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RESEARCH NOTE

Flood Tolerance in Common Buckthorn (*Rhamnus cathartica*)

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ABSTRACT: *Rhamnus cathartica* is a Eurasian shrub that has invaded woodland habitats of eastern North America. While historically known from more mesic habitats, it is often found in wetland habitats in Illinois, Minnesota, and Wisconsin, USA. This study assessed *R. cathartica's* growth, architecture, and biomass allocation across multiple flooding treatments representing a soil moisture gradient spanning upland (mesic soil moisture) to wetland habitats (saturated within 30 cm of the soil surface, periodic flooding, and permanently flooded conditions) for two age classes of saplings of *R. cathartica*. Our results on plant growth patterns under these treatments show that young *R. cathartica* saplings were able to tolerate saturated soil conditions, while old saplings were able to tolerate periodic flooding. Allocation of biomass to above- versus below-ground tissues showed that both young and old saplings have similar biomass allocation patterns in relation to soil moisture treatments. Collectively, our results suggest that *R. cathartica* exhibits tolerance to periodic flooding, and that this may partly explain its invasion of certain wetland habitats in North America.

Index terms: flooding tolerance, plant age, *Rhamnus cathartica*

INTRODUCTION

Rhamnus cathartica L., a Eurasian shrub, has been established in North America since at least 1806 (Kurylo and Endress 2012). In parts of the upper eastern and central United States and adjacent regions of Canada, *R. cathartica* has been particularly aggressive in invading woodlands and disturbed areas. *Rhamnus cathartica* is considered an upland species throughout most of its native range (Kurylo et al. 2007), but is also found in fens in England (Godwin 1943) and Central Europe (Hegi 1965). Similarly, *R. cathartica* is considered an upland species throughout most of its introduced range, but in Wisconsin, Minnesota, and Illinois it is also found as a dominant component of wetland habitats (Kurylo et al. 2007). For example, in wetland habitats near Chicago, Illinois, *R. cathartica* is found in 36.5% of surveyed wetlands, dominating, by cover, 19.7% of those wetland sites (Kurylo 2007). For this reason, this species has been recently reclassified as a facultative species in the Midwest and Northcentral/Northeast Regions (Lichvar and Kartesz 2009). More information about the life history, ecology, and ecosystem impacts of *R. cathartica* can be found in Knight et al. (2007).

Little experimental work has been conducted on the hydrologic tolerance of *R. cathartica* in either its native or naturalized ranges. At Wicken Fen in England, Godwin and Bharucha (1932) noted that *R. cathartica* seedlings left unwatered in pots appear to grow well. However, the species was also a dominant within certain areas of the fen. In Germany, growth of *R. cathartica* seedlings was inhibited when placed in stagnant water for four months, and showed little recovery during a follow-up period of well-drained conditions; the species was more susceptible to frost injury during the follow-up period (Frye and Grosse 1992). Upon exposure to partial flooding (15.2 cm tall, 1.64 L pots set in 7.2 cm of water), four-month-old *R. cathartica* seedlings showed leaf epinasty and reduced photosynthetic rates, but were able to adjust as evidenced by recovery of photosynthesis and normal shoot development in a 49-day-long greenhouse study in Iowa (Stewart and Graves 2004). Based on field observations of stand structure of *R. cathartica* in wet versus dry woodland habitats, Gourly (1985) posited that if *R. cathartica* successfully established in a dry year, individuals may survive subsequent flooding and grow rapidly under subsequent dryer conditions. In summation, the experimental work and observations above indicate that *R. cathartica* may have a broader soil moisture tolerance than it is often perceived to have.

Our objective was to study the tolerance of young *R. cathartica* plants at varying durations and depths of saturation and or inundation to address the underlying question of whether tolerance of saturation and or inundation allows *R. cathartica* to establish in wetland habitats.

