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# Summer Drought Reduces the Growth of Invasive Tree-of- Heaven (*Ailanthus altissima*) Seedlings

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**ABSTRACT:** Tree-of-heaven (*Ailanthus altissima*) is an invasive species in North America that is becoming widespread in the eastern part of the continent. In the drier, western interior of North America, however, the spread of tree-of-heaven appears to be limited to areas where supplemental water is available such as in urban areas or in riparian environments. To explore the effect of summer drought on tree-of-heaven seedlings and to look for genetic variation for drought tolerance among half-sibling families, we collected samaras from 12 open-pollinated mother trees growing in Utah County, Utah, and measured the samaras' area, maximum width, length, and weight. We then planted 10 samaras per mother tree into 10-cm pots in the greenhouse, measured the height of each resulting seedling, and randomly assigned them to a watering treatment (well-watered or droughted) that lasted for 20 wk. We examined the relationship between tree-of-heaven samara size parameters and seedling height before we started our drought treatment and for additional growth parameters after our drought treatment. Several growth parameters (relative growth, final height, final dry mass, final stem dry mass, final dry root mass, and root-to-shoot ratios) were reduced significantly by drought but differed among seedlings from different mothers only for relative growth. There was no genetic variation for drought tolerance observed for any of the growth parameters. These results suggest that tree-of-heaven seedlings from this part of western North America are uniformly and negatively affected by drought and may explain the relative dearth of tree-of-heaven in the interior West.

*Index terms:* drought tolerance, invasive, samara, seedling, tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle)

## INTRODUCTION

Tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle) is an invasive species in North America that is especially prevalent in the eastern portion of the continent where it was introduced in 1784 (Wickert et al. 2017). The species now occupies most states in the United States and has the potential to substantially expand its distribution (Albright et al. 2010). Tree-of-heaven is a shade-intolerant, dioecious tree that aggressively reproduces clonally and mature females bear an abundance of wind-dispersed samaras, each containing one seed (Landenberger et al. 2007). The tree grows rapidly, and exudes an allelopathic compound called ailanthone, which may increase its competitive ability and limit damage from herbivores (Heisey 1996). Tree-of-heaven typically occurs in moist habitats. Albright et al. (2010) showed that tree-of-heaven was much less likely to occur in the United States west of 100°W, as compared to east of 100°W. This was true both based on their search of Internet databases for occurrence records and their models' relative occurrence probability. Additionally, as early as the late 19<sup>th</sup> century, Keffer (1895) reported that tree-of-heaven performed poorly in the dry seasons of the midwestern state of Kansas. Although research has been conducted on the effects of drought on tree-of-heaven (e.g., Trifilò et al. 2004; Filippou et al.

2014), research has yet to be conducted to examine genetic variation for drought tolerance in half-sibling families produced by open-pollinated mother trees.

Based on our observations in Utah County, Utah, it appears that tree-of-heaven is restricted to urban areas where supplemental water is available or to riparian corridors. Our study was designed to examine the effects of summer drought conditions on seedling growth parameters using seeds sourced from local populations and to determine if populations of half-sibling families expressed genetic variation for drought tolerance or were uniformly affected by drought.

Gilbert and Medina (2016) defined drought as a soil water deficit that results from decreased water inputs into a system. Drought can damage plants and reduce their overall growth and relative growth rates, and alter the amount of biomass partitioned into root vs. shoot systems (Gilbert and Medina 2016). Tree-of-heaven has been shown previously to have relatively high root-to-shoot ratios (Pan and Bassuk 1986; Moore and Lacey 2009). Intuitively, one might expect that droughted plants could avoid damage with greater root-to-shoot ratios, but an overall reduction in growth brought on by drought could also result in lower root-to-shoot ratios.

We hypothesized that tree-of-heaven seedling populations would be adversely affected by drought overall but would express genetic variation for drought tolerance and that droughted seedlings would produce relatively more roots than their well-watered controls. We further hypothesized that maternal provisioning—in the form of samara size—would confer a greater ability to tolerate drought on tree-of-heaven seedlings.

