, we report the outcome of a series of complementary controlled environment and field experiments in cool and warm deserts using a diversity of grasses and biocrust types. The following questions were addressed:

1. Do biocrusts differentially influence emergence/early establishment of native and non-native grasses?
2. Does grass emergence/early establishment depend on the developmental stage and/or type of biocrust (e.g., bare soil vs. light biocrust vs. dark biocrust; pinnacled vs. rugose)?

We predicted that in both deserts, biocrusts would reduce recruitment of non-native grasses compared with that of native grasses and that dark biocrusts (more developed and with a greater lichen component) would reduce recruitment to a greater extent than light biocrusts and bare soil.

MATERIALS AND METHODS

Study sites and species

We conducted our studies in two North American deserts: the Sonoran Desert and the Colorado Plateau. The Colorado Plateau is a cool desert with a 70- to 180-d growing season (Tuhy et al. 2002). Annual precipitation (136–668 mm; USGS 2002) is a combination of winter snow and summer rainfall (Tuhy et al. 2002). The Sonoran Desert is a warm desert with continental, subtropical climate which can remain frost-free 8–12 months/yr (Shreve 1951). Annual precipitation averages 76–400 mm and is bimodal with a pronounced summer monsoon (Ingram 2000).

Complimentary experiments in each desert were conducted in field sites (hereafter, field experiments) and with small pots in an outdoor open-sided “hoop house” with a clear plastic roof (hoop house experiments; Black et al. 2011). We also conducted an experiment with small pots in a climate-controlled greenhouse solely in the Sonoran Desert (greenhouse experiment).

Sonoran Desert.—Within the Sonoran Desert, our three sites (spaced at least 400 m apart) were located within the Santa Rita Experimental Range (31.9, –110.9; ~880 m elevation). The Santa Rita Experimental Range lies on the edge of the Sonoran Desert and its transition to the Madrean Archipelago/Apache Highlands (TNC 2008; EPA 2016). Surface soils were gravelly sandy loam with predominantly cyanobacteria biocrust communities, with patchy lichens and scattered mosses. Vegetation consisted of desert shrubs (*Prosopis velutina* and *Acacia* spp.), succulents (*Opuntia* and *Cylindropuntia* spp.), and native (*Aristida*, *Digitaria*, *Bouteloua* spp.) and non-native (*Pennisetum ciliare*) grasses. The Sonoran Desert sites receive 337 mm precipitation annually with ~60% occurring during the warm season (April–September). Mean annual temperature at the Sonoran Desert sites is 19.7°C with the warm season averaging 25.6°C and the cool season (October–March) averaging 13.9°C. Mean temperatures are lowest (10.4°C) in December and highest (29.4°C) in July (PRISM 2019). Bare soil for greenhouse/hoop house experiments was obtained from one of the three sites whereas biocrusts were obtained from all three sites.

Colorado Plateau.—Within the Colorado Plateau, the three sites were located on lands managed by the Moab Field Office, Bureau of

Land Management (38.27, -109.56; ~1780–1900 m elevation) spaced ~3 km apart. Surface soils were sandy loams with predominately cyanobacteria and moss biocrusts with sparse lichens. Vegetation was predominately native (*Bouteloua*, *Achnatherum*, *Hesperostipa*, *Pleuraphis*, *Sporobolus* spp.) and non-native (*Bromus tectorum*) grasses with scattered shrubs (*Artemisia* spp. and *Atriplex canescens*). Annual precipitation averages 336 mm with ~52% occurring during the warm season (April–September). Annual temperature averages 10.9°C with the warm season averaging 18.7°C and the cool season (October–March) averaging 3.2°C. Mean temperatures are lowest (−1.6°C) in January and highest (24.5°C) in July (PRISM 2019). Biocrusts for all experiments and bare soil for greenhouse/hoop house experiments were obtained from a nearby rock outcrop/*Juniperus* spp. site with scattered grasses and sandy loam to loamy sand soils.

Species.—Across our experiments, we report on four native (*Aristida purpurea*, *A. purpurea* var. *longiseta*, *Bouteloua gracilis*, *Vulpia octoflora*) and three non-native grasses (*Bromus rubens*, *B. tectorum*, *Pennisetum ciliare*). Trials included additional native grasses that spanned a broader range of seed attributes but are not included here owing to low emergence/establishment and/or identification challenges (Appendix S1: Table S1). With the exception of *B. tectorum* and *B. rubens* seeds hand-collected near Moab, Utah and Tucson, Arizona, respectively, seeds were obtained from commercial sources (Appendix S1: Table S1). The night

prior to seeding in the field experiments, we soaked seeds (except *Bromus* spp.) in water to promote imbibition and stimulate germination. So as to conduct trials under realistic seasonal or climatic conditions, not all species were used in each desert or in each run of an experiment. For example, Colorado Plateau autumn field and hoop house trials only included *B. tectorum* (only species attempted) and most spring trials included all species. Trials with warm-season species in the subtropical Sonoran Desert were conducted during the summer monsoon season, whereas trials involving cool-season species were generally conducted in winter. We only report species X trial combinations with >5% viable seed emergence/establishment and at least five emerged seedlings (Table 1).

Field early establishment experiment

At each of three field sites within each desert, we established a barbed wire enclosure (bottom strand smooth on Colorado Plateau). To minimize small mammal access, we fenced the bottom of the Colorado Plateau enclosures with chicken wire and covered the Sonoran Desert plots with hardware cloth (1.27-cm mesh, ~5 cm above the surface, which reduced illumination by $19 \pm 4\%$ [LX-101 Lux Meter]). Each enclosure contained a series of contiguous grids consisting of 10×10 cm cells, with <2 cm buffer zones separating adjoining cells and grids (total size = $3.9 \text{ m} \times 1.0 \text{ m}$ (Sonoran Desert) or $2.9 \text{ m} \times 0.7 \text{ m}$ (Colorado Plateau); Appendix S1: Fig. S1).

Table 1. Native and non-native grass species included in analyses by study setting (field, hoop house, greenhouse), location (Sonoran Desert, SD; Colorado Plateau, CP; University of Arizona, UA), and season (only those with sufficient emergence to include in analyses are shown).

