Beneath it all: Size, not origin, predicts belowground competitive ability in exotic and native shrubs 1, 2

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Beneath it all: Size, not origin, predicts belowground competitive ability in exotic and native shrubs[1,2]

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Abstract. Traits associated with root morphology and nutrient uptake rate may contribute to the competitive ability of invasive species by determining their access to soil nutrients and their ability to extract those resources. Here, we tested the hypotheses that (a) exotic woody shrubs would be superior belowground competitors for nitrogen in heterogeneous soil resulting from key aspects of root architecture and (b) larger plants would be superior belowground competitors. We tested these hypotheses using two native shrubs, *Rubus allegheniensis* and *Viburnum dentatum*, and two invasive exotic shrubs, *Rubus phoenicolasius* and *Berberis thunbergii*, all four of which can become abundant in plant communities in the eastern United States. We grew replicate plants from each species with interspecific competitors, with intraspecific competitors, and individually in a randomized layout in a greenhouse in two temporal blocks. Each experimental container had a central soil patch amended with ^{15}N-labeled litter. We measured above- and belowground growth, root morphology, and nitrogen uptake to assess the effects of intra- and interspecific competition on plant growth and nitrogen uptake. All species grew better in the second temporal block, but we did not detect any differences in the competitive ability or root traits for exotic versus native species; rather, plant size was the key trait that predicted competitive effects. Both *Rubus* species, which capitalized on the extended growing season offered by our greenhouse conditions, were stronger competitors and typically larger plants than *B. thunbergii* and *V. dentatum*. Both *Rubus* species exerted measurable competitive effects on other species, resulting in decreased aboveground size of competitors by 50% or more relative to control plants, but did not routinely decrease ^{15}N uptake or root biomass of competitors. When competing with *Rubus*, leaf C:N ratios of all species except *R. phoenicolasius* were greater than when grown alone, suggesting that large *Rubus* plants did decrease the total nitrogen available to competitors. Our data suggest that belowground competitive ability in shrubs may be more closely associated with plant size and growth rate than plant origin. In addition, plant species that exhibit plastic growth phenology, such as those in the genus *Rubus*, may gain a competitive advantage during years with warmer autumn months by extending their growing seasons, facilitating their invasion and establishment in new habitats.

Key words: belowground competition, biological invasions, exotic plants, invasive species, nitrogen, roots

The role of roots is rarely addressed in the search for traits that contribute to invasion success, but could help explain invasiveness and post-invasion impacts (Fargione and Tilman 2006). Root traits and belowground competition may be especially important in forested systems where many of the most damaging invasive species are woody shrubs (Webster, Jenkins, and Jose 2006). Interspecific differences in root morphology and nutrient uptake rate may contribute to the competitive ability of exotic shrub species by facilitating access to soil nutrients and providing a more rapid means of extracting those resources (Wilson 1988, Coomes and Grubb 2000).