MATERIALS AND METHODS

Drupes were harvested in November 2004 and 2005 from at least three individuals from each of three scrub-shrub wetlands' edges around Chicago, Illinois. Therefore, saplings of two age classes were used: 4–8 months old ("young saplings" hereafter) from the 2005 collection, and 17–20 months old ("old saplings" hereafter) from the 2004 collection. Seeds were hand extracted and germinated on greenhouse soil mix (local topsoil, perlite, and peat moss in a 1:1:1 ratio) in flats in a greenhouse on the University of Illinois Urbana-Champaign campus. Old saplings were overwintered in a shade house adjacent to the greenhouse to avoid common greenhouse pests. Due to low numbers of unbranched old saplings, branched old saplings were also used. All young saplings were single stemmed and approximately the same height (~80 cm). Individuals were transplanted into 8.8 L pots filled with the greenhouse soil mix and acclimatized for two weeks inside the greenhouse.

Twenty-eight sets of old and young saplings were paired and assigned to one of four treatments (Figure 1): (1) flooded (FD); (2) fluctuating (FX); (3) saturated (S); and (4) control (C). The FD treatment represents plants growing in areas of permanent or near permanent soil inundation (Figure 1). The FX treatment represents plants growing in areas that flood regularly for variable time intervals (i.e., storm water basins, depressions near rivers or streams, etc.). The randomly chosen flooding schedule for the FX treatment and water depths for all treatments are depicted in Figure 2. For the FD and FX treatments, a set of young and old saplings were placed in 242-L clear plastic bins and water levels were kept at approximately five cm above the soil medium surface. Water level was marked on the bins and kept constant. During drawdown for FX treatment, bins were emptied, pots drained out overnight, and bins emptied again the next day. These plants were then watered as needed to keep the soil medium moist. The S treatment represents plants growing in areas where the water table sits within 30 cm of the surface. This treatment was accomplished by placing a pair of plants in a standard black greenhouse flat without holes and keeping the tray full of water (approximately five cm deep). Lastly, the C treatment represents plants growing in a mesic upland position. Pairs of C plants were placed in same aforementioned flats and watered as needed to maintain a moist soil medium.

Plants were sprayed as needed for spider mite and white fly control. In week seven, each plant received 237 ml of liquid fertilizer (a 20N:10P:20K mixed to 250 ppm of N).

Plant height and the number of growing vegetative tips, to quantify plant architecture, were recorded at the start of the trial and each week during the 11-week duration of the study. At the end of 11 weeks, plants were harvested by plant part (leaves, roots, and shoot (stem + branches)), dried, and weighed to determine above- versus below-ground biomass allocation.

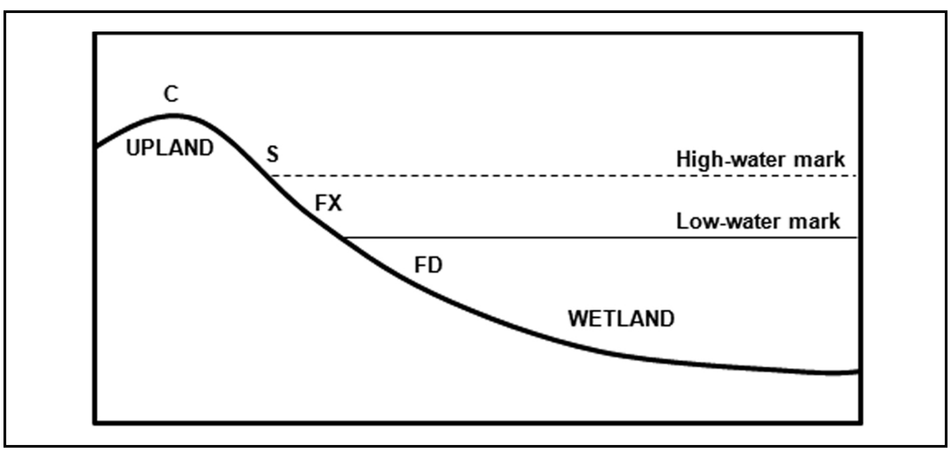

Figure 1. Schematic representation of flooding treatments used in this study in relation to the wetland to upland habitat gradient colonized by *Rhamnus cathartica* in its invaded range. Treatments used in this study include Control (C), Saturated (S), Fluctuating (FX), and Flooded (FD).

DATA ANALYSES

Changes in plant growth (plant height) and architecture (proportion change in growing tips relative to initial number of tips) were analyzed using repeated measures ANOVA with flooding treatment as a fixed between subjects factor and sampling week ("time" hereafter) as a within subjects factor. The data were iteratively analyzed by assuming different variance-covariance structures, specifically compound symmetry, unstructured, autoregressive, and autoregressive with heterogenous variances. The best fit model was then selected using relative AIC values and -2 Log Likelihood scores (Littell et al. 1996). Post hoc evaluation of differences between flooding treatments for a given sampling time was done by examining overlap of confidence intervals.

