

Early taproot development of a xeric shrub (*Larrea tridentata*) is optimized within a narrow range of soil moisture

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Abstract Effects of watering amount and frequency on root biomass accumulation and taproot elongation were examined 16–17 days post-germination in seedlings of *Larrea tridentata*, a dominant shrub in North American hot deserts. Two experimental variables manipulated in a full factorial design greenhouse study were (i) number of “triggering” days: consecutive days (2, 3, 4 or 5) at the start of the experiment on which seedlings received 10 mm of water per day; and (ii) “post-trigger” watering frequency: 5 mm of water either daily or every other day. We hypothesized that taproot elongation would increase with greater numbers of triggering days, whereas higher post-trigger watering frequency would enhance root biomass development. Increasing the number of triggering days from two to four promoted taproot extension without affecting root biomass, and higher watering frequency in the post-trigger phase generally increased root biomass, as expected. Contrary to expectations, root biomass and taproot length were significantly reduced when daily watering followed five consecutive triggering days. Taproot length correlated with root biomass, but irrigation regime also had a biomass-

independent effect: with either two or five triggering days, taproots were shorter than expected based on root biomass. Thus, both too little and too much water stymied taproot extension. In natural settings, the adverse response of taproots to too little or too much water could reduce seedling survivorship and restrict establishment to a narrow range of environmental conditions.

Keywords Recruitment · Threshold · Xerophyte · Sonoran Desert · Episodic establishment · Creosote bush

Introduction

Patterns of early seedling mortality may have profound effects on the abundance, dynamics, and spatial distributions of adult plants (de la Cruz et al. 2008; Pico and Retana 2008), responses of communities to climate change (Lloret et al. 2009), and the maintenance of species diversity (Connell 1978; Grubb 1977; Janzen 1970). In perennials, just-emerged seedlings have higher mortality rates, by far, than all subsequent life history stages (Fenner 1987) and are arguably at peak sensitivity to environmental and biotic factors. As they grow, develop root systems, and accumulate reserves and defense compounds they become better protected against moisture shortage and herbivory (Ackerman 1979; Elger et al. 2009; Padilla et al. 2007; Padilla and Pugnaire 2007), two of the most frequent

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mortality factors amongst first-year seedlings (Moles and Westoby 2004). While the physiological ecology of germination and post-emergence seedling development is widely regarded as critical to understanding plant population dynamics, much less is known about the processes that govern growth and survivorship of seedlings compared to those that govern mature plants. This reflects the facts that seed germination is difficult to detect in the field until cotyledons emerge (Fenner 1987), the time between emergence and death may be short and easily missed by all but the most diligent sampling schemes (Bowers 2004), and significant recruitment events may occur infrequently (e.g., Ackerman 1979; Barbour et al. 1977).

Germination and establishment of desert plants depend strongly on temperature and precipitation patterns (Beatley 1974b). Species differ in the minimal amount of precipitation necessary to break seed dormancy, as well as the amount of follow-up rain necessary to support seedling growth until taproots are deep enough to supply the shoots with a steady flow of water (Padilla and Pugnaire 2007). The diversity of germination and establishment requirements among species is recognized as the “regeneration niche” (Grubb 1977) and is thought to be an important component of maintaining species richness in desert plant communities (Chesson and Huntly 1997; Pake and Venable 1995, 1996). The conditions required for the establishment of long-lived desert shrubs are challenging to discern, because long-lived species need not recruit very often to maintain their populations. A typical example is *Larrea tridentata* (DC.) Coville (creosote bush, family Zygophyllaceae), the dominant evergreen shrub in all three North American warm deserts (Hunter et al. 2001; Hunziker et al. 1972).

Two principal climatic factors have been suggested as delimiters of *L. tridentata*'s range: minimum temperatures and high precipitation. Its northern boundary corresponds to low winter temperatures and may result from freezing-induced xylem cavitation (Turner et al. 1995, p. 152; Pockman and Sperry 1997; Arundel 2005). In the Mohave Desert both altitudinal and latitudinal limits match an upper limit of 183 mm mean annual precipitation (Beatley 1974a). *L. tridentata*'s western boundary appears limited by mean minimum July–August (monsoon) temperatures below 18°C (Arundel 2005), suggesting a link with temperature requirements for germination

and root growth, since seedling root growth is greatly reduced at 16°C and the mean low temperature limit for germination is 20°C (Barbour 1968).

