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Soil properties and climate mediate the effects of biotic interactions on the performance of a woody range expander

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Citation: Tomiolo, S., and D. Ward. 2018. Soil properties and climate mediate the effects of biotic interactions on the performance of a woody range expander. Ecosphere 9(4):e02186. 10.1002/ecs2.2186

Abstract. Expansion of trees into grasslands and old fields is a complex process that leads to a decline of biodiversity and reduces rangeland availability. Climate and land-use change contribute to accelerated rates of range expansion. However, the role of biotic interactions in promoting or hindering woody range expanders is still unclear. We investigated the combined effects of abiotic (soil properties and climate) and biotic (simulated grazing and intra- and interspecific plant–plant interactions) factors on a woody range-expander, *Juniperus virginiana,* which has been spreading into grasslands and old-field habitats in North America. We hypothesized that interspecific competition would negatively affect growth and survival of *J. virginiana* due to belowground competition with herbaceous species; grazing would favor *J. virginiana* via competitive release, and intraspecific interactions would be beneficial to tree seedlings during early life stages by means of facilitation. We also predicted that a thicker winter snowpack would have a positive impact on tree growth by providing protection from frost damage. In a multisite field experiment, we exposed *J. virginiana* seedlings to intra- and interspecific interactions, as well as simulated grazing of surrounding herbaceous species. These treatments were repeated at three different sites that vary in soil properties and that are situated along a precipitation gradient. Additionally, we conducted a snow-manipulation experiment at one of the sites. We conducted our monitoring for two consecutive growing seasons characterized by very different rainfall conditions, the second growing season receiving between 6% and 14% more rainfall than the first. Under lower rainfall availability, interspecific interactions between tree seedlings and herbaceous species negatively affected seedling growth rates. However, this effect was detectable only during the drier year and at the site characterized by more favorable soil properties. During winter, we found that deeper snow cover was associated with decreased growth rate of plants, probably due to repeated freeze-thaw cycles. Our results indicate that the role of biotic interactions had an effect only under harsh climatic conditions and that abiotic factors may affect range expansion directly and indirectly via biotic interactions.

Key words: biotic interactions; competition; grazing; invasion ecology; *Juniperus virginiana;* range-expanding species; stress gradient; woody encroachment.

Received 23 February 2018; accepted 6 March 2018. Corresponding Editor: Laureano Gherardi.

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INTRODUCTION

The expansion of woody plant species into grasslands and prairies has caused great concern and fueled a plethora of studies (Van Auken 2009, Eldridge and Soliveres 2014, Ratajczak et al. 2014). Tree and shrub encroachment may significantly reduce biodiversity in the span of a few decades (Briggs et al. 2002*b*, Limb et al. 2010, 2014, Starks et al. 2011). This process has

also gained attention due to its negative impacts on livestock ranching and on regional economies (Briggs et al. 2002*a*, Limb et al. 2011). At larger spatial and temporal scales, tree range expansion is predicted to modify nitrogen and carbon balance (Oechel et al. 2000, Wheeler et al. 2007, Neff et al. 2009, Blaser et al. 2014) as well as hydrogeological cycles (Sturm et al. 2005, Hallinger et al. 2010, Acharya et al. 2017), with detrimental effects on ecological processes (Hoch et al. 2002, Bond 2008, Limb et al. 2010, Ward et al. 2014).

Shifts in land use and management, such as fire suppression and changes in fire regime, have facilitated tree encroachment into prairies and grasslands (Van Auken 2000, Briggs et al. 2005). This process has been further promoted by increased grazing pressure, which removes standing biomass that serves as fuel for fires (Van Auken 2009, Ratajczak et al. 2014). Concurrently, climate also has complex effects on range expansions (Thomas et al. 2001, Chen et al. 2011, Ward et al. 2014). In temperate regions, fluctuations in winter temperatures below and above freezing may cause freeze-thaw cycles that can increase risk of frost damage to plants (Zhang 2005, Groffman et al. 2006, Mellander et al. 2007), cause nutrient leakage (Shachak et al. 1998, Comerford et al. 2013), and decrease the richness of soil microbiota (Campbell et al. 2005). In addition, summer droughts may either hinder or facilitate range expanders, depending on their ability to withstand water scarcity (Volder et al. 2010). Lastly, growing attention has been paid to the effects of biotic interactions on range expansions (Alexander et al. 2016; S. Tomiolo and D. Ward, *in revision*). Range-expanding species may enter new communities where their performance may be favored by release from natural enemies (Van Grunsven et al. 2010, Morriën and van der Putten 2013) or hampered by the presence of new competitors. However, little is known about such interactions and their effects on successful establishment of range expanders (Kopp and Cleland 2015). Although a recent study suggests the negligible contribution of biotic interactions to the process of range expansion (Katz and Ibanez 2017), other studies found the role of biotic interactions to be important (Berlow et al. 2002, Bohrer et al. 2008, Batllori et al. 2009). Moreover, the combined effects of land use, climate, and biotic interactions are rarely addressed simultaneously.