Resource allocation, in terms of biomass allocated to roots versus shoots (i.e., root: shoot ratio), was analyzed using one-way ANOVA with flooding treatments as a fixed effect and root:shoot ratio as the response variable. Post hoc pairwise comparisons were made using Tukey's HSD (Zar 1999).

Prior to analysis, height data were log transformed and the proportion data (change in growing tips, root:shoot ratio) were logit transformed to improve conformity of data to assumptions of normality and equal variance. All analyses were done using R version 2.15.2 (R Core Team 2012).

RESULTS

Plant Growth and Architecture

Plant Growth

The best fit models for both old and young saplings were those with autoregressive covariance with heterogenous variances. For both old and young saplings, there was a significant effect of flooding treatment and time on plant growth; these effects were not independent of each other as evident from the significant interaction term (*Young Saplings*: Treatment – $F_{3,288} = 164.83$, $P < 0.001$; Time – $F_{11,288} = 204.33$, $P < 0.001$;

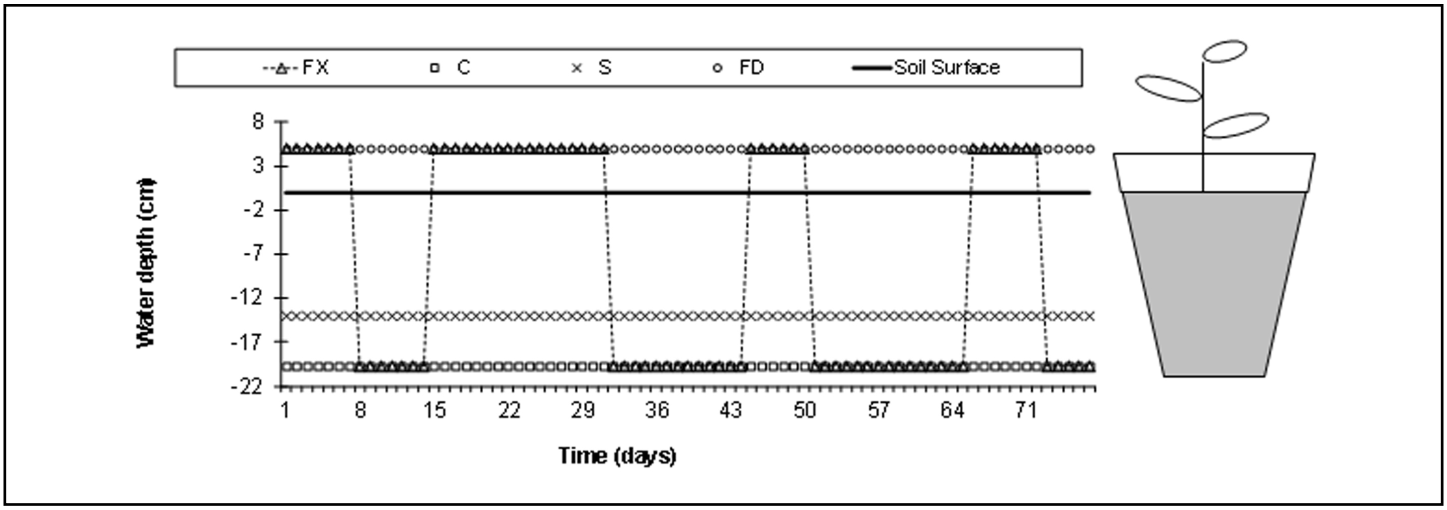

Figure 2. Depiction of water depths for all treatments (Control [C], Saturated [S], Fluctuating [FX] and Flooded [FD]) and schedule for the FX treatment.

Treatment*Time – $F_{33,288}$ = 21.77, P < 0.001. *Old Saplings*: Treatment – $F_{3,288}$ = 20.72, P < 0.001; Time – $F_{11,288}$ = 123.97, P < 0.001; Treatment*Time – $F_{33,288}$ = 4.28, P < 0.001).