## METHODS

### Samara Collection and Seed Propagation

We collected mature dry fruits (samaras) from 18 open-pollinated mother trees in central, urban Utah County, Utah, in November 2015. These were used to generate 18 half-sibling families for our greenhouse study. Each half-sibling family had a known mother tree but an unknown source of paternal DNA. Samaras were stored in paper bags for 5 mo and then 10 samaras per mother were randomly selected for inclusion in the study ( $n = 180$  samaras). Before planting, we weighed and scanned these samaras using a portable leaf area meter (LI-3000C) with a transparent belt conveyor accessory (LI-3050C; LI-COR Biosciences, Lincoln, Nebraska, USA) to determine the area, maximum width, and length of each samara. On 7 April 2016, we planted each of the 180 samaras (each samara contained one seed) into separate 10-cm pots containing 0.8 L of Sunshine Mix #2 potting soil (Sun Gro Horticulture Distribution Inc., Agawam, Massachusetts, USA). The pots were randomly positioned in the Utah Valley University greenhouse with only ambient sunlight. Temperatures were maintained between 21 °C and 24 °C. Initially, all seedlings were well-watered to maximize germination and growth. By early May, 119 of the 180 seeds had germinated (66.1%). This rate of germination is on the high end of a range of tree-of-heaven germination rates observed by Wickert et al. (2017). Only half-sibling families with at least seven seedlings that germinated were used in this study. This eliminated 6 of the original 18 half-sibling families. Results are based on 102 seedlings from 12

half-sibling families with 7–10 seedlings per family generated from 12 mother trees growing in Utah County, Utah (Figure 1).

### Experimental Design and Watering Treatment

In the Utah Valley University greenhouse, we set up a common garden experiment with two watering treatments (well-watered and droughted). Watering treatment was randomly assigned to germinated seedlings and we randomly positioned half-sibling replicates from 12 tree-of-heaven families into the split-plot design, with watering treatment crossed at the whole-plot level and half-sibling family as a sub-plot. The 24 treatment combinations were replicated across five blocks for a potential total of 120 seedlings, which was reduced to 102 seedlings since not all families yielded 10 seedlings each (i.e., some families had as few as seven seeds germinate).

The watering treatment began on 30 May with the well-watered seedlings receiving 0.3 L of water and the droughted seedlings receiving 0.03 L of water, once per week. The amount of water provided to the seedlings in our drought treatment was selected to approximate natural levels of summer precipitation in Utah County, Utah, but also to ensure seedling survival throughout the experiment. On 4 July, we increased the amount of water to 0.06 L once per week to prevent excessive leaf loss as the seedlings grew and summer progressed. The water treatment for the well-watered seedlings remained unchanged. On 18 July, all seedlings received Osmocote 8–9 month slow-release fertilizer (18:6:12 N-P-K + micronutrients; Marysville, Ohio, USA) at a rate of 1.75 g/L of soil.

### Growth Measurements

On 27 May, immediately before the water treatment began, we measured the initial height of each seedling. Height was determined by measuring from the soil surface to each seedling's apical meristem. Measurements were done once a week until the end of the growing season when seedlings from both treatments began to drop their leaves due to senescence. Final

height was assessed on 15 October. Relative growth was calculated as  $[\ln(\text{final height}) - \ln(\text{initial height})]$  (Hoffmann and Poorter 2002). On 21 October, we harvested each seedling to determine its final stem and root biomass. Stems were severed at the soil surface and roots were rinsed free of soil. Stems and roots were placed in separate paper bags and dried to a constant weight in a low-temperature (60 °C) oven for 72 hr. Leaves were omitted from biomass measurements because some of the seedlings had already lost their leaves due to senescence before our harvest began.

### Data Analysis

The effects of watering treatment, family, and their interactions, on relative growth, final height, final dry mass, final dry stem mass, final dry root mass, and root-to-shoot ratio were analyzed with a mixed-model, two-factor split-plot ANOVA using JMP Version 13.0.0 (SAS Institute 2016). Watering treatment was considered a fixed effect and family was considered a random effect. Block was initially included in the model as a random variable, but was eliminated because its effect was not statistically significant (Sokal and Rohlf 1995). Watering treatment was analyzed as a whole-plot effect and family was incorporated as a sub-plot factor within the whole-plot treatment. All interactions between watering treatment and family were included as sub-plot interactions. In the split-plot analysis, a whole-plot error term (replicates within whole-plot error) was used to test the whole-plot effect, while a split-plot error term (residual error) was used to test the sub-plot effect. Final height, final dry stem mass, and root-to-shoot ratio displayed normal distributions and similar variances and were not transformed, whereas relative growth, final dry mass, and final dry root mass were log-transformed to normalize their distributions and reduce heteroscedasticity. To assess correlations between samara size parameters and seedling height before we started our watering treatment and between samara size parameters and seedling height, final dry biomass, and root-to-shoot ratios after our watering treatment, we used linear regression in JMP Version 13.0.0 (SAS Institute 2016).