L. tridentata appears limited on its eastern boundary in Sonora, Mexico, by mean monsoon precipitation greater than 215 mm (Arundel 2005). Relatively high monsoon rainfall can increase herbaceous growth and hence fine fuel loads and fire frequency, commonly a factor in suppressing woody plant populations (McPherson 1995). Vegetative regeneration after fire is low in *L. tridentata*, particularly in seedlings (Brown and Minnich 1986; McLaughlin and Bowers 1982). Alternatively, higher monsoon rainfall may restrict this species' range more directly, via soil moisture levels. *L. tridentata* is typically absent from poorly drained areas and soils with well-developed argillic (clay-rich) horizons, but is dominant in adjacent areas with lower soil clay content (McAuliffe 1994). *L. tridentata* seedlings' high oxygen requirement for root growth (Lunt et al. 1973) presents a possible mechanism behind these range limitations.

Several factors may influence fine-scale distribution of *L. tridentata*. Individuals tend to be clumped when small and regularly spaced when large (Phillips and McMahon 1981). Small individuals are sometimes clustered under *Ambrosia dumosa*, though it is unclear whether *A. dumosa* enhances *L. tridentata* establishment or whether both are responding to edaphic microsite conditions (McAuliffe 1988). Allelopathy may inhibit root elongation (Mahall and Callaway 1992) and may progressively lead to even distributions, while vegetative reproduction can produce clonal rings several thousand years old and up to 16 m in diameter (Vasek 1980).

A notable feature of many communities of this very long-lived shrub is that stands are often of only one or several ages, the key determinant appearing to be highly episodic recruitment (Barbour 1969). Recruitment appears to occur on the order of once every 30–100 years (Bowers 2004; Goldberg and Turner 1986). *L. tridentata* does not appear to form a persistent seed bank (Barbour et al. 1977; Reichman 1984), and while germination and first-year survival are exceedingly rare in this species (Barbour 1968), if its seedlings survive their first year, subsequent annual survivorship can be remarkably high (92% over the first 7 years, Goldberg and Turner 1986).

L. tridentata germination requires continuous, plentiful moisture for 24 h (Barbour 1968), and

Table 1 Long-term (1975–2005) storm duration frequencies and average summer monsoon season (July–September) rainfall (mm) at the Santa Rita Experimental Range (SRER) in southeastern Arizona, USA (SRER 2007), compared with treatments used to trigger germination in this study

| Precipitation at SRER, southeast Arizona | | | Equivalent experimental germination trigger | | Cumulative water applied in 5 mm increments in post-trigger phase (mm) | |
|---|--|--|---|---|--|-----------------------------|
| Number of consecutive days of rain in July–Sept | Frequency of the event (year ⁻¹) | Average cumulative rainfall during period (mm) | Number of days at 10 mm per day | Water delivered during trigger phase (mm) | Irrigated daily | Irrigated on alternate days |
| 5 | 0.32 | 55.6 | 5 | 50 | 50 | 25 |
| 4 | 1.13 | 36.3 | 4 | 40 | 60 | 30 |
| 3 | 3.10 | 25.0 | 3 | 30 | 60 | 30 |
| 2 | 7.26 | 15.5 | 2 | 20 | 70 | 35 |

Also shown are the total amounts of water applied after the initial germination trigger

seedling growth and survival can be greatly enhanced by watering repeatedly immediately afterwards (Sheps 1973; Went and Westergaard 1949; Ackerman 1979). Under well-watered greenhouse conditions, *L. tridentata* seedlings grew 3% per day with relatively low root:shoot ratios of 0.3–0.6 (Barbour et al. 1974; Walters and Freeman 1983) whereas adult root/shoot ratios are typically close to or well over 1.0 (Allen et al. 2008; Barbour et al. 1977). Thus, under favorable conditions, *L. tridentata* can compensate for low maternal provisioning in its small seeds (Reichman 1976; Walters and Freeman 1983) by promoting shoot growth for carbon uptake, at the expense of root growth. Such an allocation pattern would amplify the need for continued moisture in the days and weeks following germination. However, continuous wet conditions also have disadvantages, including promotion of fungal growth, which can kill seedlings (Duniway and Gordon 1986; Vallentine and Gerard 1968) and adult plants (Ewing and Dobrowolski 1992).

