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Edaphic constraints on seed germination and emergence of three *Acacia* species for dryland restoration in Saudi Arabia

C. E. Mayence · J. C. Stevens · P. Courtney · K. W. Dixon

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Abstract In situ edaphic factors affecting seed germination and seedling emergence of three framework species of *Acacia* were investigated with the intent of developing fundamental and scalable restoration capacity for Arabian dryland restoration. Direct seeding represents the most efficient means to restore vegetation at the landscape scale and this study provides insight into edaphic and ecological limitations, as well as effective protocols governing the use of native seeds for restoration in hyper-arid environments. The study was conducted in extant *Acacia* woodland habitat on conserved land (Thumamah Nature Park) in close proximity to Riyadh, Saudi Arabia. Broad-scale direct seeding using un- and pretreated *Acacia gerrardii*, *A. tortilis*, and *A. ehrenbergiana* seed, and two seed burial depths were implemented across three sites with distinct soil surface characteristics. Eight weeks post-sowing, random samples for each species × seed treatment × burial depth combination were excavated, sieved, and categorized as follows: failed to germinate, germinated but died prior to emerging, or successfully emerged. We show that germination and emergence of *Acacia gerrardii*, *A. tortilis,* and *A. ehrenbergiana* were driven by a three-way interaction among species, site, and seed burial depth. Treating seed with the signaling compound Moddus did not have a definitive effect, positive or negative, on any of the species investigated. *Acacia gerrardii* was the only species that exhibited widespread emergence, though emergence was not consistent across sites or burial depths. Germination was highest in disturbed soil (up to 69% for *A. gerrardii*), but very few (<2%) successfully emerged; a greater proportion of germinants in sandy soil emerged (up to 44% for *A. gerrardii*) even though the overall germination was less. Though species-dependent, a 2-cm sowing depth was most effective in sand; while in disturbed soil, sowing depths of 1 and 2 cm were comparable; and no germination was observed in gravelly clay soil. Sandy soil exhibited rapid water infiltration (107.6 mm min^{-1}), and post-sowing surface crusting was a non-factor (0.44 kg cm^{-2}). Disturbed soil exhibited moderate water infiltration (1.46 mm min^{-1}) and post-sowing surface crusting

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was double that of sand (0.88 kg cm^{-2}) and restrictive on seedling emergence. Gravelly clay exhibited extremely poor water infiltration (0.12 mm min^{-1}), and surface crusting was severe (4.49 kg cm^{-2}) and an order of magnitude greater than sand. The medium-coarse sand fraction, a key driver of the observed soil surface processes, was greatest in sand (55%) and significantly less and uniform in the disturbed (22%) and gravelly clay (22%) soils. Our findings demonstrate that soil surface characteristics and associated processes can dictate ecological processes at depths as shallow as 1–2 cm, and that soil crusts that slow water infiltration and impede seedling emergence rapidly reconstitute after disturbance; both are important considerations for restoring dryland vegetation.

Keywords *Acacia ehrenbergiana* · *Acacia gerrardii* · *Acacia tortilis* · Arid environment · Desert habitat · Penetration resistance · Seed burial · Seedling establishment · Soil crusting

Introduction

The rapid growth of Saudi Arabian cities and associated camping and recreational activities in ecologically sensitive outlying areas is ongoing and has led to large-scale loss of plant cover and soil degradation across the Arabian Peninsula (Mubarak 2004). These impacts in combination with desertification driven by a drying climate and livestock overgrazing have resulted in 60% of Saudi Arabia's rangelands becoming significantly degraded, less biodiverse, and not capable of delivering key ecosystem services (Shaltout et al. 1996). Moreover, changes in political, social, and cultural practices associated with grazing, including the collapse of traditional resource management systems, have concentrated grazing into increasingly marginal habitat, leading to yet more land degradation (Al-Rowaily 1999; Barth 1999; Gardner 2003). These changes have resulted in comprehensive strategic plans being established (e.g., Strategic Plan for the Arriyadh Region, Metropolitan Development Strategy for Arriyadh) that include developing large conservation zones across ecogeological units to improve opportunities for tourism and environmental protection (ADA 2003).

To reverse desertification trends, programs aimed at conserving existing habitat and biodiversity are being considered, though in Saudi Arabia most remain in their infancy. A focus of these programs is *Acacia* woodland restoration, given their diminished vegetation cover, rarity of recruitment events, high mortality, and critical ecological role in biodiversity and ecosystem health throughout the Middle East (Ward and Rohner 1997). Current programs, which have been only marginally successful, often include sporadic tree planting activities or urban landscaping efforts (e.g., Wadi Hanifa, ADA 2015) requiring large, unsustainable water inputs. Such projects have relied on nursery-grown transplants and lack systematic monitoring, so scientific data documenting plant performance and survival rates typically go unrecorded. In practice, these programs have not been driven by ecosystem restoration principles, though many aspire to reinstate pre-disturbed landscapes and ecosystems. Requirements for restoration projects including agreement on objectives, planning, capacity building (particularly in plant production technology), and long-term strategy development are now being considered by Saudi governmental agencies. Identifying restoration frameworks and processes is being matched by investment in science programs to guide the development of best practice restoration. This study exemplifies the dedicated funding model where interest in scalable and cost-effective science-based revegetation approaches led to this study of the linkages between seed ecology, hydrology, and soil processes to inform critical habitat restoration.