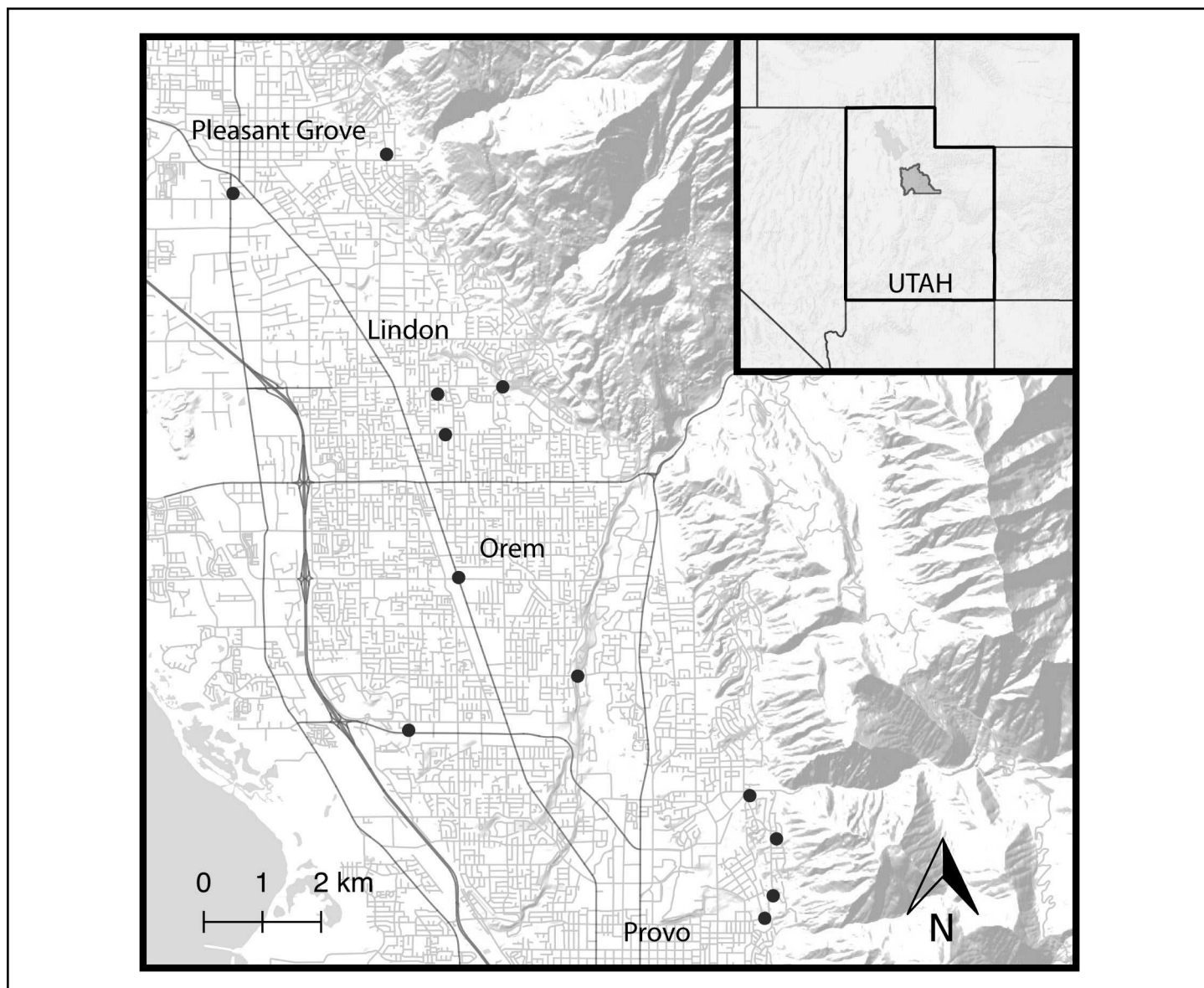


Figure 1. Locations of the 12 mother tree-of-heaven trees used in this study in Utah County, Utah.