Species	Common name	Species provenance	Season	Field	Hoop house	Greenhouse
<i>Aristida purpurea</i>	Purple threeawn	Native	Warm	SD (summer: '15)	SD (summer: '16 [2]) CP (spring: '16)	UA (summer '17)
<i>Aristida purpurea</i> var. <i>longiseta</i>	Red threeawn	Native	Warm		SD (summer: '15, '16) CP (spring: '16)	
<i>Bouteloua gracilis</i>	Blue grama	Native	Warm		SD (summer: '15 [2], '16 [2]) CP (spring: '17)	UA (summer '17)
<i>Bromus rubens</i>	Red brome	Non-native	Cool	SD (winter: '16)	SD (winter: '16, '17)	
<i>Bromus tectorum</i>	Cheatgrass	Non-native	Cool	CP (fall: '15)	CP (fall: '15, '16 [2], spring: '17)	
<i>Pennisetum ciliare</i>	Buffelgrass	Non-native	Warm	SD (summer: '15)	SD (summer: '16 [2])	
<i>Vulpia octoflora</i>	Sixweeks fescue	Native	Cool	SD (winter: '16)	SD (winter: '15) CP (spring: '16)	

Notes: The field experiment quantified early establishment over 28–30 d; hoop house and greenhouse trials ran 14–28 d.

Biocrusts are amenable to transplanting (Bowker et al. 2014). Accordingly, biocrust patches [typically 10×20 cm (Colorado Plateau) or 10×30 cm (Sonoran Desert)] in the vicinity of the enclosures (Sonoran Desert) or from a single, separate location (Colorado Plateau) were wetted, harvested (including the underlying ~ 1 cm of soil), placed in cardboard boxes for transport (with patches sometimes separated by nursery foam) and then transplanted into grid cells to be roughly flush with the surrounding ground surface. Within each grid (grid row on Colorado Plateau), cells were randomly assigned surfaces for seedling establishment trials: bare ground, light biocrust (typically cyanobacteria-dominated), or dark biocrust (typically with lichens present). We seeded a single species within each grid to aid in seedling identification. Depending on the trial and desert, each grid had one to three replicate cells of each substrate and each site had a total of three replicates of each species $\times$ substrate combination per trial. Soils were standardized by scraping the top ~ 0.1 – 1 cm of surface soil to remove existing biocrusts (light in Colorado Plateau, and light and dark in Sonoran Desert), seeds, plants, and litter and create an even, consistent base substrate (“bare soil” hereafter).

Biocrust “level of development” (LOD), modified from Belnap et al. (2008) to include lichen and moss constituents, was quantified in each grid cell using seasonal photographs. Light (median LOD = 3) and dark (median LOD = 6) biocrusts used at the Colorado Plateau were somewhat more developed than the light (median LOD = 2) and dark (median LOD = 5) biocrusts used at the Sonoran Desert. Lichens in Colorado Plateau dark biocrusts included *Collema* spp. with some *Placidium* spp., whereas *Peltula* spp. and *Placidium* spp. occurred on Sonoran Desert dark biocrusts. Within the Sonoran Desert, we observed a decrease in lichen cover from year 1 to year 2. Overall, lichen cover was $<5\%$ for dark biocrusts in both deserts.

The Sonoran Desert field experiments occurred in July–August 2015 (hereafter, “summer ’15”) and December 2016–January 2017 (winter ’16) (Table 1). The Colorado Plateau experiment occurred in September–October 2015 (fall ’15). For each trial, we scattered 20 seeds of a given grass species onto each 10×10 cm cell. Grass

species deployed varied by season (Table 1). We recorded the number of seedlings present within each grid cell weekly for ~ 4 weeks and distinguished between our “seeded” species and others that might have emerged coincidentally. Due to logistical constraints, the Colorado Plateau trial was only assessed 30 d after planting. “Early establishment” calculations are outlined in *Methods: Analyses*. The same species was generally seeded into the same location in subsequent trials conducted ~ 4 weeks later. During trials with low or no rainfall, we supplemented with hand watering. Air temperature and precipitation were tracked at each site with an automated system (HOBO RG3 rain gauge with UA-003-64 temperature sensor/data recorder inside RS1 solar radiation shield; Onset Computer Corp, Bourne, MA). Weather during the trials is summarized in Appendix S1: Table S2.

Hoop house emergence experiment

We constructed hoop houses (modifications of Black et al. 2011) at The Nature Conservancy Canyonlands Research Center near Monticello, Utah (Colorado Plateau), and at the University of Arizona Campus Agriculture Center in Tucson (Sonoran Desert). The hoop houses served as “semi-controlled environments” by excluding natural precipitation while generally tracking ambient temperature and allowing some wind (sides raised). The plastic reduced illumination by $22 \pm 9\%$ (LX-101 Lux Meter), elevated daily average temperature by 0.5°C (Colorado Plateau) and 1.0°C (Sonoran Desert), elevated daily maximum temperatures by 3.7°C (Colorado Plateau) and 3.4°C (Sonoran Desert), and reduced daily minimum temperatures by 1.1°C (Colorado Plateau) and 0.0°C (Sonoran Desert). During year 2, we lined the plastic with neutral density shade cloth (Sun Screen Fabric, Harvest Wheat) to bring air temperatures more in line with ambient conditions. Adding the shade cloth had modest influence on daily average temperatures (0.1°C [Colorado Plateau] and 0.3°C [Sonoran Desert] closer to ambient) but reduced the elevation of maximum daily temperatures by 1.2°C (Colorado Plateau) and 2.5°C (Sonoran Desert) and depression of minimum daily temperatures by 0.7°C (Colorado Plateau) and 0.2°C (Sonoran Desert). Grass seeds and biocrusts were placed in pots on benches ~ 0.7 m above ground level. We

include seven Sonoran Desert and six Colorado Plateau hoop house trials, with each trial consisting of five replicates of each grass species $\times$ substrate combination. Trials in the Sonoran Desert (Table 1) were conducted in July–August 2015 (hereafter “summer ’15”; 2 trials), December 2015–January 2016 (winter ’15), July–August 2016 (summer ’16; 2 trials), November 2016 (winter ’16), and February 2017 (winter ’17). Colorado Plateau trials were conducted in September 2015 (fall ’15), March–April 2016 (spring ’16), August–September 2016 (fall ’16; two trials), and March–May 2017 (spring ’17; two trials). Appendix S1: Table S2 summarizes the temperature, relative humidity, and watering during the trials.

Tapered pots ($9.5 \times 9.5 \times 8.5$ cm; ITML Traditional Square Pots, model SQN0400) were used as experimental units (analogous to “cells” in the field experiment); bottoms were perforated to allow drainage. Pots were partially filled with nursery foam and vermiculite then topped with ~ 1 cm of Sonoran Desert “bare” soil or Colorado Plateau soil (Colorado Plateau biocrust pots used soil from beneath biocrusts, Colorado Plateau “bare” soil pots used “bare” soil). Biocrusts were collected as described in *Methods: Field experiment*, along with “bare” soils (0–3 cm) from areas with no or poorly developed biocrusts or loose soil. Soils were sieved (2-mm mesh) and roughly homogenized before placing in pots. We topped each pot with a light or dark biocrust that had been wetted and carefully trimmed to fit pots. Pots in the “bare soil” treatment were topped with additional bare soil.