Soil moisture dynamics, driven by soil receptivity to precipitation relative to losses associated with runoff and evaporation, influence infiltration and soil moisture retention (Yang et al. 2010). Soil moisture dynamics, in conjunction with seed viability and type of dormancy, are factors that affect dormancy loss (Baskin and Baskin 1998; de Villalobos and Peláez 2001), seed germination (Call and Roundy 1991; Hardegree et al. 2013), and seedling emergence and survival (Montes-Recinas et al. 2012; see Walck et al. 2011 for extensive review). The influence of soil moisture on these processes is heightened in arid environments (Lundholm and Larson 2004) where precipitation timing and amount is highly variable (Caldwell et al. 2009), with pulses of moisture being more infrequent (Watson et al. 1997; Wiegand et al. 2004) and ephemeral (Noy-Meir 1973) compared to mesic systems. In arid systems, the probability of seed successfully dispersing to safe sites where germination and establishment can occur is rare (Nano et al. 2013; Nathan and Muller-Landau 2000). Nonetheless, seedling recruitment occurs, but the time between significant natural recruitment events can be on the order of decades or longer (Fehmi et al. 2014).

Precipitation events in arid environments are interspersed with extended dry periods (Al-Saleh 1997) during which surface materials are subject to redistribution by wind and alteration by physical and chemical weathering (Brady and Weil 2002; Ravi et al. 2010). These processes, together with inherent soil qualities (e.g., texture, chemistry, organic matter content) may promote the formation of surface conditions (i.e., crusting) that restrict seed burial, limit moisture infiltration (Hussein et al. 2010; Maestre et al. 2003), and impede seed imbibition and germination through poor seed–soil contact (Fei et al. 2012). Seedling emergence can also be constrained, as the amount of force required for emergence can exceed what seedlings are capable of generating (Azam et al. 2012). In hyper-arid environments tree recruitment is largely confined to hydrological features (e.g., wadis, washes, arroyos) where soil is unconsolidated, and infiltration occurs more rapidly. These attributes contribute to groundwater recharge and deep-rooted species (e.g., *Acacia*) capitalize on these conditions (Padilla and Pugnaire 2007).

In arid environments, soil conditions suitable for germination are highly transient and must be immediately exploited if seedlings are to emerge and establish. Soil parameters that constrain emergence also delay photosynthesis and slow growth, making it difficult for seedlings to take advantage of the abbreviated establishment period. Success is dependent on precipitation, depth of seed burial, plant growth rate and desiccation tolerance, and soil texture (Walck et al. 2011). Though not without risk, sowing pretreated seed can enhance germination at soil moisture levels below that required by dormant seed (Burrows et al. 2009; Wagner et al. 2011), and is one means for capitalizing on infrequent, low-intensity precipitation events.

Thus the aims of this study were to:

1. Assess seed germination and seedling emergence of three *Acacia* species sown under prevailing (low) soil moisture conditions, determining the relative importance of burial depth across sites differing in landscape position, soil surface texture, and disturbance history.
2. Identify linkages among soil texture, infiltration rate, and surface crust formation and their influence on seed germination and emergence to inform ecological restoration in a hyper-arid environment.

Materials and methods

Study area

All research was conducted in Thumamah Nature Park, an iconic desert park ~80 km north of Riyadh, Saudi Arabia (lat 22°45′19″N, long 46°12′32″E). Thumamah Park is an area of ~170 km^{-2} and features vegetation and geomorphic features characteristic of the Middle East and North Africa (El-Sheikh et al. 2013). The landscape comprises *Acacia*-dominated wadis, perennial shrub and grassland habitat, gravelly plains, and prominent sandstone escarpments (Fig. 1a, b) (Brown 1960). Mean annual minimum and maximum temperatures range from 15 to 37 °C, with minima occasionally dipping to 0 °C and maxima periodically reaching 50 °C. The climate is arid with mean annual rainfall of ~110 mm, most falling in winter and spring. Relative humidity varies between 8 and 20% (day and night) with sand and dust storms common during summer, which are thought to be exacerbated by the loss of regional vegetation cover.

Three sites indicative of soils and topography of the region yet with different soil surface textures (Fig. 1c–e) and landscape positions were utilized in this investigation: (1) a gently sloping unvegetated plain with scattered surface gravels imbedded in a surficial clay matrix, (2) an undulating sandy plain with scattered small (<0.25 m) shrubs, and (3) an area intermediate between the gravelly clay and sandy plain disturbed by earthmoving equipment but leveled prior to sowing. Sites were ≤500 m apart, adjacent to an ecologically intact wadi with healthy tree and shrub cover, all influenced by the same precipitation regime.

Focal species and seed collection

Three framework *Acacia* species were investigated: *A. ehrenbergiana* Hayne, *A. gerrardii* Benth. subsp.