Juniperus virginiana L. (Cupressaceae) is one of the most rapidly expanding native species in the northeastern United States (McKinley and Blair 2008, Bihmidine et al. 2009, Riddle et al. 2014), due to shifts in fire and grazing regimes (Briggs et al. 2002*a*, Bihmidine et al. 2009, DeSantis et al. 2011). Field observations report complete conversion of grasslands into closed-canopy monospecific stands over the span of decades (Briggs et al. 2002*b*, Limb et al. 2010, 2014, Starks et al. 2011). The rapid expansion of this species has been attributed in part to the high concentration of terpenes and essential oils in its leaves (Stewart et al. 2014), which makes the species relatively unpalatable to grazers (Horncastle et al. 2004). Another feature that has been linked to *J. virginiana*'s successful establishment is the tolerance of dry summers and cold winters (Eggemeyer et al. 2006, 2008). Due to high water-use efficiency, low stomatal conductance, and high photosynthetic efficiency (Eggemeyer et al. 2006, 2008, Bihmidine et al. 2009), *J. virginiana* can withstand water scarcity during summer droughts, when most herbaceous species senesce (Awada et al. 2013), and can recover from drought stress during fall, when water becomes available (Eggemeyer et al. 2006).

We describe an experiment where we monitored the performance of young individuals of *J. virginiana* across three sites with different precipitation regimes and soil properties, and under different treatments that simulated grazing and intra- and interspecific plant–plant interactions. We monitored growth, survival, and biomass production of *J. virginiana* seedlings and saplings for two consecutive years. The first year had below-average rainfall (between 7% and 14% less than long-term average at the three sites), and the second year received rainfall consistent with or higher than long-term average (between −2% and +16% compared to the long-term average across the three sites). This fortuitous difference in rainfall abundance across years allowed us to observe how the effect of treatments and site-specific features may differentially affect our target species. We then combined our multisite experiment with a snowfall manipulation at one of the three sites to test the effect of different snow

depths on winter survival and growth of target trees.

For woody range-expanding species, early life stages can be critical for successful establishment as the plants are most vulnerable to climate fluctuations and local disturbances (in accordance with the demographic bottleneck model; Jeltsch et al. 1998). At this early stage, the root system of tree species is superficial. Consequently, belowground competition with neighboring individuals may exert a comparatively stronger effect on small seedlings and saplings than on adult trees (Daly et al. 2000, Nippert and Knapp 2007, Grellier et al. 2012, Tjelele et al. 2015).

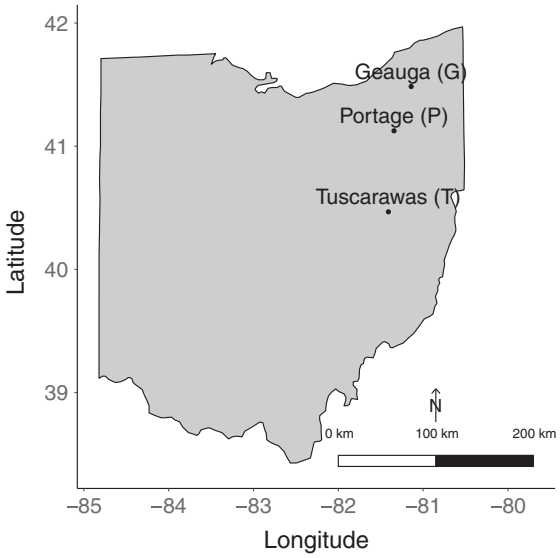
We predicted that (1) interspecific competition from plant communities in old fields would be highly detrimental to the growth and survival of *J. virginiana* seedlings; (2) intraspecific interactions with conspecific seedlings would facilitate survival and growth, at least during the early stages of establishment; and (3) simulated grazing of neighboring herbaceous plants may positively affect *J. virginiana* seedlings via competitive release. Finally, we predicted that tree seedlings would benefit from the protection of a deeper snowpack during the winter months.

Materials and Methods

Sites

We conducted a two-year study at three sites in northeast Ohio located over a range of 120 km (Fig. 1). The sites are respectively in the counties of Geauga (41°48′39″ N, 81°14′99″ W), Portage (41°12′73″ N, 81°34′47″ W), and Tuscarawas (40°46′78″ N, 81°40′93″ W), which are situated at increasing distance southward from Lake Erie (one of the North American Laurentian Great Lakes). Northeast Ohio is affected by lake-effect snow from Lake Erie (Burnett et al. 2003), with regions closer to the lake receiving more winter snowfall when cold wind masses move over the warmer lake surface (Niziol et al. 1995). Lake-effect snow can lead to extreme snowfall, for example, 150–250 mm snow in a multi-day event (Niziol et al. 1995), and is known to influence vegetation distribution in the affected regions (Henne et al. 2007). Despite large interannual variability, our three sites differ substantially in the amount of snow received through the winter (data relative to the period 1988–2017, obtained from the Midwestern Regional Climate Center: http://mrcc.isws.illinois.edu/CLIMATE/). The Geauga site receives an average of 2.2 times more snowfall than the Portage site, and 4.5 times more than the Tuscarawas site.