Precipitation patterns have well-known effects on soil moisture dynamics, including infiltration depth. The larger the rainfall event, the deeper moisture infiltrates and the less susceptible it is to evaporation. Thus, larger rainfall events result in soil moisture pulses which affect a larger proportion of the soil column and last longer (Loik et al. 2004; Noy-Meir 1973). It is well understood that large precipitation events are particularly important for seedling establishment (Beatley 1974b; Bowers 2004), but the nature of the relationship between event size and subsequent

seedling growth have seldom been considered in detail.

In the Sonoran Desert of southern Arizona, USA, convection storms large enough to trigger germination are not uncommon during the summer monsoon. While two consecutive rainy days typically deliver less soil moisture, on average, than the 20–25 mm ostensibly required for *L. tridentata* emergence (Bowers 2004), three to four consecutive rainy days can potentially meet this triggering requirement; and such conditions occur several times between July and September in an average year, while longer rain periods tend to occur only several times per decade (Table 1). What are the consequences of precipitation frequency and amount for *L. tridentata* establishment?

To address this question, we sought to quantify germination, growth and early seedling development of *L. tridentata* in response to watering patterns varying from small events which typically occur several times a year, to larger events which occur every few years, and followed by either average or above-average monsoon precipitation.

Methods

We expected that initial pulses of water would largely determine infiltration depth, and that subsequent, more gradual watering over a longer duration would have less influence on infiltration depth but would affect the overall amount of available soil moisture and thereby influence photosynthesis rates. Therefore, as roots

cannot grow into overly dry soil, we hypothesized that taproot elongation would be limited by the magnitude of initial events delivering water at a relatively high rate over a short time period. Our second hypothesis was that, following the initial pulse of moisture, small daily waterings (representing above-average rainfall) would increase overall rates of root biomass accumulation compared to small waterings every other day (representing average rainfall). We did not intend to establish differences in mortality. Rather, we sought to examine how precipitation patterns may affect root development in the first stages of life, as an indicator of the ability of seedlings to survive inevitable dry-down events at later stages.

Experimental design

The experiment was conducted in a greenhouse at the University of Arizona Campus Agricultural Center in Tucson, Arizona in June 2006. Seeds of *L. tridentata* were supplied by Desert Seed Source, Tempe, Arizona, USA. Collected directly from mature plants in the vicinity of Oracle, Pima County, Arizona, they likely represent a limited range of genotypes. Pericarps were removed by rubbing the seeds on a sieve with sandpaper. Seeds were soaked for 24 h in water in the dark and planted ($n = 4$) into each of 96 pots ($7.6 \times 7.6 \times 35.6$ cm; Zipset™, Monarch Manufacturing Inc., Salida, Colorado, USA) filled with a locally collected sandy loam soil and sealed at the bottom with weed barrier cloth to allow water to drain while retaining the soil. Pots were arranged in three blocks by distance from an evaporative cooler and treatments were randomly distributed within blocks.

Our experimental design was full factorial with four initial watering treatments (triggering days = 10 mm day⁻¹ for 2, 3, 4 or 5 successive days) and two follow-up watering regimes (post-trigger watering frequency = 5 mm daily or every other day) for a total of eight treatment combinations. These treatments were based on an analysis of a 30 year record (1975–2005) of daily rainfall from July to September at the Santa Rita Experimental Station, in southeast Arizona (SREER 2007; Table 1).

Pots were irrigated individually through a drip line system (Bowsmith® 2 gallon h⁻¹ 6-way emitters), with a flow meter (Sensus™) calibrated to deliver 5 mm per pot in a single session. On triggering days, pots received 5 mm in the morning and 5 mm in the

evening. In the post-trigger phase, 5 mm were applied either once per day or every other day, in the morning. Thus, we irrigated when evaporative demand was below its afternoon peak, establishing conditions analogous to those expected under natural storm conditions, i.e., reduced light intensity and temperature.