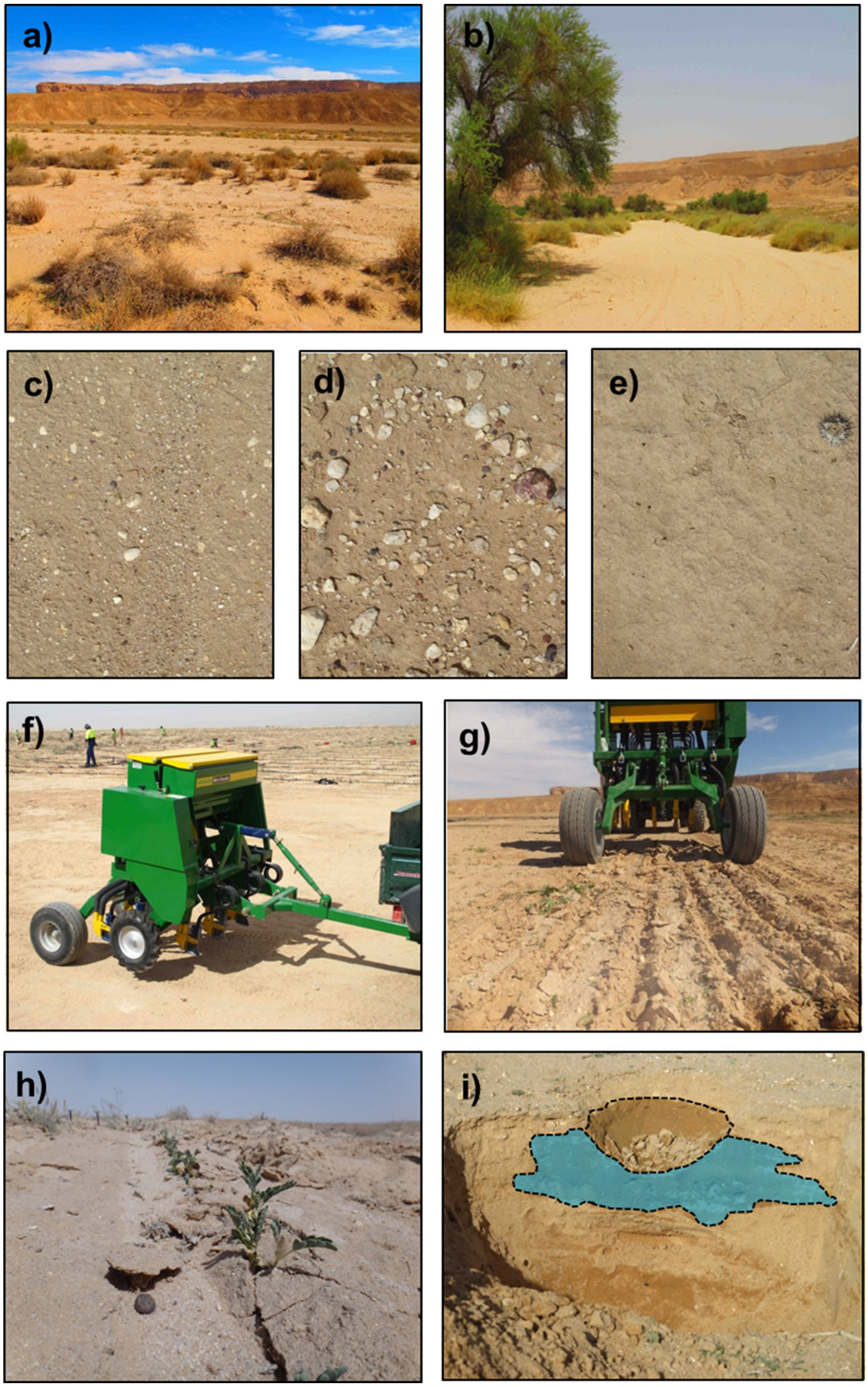

Fig. 1 Images of **a** terrain adjacent to study area; **b** healthy wadi vegetation cover; **c** disturbed; **d** gravelly clay, and **e** sandy soil surface appearances; **f** Aitchison mini seed drill; **g** post-sowing furrow spacing; **h** *A. gerrardii* seedlings in sand with minor soil crusting; **i** soil wetting demonstration showing (*shaded area*) lateral relative to vertical movement

negevensis var negevensis, and *A. tortilis* (Forssk.) Hayne subsp. s*pirocarpa*, all priority species for habitat restoration throughout the Arabian Peninsula and portions of northern Africa where their prevalence has been much reduced by fuel wood cutting, diminished recruitment, and fodder harvesting for livestock. Seed of local provenance was collected the previous year, cleaned, dried, and stored at −18 °C in a seed bank facility.