The study region is also characterized by strong edaphic variation resulting from Quaternary glaciations. Soils in Tuscarawas are sandy and well drained, whereas soils in Geauga and Portage are richer in clay and comparatively less permeable (data from https://www.nrcs.usda.gov/wps/portal/nrcs/surveylist/soils/survey/state/?stateId=OH). Such differences are also reflected in different soil chemical and nutrient properties at the three sites (analyses conducted on soil samples collected on site were performed by the



	Geauga	Portage	Tuscarawas
pH	6.46 ± 0.13	5.29 ± 0.05	6.67 ± 0.38
%N	0.23 ± 0.01	0.15 ± 0.01	0.18 ± 0.01
%C	2.40 ± 0.11	1.61 ± 0.14	2.11 ± 0.06
P(μg/g)	15.00 ± 0.47	4.52 ± 0.94	65.26 ± 9.46

Fig. 1. Map of the experimental sites and table indicating soil properties across sites showing mean ± 1 standard error values for pH, nitrogen content (N), carbon (C), and phosphorus (P). Soil samples were collected at each site (N = 5 per site) at the beginning of the experiment.

S.T.A.R. Lab at Ohio State University). Soils in Tuscarawas and Geauga have higher pH levels than in Portage; similarly, the concentration of phosphorus in Tuscarawas is the highest among the three sites (Fig. 1). The vegetation at the three sites is typical of old-fields (Appendix S1) with some overlap in species, such as *Erigeron strigosus*, *Erigeron canadensis*, *Rumex crispus*, *Muhlenbergia schreberi*, and *Agrostis scabra*.

Experimental design

In May 2016, we planted *Juniperus virginiana* seedlings at each of the three sites within a fenced area to prevent white-tailed deer (*Odocoileus virginianus*) trampling and grazing. Seedlings were purchased from a local nursery and measured on average 28 cm height (standard error [SE] = 0.8). Prior to planting, the fenced area at each site was mowed in order to remove vegetation and facilitate seedling transplants. Each seedling was planted at the center of a 50 × 50 cm plot. The following treatments were applied: (1) *control*, where herbaceous vegetation growing around seedlings was regularly removed (roots included); (2) *grazing*, where we let vegetation grow around the focal seedling and afterward we cut it weekly to a height of 1.5 cm (because *J. virginiana* is relatively unpalatable to mammalian herbivores, no clipping was applied to tree seedlings); (3) *intraspecific competition*, where three *J. virginiana* seedlings were planted around the target seedling at a distance of approximately 20 cm; and (4) *interspecific competition*, where the herbaceous vegetation native to each site grew undisturbed around the target *J. virginiana* seedling. Each treatment was replicated in eight blocks at each site (N = 32 plants per site). In each block, the position of the four treatments was randomized, and the distance between adjacent plots was 50 cm. We monitored mean monthly growth rate (calculated as final height − initial height/number of months) and mortality during two consecutive growing seasons and the intervening winter. At the end of the second growing season (summer 2017), trees were harvested and dried at 70°C for 48 h to record their above- and belowground biomass.

The first year was characterized by a drought, and the sites of Geauga, Portage, and Tuscarawas (Fig. 2) received 7%, 14%, and 10% less rainfall, respectively, than the long-term average rainfall measured over the past 30 yr. The driest months were May, June, July, September, and November, when sites received between −10% and −70% of the long-term monthly rainfall. During the second year, rainfall was more plentiful; the sites of Geauga and Tuscarawas received 16% and 4% above annual average rainfall, respectively, whereas Portage received 2% less than the long-term rainfall average. To avoid total loss of our plants due to drought and transplant shock, we watered our trees manually once a week during the peak of the drought. Nevertheless, most seedlings experienced foliar damage (i.e., browning of the tips). We recorded foliar damage as a categorical variable with two levels of damage: medium damage for individuals with 25–50% of browned tips and high damage for individuals with 50–75% of browned tips.

Snow-depth manipulation experiment

To disentangle the effects of soil properties and winter snowfall across sites, we set up a snow-manipulation experiment at the central site in Portage County. At the same time of planting for the multisite experiment, we had planted 24 additional seedlings of *J. virginiana,* each in 1 × 1 m plots. Surrounding vegetation grew undisturbed around seedlings until the end of the first growing season, when we removed neighbors from half of the plots (N = 12). This allowed us to tease apart the effects of snow alone from those of the herbaceous vegetation surrounding tree seedlings. Plots were grouped in three blocks, each representing the snow level experienced at the corresponding site. During winter, snow was added to or removed from the plots that mimicked snow depth at each site. That is, snow was added to approximate higher snowfall in Geauga, and removed to simulate lower snow cover in Tuscarawas, depending on concomitant snowfall patterns recorded at each site. However, fluctuating winter temperatures (Appendix S2: Fig. S1) led to snow melting and refreezing at the Portage site. Thus, snow manipulations could be carried out only twice (in December and January).