The median level of development (LOD) of biocrusts used in pot trials (assessed as per *Methods: Field*) was 3 (light) and 5 (dark) for the Colorado Plateau crusts and 2 (light) and 6 (dark) for Sonoran Desert crusts. These LODs were within one category of those of the biocrusts in the field grids in each desert. Lichens in Colorado Plateau pot dark biocrusts were mostly *Collema* spp. with some *Placidium* and *Peltula* spp., whereas lichens in Sonoran Desert dark biocrusts were mostly *Peltula* spp. with some *Collema* spp. Lichen content of pots with dark crusts in the Sonoran Desert trials (25%) was, on average, higher than that of those in the Colorado Plateau trials (4%).

Pots (one per biocrust or bare soil surface treatment) were randomly arranged within grids on parallel tables for each trial (Appendix S1: Fig. S1). To facilitate identification, a single species was seeded into each grid, and each species $\times$ substrate combination was replicated five times per trial. Seeds ($n = 20$) of the target species were scattered on the surface and emergence (radicle or cotyledon visible) recorded daily for 14–28 d (with seedlings removed subsequent to their emergence). We hand-watered pots (~ 60 mL) except when pots were thoroughly, visibly wet due to variation in ambient temperature and humidity. Based on Ward et al. 2006, watering was typically for 3 (Year 1) or 4 (Year 2) consecutive days per week followed by 4 or 3 d without water but ranged from daily to twice weekly. Seeds washed to pot sides were repositioned onto the substrate. “Emergence” calculations are outlined in *Methods: Analyses*.

Greenhouse emergence experiment

Upon conclusion of the hoop house experiments, we transported a subset of Sonoran Desert and Colorado Plateau pots to a University of Arizona greenhouse. This allowed us to directly compare emergence of two native grasses (*Aristida purpurea* and *Bouteloua gracilis*; Table 1) on biocrusts and bare soil from each desert under the same growing conditions (e.g., a “common garden” experiment) to test our perception that Colorado Plateau and Sonoran Desert biocrusts differed in their influence on seedling emergence. We only included native grasses due to logistical constraints. Five replicates of the three substrate types from each desert per species were used in the experiment: light biocrusts, dark biocrusts, and bare soil. Pots were randomly assigned to locations in flats on one of four greenhouse benches for three 2-week trials during June–August 2017 (summer ’17; Table 1). Dark Sonoran Desert biocrusts (median LOD = 6) were more developed compared with those from the Colorado Plateau (median LOD = 4.5) and had higher cover of lichen micropatches (44% vs. 10%) (based on July 2017 assessments). Although the median LOD of light biocrusts from the Sonoran Desert was comparable to those from the Colorado Plateau (3 and 2.5, respectively), Sonoran Desert light biocrusts had greater cover of cyanobacteria micropatches

(94% vs. 60%) and Colorado Plateau light biocrusts had higher cover of bare micropatches (40% vs. 6%). Mean ($\pm$ SE; unitless) roughness of light and dark biocrusts from the Colorado Plateau (1.33 ± 0.04 and 1.39 ± 0.04 , respectively) was greater (pairwise $P < 0.03$) than that of light and dark Sonoran Desert biocrusts (1.14 ± 0.02 and 1.19 ± 0.02) [surface distance / straight line distance from chain method (Saleh 1993) along orthogonal transects intersecting at the center of each pot].

We scattered 20 seeds of either *A. purpurea* or *B. gracilis* into each pot and tracked emergence daily for 14 d, removing emerged seedlings. For the last two (of three) trials, we recorded the micropatch type (bare soil, cyanobacteria, lichen, below surface, crack, or biocrust anomaly) associated with the emerging seed callus/base. We watered pots (reverse osmosis filtered water) with a hand-held sprayer for four consecutive days, adding ~60 mL of water on the first day and up to that amount on subsequent days depending on the apparent moisture in the pots. Un-emerged seeds were removed after each trial. "Emergence" calculations are outlined in *Methods: Analyses*. Appendix S1: Table S2 summarizes the temperature, relative humidity, and watering during the trials.

To elucidate potential mechanisms underlying the patterns of seedling emergence, we quantified water absorption of seeds placed in the pots with our different substrates. Pots with a light biocrust, a dark biocrust, or bare soil substrate ($n = 5$ per grass species) were arranged in the same locations used in the above emergence experiment. Seeds of either *A. purpurea* or *B. gracilis* were weighed and placed on the surface of each pot (20 seeds/pot). Pots then received ~60 mL of reverse osmosis filtered water. After 24 h, seeds were collected and re-weighed. We conducted three water absorption trials in March–April 2018 (spring '18; Table 1; Appendix S1: Table S2).

Analyses

Throughout the manuscript, marginal means (model-based estimates of mean response per fixed-effect, least-squares means; Lenth et al. 2020) are back-transformed and reported $\pm$ their standard error (SE). We excluded species (and associated pot/cell characteristics) from analysis when <5% of viable seeds emerged (established) and <5 seeds within a trial emerged (established).

We summarized our data into four response variables to summarize the frequency, magnitude, and timing of emergence (early establishment). We used R (ver. 4.0.2) for statistical analyses.

We assigned a binary (1/0) value for the presence/occurrence of emergence (early establishment) to each pot (cell) for all trials (i.e., 1 = one or more seeds emerged [hoop house and greenhouse] or one or more seedlings present after ~28 d [field; early establishment]) in order to model the frequency of emergence (early establishment). For magnitude of emergence (early establishment), we divided the total number of seedlings emerged (greenhouse and hoop house) or present after ~28 d (field; early establishment) within each pot/cell by the seed viability * 20 (=the number of seeds placed in a pot/cell) for all trials. To account for differences in viability/germinability between seed lots and to enable fair comparisons across species, emergence [early establishment] was scaled relative to the emergence of seeds in a near-optimal controlled environment setting (estimate of seed viability; Appendix S1: Table S3). If the observed number of seeds emerging exceeded the number of emerged seeds under controlled conditions, then scaled magnitude was >100%. If no seeds emerged (established), scaled magnitude (establishment) was 0%.

We determined days to 50% of total emergence (t_{50} ; Coolbear et al. 1984) for greenhouse and hoop house experiments with the R *germination-metrics* package (v. 0.1.4). Our t_{50} values reflect pots for which seedling emergence was observed (pots with no emergence excluded). Because hoop house trials differed in duration, we scaled t_{50} values relative to trial length within a given trial. We similarly scaled t_{50} for greenhouse trials for comparisons with the hoop house trials. We determined the week with the maximum number of seedlings ($W_{\max}$) for each cell (species $\times$ substrate combination) for field trials and similarly scaled $W_{\max}$ values based on trial duration. If t_{50} ($W_{\max}$) equaled the trial length, then t_{50} ($W_{\max}$) was set to 0.9999 to enable the use of the beta distribution.