Edaphic parameters

The in situ edaphic environment at each site was characterized by determining surface soil texture, bulk density, penetration resistance (PR), and infiltration rate. Surface soil texture was determined from five samples per site obtained from a depth of 0–5 cm. Samples were divided into five classes adapted from Krumbein (1934) based on particle size (dry sieved): <0.355 mm (fine sand, silt and clay), 0.355–0.84 mm (medium sand), 0.85–1.69 mm (coarse sand), 1.70–2.36 mm (very coarse sand), and >2.36 mm (very fine gravel and larger). Bulk density (g cm^{-3}) was determined at five locations per site, and soil from each site was analyzed for Ec (1:5 water), pH (1:5 water), organic C (Walkley and Black 1934), total N (Kjeldahl digestion), and other macronutrients [K, Ca, Mg, P, and S (Mehlich No 3 for all, Mehlich 1984)]. For chemical properties, a composite sampling approach was used in which five samples per site were bulked, yielding one for analysis.

Penetration resistance was measured using a soil penetrometer (Geotester, Civilab Pty Ltd, AUS). Measurements (kg cm^{-2}) were made at five locations and four depths (surface, 5, 10, and 20 cm) per site in unsown (reference) and sown areas. Unsown areas were measured to establish baseline conditions while sown areas were measured (post-sown and surface only) to characterize surface crust redevelopment. In all cases, five replicate samples were obtained. In sown areas where no emergence was observed, PR was measured in seed drill furrows and adjacent inter-furrow areas. When emergent seedlings were present, PR was measured at three locations in conjunction with furrows: center, off center, and inter-furrow. Infiltration rate (mm H_2O min^{-1}) was measured with a mini disk infiltrometer (Decagon Devices, Inc, USA) at five random locations in furrows (sown) and analogous unsown areas.

Direct seeding trial

Prior to sowing, *A. gerrardii* and *A. tortilis* seed was manually scarified to alleviate physical dormancy. Half of the scarified seed for both species was then chemically treated with Moddus (trinexapac-ethyl) (Syngenta Ltd, GBR) by soaking for 2 h in 0.5% solution (50 ml 10L H_2O). Moddus is an agro-industrial plant signaling and growth regulating compound shown to increase crop yield (Syngenta 2013), and anecdotally reported to enhance plant stress tolerance. Codes for seed treatments are as follows: untreated (−M) and pretreated (+M). To eliminate priming effects, all remaining (control) *A. gerrardii* and *A. tortilis* seed was soaked in freshwater for 2 h. *Acacia ehrenbergiana* seed is not physically dormant (Aref 2000) and was not scarified, but was soaked in Moddus and freshwater as described previously. Representative samples of each field-sown seed lot were tested for germinability under controlled environment conditions (25 °C, dark incubator).

Seed was sown in winter using an Aitchison mini seed drill, Model MS06 (Fig. 1f–g) (Reese Group Ltd-Aitchison, NZL). Sowing occurred in six parallel rows separated by ~20 cm and at two depths: 1 and 2 cm. Being a field trial, sowing rate (~100 seeds m^{-1}) was greater than would be employed in actual restoration. Soil moisture content at sowing was uniform across sites and best described as dry (<1% VSW). After sowing, each site was overhead irrigated three times (~25 mm $event^{-1}$ over 3 weeks = 75 mm) to simulate average season breaking precipitation. Ambient rainfall amounted to an additional 25 mm over the course of the study.

After a period of 8 weeks, seed germination and seedling emergence were assessed. First, each drill-sown line (one line per species and sowing depth) was divided into 10 1 m sections, with three of the 10 randomly chosen to serve as representative samples of each species × seed burial depth × seed treatment combination. The number of emergent seedlings (live and dead) in each 1 m section was tallied. Second, the first 3 m of each line were excavated and sieved to recover all seed and seedling material. Excavated sections differed from the three 1 m sections where emergence was assessed because the latter remained intact for tallying seedling survival. Seed and seedling material were classified as follows: (1) ungerminated (Ungerm), (2) germinated but died before emerging

(Germ + died), and (3) emerged (Emerged). Emergent seedlings were described as either dead (Emerged + died) or alive (Emerged + alive).

Statistical analyses

SAS Version 9.2 was used for all statistical analyses. To test for differences in edaphic parameters one-way ANOVA was used, the exception being for pre- and post-sowing PR for which paired *t* tests were used. Differences in germination and emergence were assessed using either multi-factor ANOVA (for equal sample sizes) or a GLM (for unequal sample sizes). Continuous data types were log (natural) transformed while discrete germination and emergence data were arcsin-transformed to adjust for unequal variances. In figures and tables, actual treatment means are presented. A significance level of $\alpha = 0.05$ was used for all statistical analyses, and Tukey's post hoc multiple comparison procedure was used because of small sample sizes.

Results

Edaphic parameters

Not all edaphic metrics varied across sites (Table 1). Infiltration rate was 70–900 mm·min^{-1} greater ($P < 0.05$) for the sandy soils compared to the disturbed and gravelly clay soils. Bulk density on the other hand did not vary noticeably (1.72–1.76 g cm^{-3}; $P = 0.52$). Chemical properties did not differ significantly across sites; as such only ranges are reported: Ec (6–7 mS m^{-1}), pH (9.1–9.2), organic C (0.06–0.19%), total N (0.006–0.016%), P (0.9–2.6 mg g^{-1}), K (52–72 mg kg^{-1}), Mg (150–190 mg kg^{-1}), S (8–13 mg kg^{-1}), and Ca (all ~5500 mg kg^{-1}).