Statistical analyses

To control for Type I statistical error, we tested how site, treatment, and their interaction affected damage, growth rate, and biomass using a

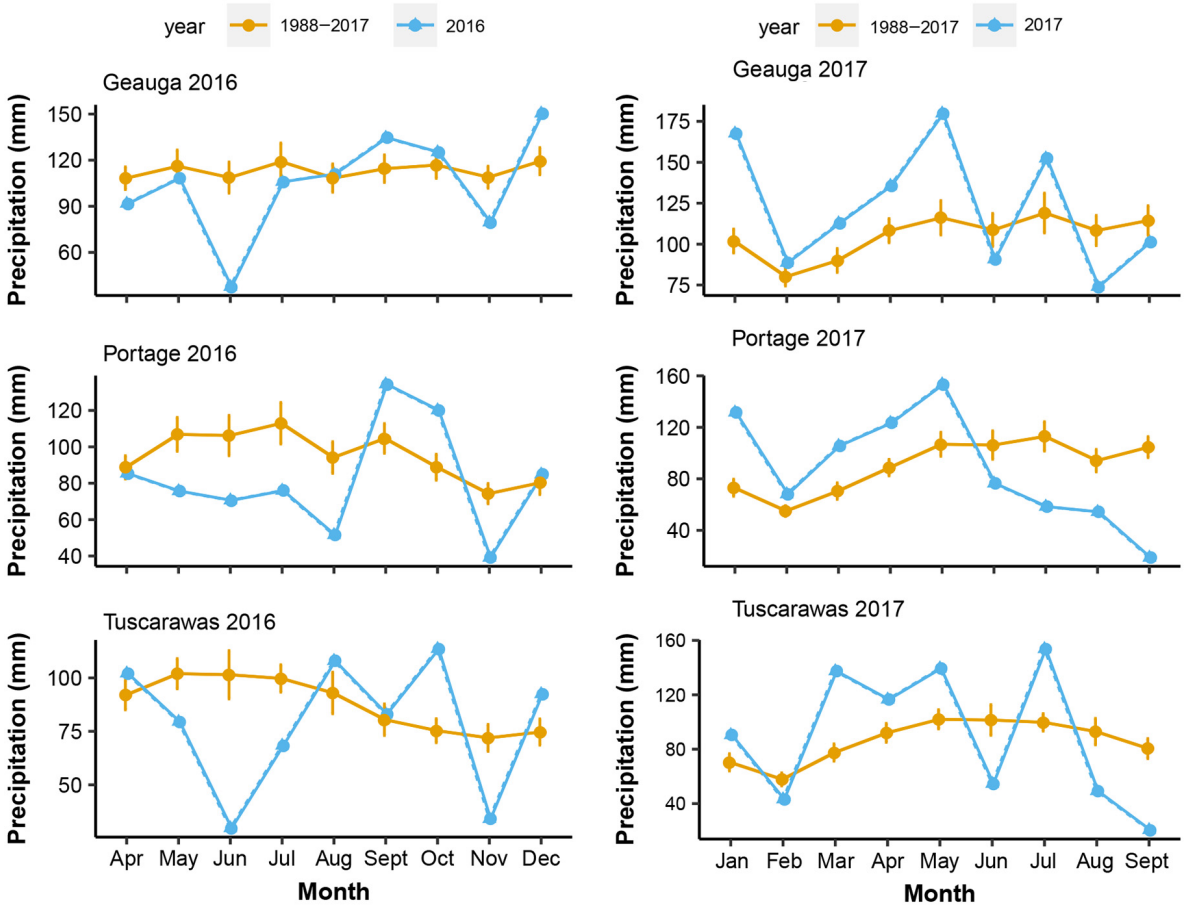


Fig. 2. Comparison of long-term mean total monthly precipitation patterns ± 1 standard error (orange lines) and monthly precipitation during each of the two consecutive years (light-blue lines) 2016 and 2017 for each site. Long-term precipitations were calculated using data for the past 30 yr (1988–2017).