Day of emergence was recorded for all seedlings. After the first seedling emerged in a pot, subsequent seedlings were removed to maintain one plant per pot. Start dates were staggered over five consecutive days, such that the post-trigger phase of the experiment began on the same day in all treatments. Harvests at the end of the experiment were also staggered, occurring over five days. Pots receiving three or five triggering days were harvested after 16 days; pots receiving two or four triggering days were harvested after 17 days. This allowed us to vary trigger duration independently of post-trigger watering frequency and avoid watering patterns immediately prior to harvest being influenced by trigger duration (i.e., the final watering day for all treatments was two days before harvest, irrespective of trigger duration). At harvest, pots were cut open and intact root systems were carefully separated from the soil. Roots and shoots were oven dried at 70°C for 48 h and weighed.

Soil characteristics

The soil had low gravimetric N and organic C content ($0.11 \pm 0.01\%$ and $1.07 \pm 0.03\%$, respectively) and high carbonate C content ($5.85 \pm 0.17\%$; $n = 6$ samples; ECS 4010 elemental analyzer, Costech Analytical Technologies Inc., Valencia California; Harris et al. 2001). In these respects, the soil was broadly typical of drylands such as the Sonoran Desert (Pitty 1979; Throop and Archer 2008). Texture was determined by hand to be sandy loam (Thien 1979). Bulk density was 1.43 ± 0.06 g cm⁻³ ($n = 4$ pots) and approximated that of soils at a nearby field site (Throop and Archer 2008). Saturated water content was $16.8 \pm 1.6\%$ w/w ($n = 6$).

Statistical analysis

Statistical tests are summarized in Table 2. To test our hypotheses, we performed analysis of variance (ANOVA) on log(taproot length) and log(root biomass), with triggering days, post-trigger watering

Table 2 Summary of statistical tests (ANOVA, ANCOVA and regression analyses, according to the classes of explanatory variable(s))

| Dependent variable | Explanatory variables | | | |
|--|-----------------------|------------------------|---------------------|------------------------------|
| | Categorical | | | Continuous |
| Day of emergence | Trigger days | Post-trigger frequency | Trigger × frequency | |
| Arcsin√(emergence rate (%)) ^{a,c} | Trigger days | Post-trigger frequency | Trigger × frequency | |
| log(root biomass) ^{b,c} | Trigger days | Post-trigger frequency | Trigger × frequency | |
| log(shoot biomass) ^b | Trigger days | Post-trigger frequency | Trigger × frequency | |
| √(root/shoot biomass) | Trigger days | Post-trigger frequency | Trigger × frequency | |
| log(taproot length) ^{b,c} | Trigger days | Post-trigger frequency | Trigger × frequency | |
| log(taproot length) ^d | Trigger days | Post-trigger frequency | Trigger × frequency | log(root biomass) |
| log(taproot length) ^b | Trigger days | | | log(root biomass) |
| log(taproot length) ^e | | Post-trigger frequency | | Trigger days (2–4 days only) |
| log(root biomass) ^e | | Post-trigger frequency | | Trigger days (2–4 days only) |
| log(total biomass) | | | | Day of emergence |

Treatments were 10 mm water per day for 2, 3, 4 or 5 initial trigger days, followed by 5 mm water at a frequency of either once every day or every other day

^a Data are presented in Fig. 1

^b Data are presented in Fig. 2

^c Statistical results are presented in the text and in Table 3

^d Statistical results are presented in the text and in Table 5

^e Statistical results are presented in the text and in Table 4

frequency and their interaction as explanatory variables. To enable discussion of taproot elongation in the context of seedling emergence and biomass accumulation more generally, we also performed ANOVAs on day of emergence, arcsine√(proportion of emergence), log(shoot biomass), and √(root/shoot biomass), again with triggering days, post-trigger watering frequency and their interaction as explanatory variables. Proportion of emergence was based on all four seeds planted in each pot. All other statistics were based on only the first-emerging seedling of each pot, these being the seedlings that were allowed to go through to harvest.

As log(root mass) and log(taproot length) responses to trigger duration were markedly different at five triggering days, we performed post hoc analyses of covariance (ANCOVA) on these dependent variables confined to 2–4 triggering days, triggering days being the covariate (regression component of the ANCOVA) and watering frequency being a categorical (ANOVA component of the ANCOVA) (Doncaster and Davey 2007). To determine treatment effects on taproot length independently of root mass, ANCOVAs were performed on log(taproot length) with log(root mass)

as the continuous covariate and (a) triggering days, (b) triggering days, post-trigger watering frequency and their interaction as categorical explanatory variables. To assess the influence of time to emergence on total biomass at harvest, we performed a regression with emergence day as explanatory variable and log(total biomass) as dependent variable.