Unsurprisingly, both old and young saplings exhibited a logistic trend in growth over time (Figure 3a, b). The growth patterns of young saplings were similar until Week three, after which plants in the C and S treatments were taller than those in the FX and FD treatments (Figure 3a). From Week eight onwards, plants in the C treatment were taller than those in the S treatment (Figure 3a). The height of the plants in the FX and FD treatments did not differ from each other over the entire duration of the study (Figure 3a). In contrast to the young saplings, old saplings in the S treatment were the tallest on average at the end of the study duration (Figure 3b). Old saplings in the S treatment (243.33 ± 24.73 cm; mean ± 95% CI) were significantly taller than those in the FD treatment (164.70 ± 29.85 cm), but did not differ relative to the other two treatments (C: 203.86 ± 29.19 cm; FX: 199.94 ± 25.31 cm; Figure 3b).

Architecture

There were no differences in the architecture of either old or young saplings between flooding treatments over the course of the experiment (Figure 3c, d). There were, however, marginal changes in the production of new tips over time (*Young Saplings*: Time – $F_{10,264}$ = 1.82, P = 0.06. *Old Saplings:* Time – $F_{10,264}$ = 4.78, P < 0.001).

Resource Allocation

Allocation of biomass to roots, relative to shoots, was similar in both old and young saplings across the flooding treatments (Figure 4). For both age-classes, post hoc pairwise comparisons showed that plants in C and S treatments had significantly higher root:shoot ratios relative to plants in the FX and FD treatments (*Young Saplings*: Treatment – $F_{3,24}$ = 65.05, P < 0.001. *Old Saplings*: Treatment – $F_{3,24}$ = 15.50, P < 0.001; Figure 4a, b). There was greater variability in biomass allocation patterns in old sapling plants in relation to the flooding treatments in comparison to young sapling plants (Figure 4a, b).

DISCUSSION

Young *R. cathartica* saplings appear to tolerate saturated soils quite well as indicated by their growth relative to control plants. However, they did not tolerate inundated conditions (FX or FD) very well. Old saplings appeared to tolerate saturated and intermittently inundated conditions (FX), as well as plants growing in conditions mimicking upland soils. This suggests that young saplings are capable of establishing in saturated conditions and, once established, they are capable of surviving intermittent flooding. Both old and young saplings had much higher root to shoot ratios in the C and S treatments versus the FX and FD treatments. Interestingly, young saplings tended to invest more in above-ground biomass in the S treatment, while old saplings tended to invest more in above-ground biomass in the C treatment. Collectively, our results suggest that *R. cathartica* exhibits tolerance of at least periodically flooded environments.

Acclimation is a potential biological mechanism that confers flood tolerance in plants. Exposure to flooded conditions at an early age could flood harden, or acclimate, young plants, giving them better endurance to subsequent flooding events (Keeley 1979; McKevlin et al. 1998; Craine and Orians 2006). For example, *Pinus rigida* Mill. (pitch pine) seedlings with previous exposure to root flooding were more tolerant of flooding during the next growing season than seedlings that had no previous flooding exposure (Craine and Orians 2006). Gourley (1985) suggested *R. cathartica* may be establishing in drier years, surviving subsequent flooding, then putting on growth in less wet years. However, this assumes that younger plants are less tolerant of excessive soil moisture. Our results suggest that this may not be the case. The tolerance of young *R. cathartica*