MANOVA, and used block as a random factor. Following that, we analyzed how mean monthly growth rate of *J. virginiana* varied across sites, treatments, classes of foliar damage, and their interactions, for each growing season and the intervening winter separately. We also analyzed the effects of these factors on biomass production (after square-root transformation). We applied linear mixed models using the R package nlme (Pinheiro et al. 2017) in these cases and used block as a random factor. Because the residual spread varied across levels of the fixed factors, we specified the variance structure in our model (Zuur et al. 2009). To test the effect of snow depth on winter mean monthly growth in our snow manipulations, we applied linear models and used square-root-transformed growth rate as the response variable. We used generalized linear models with a binomial distribution and logit-link function for analyzing survival in response to site, treatment, and foliar damage. We also analyzed how the number of surviving trees in intraspecific treatments varied across sites, using generalized linear models with a Poisson distribution. To assess whether site, treatment, and initial height affected the initial level of damage observed in focal seedlings, we applied generalized linear models with a binomial distribution and logit-link function using damage class as response variable. For all models, significant differences were tested using post hoc tests in the package lsmeans (Lenth 2016). For the MANOVA, we used SPSS v. 24 (IBM SPSS, Armonk, New York, USA). All other

analyses were conducted using R3.3.3 (R Development Core Team 2014).

Results

The MANOVA showed a significant effect of site (Wilks' lambda = 0.681, $P = 0.005$) and treatment (Wilks' lambda = 0.631, $P = 0.012$) but no significant interaction (Wilks' lambda = 0.620, $P = 0.465$). The results were significant during the first ($F_2 = 4.141$, $P = 0.020$) as well as during the second year ($F_2 = 4.583$, $P = 0.010$) and in terms of damage level ($F_2 = 7.510$, $P = 0.001$). Treatment had a significant effect on summer growth during the first year ($F_3 = 3.225$, $P = 0.027$) and on winter growth ($F_2 = 6.203$, $P = 0.001$).

We present the results of univariate statistics following the chronological order of our experiment: first growing season (2016), intervening winter, second growing season (2017). During the first growing season (2016), mean monthly growth rate varied considerably across sites and treatments. On average, seedlings grew more in Tuscarawas than in the other two sites (Table 1, Fig. 3A). Although we found consistent trends in growth rate among treatments across the three sites, such differences were significant only in Tuscarawas (Fig. 3A), where interspecific-competition treatments were associated with the lowest growth rates. At all sites, growth rate was negatively affected by foliar damage. Mortality amounted to 36% (35/96) of the target individuals and was primarily driven by foliar damage ($\text{Deviance}_1 = 10.426$, $P = 0.001$), whereas the effect of site was marginally significant ($\text{Deviance}_2 = 5.631$, $P = 0.059$) and treatment had no effect ($\text{Deviance}_3 = 7.142$, $P = 0.067$; Appendix S2: Fig. S2).

Remarkably, no tree seedlings in our experiment were undamaged. Binomial models showed that foliar damage was unrelated to treatment, but was unevenly distributed among sites. In Tuscarawas, 15.6% of the target individuals suffered from severe foliar damage as contrasted with 37.5% at Portage and 59.3% at Geauga.

During winter, initial foliar damage did not affect growth rate. However, significant differences among sites and treatments were found, with the highest mean growth rates being achieved at the Portage site (Table 1, Fig. 3B). At this site, individuals in control and intraspecific treatments attained higher growth rates than those in grazing and interspecific treatments. Winter mortality was much lower than in the previous summer; only seven individuals died.

In the snow-depth manipulation at the Portage site, greater snow depth hindered growth rates (Fig. 4), and individuals exposed to snow removal (simulating the snowfall depth in Tuscarawas) attained the highest growth rate compared to treatments in which trees were exposed to snow (simulating the snow depth at Portage and Geauga). However, such differences were significant only in neighbor-removal treatments ($F_2 = 5.495$, $P = 0.024$), whereas no significant differences among snow-depth treatments were found when herbaceous neighbors surrounded target trees ($F_2 = 0.556$, $P = 0.596$).

During the second, wetter growing season (2017), no differences were found in growth rates across treatments. Site was the only factor that significantly affected growth rates, following a pattern consistent with the previous year (Table 1, Fig. 3C). Initial foliar damage did not have an effect on growth rate (Table 1) and no

Table 1. Linear mixed model results for growth (summer 2016, winter 2016/2017, summer 2017) and biomass of *Juniperus virginiana*.

Variable	Site			Treatment			Damage			Site × treatment		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Growth rate (summer 2016)	5.330	2,65	**0.006**	3.572	3,65	**0.017**	50.017	1,65	**<0.001**	1.891	6,65	0.093
Growth rate (winter 2016/2017)	24.388	2,38	**<0.001**	7.431	3,38	**<0.001**	3.030	1,38	0.089	3.557	6,38	**0.006**
Growth rate (summer 2017)	4.182	2,32	**0.024**	0.874	3,32	0.464	0.394	1,32	0.534	0.576	6,32	0.745
Biomass	11.870	2,32	**<0.001**	5.996	3,32	**0.002**	33.099	1,32	**<0.001**	1.453	6,32	0.225

Notes: Linear mixed models were applied to growth rate across seasons and biomass using site, treatment, and initial damage level as explanatory variables. Rows correspond to each of the four models and columns to explanatory variables. Significant *P*-values ($P < 0.05$) are in bold characters.