Due to the staggered experimental design, seedlings grew for either 16 or 17 days. To determine whether this had any unintended effects, we analyzed final harvest data in two ways, either using the raw harvest data as measured or adjusting the harvest data in groups that grew for 17 days by multiplying by 16/17. There were only minimal discrepancies in the *P* values calculated for the raw and adjusted data sets (*P* values <0.05 typically decreased, by up to 20%, using the adjusted data); and there were no changes in statistical conclusions, in that raw and adjusted data showed exactly the same relationships to be significant for all response variables. Here, we report only results based on analyses of unadjusted raw data except for the one instance where adjusting the data for experiment duration increased a *P* value that was <0.05. For that case, the regression of log(total biomass) against

emergence day, we report the results for both the raw and the adjusted data.

For all tests, $\alpha = 0.05$. Data transformations were applied as necessary to achieve homoscedasticity and normality of residuals. We used the Tukey–Kramer test for multiple comparisons, with a global error rate of 0.05. Block was not a significant factor except for emergence proportion, so we eliminated block as a factor in the analysis of all other dependent variables but analyzed emergence proportion as for a blocked design by taking means within each block. We used SAS 9.2 (SAS Institute Inc., Cary, North Carolina) for all analyses.

Results

At harvest, each seedling still had both cotyledons and had produced no more than two true leaves. Maximum taproot length was 30 cm; none were long enough to have become significantly constrained in the 35 cm deep pots. There was no mortality prior to harvest.

Emergence rates, based on all four planted seeds and averaged by block, were significantly increased by higher numbers of triggering days and by higher post-trigger watering frequency (Table 3). However, the only significant pairwise differences were that emergence proportion was lower under 55 mm total water than under treatment combinations with 90 or 100 mm total water (Fig. 1).

There was a very weak negative relationship between emergence day and total biomass at harvest [$\text{adj } R^2 = 0.037$, $P = 0.0570$ for regression of $\log(\text{total biomass})$ against emergence day; $\text{adj } R^2 = 0.049$, $P = 0.0488$ for regression of $\log(\text{total biomass per$

day) against emergence day]. Seedlings allowed to go through to harvest emerged between days 6 and 12 of the experiment and within this set there were no significant treatment effects on emergence day.

There were no significant treatment effects on shoot biomass (Fig. 2a). By contrast, root biomass was affected by the number of trigger days, the post-trigger watering frequency and their interaction, which together explained 34% of the total variation (Table 3). Higher watering frequency in the post-trigger phase increased root biomass, except among seedlings experiencing five triggering days (Fig. 2b).

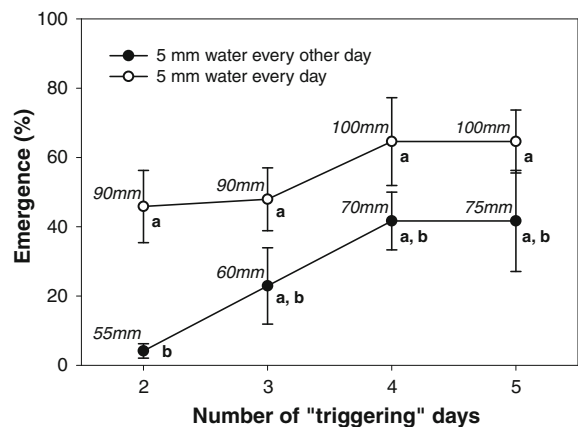


Fig. 1 Mean \pm SE emergence (%) of all seeds planted as functions of the number of triggering days and post-trigger watering frequency (daily vs. alternate days; Table 1). Means based on 48 seeds (four seeds pot⁻¹; four pots block⁻¹; three blocks treatment⁻¹). See Table 3 for ANOVA summary. Values with *different letters* were significantly different (Tukey–Kramer test, $\alpha = 0.05$, with arcsine square root transformation). Values are annotated in *italics* with total depth of water applied (mm)