## RESULTS

Our drought treatment significantly reduced the relative growth, final height, and final dry mass of the tree-of-heaven seedlings in our study (Figure 2). For droughted seedlings, relative growth from 27 May to 15 October was 27.3% less than that of well-watered seedlings ( $P = 0.002$ ), while final height was 19.8% lower ( $P = 0.002$ ) and final dry biomass was 68.6% lower ( $P < 0.001$ ). Family differences were significant ( $P = 0.035$ ) for relative growth, but were not significantly different for either of the other two growth parameters. No significant treatment-by-family

interactions were found for any of the three growth parameters (i.e., no genetic variation for drought tolerance; Figure 2).

In addition to differences in final mass between the two treatments, droughted seedlings had less stem and root mass than well-watered seedlings had (Figure 3). Final stem mass was 46.4% lower ( $P < 0.001$ ) and final root mass was 71.2% lower ( $P < 0.001$ ). Further, root-to-shoot ratios differed in the two treatments (Figure 3). The mean root-to-shoot ratio for well-watered seedlings was 9.36, while the ratio for droughted seedlings was 5.06 (45.9% lower for droughted seedlings;  $P < 0.001$ ). Families did not differ statistically for either

dry stem mass, dry root mass, or root-to-shoot ratio, however, treatment-by-family interactions were marginally significant for root-to-shoot ratios ( $P = 0.088$ ; Figure 3).

We also examined the relationship between tree-of-heaven samara size parameters and seedling height before we started our drought treatment using linear regression. Pre-treatment height (on 27 May) was positively correlated with samara area ( $r = 0.201$ ,  $P = 0.044$ ), maximum width ( $r = 0.282$ ,  $P = 0.004$ ), and weight ( $r = 0.236$ ,  $P = 0.017$ ) and positively and marginally correlated with samara length ( $r = 0.194$ ,  $P = 0.052$ ).