Soil particle size varied significantly across sites ($F_{14,60} = 260.31$; $P < 0.0001$) and for each diameter class (Table 2). The disturbed and gravelly clay soils were composed of similar fine (<0.85 mm) but not coarse-textured (>2.37 mm) materials, and compared to the sandy soil, the fine-textured fractions (<0.84 mm) of the disturbed and gravelly clay soil were significantly less (27 and 24% less, respectively). The >0.85 mm diameter fraction was significantly greater for the disturbed and gravelly clay compared to the sandy soil (84 and 83%, respectively). The medium-grain sand fraction (0.36–0.84 mm) was dominant in the sandy soil.

Penetration resistance (PR) varied significantly across sites and most depths. Surface PR was ~1.5 kg cm^{-2} greater ($P < 0.05$) for the gravelly clay (5.9 kg cm^{-2}) compared to similar resistance in disturbed (3.8 kg cm^{-2}) and sandy (3.9 kg cm^{-2}) soils. Appreciable across-site differences were not observed at 5 cm ($P = 0.75$), but differences at 10 and 20 cm were significant ($P < 0.05$ for both) [ranging from 2.24 to 4.9 kg cm^{-2} (sand–disturbed) at 10 cm to 2.9–5.7 kg cm^{-2} (sand–disturbed) at 20 cm]. Within site, PR was also depth-dependent, with PR increasing from 5 to 20 cm in the disturbed soil ($P < 0.05$), but decreasing over the same distance for the gravelly clay and sandy soils ($P < 0.05$ for both).

Table 1 Site-level differences in water infiltration and bulk density

	Soil metric	
Site/soil	Water infiltration (mm min^{-1})[a]	Bulk density (g cm^{-3})
Disturbed	1.46 ± 0.51^{b}	1.76 ± 0.02^{a}
Gravelly clay	0.12 ± 0.02^{c}	1.72 ± 0.01^{a}
Sand	107.6 ± 32.78^{a}	1.73 ± 0.02^{a}
F value$_{[df\ 2,12]}$	123.53*	0.68$^{n.s.}$

Means with the same letter in the same column are not statistically significant ($P > 0.05$)

Values are mean ± SE

n.s. Non-significant difference ($P > 0.05$)

* Significant difference ($P < 0.05$)

[a] Test statistics are for log-transformed data

Table 2 Distribution of soil particle size classes (as a proportion of total for each site)

Diameter (mm)	Site/soil			F value$_{[df\ 2,12]}$
	Disturbed	Gravel	Sand	
<0.355	$0.45 \pm 0.03^{a,b}$	$0.48 \pm 0.01^{a,b}$	$0.55 \pm 0.01^{a,a}$	8.39*
0.355–0.84	$0.22 \pm 0.02^{b,b}$	$0.22 \pm 0.00^{b,b}$	$0.39 \pm 0.01^{b,a}$	82.02*
0.85–1.69	$0.18 \pm 0.04^{b,a}$	$0.07 \pm 0.00^{c,b}$	$0.04 \pm 0.00^{c,b}$	21.58*
1.70–2.36	$0.04 \pm 0.00^{d,a}$	$0.03 \pm 0.00^{d,b}$	$0.01 \pm 0.00^{d,c}$	142.87*
>2.36	$0.10 \pm 0.00^{c,b}$	$0.20 \pm 0.01^{b,a}$	$0.00 \pm 0.00^{e,c}$	438.98*
F value$_{[df\ 4,20]}$	62.67*	937.86*	1552.16*	

Means with the same letter in the same column or row are not statistically significant ($P > 0.05$). All analyses performed on arcsin-transformed data. First letter corresponds to within-site F value (bottom row), second to across-site F value (right column)

Values are mean ± SE

* Significant difference ($P < 0.05$)

The disruption to the soil surface caused by the seed drill during sowing resulted in a 77% decrease in surface PR in the disturbed soil ($P < 0.0001$), a 24% decrease in the gravelly clay ($P = 0.0003$), and an 89% decrease in the sandy soil ($P < 0.0001$) (Table 3). Soil PR varied significantly across sites before and after sowing but post-sowing differences were greater due to the large decreases by the disturbed and sandy soils relative to the gravelly clay (which nearly returned to the pre-sowing PR after 8 weeks).

Seed germination and seedling emergence

Seed germination was not observed in the gravelly clay soil regardless of species, sowing depth, or seed treatment. Germination and emergence were only observed for the sandy and disturbed soils, and the proportion of seed that germinated and emerged differed across site, species, seed treatment, and sowing depth (germination: $F_{23,74} = 7.25$; $P < 0.0001$; emergence: $F_{23,74} = 8.17$; $P < 0.0001$).