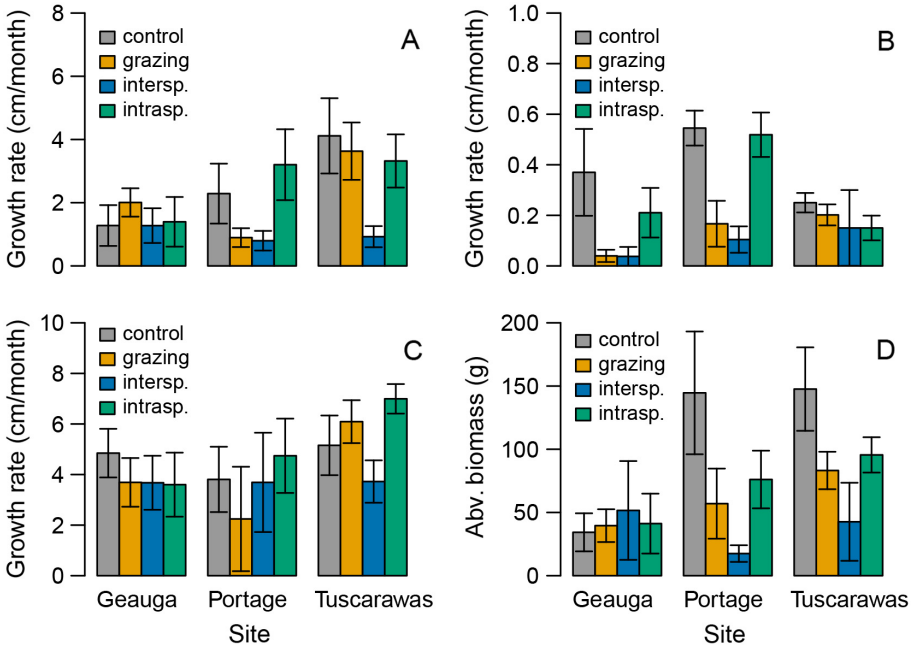


Fig. 3. *Juniperus virginiana* performance in response to control, simulated grazing, interspecific competition (intersp.), and intraspecific (intrasp.) interactions across three sites located along a soil and snowfall gradient. (A) Mean monthly growth rate (cm/month) ± 1 standard error during the first growing season (summer 2016). (B) Mean monthly growth rate (cm/month) ± 1 standard error (SE) during winter (2016/2017). (C) Mean monthly growth rate (cm/month) ± 1 SE during the second growing season (summer 2017). (D) Aboveground (Abv.) biomass (g) ± 1 SE.

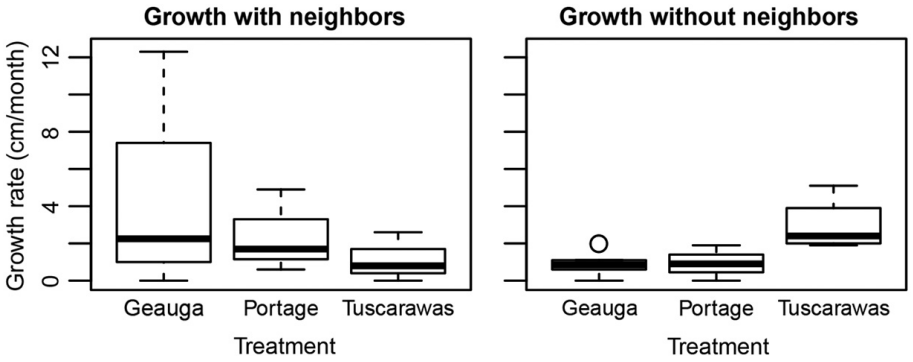


Fig. 4. Boxplot of mean winter growth rate (cm/month) across snow-depth manipulation treatments simulating the mean level of snow received at each of the three experimental sites: Geauga (snow addition), Portage (control treatment), and Tuscarawas (snow removal), with and without neighbors.

traces of browned tips were recorded on the target seedlings at the beginning of the season. During this second growing season, only nine individuals died. Mortality was not affected by site ($\text{Deviance}_2 = 2.19$, $P = 0.347$), treatment ($\text{Deviance}_2 = 2.24$, $P = 0.523$), or initial damage ($\text{Deviance}_2 = 0.157$, $P = 0.691$). The total number of surviving individuals in intraspecific treatments (i.e., targets and neighbors) varied significantly across sites and was significantly higher in

Tuscarawas than at the other two sites (Deviance$_2$ = 8.37, P = 0.015).