We utilized the R *glmmTMB* package (v. 1.0.2.1) to calculate mixed-effects models, the R *car* package (v. 3.0-8) to calculate Wald chi-squared (χ^2) test (type II) of the models' fixed effects, and the R *emmeans* package (v. 1.4.8) to estimate marginal means on the response scale and to compute

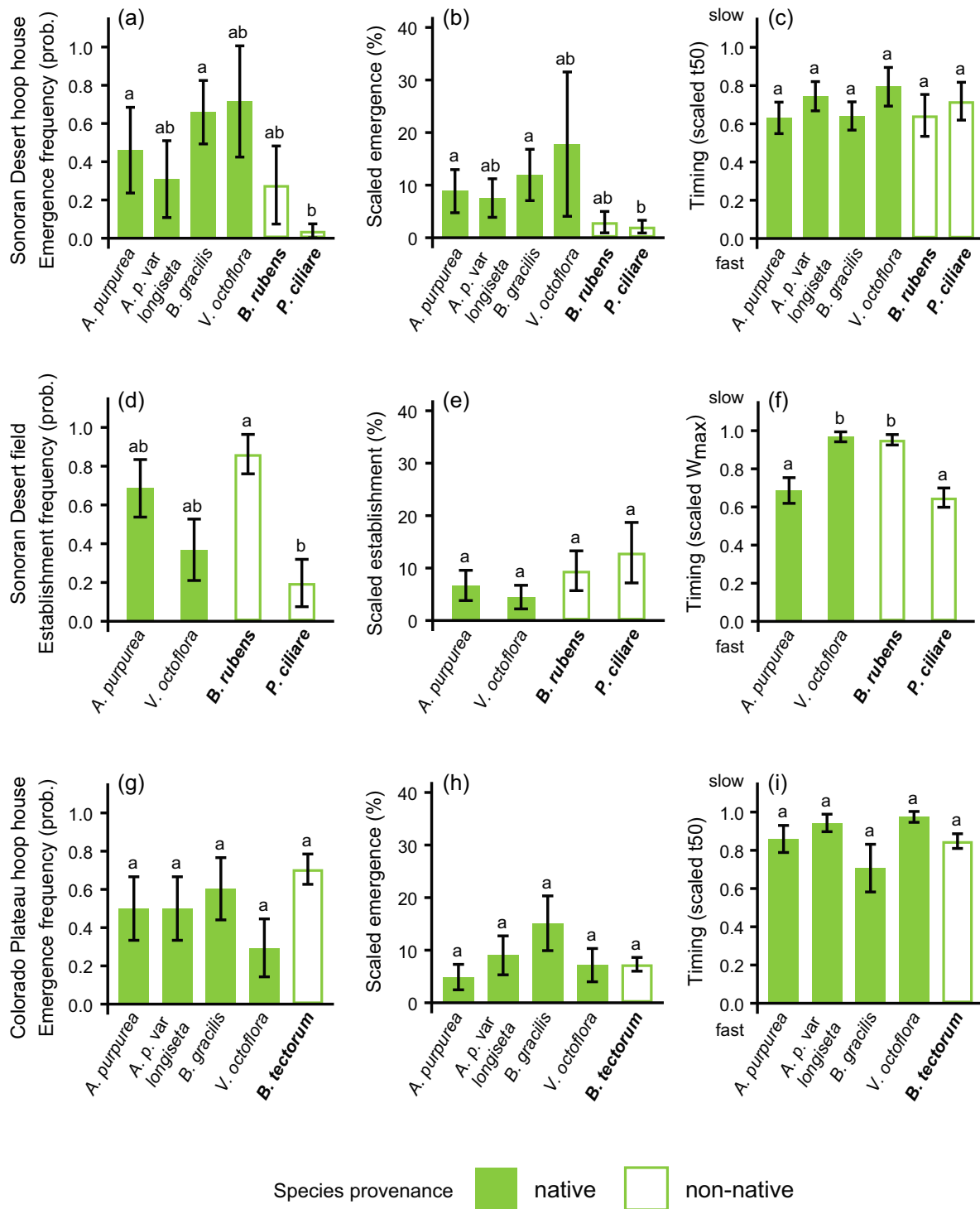


Fig. 1. Estimated marginal mean ($\pm$ SE) of emergence (hoop house) or early establishment (field) frequency, magnitude (%; scaled to viability), and timing (scaled t50 or W_{max}) for native and non-native (bold labels) grasses on biocrusts (types pooled) from Sonoran Desert hoop house (a–c) and field (d–f) environments and Colorado Plateau hoop house trials (g–i). Smaller scaled timing values indicate more rapid emergence. Different lowercase

(Fig. 1. *Continued*)

letters within a panel indicate significant differences (Tukey adjustments, $\alpha = 0.05$). Type II chi-squared test results of mixed-effects models given in Table 2.

pairwise comparisons ($\alpha = 0.05$). Differences were assessed using mixed models with trial, site (field experiments), and grid (row) as nested random effects. We checked model residuals with the R *DHARMa* package (v. 0.3.2.0), adjusted random effects and dispersion formulas as needed, and retained models we deemed robust (Hartig 2020), such as those for which the only significant test ($P < 0.05$) was for quantile regression on the residuals or a residual outlier. However, in one instance we retained a model with over-dispersed data and report it in the *Results*. For each experimental setting/location, we ran models of grass species on biocrusts (biocrust types pooled and separate) to evaluate the differential influence of biocrusts. Also, within each experimental setting/location, we ran models of grass species plus substrate type (light biocrusts, dark biocrusts, or bare soil) and source desert (greenhouse only) and checked for interactions, retaining interaction terms when $P < 0.1$, to evaluate the influence of biocrust development and type. Although our experimental design in the field and hoop house trials confounded block (grid) and species effects, our data were analyzed as a randomized-block design with block (grid) as a random effect whenever possible. We utilized the binomial distribution for models of frequency of emergence (early establishment), the Tweedie distribution for emergence (hoop house) and early establishment (field) magnitude due to the preponderance of zeros, the Gaussian distribution for emergence magnitude in greenhouse environments, the beta distribution for emergence (early establishment) timing, and the Gaussian distribution for water absorption.

RESULTS

We first compare seedling emergence (early establishment) of native and non-native grass species on biocrusts (types pooled). We then compare emergence (early establishment) across both species and biocrust development/type. Within each desert, we sequence results, tables, and figures from most to least controlled

environmental settings (e.g., hoop house pots to field plots). For biocrust development, we then present results from the greenhouse trials, which included biocrusts from both deserts.

Differential influence of biocrusts

In this subsection, we present data from three of our locations/settings where we had sufficient data on both native and non-native grasses. Fig. 1 shows estimated marginal means for grass species on biocrusts (light and dark biocrust types pooled) by locations/settings; Table 2 shows mixed model results. Models did not include biocrust type as it was significant only for a single model: an interaction with species for establishment timing ($W_{\max}$) in Sonoran Desert field sites ($P = 0.007$).

