Shrub Seedling Root Development, Establishment and Encroachment Potential

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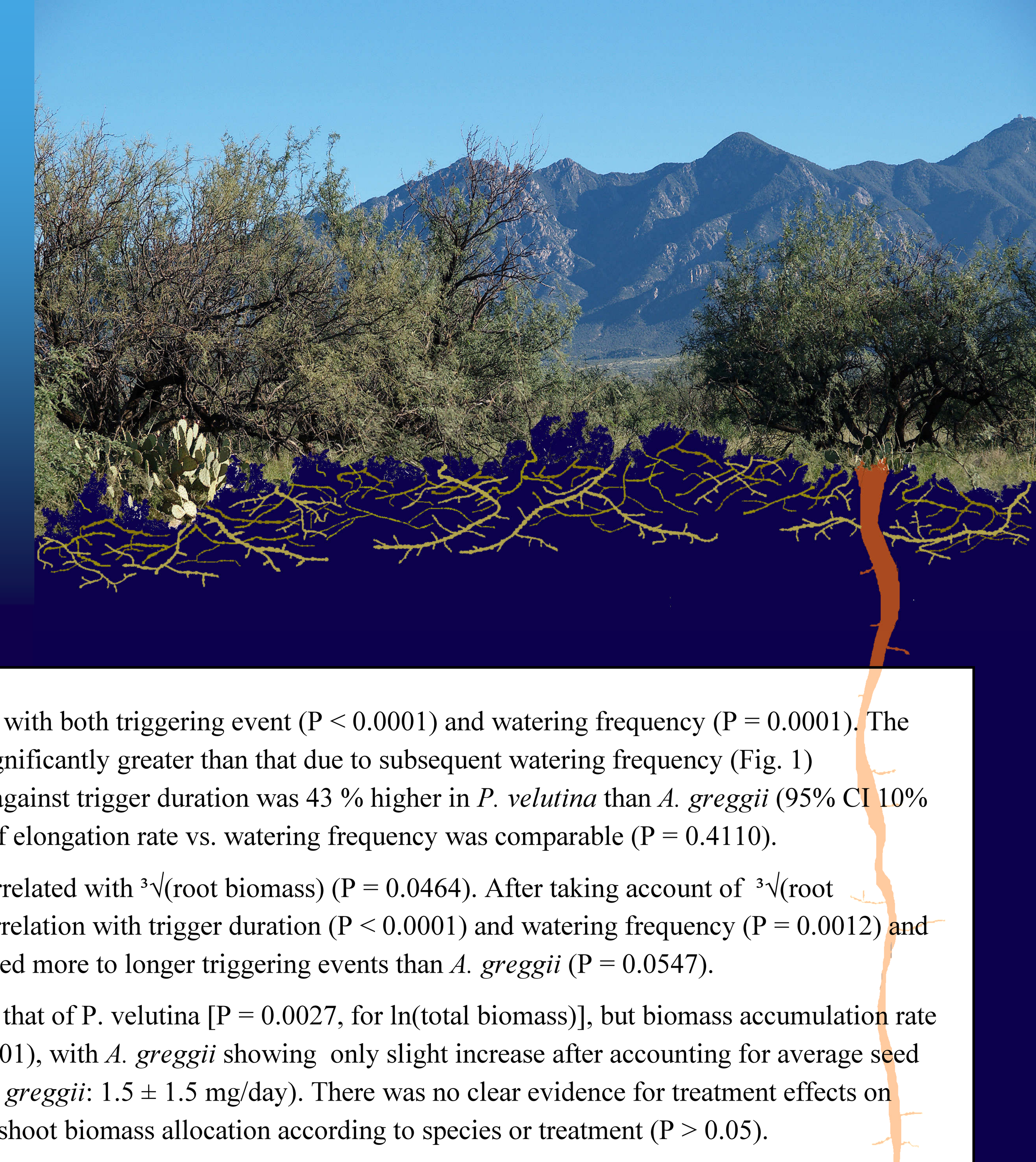

Abstract

• Encroachment of woody plants into arid and semi-arid grasslands is well-documented. Effects on nutrient cycles and community composition are profound, but it remains unclear why some native shrubs have spread dramatically while others have not. We suggest that the capacity for rapid taproot elongation by seedlings under a wide range of moisture conditions is associated with encroachment potential.