Table 3 Analysis of variance summary for *Larrea tridentata* seedling emergence, based on four seeds per pot; and final harvest data, based on the first seedling to emerge per pot

| Treatment | Log taproot length | | | | Log root biomass | | | | Arcsin $\sqrt{}$ (emergence rate (%)) | | | |
|------------------------|--------------------|------|---------|---------|------------------|------|---------|--------|---------------------------------------|------|---------|--------|
| | df | SS | F ratio | P | df | SS | F ratio | P | df | SS | F ratio | P |
| Model | 7 | 1.57 | 5.36 | 0.0001 | 7 | 2.87 | 4.27 | 0.0008 | 7 | 1.36 | 4.85 | 0.0043 |
| Trigger days | 3 | 1.12 | 8.96 | <0.0001 | 3 | 1.47 | 5.09 | 0.0035 | 3 | 0.56 | 4.69 | 0.0156 |
| Post-trigger frequency | 1 | 0.10 | 2.38 | 0.1285 | 1 | 0.44 | 4.58 | 0.0367 | 1 | 0.69 | 17.17 | 0.0008 |
| Days \times Freq | 3 | 0.36 | 2.84 | 0.0460 | 3 | 0.88 | 3.06 | 0.0355 | 3 | 0.11 | 0.91 | 0.4568 |
| Error | 55 | 2.30 | | | 56 | 5.39 | | | 16 | 0.64 | | |

SS sums of squares, df degrees of freedom

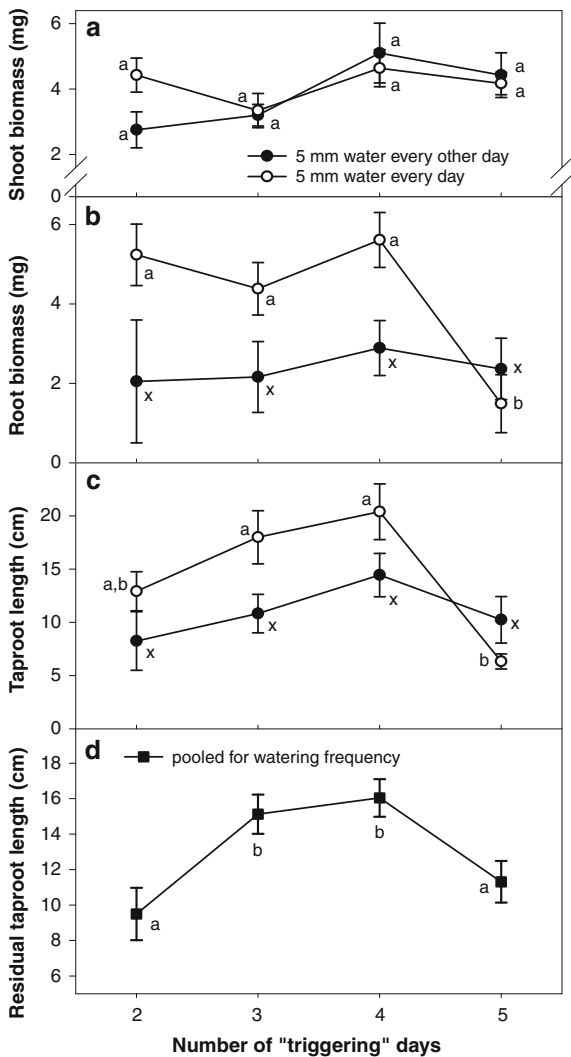


Fig. 2 Influence of the number of triggering days and post-trigger watering frequency on mean **a** shoot biomass; **b** root biomass; **c** taproot length; and **d** marginal taproot length after adjusting for the effect of root biomass (bars indicate SE). Within each post-trigger frequency (**a**, **b**, and **c**), values with different letters were significantly different (Tukey–Kramer test, $\alpha = 0.05$). In **d** the data were pooled for post-trigger frequency, since this factor had no significant effect in the analysis of covariance (see Table 4)

Across the experiment, the mean \pm SE root/shoot ratio was 0.93 ± 0.09 and $\sqrt{(\text{root/shoot biomass ratio})}$ was 0.90 ± 0.04 . Treatment main effects on $\sqrt{(\text{root/shoot biomass ratio})}$ were non-significant, but a significant interaction term ($P = 0.0370$) reflected that with daily follow-up watering, $\sqrt{(\text{root/shoot biomass ratio})}$ was higher with three or four trigger days than with five trigger days.