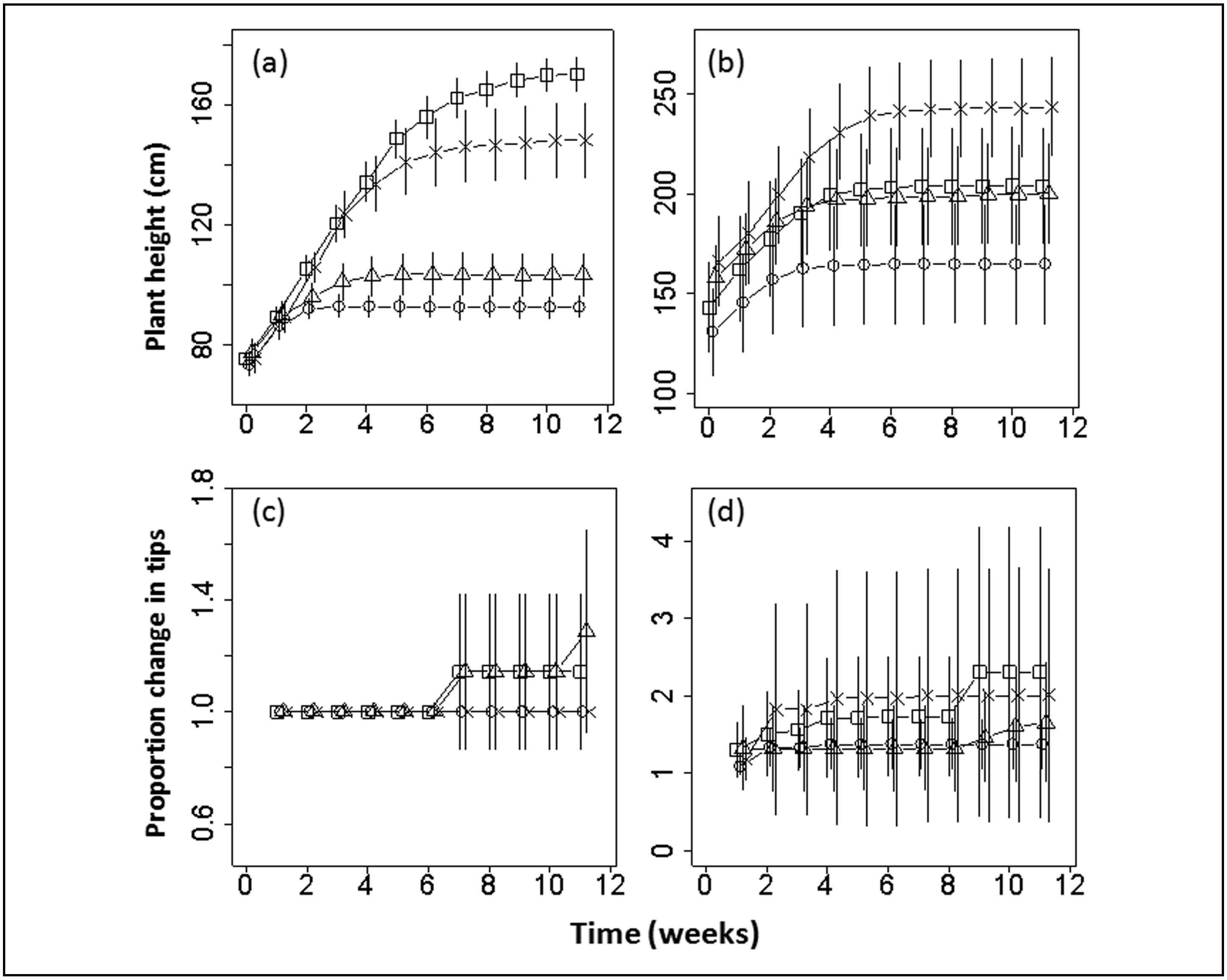

Figure 3. Change in growth ((a) young sapling, (b) old sapling) and architecture ((c) young sapling, (d) old sapling) over time in *Rhamnus cathartica* in relation to different soil moisture treatments. Plots are means and error bars are 95% confidence intervals. Treatments are depicted by different symbols: Control (□; C), Saturated (×; S), Fluctuating (Δ; FX) and Flooded (O; FD). Seed was collected from three sites in the Chicago, Illinois, region in 2004 and 2005.

saplings to saturated environments and the associated tolerance of old saplings to periodic inundation suggest that acclimation may allow the species to establish in wetlands. However, this alone may not explain the differential colonization of wetlands by this species in its native versus invaded range.

Besides acclimation, genetic variation may also confer tolerance of high levels of soil moisture in *R. cathartica*. This may manifest itself in the form of genotypic differences in flood tolerance. If the introduced genotypes of *R. cathartica* were from areas in or around the English fens (Godwin 1943) it is known to occur in, for example, then a higher degree of flood tolerance may have been present versus genotypes from other parts of its native range where it is absent from wetland habitats, such as in Morocco and Siberia (Kurylo et al. 2007). This may partly explain why it appears to be a common component of wetland habitats in parts of its invaded range in contrast to its native range. Genotypic variation in relation to soil moisture is well known among plants occupying broad moisture gradients. For example, the legume *Chamaecrista fasciculata* Michx. (partridge pea) is commonly found on dry sandy soils in eastern North America, while *C. fasciculata* var. *macrosperma* Fernald inhabits fresh-water tidal marshes within Virginia's central coastal plain (Fenster 1997).

