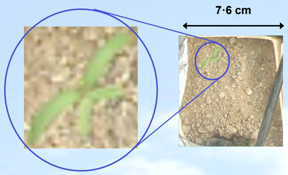
# Precarious seedling establishment in *Larrea tridentata*: soil moisture and a taproot elongation threshold





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## Abstract

***Larrea tridentata*, the dominant shrub in North American hot deserts, has proliferated in semi-arid grasslands over the past century. Effects on nutrient cycles and community composition are profound, impacting ecosystem water balance, water flows and erosion. Encroachment depends on rare and sporadic recruitment, the seedling establishment phase being critical. However, the mechanistic basis remains elusive.**

**Assuming rapid taproot elongation is essential for successful establishment, we hypothesized that precipitation patterns at germination would strongly influence taproot development. To test this hypothesis, we compared *L. tridentata* seedling emergence and growth in a controlled environment for 2.5 weeks, varying the number of germination-triggering watering days (2,3,4, or 5 days with 10 mm/day) and follow-up watering frequency (5mm every or every other day).**

**Taproot elongation showed a linear increase from 2 to 4 triggering days and a sharp decrease from four to five days. This pattern was stronger than expected based solely on root biomass, indicating that soil moisture levels can influence taproot elongation, independent of effects on overall root growth. Greater trigger duration and follow-up watering frequency increased total seedling emergence but did not affect time to emergence.**

**Vigorous taproot development in *L. tridentata* may be matter of striking a fine balance between too little and too much water in the expansion zone of the root system. Long precipitation episodes may stimulate high emergence, but could lessen seedling survival, as reduced taproot elongation delays escape from topsoil desiccation and below-ground competition from grasses. Short precipitation episodes reduce emergence and constrain taproot elongation to a shallow infiltration depth. Thus, aridland precipitation patterns may have profound long-term consequences, through influences on establishment of shrubs such as *L. tridentata*.**


## Methods

**The greenhouse experiment was conducted at the University of Arizona Campus Agricultural Center in Tucson in July 2006. *L. tridentata* seeds which were soaked for 24 h in water in the dark after removing pericarps, then planted into pots.**

**Four seeds were planted into each of 96 pots (35.6 cm tall x 7.6 cm square Zipset™) filled with a sandy loam soil and irrigated via a calibrated drip line system.**

**The experimental design was a complete factorial with 4 initial watering treatments ("triggering days" = 10 mm per day for 2, 3, 4 or 5 successive days) and 2 follow-up watering regimes ("post-trigger watering frequency" = 5 mm every day or every other day) for a total of 8 treatments. These treatments reflect a range of precipitation patterns likely to trigger germination and representing common to relatively rare events at the Santa Rita Experimental Range near Tucson, AZ.**

**Day of seedling emergence was recorded. Seedlings were thinned to one per pot and harvested 16 or 17 days after the start of the experiment. Taproot length was measured. Seedling roots and shoots were dried at 105 ºC for 48 h and weighed.**

**Analysis of variance was performed on taproot length, log(root biomass), log(shoot biomass), log(root/shoot biomass), day and proportion of emergence, with triggering days and post-trigger watering frequency as fixed effects.**

*Background photograph: Lisa Benton. Insets: Miranda Lanning.*

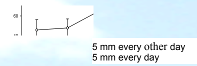


Figure 1. Mean ±SE emergence rate as a function of number of triggering days and post-trigger watering frequency.

| Treatment | df | Emergence rate (%) | |
|---|---|---|---|
| | | %SS | p |
| Trigger days | 3 | 25 | 0.035 |
| Post-trigger frequency | 1 | 35 | 0.001 |
| Days×Freq | 3 | - | 0.761 |

Table 1. ANOVA results for seedling emergence.

| Treatment | df | Taproot length | |
|---|---|---|---|
| | | %SS | p |
| Root biomass | 1 | 39 | <0.001 |
| Trigger days | 3 | 12 | 0.006 |
| Post-trigger frequency | 1 | - | 0.943 |
| Days×Freq | 3 | - | 0.426 |

Table 2. ANCOVA results for taproot length.