Seed germination at 1 cm in the sandy soil varied by species, with the greatest germination (24%) in *A. gerrardii* ($F_{5,12} = 185.51$; $P < 0.0001$), followed by *A. tortilis* at 13% ($F_{5,24} = 173.56$; $P < 0.0001$) and *A. ehrenbergiana* at 1% ($F_{5,21} = 1039.55$; $P < 0.0001$) (Fig. 2a). Most germinants were +M; however, all failed to emerge. Seed sown at 2 cm exhibited a different pattern (Fig. 2b), with germination by *Acacia ehrenbergiana* increasing to 29 and 38% (+M and −M, respectively) ($F_{5,15} = 11.99$; $P < 0.0001$), but as with the 1 cm depth, none emerged. *Acacia gerrardii* germination increased to 41 and 74% (+M and −M), and of the 74% of −M germinants, 44% emerged ($F_{5,15} = 5.03$; $P = 0.0066$). All 41% of +M germinants successfully emerged. Germination by *A. tortilis* at the 2 cm depth increased to 49 and 93% (+M and

Table 3 Pre- (non-furrow) and post-sowing (furrow) PR (kg cm^{-2})

Time	Site/soil			F value$_{[df\ 2,72]}$
	Disturbed	Gravel	Sand	
Pre-sowing	$3.77 \pm 0.22^{a,b}$	$5.91 \pm 0.11^{a,a}$	$3.98 \pm 0.31^{a,b}$	20.27*
Post-sowing	$0.88 \pm 0.09^{b,b}$	$4.49 \pm 0.27^{a,b}$	$0.44 \pm 0.05^{b,c}$	137.79*
t value$_{[24]}$	13.52*	4.27*	14.09*	

Means with the same letter in the same column or row are not statistically significant ($P > 0.05$). All analyses performed on log-transformed data. First letter corresponds to within-site t value (bottom row), second to across-site F value (right column)

Values are mean ± SE

* Significant difference ($P < 0.05$)

−M). Of the 49% of +M germinants, nearly all (99%) died prior to emerging ($F_{5,12} = 6.90$; $P = 0.003$). Of the 93% of −M germinants, most failed to emerge, leaving 10% that emerged successfully.

Seed germination at 1 cm in disturbed soil also varied across species with the greatest germination (60%) in *A. gerrardii* ($F_{5,12} = 4.26$; $P = 0.0185$), followed by *A. tortilis* at 58% ($F_{5,12} = 17.59$; $P < 0.0001$), and *A. ehrenbergiana* at 33% (Fig. 3a). For *A. ehrenbergiana,* only −M seed germinated and all failed to emerge. Of the 60% of +M *A. gerrardii* germinants, only 8% successfully emerged. All 8% of the −M *A. gerrardii* germinants failed to emerge, and none of the 52 and 58% (+M and −M) of *A. tortilis* germinants emerged. Results were different for two of the three species at the 2 cm depth (Fig. 3b). *Acacia ehrenbergiana* germination decreased to 6% with deeper burial and none emerged ($F_{5,9} = 113.38$; $P < 0.0001$). *Acacia gerrardii* germination was 27 and 69% (−M and +M). Of the 69% of +M seed that germinated, only 2% emerged ($F_{5,12} = 21.21$; $P < 0.0001$); the 27% of −M germinants exhibited similarly low (1%) emergence. For *A. tortilis,* 18 and 52% of seed germinated (+M and −M) but all died prior to emerging ($F_{5,9} = 22.41$; $P < 0.0001$).

In terms of trends across sites and species, overall germination was higher in the disturbed soil, but the fraction of emergent seedlings was greater in the sandy soil. Sowing depth was not important in disturbed soil, whereas in sand the 2 cm sowing depth resulted in 88% greater germination and 100% greater emergence compared to 1 cm. +M seed represented the majority of germinants at 1 cm in the sandy soil. When averaged across sites, −M seed accounted for a greater proportion of germination and emergence. *Acacia tortilis* exhibited the greatest overall germination which was comparable at 2 cm in sandy soil and 1 cm in disturbed soil, while *A. gerrardii* exhibited the greatest overall emergence.

Under closer inspection of the sandy soil, *A. gerrardii* emergence and surface crusting varied across the site and at the scale of the furrow made by the seed drill. In areas with pronounced surface crusting (~2.1 kg cm^{-2}), 96% of seed either failed to germinate or germinated and failed to emerge. However, in areas with less crusting (~0.6 kg cm^2),