Sonoran Desert.—Within the Sonoran Desert hoop house, emergence frequency (probability of any seeds emerging within a pot) and emergence magnitude (% of seeds emerging, scaled to seed viability) on biocrusts (types pooled) were reduced for non-native *P. ciliare* compared with two of four native grasses (*A. purpurea* and *B. gracilis*). However, the frequency and magnitude of non-native *B. rubens* emergence was not different ($P > 0.05$) from that of the four native grasses or *P. ciliare*. Emergence timing (scaled t50) was similar among all native and non-native grasses in the Sonoran Desert hoop house. In the Sonoran Desert field environments, the frequency of early establishment (one or more seedlings present within a cell ~28 d after seeding) of *B. rubens* was higher than that of *P. ciliare*, but both were the same as that of native grasses. In contrast, the native and non-native grasses had similar early establishment proportions. In the Sonoran Desert field sites, the warm-season grasses (native *A. purpurea* and non-native *P. ciliare*) reached their maximum number of seedlings earlier than the cool-season grasses (native *V. octoflora* and non-native *B. rubens*), after accounting for differences in dispersion (Fig. 1, Table 2).

Colorado Plateau.—Within the Colorado Plateau hoop house, accounting for differences in dispersion, the frequency, magnitude, and

Table 2. Type II chi-squared test results of mixed-effects models of effect of grass species (native and non-native) on emergence (hoop house) or early establishment (field) frequency, magnitude (%; scaled to viability), and timing (time to 50% of maximum emergence [t50; scaled] or weeks to maximum number of seedlings [$W_{\max}$; scaled] on biocrusts (light and dark pooled) in Sonoran Desert hoop house and field and Colorado Plateau hoop house trials. Estimated marginal means and pairwise comparisons shown in Fig. 1.

Experimental setting	Response variable	<i>N</i>	Fixed effect	<i>df</i>	χ^2	<i>P</i>
Sonoran Desert hoop house	Frequency of emergence	132	Species	5	20.7	0.001
	Emergence %	132	Species	5	18.7	0.002
	t50	65	Species	5	4.3	0.505
Sonoran Desert field	Frequency of emergence	72	Species	3	9.7	0.022
	Establishment %	72	Species	3	3.7	0.298
	$W_{\max}$	45	Species	3	21.1	<0.001
Colorado Plateau hoop house	Frequency of emergence	80	Species	4	5.0	0.285
	Emergence %	80	Species	4	5.0	0.283
	t50	47	Species	4	6.3	0.179

timing of non-native *B. tectorum* emergence on biocrusts was not statistically significantly different than the four native grasses (Fig. 1, Table 2). Establishment levels in Colorado Plateau field trials on biocrusts were too low to enable comparisons between native and non-native grasses.

Influence of biocrust development and type

Here, we compare across species and contrasting substrates (bare soil, light, and dark biocrusts). As above, we analyzed our data and present results separately by study location/experimental setting (Fig. 2, Table 3). Greenhouse trials only used native grasses and were designed to compare Colorado Plateau and Sonoran Desert substrates (Fig. 3, Table 4).

Sonoran Desert.—The frequency and magnitude of emergence in Sonoran Desert hoop house trials were higher on bare soil than on light or dark biocrusts within each species. Emergence was also faster on bare soil than on dark biocrusts within each species in the Sonoran Desert hoop house trials. Additional details beyond those in Fig. 2 are given in Appendix S2: Tables S1–S2. In Sonoran Desert field trials, the frequency of early establishment varied by grass species, but was similar among all substrate/grass species combinations. Although the influence of substrate on the magnitude of early establishment varied by species, pairwise comparisons did not indicate any significant differences. Within each grass species, the maximum number of seedlings

occurred sooner on bare soil than light biocrusts (Fig. 2, Table 3).

Colorado Plateau.—Within the Colorado Plateau hoop house trials, the emergence frequency was comparable across substrates (bare soil, light and dark biocrusts) and grass species. The magnitude of emergence varied by species, but pairwise comparisons of substrates within a species were not significant. However, the data were over-dispersed, so our estimates of the effect of species and substrate may be overestimated. Timing of emergence was similar among substrates and grass species in the Colorado Plateau hoop house. Within the Colorado Plateau field trial, the frequency of early establishment of *B. tectorum* was not influenced by substrate. However, early establishment percentage was higher on bare soil compared with light biocrusts for the Colorado Plateau field trial (Fig. 2, Table 3).

Greenhouse.—Within the greenhouse, emergence frequency was >95% for all species $\times$ substrate combinations. The magnitude of emergence varied among grass species plus the interaction of substrate type and its source region. Overall, emergence proportions were higher for *B. gracilis* than *A. purpurea*. The influence of substrate type depended on the substrate source region; within each desert, emergence magnitude was higher on bare soil than that on light or dark biocrusts. Biocrusts from the Sonoran Desert decreased emergence more than those from the Colorado Plateau. Emergence timing was comparable across grass species, with the influence of substrate type varying by source