Root biomass can determine a plant's nitrogen acquisition ability when it competes (Gaudet and Keddy 1988; Lamb, Stewart, and Cahill 2012), but the effect of nutrient and water limitation on the intensity of root competition is debated (Wilson 1988, Belcher, Keddy, and Twolan-Strutt; 1995, Schenk 2006). Some studies suggest that plant species that possess a superior ability to acquire nutrients benefit disproportionately in high resource environments (Gioria and Osborne 2014) and that both root and shoot competition are strongest when soil nutrients are abundant and plants are actively growing (Grime 1977; Li *et al.* 2010; Li *et al.* 2015). A recent systematic meta-
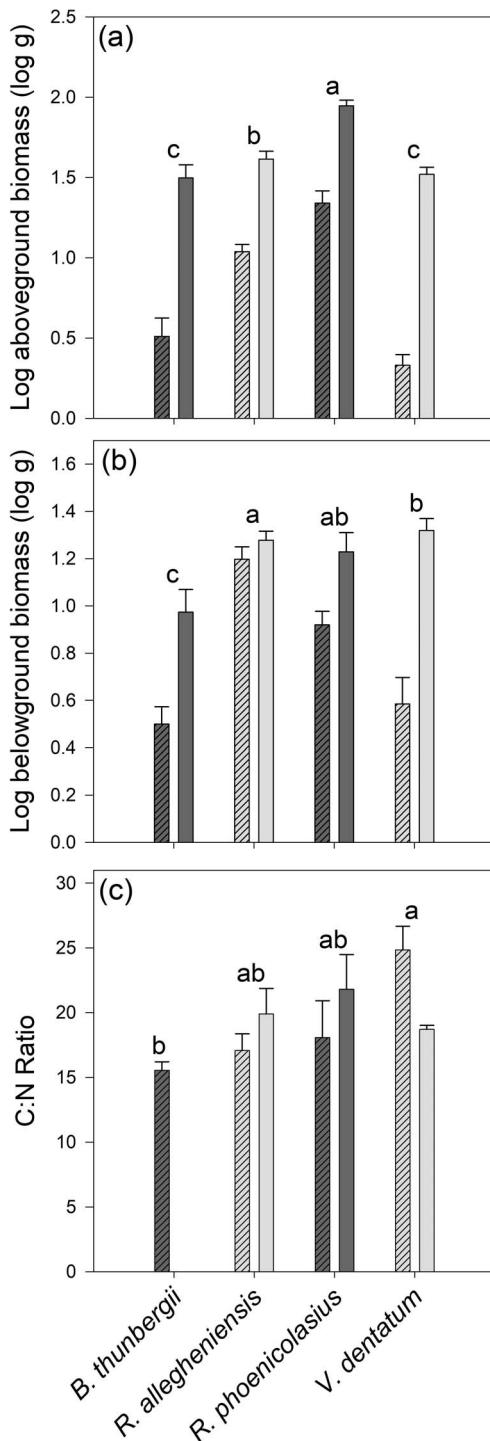
FIG. 1a–c. Aboveground and belowground biomass (log$_{10}$–transformed) and leaf C:N ratio without competition. Dark gray bars correspond to exotic species and light gray bars to native species. Hatched bars indicate the first block and unhatched bars the second block. Data were not available for

analysis, however, has reported the opposite result: that root competition intensity is generally higher in low resource environments (Kiaer, Weisbach, and Weiner 2013).

The persistence of exotic shrubs in the forest understory makes them a dominant component of invaded northeastern North American forests, at times forming dense, nearly monospecific stands that competitively exclude native plant species (Dorning and Cipollini 2006). The spread of exotic species may be further encouraged through the ongoing and widespread nutrient enrichment in temperate forests by favoring species that are fast-growing or superior belowground competitors and are able to persist in forest understories (Gilliam 2006; Perry *et al.* 2010; Caplan *et al.* 2017). Although the contribution of root traits to plant competitive ability may be particularly important for exotic woody shrubs because their perennial root systems occupy soil for long periods of time, the majority of studies examining the effects of root traits on belowground competitive ability have focused on herbaceous species (*e.g.*, Roumet, Urcelay, and Diaz 2006; Dehlin *et al.* 2008). Comparable research on woody shrubs remains sparse, especially for exotic shrubs (but see Jo *et al.* 2015).

This study addressed whether understory shrub species from forests of northeastern North America exhibit consumptive competition for nitrogen in heterogeneous soils and whether interspecific differences in root traits are associated with competitive ability. We chose four shrub species based on their high prevalence in deciduous forest understories of northeastern North America. Two are native to the region, *Rubus allegheniensis* Porter (Allegheny blackberry) and *Viburnum dentatum* L. (arrowwood viburnum). The other two species, *Berberis thunbergii* DC (Japanese barberry) and *Rubus phoenicolasius* Maxim (wineberry), are exotic species from genera known to have negative effects on native plants in invaded communities (Ehrenfeld 1999; Silander and Klepeis 1999; Xu, Griffin, and Schuster 2007; Gorchov *et al.* 2011; Gaire *et al.* 2015). We hypothesized that (a) exotic shrubs would outperform native shrubs when grown with an interspe-

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B. thunbergii C:N ratio in the second block. Different letters above bars indicate that treatment-level means differ significantly. Error bars indicate ± 1 standard error of the mean.