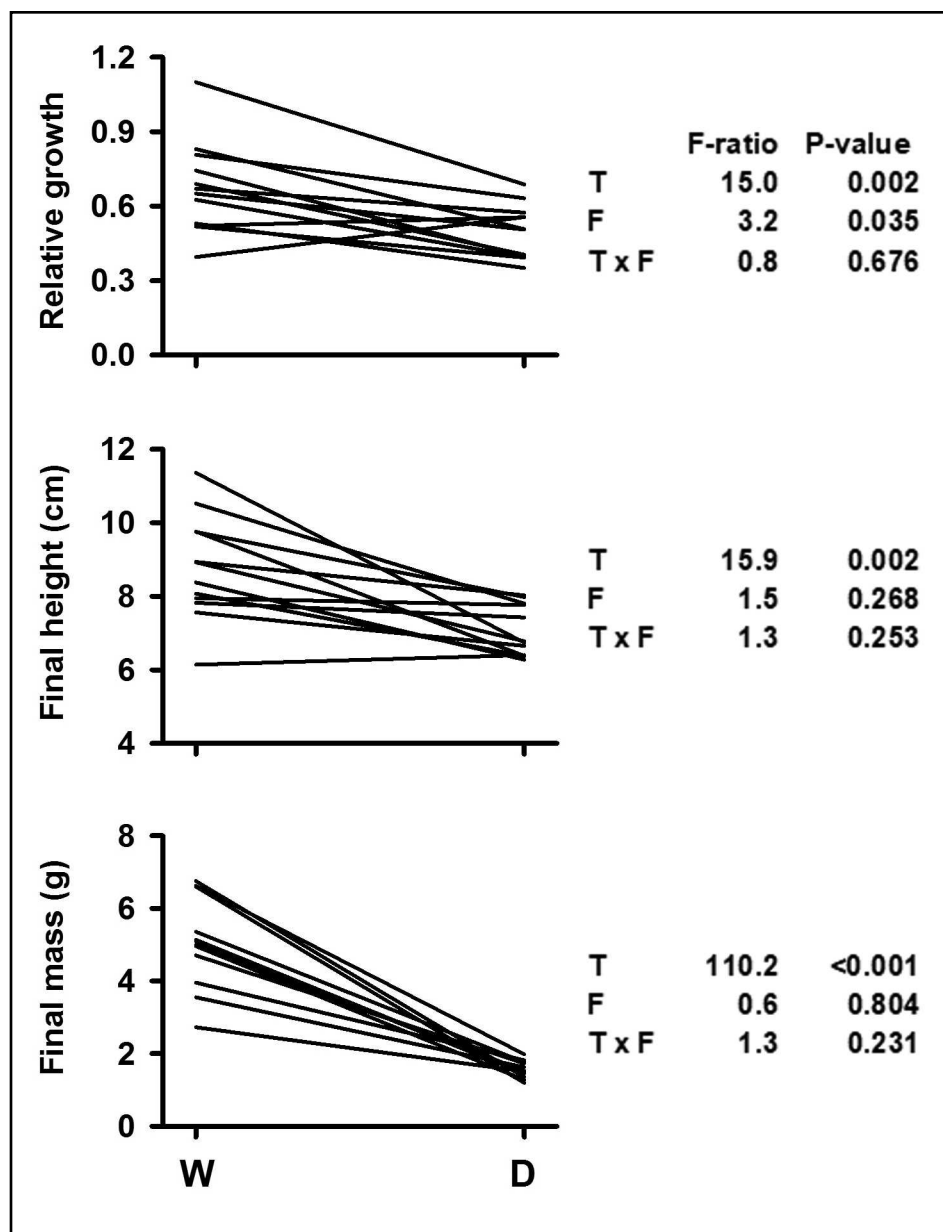


Figure 2. Norm of reaction plots for relative growth, final height, and final dry mass of tree-of-heaven seedlings in relation to watering treatment (T) (well-watered [W] vs. droughted [D]) and half-sibling family (F). *F* ratios and *P* values indicate the results of a mixed-model, two-factor split-plot ANOVA. Each line represents the mean response of ( $n = 7$ – $10$ ) seedlings in a half-sibling family in the well-watered vs. droughted condition.

## DISCUSSION

Our experimental drought conditions negatively affected relative growth, final height, and final dry mass of tree-of-heaven seedlings. These findings contradict those of Trifilò et al. (2004) and Moore and Lacey (2009) who did not find a significant effect of their drought treatment on the growth of tree-of-heaven. The severity of our drought treatment (0.03–0.06 L of water per week) was similar to the most severe treatment used by Trifilò et al. (2004) (0.05 L of water per week), but our treatment duration (20 wk) was longer than the treatment used by Trifilò et al. (2004) (13 wk). Additionally, the two-year-old seedlings used by Trifilò et al. (2004) may have been less susceptible to drought than the less than one-year-old seedlings used in our study. Our study was similar to the study done by Moore and Lacey (2009) in terms of duration and seedling age, but Moore and Lacey (2009) supplied a much greater amount of water (0.23 L of water per week) to their droughted plants than we did. Our drought treatment of 0.03–0.06 L of water per week is not overly severe as it is based on natural levels of precipitation in Utah County, Utah, where an area the same size as our pots (10 cm<sup>2</sup>) would receive only 0.01 L/week presuming that the annual precipitation of 50.2 cm (US Climate Data 2017) occurs at a constant weekly rate (and less precipitation is typically received during the summer months).

Although we found significant growth reduction due to drought and significant differences in growth among the 12 half-sibling families with respect to relative growth, we found no significant genetic variation for drought tolerance (as evidenced by no significant drought treatment-by-family interactions). This indicates that the half-sibling families in our sample are uniformly and negatively affected by drought. The lack of genetic variation for drought tolerance that we found could explain why the spread of tree-of-heaven has been more limited in the western part, as opposed to the eastern part, of North America and why we observed that tree-of-heaven was restricted to areas where supplemental water was available in Utah County, Utah. Aldrich et

By 15 October, after 4 mo of our watering treatment, there were no significant correlations between any samara size parameters and the height of well-watered seedlings, however, samara area and maximum width were both negatively correlated with root-to-shoot ratios ( $r = -0.281$ ,  $P = 0.044$ ;  $r = -0.336$ ,  $P = 0.015$ ; respectively) for well-watered seedlings.

