Are woody encroachers more resilient to drought and defoliation than other woody plant species?

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Abstract: The encroachment of woody plant species into open grasslands and savannas is a worldwide problem. We hypothesized that a species' encroachment potential is linked to higher seedling establishment success under drought and defoliation stress. To test this hypothesis, we compared early seedling growth in three leguminous shrubs native to the arid southwestern US: *Acacia greggii* and *Cercidium microphyllum* (not encroaching) and *Prosopis velutina* (encroaching). We found that all three species were very tolerant to drought and partial defoliation (seedlings did not die), but only *P. velutina* continued to grow under the highest stress level.

Introduction

Worldwide, woody plant species are invading open grasslands and savannas, a phenomenon called woody encroachment. This has profound effects on carbon, water and nutrient cycles, and reduces rangeland productivity.

Causes of woody encroachment are hotly debated and include fire suppression, increases in grazing pressure with the introduction of livestock and climate change. However, in every region, only a select few species out of much larger pool of native woody plant species become encroachers.

We sought to gain further insight into the causes of woody encroachment by comparing the growth of encroachers and non-encroachers. This study concentrated on the seedling establishment phase, the most vulnerable and tractable phase of the shrub life cycle. We hypothesized that seedlings of a woody encroacher are more tolerant to the two most common stresses encountered in grasslands and savannas: periodic drought and herbivory.

We chose three species for testing this hypothesis: *Acacia greggii* (catclaw acacia), *Cercidium microphyllum* (foothills paloverde) and *Prosopis velutina* (velvet mesquite) (Fig. 1). All are deciduous leguminous shrubs, native to the southwestern United States including southern Arizona where the experiment was conducted. Of the three species, only *P. velutina* is an encroacher. Worldwide, many problem species are in the genus *Prosopis.*

The Hypotheses

1) **With longer drought, end-of-season seedling sizes become smaller.**
2) **Growth of *P. velutina* seedlings is least sensitive to drought.**
3) **Longer drought followed by defoliation results in seedling mortality.**
4) **Stress-induced mortality is lowest for *P. velutina*.**

Acacia greggii (Catclaw acacia) | *Cercidium microphyllum* (Foothills paloverde) | *Prosopis velutina* (Velvet mesquite)

Figure 1. The three study species as mature plants.

Methods

Seedlings were grown in 384 soil-filled 3 liter pots in the greenhouse (Figure 2). The 24 species-treatment combinations (Table 1) plus one non-droughted, non-defoliated control treatment per species were randomized within and across trays.

Table 1: Experimental Design.

Factors:	Levels:
Species	3
Drought length	4 (10, 14, 22 and 26 days)
Defoliation	2 (none, 50% leaf removal)

Figure 2: A bench with 12 trays (left) and a single tray with 16 pots (right). Pots were watered individually from an irrigation manifold.

Seeds were acid-treated to break dormancy and then soaked in distilled water for 24 hours before planting. Pots were watered with 15 mm water twice a day for 5 days to induce germination and then with 5 mm every other day, except during the drought treatment. All drought treatments started on day 14. Plants were defoliated at the end of the drought treatments.

From days 3 to 48, leaf numbers per seedling and plant height were measured daily. On day 48, all seedlings were harvested to determine above and below ground biomass. Here, we only report on the results of the leaf count. We used Analysis of Variance to test for significant species and treatment effects. The significance criterion was set at the $\alpha = 0.05$ level.

Results

Very few seedlings died, but some late germinating plants were removed from the analysis. Figure 3 shows an example of leaf number growth over the course of the experiment.

Drought length did not significantly affect final leaf number in any of the three species (Fig. 4). Defoliation had highly significant effects on leaf number in *A. greggii* and *P. velutina*, and a marginally significant effect in *C. microphyllum* ($p = 0.052$). However, in *C. microphyllum*, drought-defoliation interactions were significant ($p = 0.024$), indicating that less droughted plants were able to compensate for leaf loss by accelerated leaf growth, but that with increasing drought length, defoliated plants were increasingly less able to make up for lost leaves.