Table 1. MANOVA table for differences in species traits among *Berberis thunbergii*, *Rubus allegheniensis*, *Rubus phoenicolasius*, and *Viburnum dentatum* ($N = 38$) in the absence of competition.

Factor	Wilks' lambda	F value	Num DF	Den DF	Pr > F
Species	0.0010	42.25	18	71.196	< 0.0001
Block	0.0845	45.14	6	25	< 0.0001
Species × Block	0.0779	5.8	18	71.196	< 0.0001

cific root competitor, and that (b) larger plants would be superior root competitors.

Materials and Methods. EXPERIMENTAL SETUP. Plant propagation took place at Pinelands Nursery (Columbus, NJ) using seeds collected from local populations of the respective species; seeds were cold-stratified before germination. The competition experiment took place in a greenhouse run in two consecutive full-factorial temporal blocks as we were unable to fit all experimental containers in one greenhouse bay at one time. Each container held a focal plant grown either individually or with a single competitor plant. We planted seedlings of roughly equivalent age and size (*B. thunbergii*: 4.4–14.1 cm height, *R. allegheniensis*: 0.2–3.2 cm, *R. phoenicolasius*: 0.6–2.6 cm, and *V. dentatum*: 5.6–12.2 cm) in containers using a full-factorial design. Factors included Species (4 levels) and Competitor (5 levels; none or one individual of each species), yielding 14 nonredundant treatment combinations. Containers were rectangular boxes of white corrugated plastic (46 × 20 × 25 cm) filled with field soil that was amended with sand to improve drainage. The composition of the mixture was 19% gravel, 48% coarse sand, 19% fine sand, and 13% silt and clay by mass. Field soil used in the second block had roughly seven times the inorganic N content of field soil used in the first block (46 ppm NO_3 + 3 ppm NH_4 vs. 6 ppm NO_3 + 1 ppm NH_4) due to variability in supply. To evaluate the importance of contested patches to competitive outcomes, each container included a vertically-oriented band of ^{15}N-enriched litter combined with the aforementioned soil mixture (0.75% *Lolium multiflorum* by mass, enriched to 4.2 atm %) placed across the center of the container. White corrugated plastic dividers were placed between plants aboveground to ensure that root competition occurred without the influence of shoot competition (von Wettberg and Weiner 2003). Control containers contained individuals of each species grown singly under identical conditions.

Containers were randomly placed on one of four greenhouse benches at the start of either of two temporal blocks (26 weeks each). We initially established 11 to 12 replicates of each treatment combination, targeting 10 replicates after early plant loss. Final sample sizes ranged from 10–11 replicates of each treatment combination, with 4–6 replicates per temporal block. We watered the soil in each container to field capacity 1–3 times per week, with watering dependent on plant size and environmental conditions in the greenhouse. Greenhouse shades were drawn when photosynthetic photon flux density exceeded 200 µmol m^{-2} s^{-1}, and supplemental lighting was used to maintain a 16:8 hour light:dark photoperiod throughout both temporal blocks. Temperature set points ranged from 20.5 °C to 23.9 °C during the day and from 12.8 °C to 15.6 °C at night. Greenhouse conditions were intended to mimic partly-shaded understory conditions with temperature and light regimes set to those typically experienced during the New Jersey growing season (Caplan *et al.* 2017). We did not wish to replicate deeply shaded conditions that could limit seedling establishment or growth, and thus competition for nitrogen (Ricard *et al.* 2003). Plants in the first block grew from August 2011 until February 2012, while plants in the second block grew from May until October 2012. Each block was terminated when we determined that larger plants were becoming container-bound.