For droughted seedlings, samara weight and seedling height on 15 October were still positively correlated ( $r = 0.309$ ,  $P = 0.029$ ) and samara area, maximum width, and weight were positively correlated, or positively and marginally correlated, with final dry stem biomass ( $r = 0.266$ ,  $P = 0.062$ ;  $r = 0.315$ ,  $P = 0.026$ ;  $r = 0.337$ ,  $P = 0.017$ ; respectively).

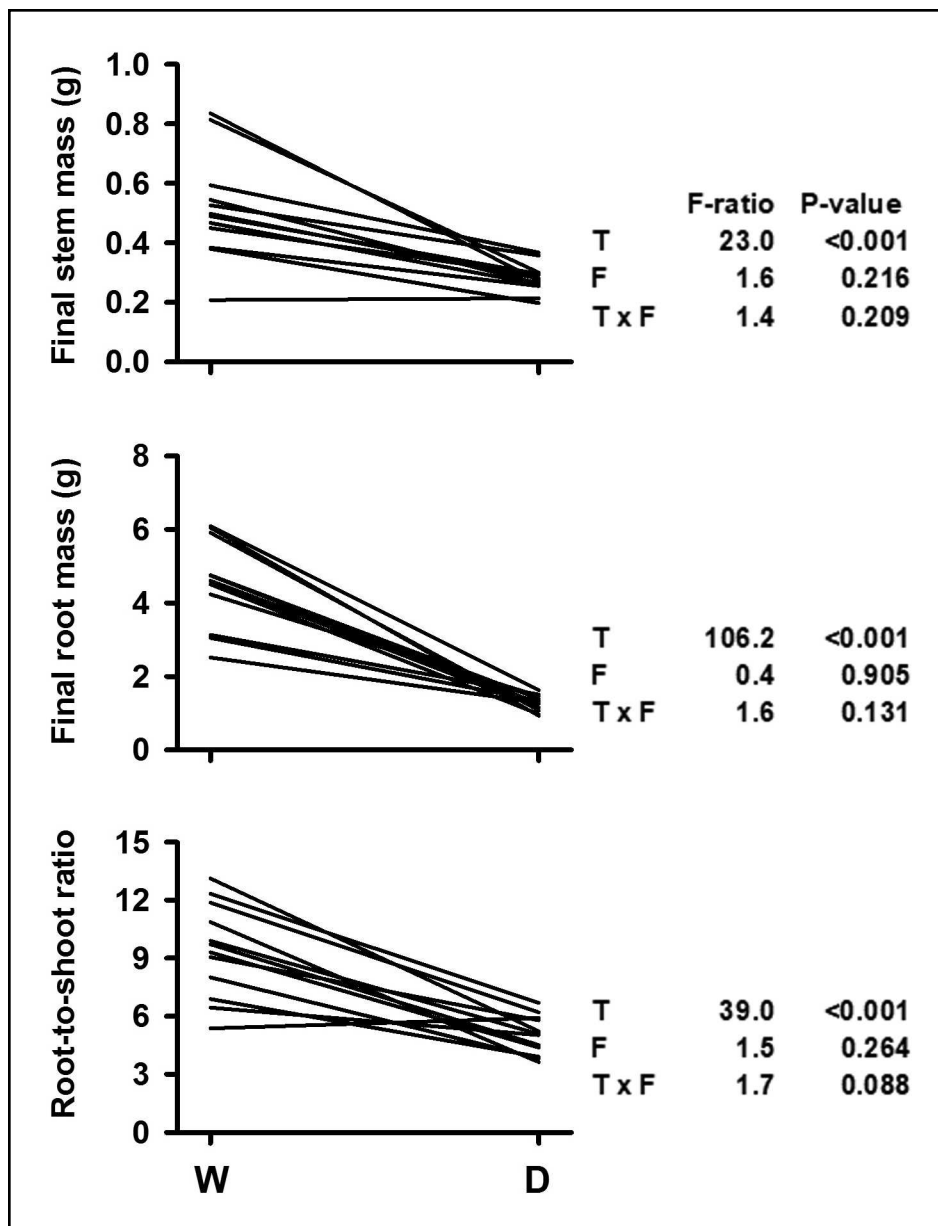


Figure 3. Norm of reaction plots for final dry stem mass, final dry root mass, and root-to-shoot ratio of tree-of-heaven seedlings in relation to watering treatment (T) (well-watered [W] vs. droughted [D]) and half-sibling family (F). *F* ratios and *P* values indicate the results of a mixed-model, two-factor split-plot ANOVA. Each line represents the mean response of ( $n = 7\text{--}10$ ) seedlings in a half-sibling family in the well-watered vs. droughted condition.

al. (2010) found significant but small genetic differences among 28 tree-of-heaven populations from across the United States using microsatellite data, but their samples from the western United States were not especially variable when compared to their other samples from the rest of the country. It is possible that with a larger geographic sample we would have found genetic variation for drought tolerance. However, a sample of 12 genotypes collected from

south-central Wisconsin was sufficient to detect genetic variation for tolerance to herbivory in trembling aspen (*Populus tremuloides* Michx.; Stevens et al. 2007).

Similar to the results of Pan and Bassuk (1986) and Moore and Lacey (2009), we found that tree-of-heaven seedlings put a proportionately large amount of their resources to root production in their first season of growth, and thus, had high root-

to-shoot ratios. It is interesting to note that our drought treatment had a more pronounced effect on root mass than on stem mass (71.2% reduction vs. 46.4% reduction). One might expect droughted seedlings to compensate for low soil water by producing more roots (Brunner et al. 2015), as is the case with plants grown under low soil nutrient conditions (White et al. 2013). However, we found shoot mass was more conserved than was root biomass, perhaps to maintain a minimum aboveground biomass for photosynthesis and competition.