• To test this hypothesis we compared seedling emergence and growth of two species with different encroachment histories in southern Arizona: *Acacia greggii* (non-encroacher) and *Prosopis velutina* (aggressive encroacher). Seedlings were grown in a controlled environment for 2.5 weeks, varying the number of watering days to trigger germination ("trigger duration"; 4 levels) and the follow-up watering frequency (2 levels).

• We hypothesized taproot elongation would be faster in *P. velutina* (H_1) and that *P. velutina* would be more responsive to water inputs both during (H_2) and after (H_3) germination. Evidence supporting H_1 was weak and there was no support for H_3. However, there was strong support for H_2: taproot elongation increased linearly with trigger duration with a slope 58% higher in *P. velutina* than *A. greggii* ($P = 0.0076$).

• This suggests newly emerged *P. velutina* seedlings are highly responsive to the magnitude of the rainfall event which triggers germination, thus reducing the time required to escape (a) topsoil desiccation and (b) strong below-ground competition from shallow-rooted competitors, such as grasses. By contrast, *A. greggii* seedlings seem less able to take advantage of triggering events.

Methods

Site Description and environmental basis for treatments

• Greenhouse experiment conducted at University of Arizona Campus Agricultural Center in Tucson.

• Watering treatments based on summer precipitation (PPT) from the Santa Rita Experimental Range (SRER), 40 km south of Tucson (Tables 1 and 2). Data sets were provided by the Santa Rita Experimental Range Digital Database (SRER 2007).

Experimental Design

• *Prosopis velutina* and *Acacia greggii* seeds were chemically scarified to break dormancy (*Prosopis* in 20% H_2SO_4 for 10 min; *Acacia* in 90% H_2SO_4 for 20 min), then soaked 24 h in distilled water in the dark.

• Seeds of each species (n=4) were planted into each of 72 pots (Zipset™) filled with a sandy loam soil (Fig. 1). Emerging seedlings were thinned to one per pot. Four pots of each species were randomly assigned within each block (tray of pots).

• Trays were allocated to one of two drip-line irrigation feeds operated by manual valves with a flow meter and calibrated to determine the volume of water required for each feed to supply 5 mm per pot.

• Triggering events (5 mm H_2O in morning and 5 mm in the evening per day) started on consecutive days to allow post-trigger watering to begin the same day for all treatments. Thereafter, one feed delivered 5 mm H_2O to each of its pots on alternate mornings; the other feed delivered 5 mm every morning.

• Harvests were staggered, 16 days after 3- and 5-day triggering events and 17 days after 2- and 4-day triggering events. No water was applied the day before harvest, and 5 mm was applied as scheduled two days beforehand. Taproot length was measured. Seedling root systems and shoots were oven dried at 105 °C for 48 h and then weighed.

• Mean green-weight seed mass was determined after removing seed coats (n = 20).

Analysis

• Measurements were converted to units per day of experiment to account for differences in experiment duration. Values for each species were averaged for each block (tray), as watering treatments were applied at the tray level.

• Multiple linear regressions were applied to taproot elongation rate, ln (root biomass), and rate of total biomass increase (root + shoot – mean seed biomass). Block location (distance from cooler pads) was a random effects variable; trigger duration and subsequent watering frequency were fixed effects. An additional regression on taproot elongation rate also included $\sqrt[3]{\text{root biomass per day}}$ as an explanatory variable. JMP 5.0.1a software was used for all analyses (SAS 2002).

Figure 1. Experimental setup.