Table 2. MANOVA table for differences in leaf ^{15}N, ^{13}C, and C:N ratio among *Berberis thunbergii*, *Rubus allegheniensis*, *Rubus phoenicolasius*, and *Viburnum dentatum* in the absence of competition ($N = 32$).

Factor	Wilks' lambda	F value	Num DF	Den DF	Pr > F
Species	0.1445	3.95	15	58.373	< 0.0001
Block	0.1623	21.69	5	21	< 0.0001
Species × Block	0.3335	3.07	10	42	0.0051

Table 3.   MANOVA table for effects of competitors on growth of *Berberis thunbergii* ($N = 48$), *Rubus allegheniensis* ($N = 49$), *Rubus phoenicolasius* ($N = 48$), and *Viburnum dentatum* ($N = 49$).

Species	Factor	Wilks' Llambda	*F* value	Num DF	Den DF	Pr > *F*
B. thunbergii	Competitor	0.3443	1.73	24	116.33	0.029
	Block	0.1402	33.73	6	33	< 0.0001
	Competitor × Block	0.2515	2.35	24	116.33	0.001
R. allegheniensis	Competitor	0.2620	2.34	24	119.82	0.001
	Block	0.0911	56.52	6	34	< 0.0001
	Competitor × Block	0.5128	1.05	24	119.82	0.407
R. phoenicolasius	Competitor	0.2504	2.36	24	116.33	0.001
	Block	0.1602	28.83	6	33	< 0.0001
	Competitor × Block	0.6634	0.61	24	116.33	0.922
V. dentatum	Competitor	0.378	1.61	24	119.82	0.051
	Block	0.0716	73.51	6	34	< 0.0001
	Competitor × Block	0.2460	2.47	24	119.82	0.0007

After 26 weeks, we harvested all aboveground plant material. We measured total stem length, counted the number of leaves, measured total leaf area using a LI-3100C Area Meter (LI-COR Biosciences, Lincoln, NE), and then measured oven-dry biomass of all aboveground material. We finely ground and homogenized leaf tissue for analysis of ^{15}N, ^{13}C, and carbon to nitrogen (C:N) ratio using continuous flow isotope ratio mass spectrometry (UC Davis Stable Isotope Facility, Davis, CA). Carbon-13 was opportunistically analyzed to determine if root competition affected plant gas exchange. Carbon is more strongly fractionated when a leaf's intercellular CO_2 concentration is greater, which occurs when photosynthesis is carried out with less water loss (Farquhar *et al.* 1989). Greater values of $\delta^{13}C$ (*i.e.*, those nearer to zero) are therefore indicative of greater water use efficiency over the course of a leaf's lifespan (Warren, McGrath, and Adams 2001). Sample sizes for tissue chemistry ranged from 6–10 samples for each treatment combination. We then washed all soil away from root systems, measured the length of the longest lateral root from each plant, and scanned this root (together with its daughter roots) on a flatbed scanner (600 dpi). Images were analyzed for total fine root length using WinRhizo 2007d (Regent Instruments, Québec, Canada) before measuring oven-dry biomass of all root material.

STATISTICAL ANALYSES. We used multivariate analysis of variance (MANOVA) to determine the effects of species and competition on leaf number, total stem length, leaf area, aboveground biomass, belowground biomass, longest root length, and total fine root length. Response variables were log_{10}–transformed to help satisfy assumptions of residual normality. Because measures of intraspecific competitors within containers were not independent, we averaged responses of the two intraspecific competitors grown within a container. This method retained the container as the experimental unit, ensuring that samples were independent. We first compared above- and belowground growth characteristics among the four focal species using plants grown without competitors. We then examined growth characteristics within each species for effects of intra- or interspecific competitors using MANOVA with mixed effects. The primary fixed effect was competitor identity; we included random effects to account for variability between temporal blocks and for Competitor × Block interactions. Additional MANOVAs for each species examined the effects of root competition on leaf ^{15}N enrichment, ^{13}C enrichment, and leaf C:N ratio. Treatment means were compared *post hoc* using Tukey's multiple comparison tests. We conducted statistical analyses in SAS 9.4 (SAS Institute 2011). Growth characteristics in our experiment were typically highly correlated; we therefore present representative figures in-text (*i.e.*, those depicting aboveground biomass, belowground biomass, and leaf C:N ratio). Remaining characteristics are presented in the Supplemental Material.