Taproot length was strongly affected by the number of triggering days, but not by the post-trigger watering frequency, and the interaction between these two factors was only marginally significant (Fig. 2c; Table 3). Considering only triggering days two through four, ANCOVAs revealed that taproot elongation increased markedly with the number of triggering days, while root biomass was not influenced by trigger duration; and higher post-trigger watering frequency significantly increased both root biomass and taproot length (Table 4; cf. Fig. 2b, c).

In ANCOVAs using root biomass as a covariate of taproot length, the number of triggering days had a significant effect on taproot length that was independent of root biomass (Fig. 2d; Table 5): taproots were shorter than expected based on root biomass alone when given two or five triggering days and longer than expected when given an intermediate number of triggering days. Thus, either too little or too much water applied during germination stunted taproot elongation.

Discussion

The first weeks of life of desert perennials are most precarious. Once the germination process is set in motion, emerging seedlings rely on continuous moisture availability at the soil surface. Some species with high maternal provisioning in seeds develop long taproots well before their cotyledons break through the soil (e.g., jojoba (*Simmondsia chinensis*), Gentry 1958), but this is not possible for small-seeded *L. tridentata*, which must fuel growth from photosynthesis soon after germination. For such a species, growth is a balancing act between shoot development (to maintain sufficient assimilation for growth) and root development (to ensure future water and nutrient supply). For *L. tridentata*, continuing availability of shallow soil moisture appears essential for maintaining this balance (Ackerman 1979; Sheps 1973; Went and Westergaard 1949). Our experiment showed that *L. tridentata*'s success in developing a deep taproot is highly variable and extremely sensitive to patterns of soil moisture input. It suggests that rainfall during and in the days immediately following seed germination may have disproportionately large effects on seedling survival compared to later precipitation patterns via effects on root early development.

Table 4 Summary of analysis of covariance results for log(root biomass) and log(taproot length) with the number of triggering days as covariate, excluding triggering days = 5

| Treatment | Log root biomass | | | | Log taproot length | | | |
|------------------------|------------------|------|---------|--------|--------------------|------|---------|--------|
| | df | SS | F ratio | P | df | SS | F ratio | P |
| Model | 2 | 1.11 | 5.89 | 0.0054 | 2 | 0.47 | 6.11 | 0.0046 |
| Trigger days | 1 | 0.12 | 1.26 | 0.2682 | 1 | 0.25 | 6.49 | 0.0145 |
| Post-trigger frequency | 1 | 1.10 | 11.68 | 0.0014 | 1 | 0.34 | 8.84 | 0.0048 |
| Error | 43 | 4.16 | | | 43 | 1.67 | | |

SS sums of squares, *df* degrees of freedom

Table 5 ANCOVA table for log(taproot length) with log(root biomass) as covariate

| Treatment | Log taproot length | | | |
|------------------------|--------------------|------|---------|---------|
| | df | SS | F ratio | P |
| Model | 8 | 2.75 | 16.46 | <0.0001 |
| log(root biomass) | 1 | 1.18 | 56.33 | <0.0001 |
| Trigger days | 3 | 0.37 | 5.76 | 0.0026 |
| Post-trigger frequency | 1 | 0.00 | 0.00 | 0.9429 |
| Days × Freq | 3 | 0.03 | 0.39 | 0.7199 |
| Error | 54 | 1.13 | | |

SS sums of squares, *df* degrees of freedom

Our irrigation design had two components, with larger irrigation events at the onset of the experiment to wet the soil column to depth, followed by smaller events meant to keep the upper portion of the soil column moist with minimal downward replenishment of soil moisture. Although we did not quantify soil moisture, visual inspection of soil columns at harvest revealed that soils were dark (wet) further down under higher trigger treatments irrespective of follow-up watering level. We expected the depth of the wetting front to limit taproot elongation, on the assumption that root tips cannot grow through dry soil. Furthermore, we expected that post-trigger watering frequency would primarily influence growth rate, and therefore the time required for roots to reach the lower portion of wetted soil. Excluding the unexpected negative response to five triggering days, these expectations were largely substantiated: seedlings watered daily did accumulate more root biomass and developed longer taproots (Fig. 2b, c; Table 4). However, while taproot length was positively correlated with the number of triggering days, root biomass was not. This suggests that the depth of sufficiently wet soil primarily affects root allometry, while the

amount of biomass allocated below ground is more a function of soil moisture within the seedling's root zone. Although seedlings that emerged earlier had slightly greater total biomass at harvest, size differences due to emergence were independent of treatment. Soil moisture effects on biomass were, therefore, due to differential growth rates and not mediated by time to emergence.