A more plausible alternative reason for the observed distribution of *R. cathartica* in wetlands may be that this species exhibits phenotypic plasticity, where the same genotypes exhibit different growth patterns in relation to soil moisture. Understanding the relative importance of genotypic differences and phenotypic plasticity will require a reciprocal transplant experiment wherein seeds of *R. cathartica* from wetlands and uplands are planted across a moisture gradient. Replicating this in

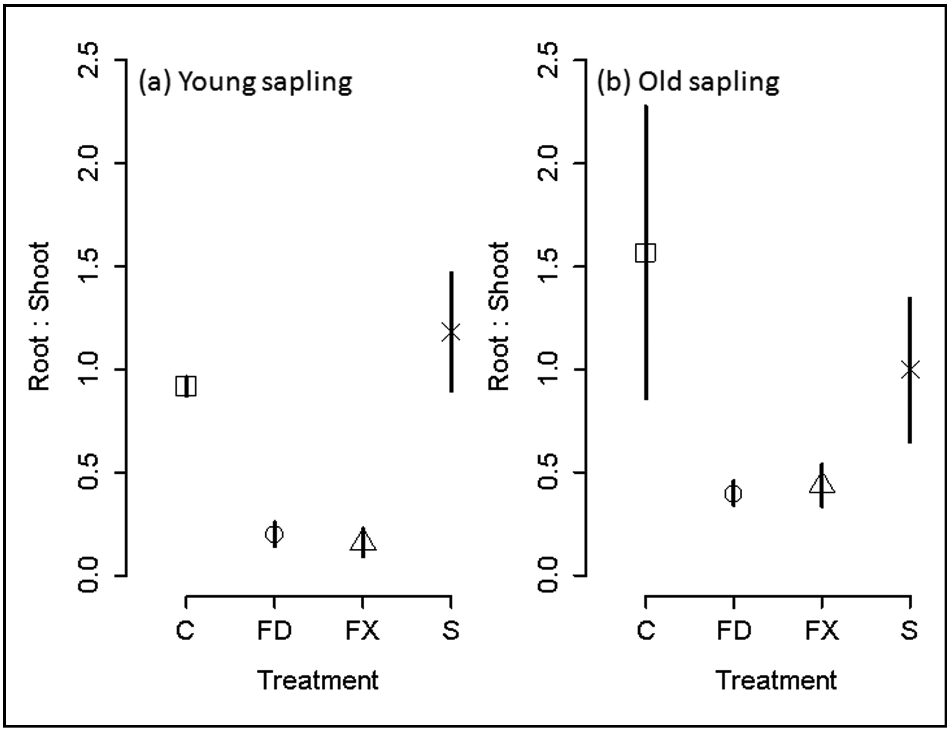

Figure 4. Biomass allocation to roots relative to shoots in (a) young saplings and (B) old saplings of *Rhamnus cathartica* across different soil moisture regimes. Plots are means and error bars are 95% confidence intervals. Treatments are depicted by different symbols and abbreviations: Control (□; C), Saturated (×; S), Fluctuating (Δ; FX) and Flooded (O; FD). Seed was collected from three sites in the Chicago, Illinois, region in 2005 and 2006.

common gardens in both the Midwest and Northeastern United States would not only shed light on how regional environmental differences affect *R. cathartica*'s growth and invasiveness, but also shed light on whether there is something unique about *R. cathartica* genotypes from the Midwest where records of this species from wetland habitats appear more prevalent. Similarly, a reciprocal transplant study spanning native versus invaded range could also shed light on the role of flood tolerance on the invasiveness of *R. cathartica*.

In conclusion, *R. cathartica* displays some tolerance of flooding and saturated conditions, suggesting that such tolerance may explain its colonization of wetland habitats in North America. Investigating the underlying mechanisms behind this tolerance may be important to both predicting its potential distribution across its invaded range, and also to inform management of this species in wetlands as well as uplands.

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