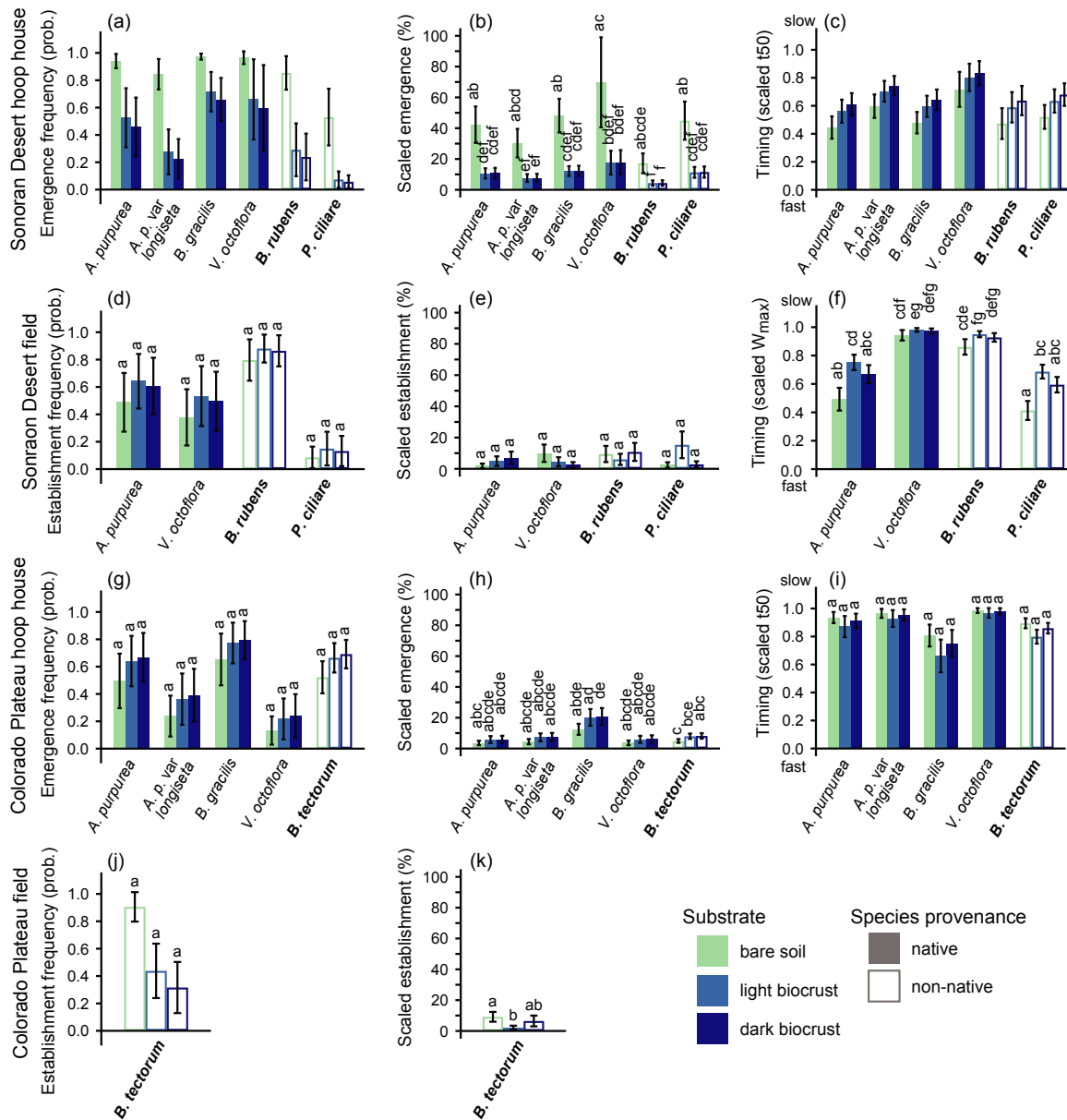


Fig. 2. Estimated marginal mean ($\pm$ SE) of emergence (hoop house) or early establishment (field) frequency, magnitude (%; scaled to viability), and timing (scaled t50 or W_{max}) for native and non-native (bold labels) grasses on bare soil, light biocrusts, and dark biocrusts from Sonoran Desert hoop house (a–c) and field (d–f) environments and Colorado Plateau hoop house (g–i) and field (j–k) environments. Smaller scaled timing values indicate faster emergence. Different lowercase letters within a panel indicate significant differences (Tukey adjustments, $\alpha = 0.05$). Panels missing lowercase letters had comparisons that were too complicated to represent here, but can be found in Appendix S2. Type II chi-squared test results of mixed-effects models given in Table 3.

region; biocrusts from the Sonoran Desert slowed emergence more than those from the Colorado Plateau. Emergence timing on dark biocrusts was similar among species and source deserts

and was always slower than that observed on bare soil (Fig. 3, Table 4).

Pots with light and dark biocrusts contained micropatches of bare soil, cyanobacteria, lichens,

Table 3. Type II chi-squared test results of mixed-effects models of emergence (hoop house) or early establishment (field) frequency, magnitude (%; scaled to viability), and timing (time to 50% of maximum emergence [t50; scaled] or weeks to maximum number of seedlings [$W_{\max}$; scaled] for grass species on light and dark biocrusts and bare soil (=substrate type) Sonoran Desert and Colorado Plateau hoop house and field trials. If interactions present, individual fixed effects not shown. Estimated marginal means and pairwise comparisons shown in Fig. 2.

Experimental setting	Response variable	N	Fixed effects	df	χ^2	P
Sonoran Desert hoop house	Frequency of emergence	198	Grass species	5	24.8	<0.001
			Substrate type	2	28.7	<0.001
	Emergence %	198	Grass species	5	10.0	0.074
			Substrate type	2	87.1	<0.001
	t50	123	Grass species	5	11.1	0.049
			Substrate type	2	28.2	<0.001
Sonoran Desert field	Frequency of establishment	108	Grass species	3	9.9	0.019
			Substrate type	2	1.1	0.568
	Establishment %	108	Grass species $\times$ substrate type	6	25.0	<0.001
			Grass species	3	32.6	<0.001
	$W_{\max}$	63	Substrate type	2	22.9	<0.001
			Grass species	4	7.9	0.097
Colorado Plateau hoop house	Frequency of emergence	120	Substrate type	2	2.4	0.299
			Grass species	4	18.0	0.001
	Emergence %	120	Substrate type	2	4.0	0.136
			Grass species	4	8.0	0.091
	t50	65	Substrate type	2	3.9	0.144
			Grass species	2	4.2	0.122
Colorado Plateau field	Frequency of establishment	27	Substrate type	2	7.6	0.022
	Establishment %	27	Substrate type	2		

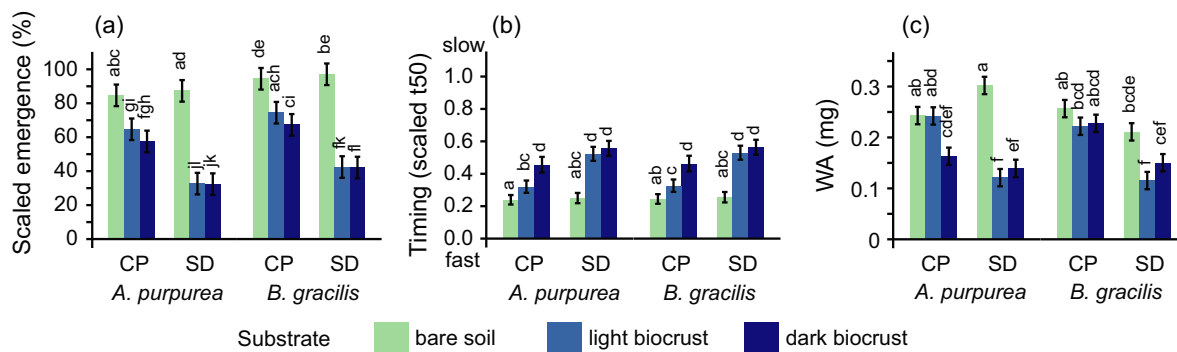


Fig. 3. Estimated marginal mean ($\pm$ SE) of emergence magnitude (%; scaled to viability; a), timing (scaled t50; b) and 24-h water absorption (WA; mg; c) of native grasses on bare soil, light biocrusts, and dark biocrusts from Colorado Plateau (CP) and Sonoran Desert (SD) source regions in a greenhouse environment. Different lowercase letters within a panel indicate significant differences (Tukey adjustments, $\alpha = 0.05$). Type II chi-squared test results of mixed-effects models given in Table 4.