All species compensated for leaf loss to some extent. To quantify this compensatory leaf growth, we calculated relative leaf growth rate over the first 9 days after defoliation as:

$$\mathrm{RLGR} = \frac{L_{d+9} - L_d}{L_d}$$

where L is leaf number and d is the day of defoliation, when leaf numbers were counted after defoliation. Overall, RLGR was significantly greater for defoliated plants and decreased with drought length (Fig. 5). *P. velutina* was the only species that still produced leaves after 26 days of drought and defoliation.

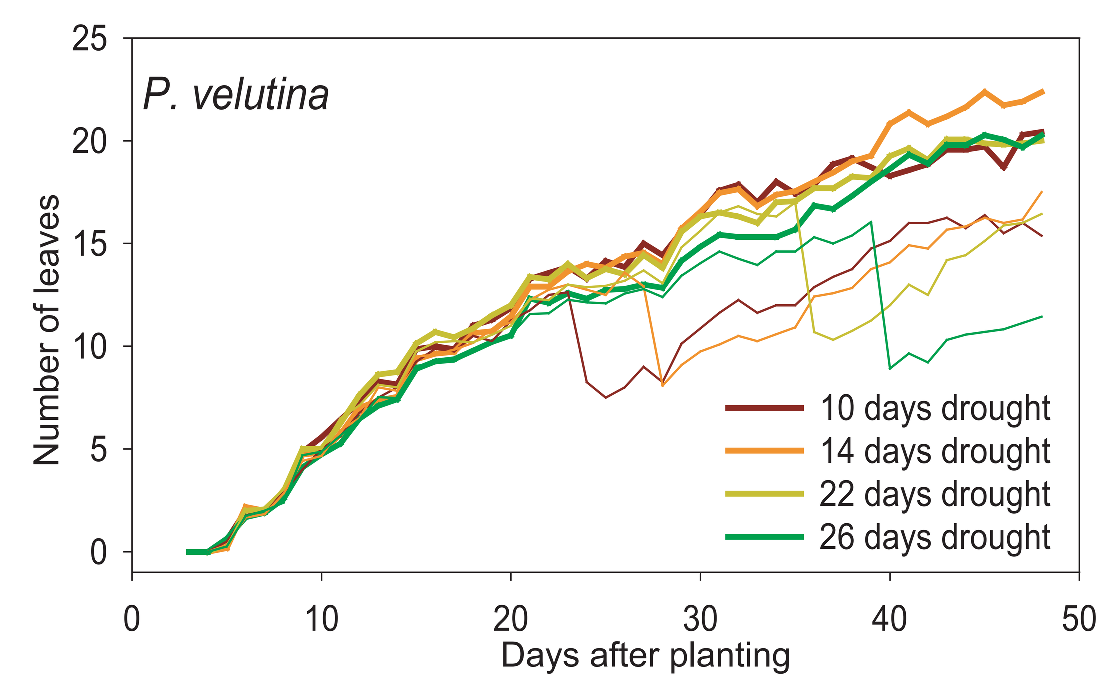

Figure 3. Leaf growth in *P. velutina* in the drought treatments. Thick lines: non-defoliated, thin lines: defoliation plants.

Results, continued...