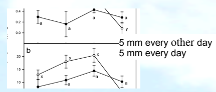


Figure 2. Root biomass, taproot length and marginal mean taproot length (based on root biomass as the covariate), as functions of number of triggering days and post-trigger watering frequency. Letter codes indicate differences among triggering days, within post-trigger frequencies. In panel 2c, data were pooled for post-trigger frequency.

| Treatment | df | log root biomass | | log taproot length | |
|---|---|---|---|---|---|
| | | %SS | p | %SS | p |
| Trigger days | 3 | 16 | 0.005 | 28 | <0.001 |
| Post-trigger frequency | 1 | 6 | 0.023 | - | 0.093 |
| Days×Freq | 3 | 11 | 0.030 | 9 | 0.046 |

Table 3. ANOVA results for final harvest data.

## Results

**Emergence rates were significantly affected by the number of triggering days and the post-trigger watering frequency (Fig. 1, Table 1). Post-trigger watering frequencies had a greater effect on emergence than did the amount of water received in the triggering phase of the experiment.**

**Taproot length was strongly affected by the number of triggering days (P < 0.001) but not post-trigger watering frequency; and the interaction between the two factors was significant (Table 3). Taproot length increased with trigger duration up to 4 days, and in this range also increased with post-trigger watering frequency (Fig. 2b). However, taproot length was sharply reduced with 5 trigger days, if followed by daily watering, giving the lowest average taproot length across all experimental groups.**

**The number of trigger days, post-trigger watering frequency, and the interaction between them all had significant effects on root biomass (Table 3). The higher watering frequency in the post-trigger phase generally increased root biomass, except when combined with 5 triggering days (Fig. 2a). There were no significant effects of treatment on shoot biomass.**

**Taproot length was strongly correlated with root biomass, but the number of triggering days also had a significant independent effect on taproot length (Fig. 3 b & c, Tables 2, 3): taproots were shorter than expected based solely on root biomass when given 2 or 5 triggering events, compared to taproots that were given an intermediate number of triggering events. Thus, either too little or too much water applied during germination stunted taproot development.**

**Emergence rates were significantly affected by the number of triggering days and the post-trigger watering frequency (Fig. 1, Table 1). In general, pots that received more water had higher emergence rates, but a higher post-trigger frequency facilitated emergence more than the amount of water received in the triggering phase of the experiment.**

## Discussion

**Root growth was facilitated by more frequent, small waterings in the post-trigger phase of the experiment, but not by a greater number of triggering days (Fig. 2a, Table 2). On the contrary, five consecutive triggering days followed by daily watering reduced root growth.**

**Taproot elongation showed a more pronounced response to the number of triggering days (initial water) than did root biomass. At low initial waterings, low soil moisture at depth appears to set a clear limit to taproot elongation, which cannot be overcome by more biomass allocation to roots.**

**At high initial watering (5 day trigger), taproots were noticeably stunted, more so than can be explained by lower root biomass. This suggests low oxygen levels may have stopped taproots from growing deeper (Lunt et al 1973). Taproot development in *L. tridentata* may require a fine balance between too little and too much water in the roots' expansion zone.**

**It appears *L. tridentata* has a narrow range of soil moisture conditions in which establishment is likely. Germination rates were maximized by the highest total amount of water supplied (four to five triggering days followed by daily watering; Fig. 1), but five triggering days stymied root growth and stunted taproots to the lowest values. *L. tridentata* recruitment may be limited by both dry and wet conditions, with dry conditions constraining germination rates and excessively wet conditions inhibiting root growth.**

**Small changes in temporal patterns of precipitation could have profound long-term effects on *L. tridentata* establishment, and thereby on plant community composition.**

**Reference**


**Lunt, O. R., J. Letey, and S. B. Clark. 1973. Oxygen requirements for root growth in three species of desert shrubs. Ecology 54: 1356-1362.**