and discontinuities (e.g., cracks; see *Methods: Greenhouse*). Of the seeds that emerged from pots with Colorado Plateau light biocrusts, nearly 50% had their callus/base associated with bare soil micropatches or were just beneath the surface of any type of micropatch. In contrast, emergence on similar micropatches from pots with

Sonoran Desert light biocrusts and Colorado Plateau and Sonoran Desert dark biocrusts was only 5–24% of the total emerged seeds. Although we scattered seeds on the surface at the start of the experiment, in pots with Colorado Plateau bare soil, >40% of emerged seeds were beneath the surface, whereas emerged seeds in Sonoran

Table 4. Type II Wald chi-squared test results of mixed-effects models of grass species seedling emergence magnitude (%; scaled to viability), time to 50% of maximum emergence (t50; scaled), and ~24-h water absorption (WA; mg) by native grass seeds for seeds on Colorado Plateau and Sonoran Desert (=source) light and dark biocrusts and bare soil (=substrate type) in greenhouse setting.

Response variable	N	Fixed effect(s)	df	χ^2	P
Emergence (%)	180	Grass species	1	11.9	0.001
		Source × substrate type	2	28.0	<0.001
t50	178	Grass species	1	0.2	0.669
		Source × substrate type	2	27.7	<0.001
WA	180	Grass species × desert × substrate type	2	6.2	0.045

Note: If interactions present, individual fixed effects not shown. Estimated marginal means and pairwise comparisons shown in Fig. 3.

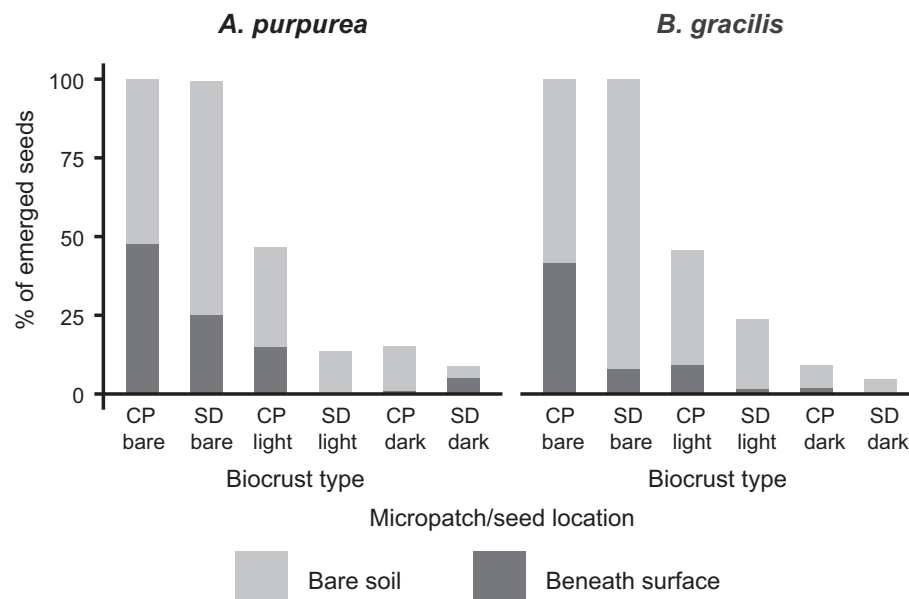


Fig. 4. Proportion of emerged native grass seeds (greenhouse environment) where seeds had their callus/seed base on bare soil micropatches or beneath the surface of any surface type in pots with bare soil, light, and dark biocrusts from the Colorado Plateau (CP) and Sonoran Desert (SD) source regions.

Desert bare soil pots were found beneath the surface less often (25% of *A. purpurea* and 8% of *B. gracilis*; Fig. 4).

Seed water uptake varied by the interaction of grass species, substrate, and source desert. For *A. purpurea* on Sonoran Desert substrates, seeds on bare soil absorbed more water compared with those on light and dark biocrust. For *A. purpurea* on Colorado Plateau substrates, seeds on bare soil absorbed more water compared to dark biocrusts with light biocrusts equivalent to the other Colorado Plateau substrates. The amount of water absorbed by *B. gracilis* seeds was similar among the Colorado Plateau substrates.

However, *B. gracilis* seeds absorbed more water on Sonoran Desert bare soil than on Sonoran Desert light biocrusts (Fig. 3; Table 4).

DISCUSSION

We conducted a coordinated series of experiments in controlled, semi-controlled, and field environments aimed at clarifying present inconsistencies regarding biocrust effects on grass emergence/establishment. Our experiments are elements of a broader goal aimed at assessing the potential use biocrusts as a component of restoration (Bowker 2007) and invasive species

management plans. Our analytical approach differed from many previous studies in that we both compared emergence/early establishment on biocrusts across a range of a grass species in addition to comparing across both species and substrates (bare soil, light biocrust, dark biocrust).

Native vs. non-native grasses

Our prediction that biocrusts would reduce emergence or early establishment of non-native grass species relative to native grass species was not consistently supported, although the variability in our data may have obscured some differences. More specifically, we did not observe differences in the emergence of non-native *B. tectorum* compared with native grasses in the Colorado Plateau hoop house, including the native annual *V. octoflora* (biocrust types pooled or separate). Our emergence magnitude finding was similar to previous work comparing emergence on biocrusts across species (*B. tectorum* to *Vulpia microstachys*, a native annual fescue; Deines et al. 2007; Serpe et al. 2008). However, we did not observe differences in germination timing as has been reported in other studies (Deines et al. 2007). We compared across annual and perennial species, and our experimental results concur with meta-analysis findings that plant longevity/duration is not a significant explanatory variable in explaining biocrust–germination relationships (Havrilla et al. 2019).

In our hoop house Sonoran Desert trials, emergence of the non-native annual *B. rubens* was similar to that of native grasses, whereas that of non-native perennial *P. ciliare* was reduced compared with some (*A. purpurea* and *B. gracilis*), but not all, native grasses. We saw a somewhat similar pattern in the Sonoran Desert field experiment. The non-native grasses used in our experiments likely evolved in association with a variety of biocrust types. The native range of *P. ciliare* spans Africa and portions of Asia and southeastern Europe (USDA ARS 2015), where biocrusts can be smooth or rolling (Colesie et al. 2016). *Bromus rubens* and *B. tectorum* are native to Eurasia and northern Africa (USDA ARS 2015), where biocrusts have smooth, rugose, pinnated, and rolling morphologies (Colesie et al. 2016). Within its native range of Israel, *B. rubens* germination does not differ between bare soil and cyanobacterial biocrusts (Zaady et al. 2003). The

non-native grasses used in our study originate from areas with biocrusts having morphologies similar to those in North America (Rosentreter and Belnap 2003), which may partially explain why we did not see a strong or consistent biocrust effect on emergence/establishment.