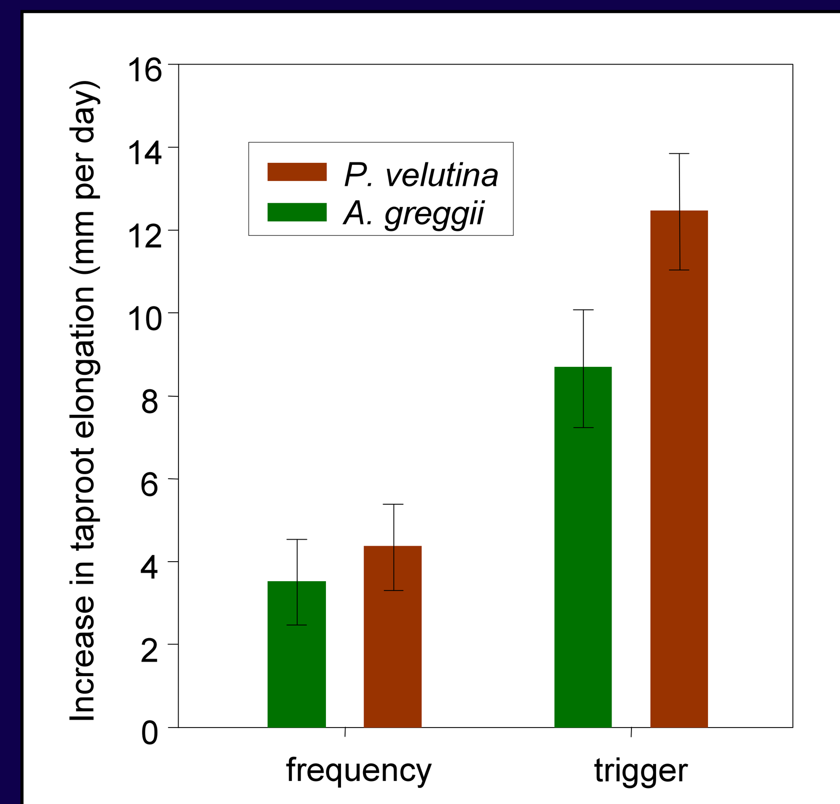

Figure 2. Root elongation responses to increased watering frequency (alternate days to every day) and increased triggering event (2 to 5 days). Bars indicate 95% CIs.

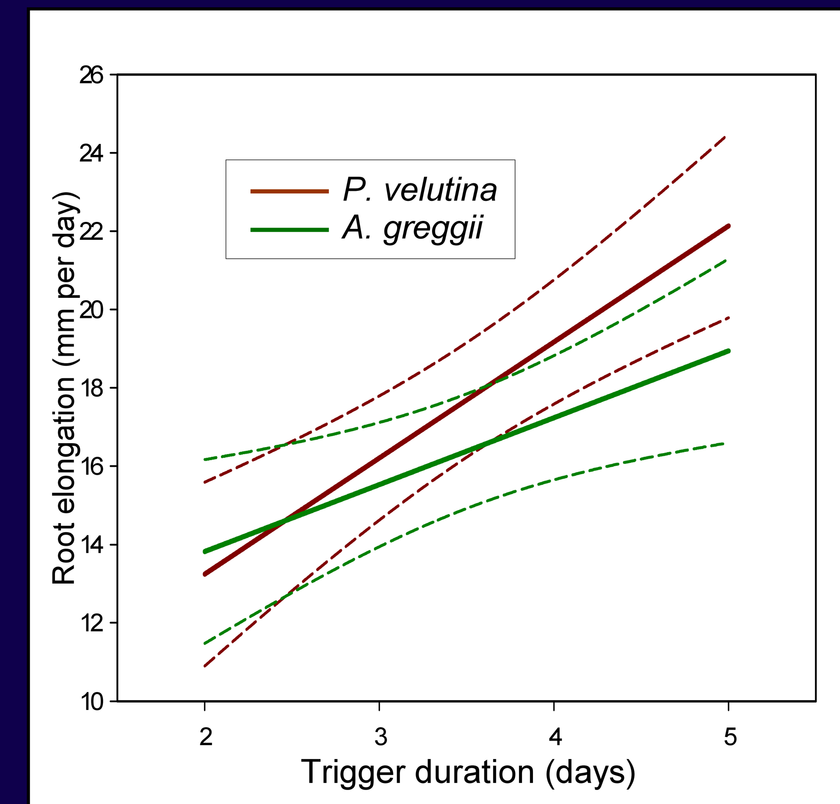

Figure 3. Plot of mean root elongation rate against triggering event, with daily subsequent watering. Dashed lines indicate 95% CIs for the means.

Santa Rita Experimental Range precipitation: single monsoon storms			Equivalent experimental germination trigger	
Number of consecutive days' rain in July - Sept	Event frequency (yr^{-1})	Average cumulative rainfall during event (mm)	Number of days	Total water delivered (mm)
5	0.32	55.6	5	50
4	1.13	36.3	4	40
3	3.10	25.0	3	30
2	7.26	15.5	2	20

Table 1. Storm duration frequencies and average rainfall, SRER, July through September, 1922-2005; compared with experimental treatments (trigger duration).