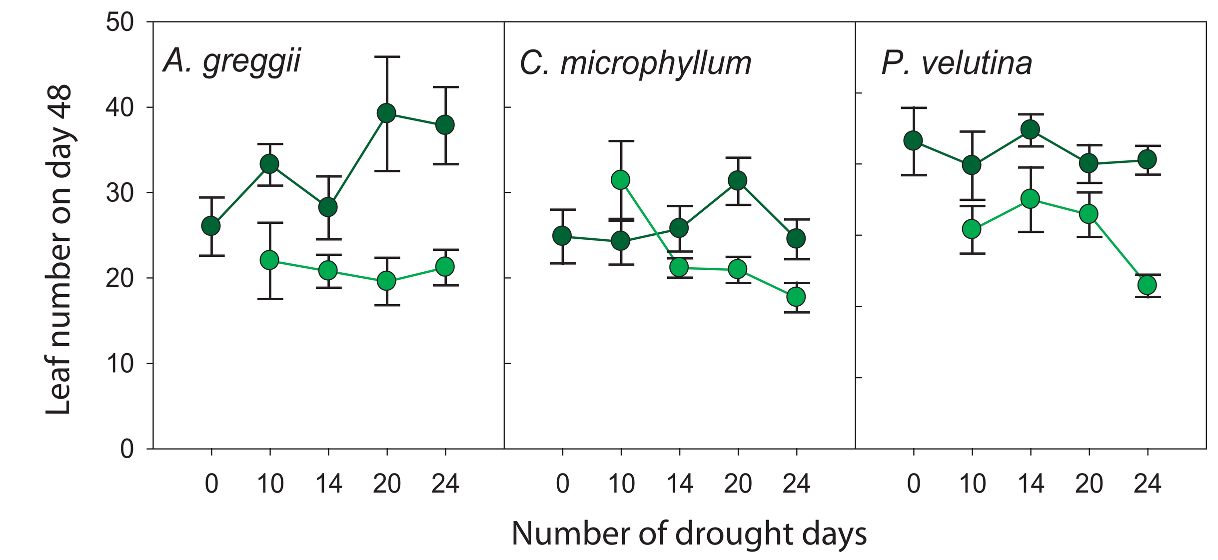

Figure 4. Effects of drought and defoliation on final leaf number. Dark green: no defoliation, light green: 50% defoliation. Error bars indicate standard errors.

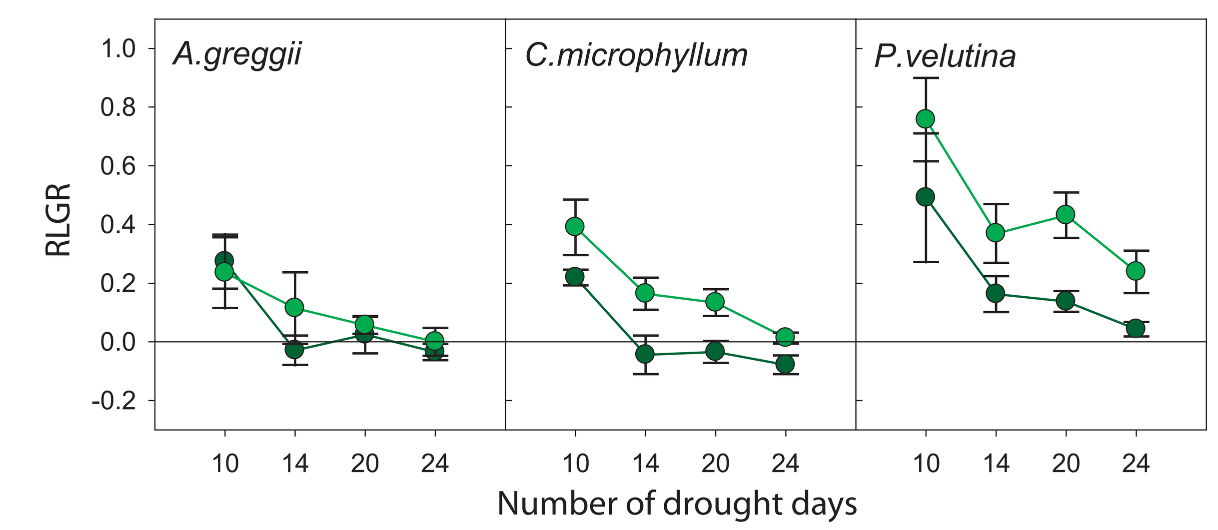

Figure 5. Effects of drought and defoliation on relative leaf growth rate (RLGR) over the first 9 days after defoliation. Colors and error bars as in Fig. 4.

Conclusion

None of our initial hypotheses were supported. For example, drought alone did not affect leaf growth in any species and additional defoliation did not kill seedlings, even at the highest drought level. In hindsight, 26 days of drought and 50% defoliation may not constitute a very severe stress level relative to the drought stress encountered in the species' natural environment. However, *P. velutina* stood out in one important way: it was the only species that could still grow after the longest drought and defoliation. In the field, this could mean that *P. velutina* seedlings are bigger at the end of the first growing season and have better chances of survival in the second. Understanding the limits of seedling stress tolerance may allow a more effective management of the world's most aggressive woody encroachers.

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