Aboveground biomass, which was positively correlated with belowground biomass ($F_{1,50}$ = 424.94, $P < 0.0001$), was significantly higher in Tuscarawas than in Geauga, but not significantly different from Portage (Table 1, Fig. 3D). In Portage and Tuscarawas, the biomass of *Juniperus virginiana* individuals exposed to interspecific competition was significantly lower than for individuals growing in control treatments. This difference among treatments was consistent for belowground biomass ($F_{2,32}$ = 5.894, P = 0.006). Damage had a negative effect on total biomass of trees growing at the three sites (Table 1).

Discussion

Contrary to our initial predictions, the effect of biotic interactions on *Juniperus virginiana* performance was limited, and likely modulated by abiotic factors such as soil properties and rainfall. Our study showed that site-specific characteristics and rainfall availability in two consecutive and climatically different years led to considerably different growth rates and biomass production in young *J. virginiana* individuals. In a lower-than-average rainfall year, tree seedlings experienced strong competition from herbaceous neighbors when exposed to interspecific competition. However, such effects were detectable only at one site with benign soil properties (Tuscarawas). Furthermore, during the subsequent (wetter) year, only site exerted an effect on tree performance. In this wetter year, overall mean growth rate was 2.2 times higher than under the drier conditions experienced during the first growing season. This is consistent with a previous study that showed that *J. virginiana* growth is positively correlated with rainfall (Riddle et al. 2014).

At the Tuscarawas site, permeable and limestone-rich soil provided better conditions for the growth of *J. virginiana* (Briggs et al. 2002*a*, Pierce and Reich 2010, DeSantis et al. 2011). In addition, this soil had higher levels of nutrients than the other two sites. Conversely, both the Geauga and Portage sites are situated on clay-rich soils with poor drainage and lower nutrient contents. Our experimental design does not allow us to fully disentangle the roles of soil properties and climate on *J. virginiana* growth. However, the performance of the species was consistently higher at Tuscarawas across two years that largely differed in rainfall availability. The deviation of precipitation from the long-term means across sites and years was significant: Portage experienced the harshest conditions in both years (with 14% and 2% less than long-term averages, respectively, in the first and in the second year). Conversely, Geauga experienced comparatively more favorable growing seasons, with 7% less precipitation during the first year and 16% higher than average precipitation during the second year. Interestingly, despite experiencing less severe drought than the other two sites, trees at Geauga performed worst. This indicates that soil conditions may have exerted a stronger effect on tree performance than climate. Interestingly, the highest winter growth rates were attained by individuals at the Portage site. Our climate diagrams (Fig. 2) suggest that September and October rainfall were higher than average at this site. As *J. virginiana* replenishes with water during fall (Eggemeyer et al. 2006), reduced water stress may have allowed for higher winter growth.

During the winter, snowfalls were often followed by fluctuations in temperature above and below 0°C. This led to numerous freeze-thaw cycles, so that in the snow-manipulation experiment at Portage, trees exposed to greater snow depth were surrounded by ice lenses (*personal observation*), unlike trees in snow-removal treatments. During winter, a deep snowpack can provide increased protection from frost (Hallinger et al. 2010), retain soil nutrients, and maintain an active microbial community (Bardgett et al. 2005), which may accelerate growth rates during the following growing season (Mack et al. 2004, Chapin et al. 2005). However, freeze-thaw cycles are known to have detrimental effects, such as increased risk of frost damage to tree roots (Zhang 2005, Mellander et al. 2007), increased nutrient leakage from soil (Shachak et al. 1998, Comerford et al. 2013), and decreased soil microbiota richness (Campbell et al. 2005). We had initially predicted that deeper snow cover would be beneficial to tree growth due to protection from frost damage (Schaberg et al. 2008, Hallinger et al. 2010, Kreyling et al. 2011). However, our results indicate that greater snow depth in combination with temperature fluctuations below

and above 0°C may impact growth rates negatively. Thus, increasingly mild winters with large fluctuations in temperatures may lead to a shift in the effect of snowpack on range-expanding species. Such effects may have an important impact on subsequent range expansions (Campbell et al. 2005). Nonetheless, a study on the seasonal distribution of precipitation on grass–shrub interactions showed complex effects and high-system resilience (Bates et al. 2006). Therefore, long-term monitoring of winter snowfall and temperature effects on *J. virginiana* performance would be desirable.

The effect of foliar damage was significant across sites and treatments. Out of the 96 target trees planted at our sites, all experienced foliar damage (i.e., browned tips) to some degree, despite application of extra water to our plots during the drought period. The lower proportion of foliar damage and higher performance in Tuscarawas suggest that at this site, favorable abiotic conditions may have contributed to lower foliar damage and thus higher growth rate. Consistently, we recorded the highest percentage of mortality (30%) at the end of the first—drier—growing season, and foliar damage had a strong influence on this process. These results partially contradict previous studies reporting success of *J. virginiana* encroachment in semi-arid areas during dry seasons (Bihmidine et al. 2009, Awada et al. 2013). However, signs of foliar damage were not evident on our target trees by the beginning of the second growing season, indicating considerable resilience to drought (Eggemeyer et al. 2006).