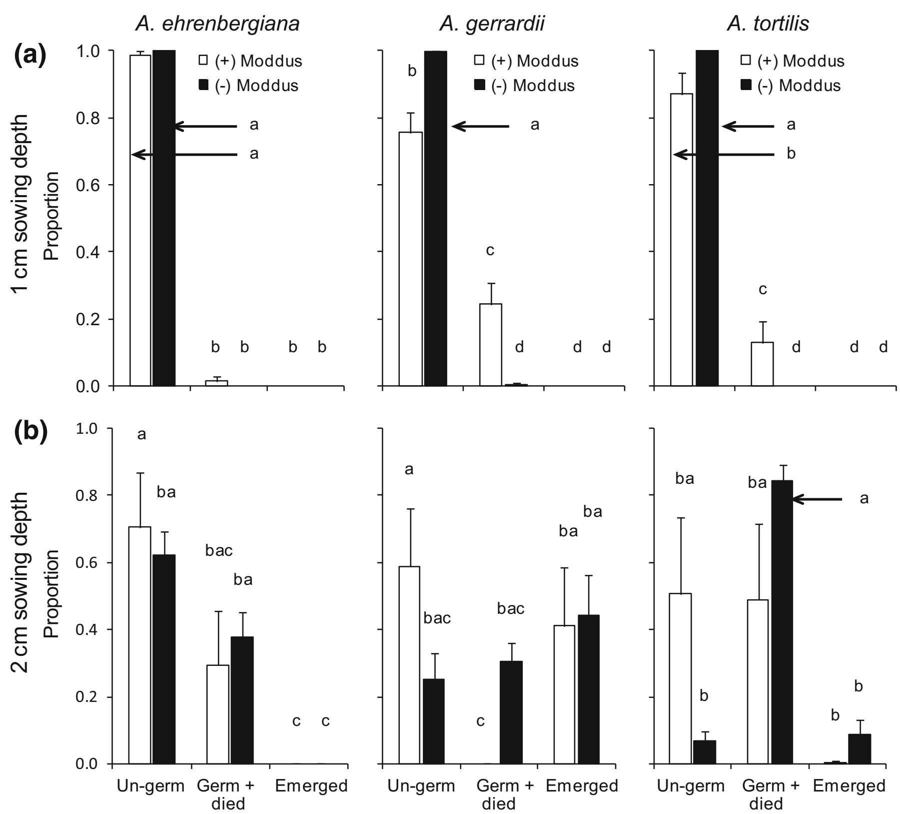

Fig. 2 Species and sowing depth differences in germination and emergence for +M and −M seed sown at **a** 1 cm and **b** 2 cm in sand. *Ungerm* ungerminated; *Germ + died* germinated and died; *Emerged* emergent seedling. *Letters over bars* represent statistical significance across all developmental stages according to species and sowing depth (Tukey's multiple comparison procedure, $\alpha = 0.05$). Test statistics are for arcsin-transformed data. Values are mean ± SE

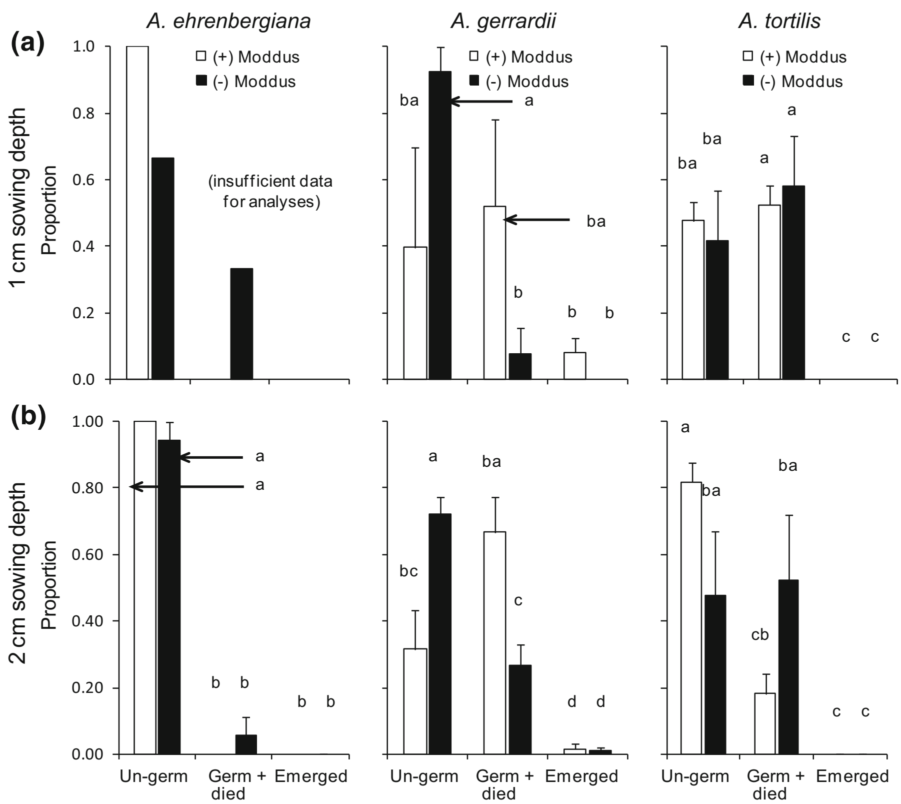

Fig. 3 Species and sowing depth differences in germination and emergence for +M and −M seed sown at **a** 1 cm and **b** 2 cm in disturbed soil. *Ungerm* ungerminated; *Germ + died* germinated and died; *Emerged* emergent seedling. *Letters over bars* represent statistical significance across all developmental stages according to species and sowing depth (Tukey's multiple comparison procedure, $\alpha = 0.05$). Test statistics are for arcsin-transformed data. Values are mean ± SE

45% of germinants emerged with 25% of those alive after 8 weeks ($F_{5,164} = 11.95$; $P < 0.0001$). Surface crust formation was not completely offset by disturbance caused by the seed drill, though post-sowing crusting was less (Table 3). Overall, sown areas exhibited less crusting compared to reference conditions ($F_{7,220} = 18.57$; $P < 0.0001$), and PR was significantly less in the center of furrows relative to off-center areas; inter-furrow PR was lower relative to reference conditions.