Biocrust development

Our prediction that dark biocrusts would be more of a barrier to grass recruitment than light biocrusts or bare soil was not supported. In our experiments, bare soil and light and dark biocrusts varied in their influence on grass emergence, although some differences may have been obscured by the high variability in our data. Emergence magnitude was higher on bare soil compared to light and/or dark biocrusts in some (Sonoran Desert hoop house, Colorado Plateau field, and greenhouse trials), but not all, settings. These inconsistencies are in accord with disparate North American studies reporting that biocrusts can reduce (Serpe et al. 2006, 2008, Deines et al. 2007, Havrilla and Barger 2018), increase (Pando-Moreno et al. 2004, Serpe et al. 2008, Havrilla and Barger 2018), or have no effect (Pando-Moreno et al. 2004, Serpe et al. 2006, 2008, Deines et al. 2007, Havrilla and Barger 2018) on grass emergence compared to bare soil or soils with biocrusts removed. Similarly, in North American field settings biocrusts can reduce or have no effect on seedling establishment (Harper and St. Clair 1985). Globally, the influence of biocrusts relative to bare soil or to soil with biocrusts removed is neutral (Havrilla et al. 2019).

Biocrust composition can significantly influence the extent to which grass germination and establishment differ from that on bare soil. Globally, lichen biocrusts reduce germination magnitude (Havrilla et al. 2019) and North American biocrusts dominated by crustose lichens reduce germination magnitude compared with bare soil (Deines et al. 2007, Serpe et al. 2008). Because our dark biocrusts had low lichen cover consisting mainly of squamulose and gelatinous morphologies (Rosentreter et al. 2007), morphology likely was not the main driver behind our findings that dark biocrusts reduced emergence compared with bare soil in some, but not all, settings.

Emergence timing relative to that on bare soil may (Serpe et al. 2006, Deines et al. 2007) or may not (Pando-Moreno et al. 2004) be influenced by

biocrust composition. Our experiments showed that some species in our Sonoran Desert trials emerged and established sooner on bare soil compared with light and/or dark biocrusts. A delay in emergence and early establishment, as we observed for many of the grass species in our experiments, may leave seeds more vulnerable to small mammal and ant predation (Reichman 1979, Fick et al. 2016).

Globally, cyanobacteria and mixed biocrusts are equivalent in their effect on germination and do not differ in their effect on germination magnitude relative to a control (Havrilla et al. 2019) and our findings generally align with this trend. Our experiments revealed a few instances where emergence/early establishment differed between light and dark biocrusts, notably when considering emergence timing and water absorption (see *Biocrust type/microtopography*).

Biocrust type/microtopography

Safe sites provide seeds with the conditions, resources, and protection needed for germination (Harper 1977). Our greenhouse experiment afforded the opportunity for a direct assessment of the microtopographic component of grass germination/early establishment “safe sites.” Emergence magnitude of the native grasses (*A. purpurea* and *B. gracilis*) was higher on the pinnacled Colorado Plateau biocrusts than on the rugose Sonoran Desert biocrusts. However, emergence magnitude on bare soil exceeded that of all biocrusts for both species. In addition, emergence on bare soil (both deserts) and on Colorado Plateau light biocrusts was accelerated, which may have been related to the bare soil micropatches within the Colorado Plateau light biocrusts. Within biocrusted soils, some have observed seeds emerging more often from non-crusted patches interspersed with biocrusts (Sylla 1987) while others have suggested that bare soil is itself a “safe site” for seed germination/seedling establishment (Reisner et al. 2013). The difference may also be due to an increased availability of safe sites on the Colorado Plateau biocrusts as some have speculated that rougher biocrusts have more safe sites for germination relative to flat biocrusts (Johansen 1986).

Water absorption by seeds on biocrusts can be influenced by biocrust composition, with crustose lichens decreasing seed water uptake relative to

that on mixed biocrusts and bare soil (Serpe et al. 2008). Although the dark biocrusts in our experiment had little in the way of crustose lichens and mosses, we observed decreases in water absorption. In our study, Sonoran Desert biocrusts decreased water absorption relative to bare soil, whereas the effect of Colorado Plateau biocrusts varied with grass species and biocrust type. Water absorption by *B. gracilis*, with its relatively small seeds, did not vary among Colorado Plateau substrates, whereas *A. purpurea*, with its larger seeds, exhibited lower water absorption on Colorado Plateau dark biocrusts. Our findings suggest potential biocrust type/composition × seed morphology interactions on seed water absorption that warrant further investigation.

Further investigations related to biocrust type/composition and seed morphology may reveal mechanisms underlying the influence of biocrusts on seed emergence. Biocrusts may reduce emergence by altering surface hydrology and temperatures; influencing rate, pattern, and depth of seed burial; and reducing seed-soil contact. These biocrust influences will, in turn, vary with the type of biocrust (Havrilla et al. 2019) and the plant species and seed attributes (Zhang et al. 2016). There is some evidence that grass germination on biocrusts may be influenced by seed morphology (Belnap et al. 2003b, Zhang et al. 2016, Havrilla et al. 2019). Accordingly, seed attributes such as seed size and shape and length of awns may be more important than species provenance in dictating grass recruitment on biocrusts.

CONCLUSION

We conducted a series of experiments to further our understanding of the role of biocrusts in grass emergence and establishment. We utilized a coordinated series of greenhouse, semi-controlled, and field environments involving native and non-native grasses and biocrusts from contrasting bioclimatic regions. Across our experiments, and contrary to our predictions, we observed no consistent differences between native and non-native grass emergences or early establishment on biocrusts. Species-specific interactions or seed attributes may be more important than species provenance in dictating grass recruitment on biocrusts. We also observed that the effect of biocrusts relative to that of bare soil on grass recruitment was

also variable and inconsistent. The topographically rugged Colorado Plateau biocrusts had higher grass emergence when compared directly with the flatter biocrusts of the Sonoran Desert lending support to the idea that biocrust microtopography is an important safe site (*sensu* Harper 1977) attribute. Although we focused on the initial “bottle-neck” phases of seedling emergence and early establishment (Leck et al. 2008), biocrusts and vascular plants interact on a variety of spatial and temporal scales (Bowker 2007) that extend well beyond the scope of our study. Given the inconsistent and variable outcomes of our coordinated experiments, restoration and invasive species management should be place-based and utilize grass species-, biocrust-, and site-specific information.

ACKNOWLEDGMENTS

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DATA AVAILABILITY STATEMENT

Data are available from Dryad: <https://doi.org/10.5061/dryad.1c59zw3v2>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3841/full>