We predicted that interspecific interactions would have a negative effect on the performance of *J. virginiana*. Our predictions were corroborated only in Tuscarawas, where strong interspecific competition inhibited tree growth (during the first year) and biomass production. Classical theories of tree–grass interactions predict that if trees are able to exploit water from deeper soil layers, they may have a competitive advantage over grasses, especially during dry years (Walter 1939, Walker and Noy-Meir 1982). However, during the early life stages, roots of tree seedlings are not fully developed and likely share the same rooting zone with herbaceous competitors (Ward and Esler 2011). Under limited rainfall availability, experienced during the first year, such effects of belowground competition may have been exacerbated (Belsky 1994, Ward et al. 2013). Conversely, during the second year, deeper tree roots may have reduced the intensity of competitive effects. We can only speculate on the role of root depth in decreased interspecific competition because we measured belowground biomass, but not root depth compared to that of surrounding herbaceous species. Interestingly though, we found that interspecific treatments were usually associated with the lowest production of above- and belowground biomass compared to other treatments. An alternative explanation is that during the second wetter season, herbaceous species may have retained water in the rooting zone, thereby increasing soil humidity with positive effects on *J. virginiana* performance. A similar process has been documented in semi-arid shrublands (Rysavy et al. 2016). Thus, higher resource availability may mitigate competitive interactions between woody and herbaceous species (Daly et al. 2000, Riddle et al. 2014). The absence of any treatment effect in Geauga and Portage suggests that at these sites, unfavorable abiotic conditions may have overwhelmed the effect of interspecific interactions.

We predicted that intraspecific interactions and grazing would have positive effects on tree performance, the first via facilitation and the second via competitive release. These results were only partially supported by our findings, because biomass production in such treatments was similar to control treatments, suggesting little or no effect of grazing and conspecifics on tree performance compared to control treatments. Interestingly, at the Portage site, *J. virginiana* individuals surrounded by conspecifics grew more than in grazing and interspecific-competition treatments during winter. A possible explanation is the protection from frost offered by the conspecifics planted around the target. Contrastingly, in grazing and interspecific-competition treatments (where herbaceous plants had senesced and died), trees may have been exposed to the numerous freeze-thaw cycles that were observed over the winter. Notably, during the second growing season we recorded an increased mortality rate of *J. virginiana* individuals in intraspecific-competition treatments, regardless of their position (focal or neighbor) within a plot. This is

not uncommon, as intraspecific interactions in woody species are expected to shift from facilitation to competition across ontogenetic stages (Miriti 2006). As individuals grow larger, and therefore closer to each other, competition for light and soil resources becomes increasingly harsh and results in thinning, a form of intraspecific competition (Li et al. 2013). Historically, heavy grazing has been correlated with higher establishment of *J. virginiana* and other woody range expanders in grasslands, prairies, and savannas (Owensby et al. 1973, Briggs et al. 2002*a*, DeSantis et al. 2011, Ward et al. 2014). The high concentration of terpenes in the leaves of *J. virginiana* (Stewart et al. 2014) makes the species relatively unpalatable to mammalian herbivores (Horncastle et al. 2004), leading to selective grazing of surrounding grasses and consequently favoring increased tree growth (Provenza et al. 2003) due to reduced competition for water and resources. Consistent with these previous studies, our simulated grazing treatments may have reduced interspecific competition for *J. virginiana* individuals (Brown and Archer 1999, D'Odorico et al. 2012, Segre et al. 2016).

Overall, our study showed a complex interplay of abiotic (soil properties, snowfall depth and persistence, summer rainfall) and biotic factors on the performance of a range expander in a novel recipient community. Although we cannot tease apart the role of climate from that of soil abiotic properties, our results indicate these factors combined may have contributed to different levels foliar damage, which in turn affected growth rate and survival. In addition, the succession of two climatically different years, in terms of rainfall abundance, allowed for observing how abiotic factors mediated the effect of biotic interactions on growth and biomass production. Given the increasing frequency of climatic variability predicted by climate-change scenarios (Adler et al. 2012, Cleland et al. 2013), plant communities may be exposed to increasing instability at both local and regional scales (Bates et al. 2006, Bai et al. 2008, Heisler-White et al. 2008, Bachman et al. 2010, Cleland et al. 2013, Germino and Reinhardt 2014). Such increasing uncertainty is likely to affect the process of range expansion in complex ways, both directly and by interacting with abiotic (e.g., soil properties) and biotic (e.g., competition and grazing) factors. This certainly calls for increased efforts in understanding how these novel communities may develop.

Acknowledgments

We thank Melissa Davis, Jean Engohang-Ndong, Jim Morales, and the staff of Geauga and Tuscarawas campuses for technical and logistic support in the field. Christian Combs and Matt Wuensch are thanked for help with fieldwork. This research was funded by the Herrick Trust, Kent State University.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2186/full