Discussion

This study demonstrates that variation in surface and near-surface soil physical attributes (e.g., texture) can lead to crusting and differential water infiltration capacity among other processes, driving differences in seed germination and seedling emergence. The ability of some soil types to retain adequate moisture in near-surface layers (driving germination through imbibition) as well as facilitate water movement to depth (driving emergence through seedling growth) in part explain what we observed. The greatest seedling emergence occurred in the sandy soil (Fig. 1h) though seed germination was greatest in the disturbed soil. Irrigation trials showed rapid infiltration to greater depth in the sandy soil, in turn supporting germination at the 2 cm sowing depth but not at 1 cm where we assume moisture retention was insufficient for seeds to imbibe. This suggests that the additional 1 cm of soil cover was adequate to enhance moisture retention and insulate seed from desiccation (Zheng et al. 2005) in a very well-drained soil. The additional soil cover was not required in the less sandy, slightly heavier disturbed soil where germination at both sowing depths was comparable and the greatest among soil types was investigated. For arid-adapted species like

Acacia, a difference of several hours of moist soil conditions around the seed is sufficient for germination (Abulfatih 1995). To increase germinability, emergence, and seedling survival, additional research targeting the absolute moisture retention capacity of these soils is warranted (e.g., Benigno et al. 2013), as is research investigating lateral water movement and the presence of subsoil preferential flow channels (Fig. 1i) (Devit and Smith 2002). Substrates such as the gravelly clay where seed completely failed to germinate (owing to the combined effects of poor infiltration, surface crust formation, and high PR) would likely benefit from engineering solutions such as combined shallow scarification and gypsum ($CaSO_4$) application that promote water infiltration (Critchley and Siegert 1991), soil structural development, and jumpstart key ecological processes (Gutterman 2001).

That each species in this trial responded differently to a uniform set of conditions highlights the natural range of variation in hydrological cues, dormancy states, and imbibition potential common in arid-adapted species (Commander 2009). Although germination and emergence trends consistently observed in this study align broadly with minimal rainfall envelopes for current distributions of two of the species investigated (*A. tortilis* <400 mm year^{-1}; *A. ehrenbergiana* >400 mm year^{-1}, FAO), understanding how germination and emergence processes are driven by available moisture above critical thresholds, such as base water potentials, is crucial for recruitment in precipitation-limited desert environments (Ogle and Reynolds 2004; James et al. 2011). For restoration activities to be successful in such environments, one must be acutely aware of the extremely narrow margins separating no germination, germination yet failed to emerge, and successful emergence as indicated by this study. Restoration practitioners should be steadfast in their attention to detail for variables within their control (e.g., species selection, seed quality and dormancy-breaking pre-treatments, site selection and site preparation) because precipitation events are uncommon in hyper-arid environments and failing to capitalize on an event due to poor planning and execution is financially and temporally costly.

Pre-treating seed with Moddus had no obvious benefit on increasing thresholds for plant establishment across germination, emergence, or seedling survival stages. The exceptions were germinants at 1 cm in sandy soil, as nearly all were +M, suggesting Moddus may stimulate germination under exceptionally dry conditions. However, doing so places germinants in an unlikely-to-recruit position unless emergence is coupled with or immediately followed by precipitation, as seedling mortality in arid environments tends to be greatest during the first dry period after emergence (Lloret et al. 1999). *Acacia gerrardii* was the only species for which +M seed emerged, again suggesting species-specific interactions, though the proportion of +M seedlings did not differ from −M seedlings. These results are somewhat novel because Moddus is marketed as a yield enhancer for widely produced agricultural species, not a seed germination stimulant. Laboratory trials are required to fully understand the potential benefit of Moddus as a germination stimulant as concentration levels and method of delivery may influence its use in seed treatment, as has been observed with other signaling compounds (Stevens et al. 2006).

In Saudi Arabia and similar hyper-arid environments where the probability of recruitment occurring annually is low and dependent on many factors (Abulfatih 1995; Ward and Rohner 1997; Aref 2000), it is essential to understand these factors and be cognizant of whether a site can support suitable conditions including seed safe sites and germination niches if large-scale, seed-based restoration activities and programs are to be effectively deployed. Although not assessed in this study, the establishment of seedlings is further reliant upon access to deep moisture, with the time required for seedlings to access and exploit this resource being too great in all but the most ecologically suitable sites in most years (Lloret et al. 1999; Azam et al. 2012).

This study addresses seed and edaphic constraints confronting the first stages of seedling recruitment in arid environments including the interaction between precipitation and soil, seed pre-treatment, and depth of seed burial. Given the research programs are only now being considered in Saudi Arabia to address large-scale restoration to support a broader conservation strategy, this study provides a platform to target future research endeavors and their application. Understanding key ecological limitations to recruitment, including seed–soil–environment interactions, will allow scalable solutions to be efficiently identified, including defining target restoration site locations and optimization of site manipulations to maximize seedling recruitment by extending the window of favorable edaphic conditions.

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