With regard to relationships between samara size parameters and growth, we found positive correlations between samara size and seedling height before our watering treatment began. Such positive correlations are often assumed (Gross 1984; Guerrero-Campo and Fitter 2001; Moles and Westoby 2004) and increased seed size has been shown to contribute to invasive success in some plant species (Hierro et al. 2013). However, in another study of tree-of-heaven, Delgado et al. (2009) did not find positive correlations between samara size and seedling size. Interestingly, the positive correlations we observed did not persist for well-watered seedlings but did persist for droughted seedlings. Perhaps the early effects of maternal provisioning are more lasting under unfavorable environmental conditions such as drought. This interpretation is in line with reports of drought-prone plants producing weightier seeds both in California (Baker 1972) and among riparian species (Stromberg and Boudell 2013). By the end of the experiment, samara area and maximum width were both negatively correlated with root-to-shoot ratios for well-watered seedlings, so the best maternally provisioned seeds produced seedlings that allocated proportionately more biomass to stems, as opposed to roots (Fenner 1983). For an aggressively growing tree like tree-of-heaven, relatively high stem production and its associated leaf production may be more important for survival and fitness than is allocation to roots. In fact, trembling aspen shows a similar pattern of growth, expressing tolerance to herbivory by allocating more resources to stems and mobilizing resources stored in

roots (Stevens et al. 2008). For droughted seedlings, samara size parameters were also positively correlated (or positively and marginally correlated) with stem biomass. In summary, under both watering treatments, samara size parameters were positively linked to initial stem height and final stem allocation. The tree-of-heaven seedlings in our sample appear to be rooty overall, but increasingly shooty when well-provisioned maternally in terms of their samaras.

Unexpectedly, the rooty nature of the tree-of-heaven seedlings in our sample did not confer a level of drought tolerance. Instead, the seedlings' overall performance on several growth parameters was adversely affected by drought and their population displayed no genetic variation for drought tolerance. This finding provides a mechanism behind the relative lack of tree-of-heaven in the dry, western interior of North America, as opposed to the eastern part of the continent, although our sample size was small. If tree-of-heaven growing in western North America evolves genetic variation for drought tolerance in the future, we predict the spread of these drought-tolerant genotypes in the West on a scale similar to what has been observed for the invasion of tree-of-heaven in eastern North America. Such an expansion would be detrimental to native plant communities and natural areas in the West.

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