	Santa Rita Experimental Range precipitation: means of peak rainfall months (mm/day)		Equivalent experimental post-trigger watering:
	July	August	frequency of 5mm waterings
lower 95% limit	0.22	0.54	—
mean	2.60	2.61	Alternate days
upper 95% limit	4.99	4.67	Every day

Table 2. Estimated mean daily summer rainfall at SRER, July and August, 1922-2005; compared with experimental treatments (follow-up watering frequency).

Results

• Taproot elongation increased linearly with both triggering event ($P < 0.0001$) and watering frequency ($P = 0.0001$). The increase due to triggering event was significantly greater than that due to subsequent watering frequency (Fig. 1) ($P < 0.0001$). Slope of elongation rate against trigger duration was 43 % higher in *P. velutina* than *A. greggii* (95% CI 10% to 89%, $P = 0.0093$; Fig. 2) but slope of elongation rate vs. watering frequency was comparable ($P = 0.4110$).

• Taproot elongation was positively correlated with $\sqrt[3]{\text{root biomass}}$ ($P = 0.0464$). After taking account of $\sqrt[3]{\text{root biomass}}$, there remained a positive correlation with trigger duration ($P < 0.0001$) and watering frequency ($P = 0.0012$) and some evidence that *P. velutina* responded more to longer triggering events than *A. greggii* ($P = 0.0547$).

• Total biomass of *A. greggii* exceeded that of P. velutina [$P = 0.0027$, for ln(total biomass)], but biomass accumulation rate was 5X greater in *P. velutina* ($P < 0.0001$), with *A. greggii* showing only slight increase after accounting for average seed mass (*P. velutina*: 8.0 ± 1.5 mg/day; *A. greggii*: 1.5 ± 1.5 mg/day). There was no clear evidence for treatment effects on total biomass, or of differences in root/shoot biomass allocation according to species or treatment ($P > 0.05$).

Discussion

• This study investigated initial seedling establishment – the most vulnerable and tractable phase of the shrub life cycle. In arid and semi-arid environments, rapid access to deeper soil moisture is likely a key factor in woody plant seedling survival and the spread of shrub and tree species into grasslands. Within typical environmental limits, taproot elongation in emerging *A. greggii* and, especially, *P. velutina* seedlings was more responsive to triggering event duration than subsequent watering, responses to triggering event being greater than expected due solely to increases with biomass.

• Results suggest early rooting depth is driven more by the size/frequency of triggering events than by the subsequent soil moisture dynamics. Deeper soil moisture is less available to grasses and forbs and lasts longer into the dry season, so achieving greater rooting depth early in the life cycle can be expected to translate into increased survival through the first dry season. Young *P. velutina* seedlings appear more able than *A. greggii* to capitalize on the water provided by larger triggering events. This may help explain why environmental changes favoring shrub proliferation in grasslands have benefited some woody species more than others and, in particular, why *P. velutina* has become a ubiquitous grassland invader in the desert southwest.

• It remains to be shown whether the trends shown in this study continue through the seedlings' first year, and whether the root elongation differences between invasive and non-invasive species apply more generally than to just these two species – the subjects of continuing experiments. Preliminary results indicate that *P. velutina*, *A. greggii* and *Parkinsonia floridia* seedlings can attain root depths of 120 cm within 60 days of germination in controlled environments. However, seedling mortality in the field reached 100% in *P. velutina* and *Larrea tridentata* and 71% in *P. floridia* (seedling n = 137, 77, 42 respectively at the Santa Rita Experimental Range in 2007) (emergence from seed was below 1% in *A. greggii*). There is doubtless a complex interplay between germination, taproot elongation, rainfall and how these may be further mediated by other factors such as soil type and herbivory.

References

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Santa Rita Experimental Range (SRER), 2007. http://ag.arizona.edu/SRER/precip/precip.xls, maintained by SRER, viewed 05/09/2007. Funding for the digitization of these data was provided by USDA Forest Service Rocky Mountain Research Station and the University of Arizona.

Acknowledgements

We are grateful for the support of NSF Ecology and NSF – REU programs, and for the help of Chad McMurtry, Hazel Cox, Miranda Lanning, Katie Lee and Julie Mudd.

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