Shoot development in *L. tridentata* was surprisingly unresponsive to irrigation regimes that caused a nearly fourfold difference in root biomass (Fig. 2a, b). This suggests that early shoot development, at least until the second true leaf stage, follows a strict developmental program, while root development is more plastic. It also suggests that the size of the root system and the survival odds of young seedlings cannot be reliably judged from shoot size.

The step from four to five triggering days elicited an entirely different below-ground response with much reduced root biomass and taproot length, especially in the daily post-trigger watering regime. The treatment combination with four triggering days and daily watering received as much water over the course of the experiment as the treatment with five triggering days and daily watering (100 mm, Table 1; Fig. 1). Nevertheless, seedlings in these two treatments showed the greatest disparity in biomass and taproot elongation (Fig. 2b, c). Differences in seedling development were thus unrelated to the total amount of water applied or the post-trigger watering schedule. Excessive moisture can lead to fungal intrusion (e.g., “damping-off”; Trout et al. 1990; Vallentine and Gerard 1968), but this is an unlikely explanation for the low root growth observed after five triggering days as there were no visible signs of fungal infection or root necrosis. Rather, the higher initial water content of the soil column after five triggering days seems a

more likely cause of stunted root development. A possible mechanism behind this response would involve *L. tridentata*'s high soil oxygen requirement, as moderately waterlogged conditions can arrest root growth (Lunt et al. 1973). Accordingly, the fifth application of 10 mm water may have sufficiently saturated the soil column such that gaseous diffusion was significantly reduced at depths below 10–15 cm, driving oxygen levels at the root tip below tolerable levels.

The experiment clearly indicated that rates of taproot elongation were not controlled solely by rates of below-ground biomass allocation, as the relationship between taproot length and biomass showed significant non-linearity with respect to the number of triggering days (Fig. 2d; Table 5). The shortest taproot lengths were seen in treatments receiving either two or five triggering days, but these patterns were produced by qualitatively different responses. Following two triggering days, taproots remained short, although plants allocated no less biomass below ground than after three or four triggering days (Fig. 2b). Either taproot thickness increased or more lateral roots were initiated. Although we did not obtain data to distinguish among these possibilities, at harvest there was no visually noticeable variation in taproot width. By contrast, after five triggering days and followed by daily watering, plants allocated much less biomass below ground than in all other trigger durations (Fig. 2b). In addition, taproot length was even shorter than expected based on below-ground biomass (Fig. 2d). Thus, lack of water infiltration during germination may confine root vertical development without necessarily impairing total biomass allocation to roots, while lack of oxygen in the root zone may impair allocation to roots; and limitations of both excessive and insufficient water appear to enhance lateral root development and/or taproot thickness.

McAuliffe (1994) noted a conspicuous absence of *L. tridentata* on geomorphic surfaces with strongly developed argillic horizons. He suggested that in relatively mesic sites this could be attributed to the vulnerability of *L. tridentata* roots to conditions of prolonged water saturation within the clay-rich portions of the soil profile. Our short-term experiment supports this scenario, as it indicates that taproot development, ostensibly essential to early seedling survival, would likely be markedly compromised under such conditions.

Though this experiment was of only short duration, it demonstrated that the very first days of seedling development can be greatly influenced by rainfall patterns, with potential consequences for post-emergence survival. In *L. tridentata*, more precipitation may be expected to produce higher germination rates (Fig. 1), but conditions producing the highest germination rates may also produce seedlings with the most impaired root systems. Many potential recruits may be lost due to insufficient post-emergence root development, unable to access the deeper soil moisture which drives both transpiration and phenology in mature plants (Kurc and Benton 2010). Our conclusion is not only that both too much and too little water inhibit the optimal development of *L. tridentata*'s root system, but that the gap between too little and too much water appears to be remarkably narrow, leaving this species with a relatively restricted range of suitable establishment conditions. This could, in part, explain the rare and episodic recruitment reported in this species. It would also suggest that changes in climate, particularly in precipitation timing, amount, frequency and variability, could impact recruitment in *L. tridentata* more than in other, less discriminating species.

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