Results. DIFFERENCES AMONG SPECIES. In the absence of competition, the four species differed significantly in above- and belowground traits; however, we found no size trend or differences in leaf tissue chemistry separating the native and exotic species (Fig. 1; Fig. S1, S2). Differences among species were much more pronounced in the second temporal block, during which all species
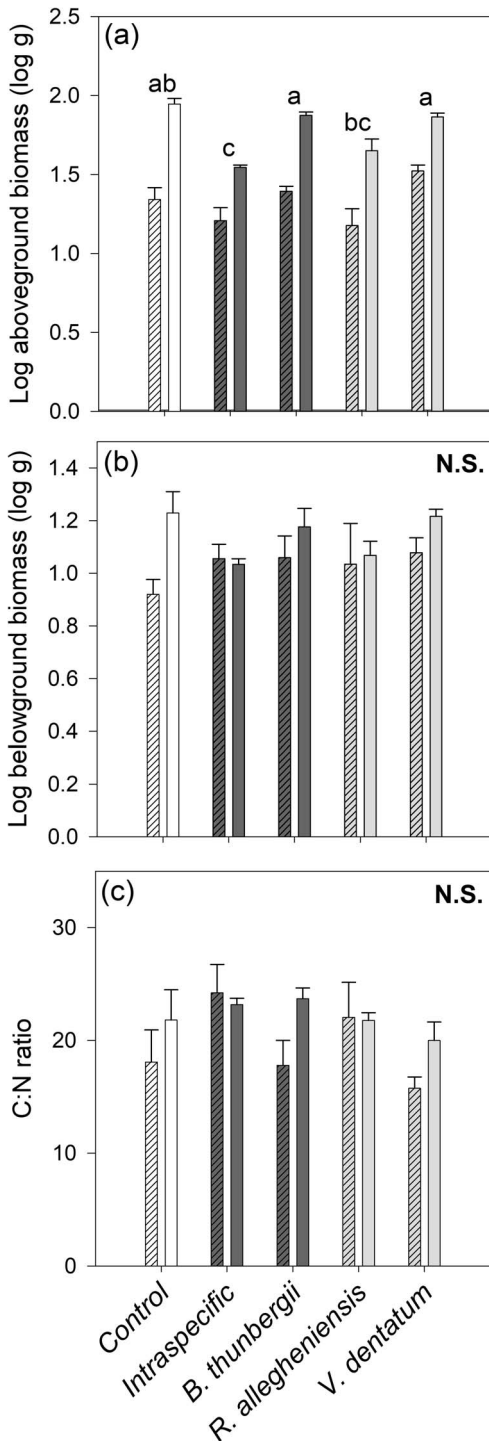
FIG. 2a–c. *Berberis thunbergii* responses to competitor treatments. Dark gray bars correspond to an exotic competitor, light gray bars to a native competitor, and white bars are plants grown without competitors. Hatched bars indicate the first block and unhatched bars indicate the second block. Data were

were more productive than in the first block (Table 1, significant Species × Block interaction). Both native and exotic *Rubus* species grew larger than either *B. thunbergii* or *V. dentatum*. While the total stem length measured for *V. dentatum* was significantly smaller than the other three species, there was no significant difference between the aboveground biomass measured for *B. thunbergii* and *V. dentatum*. *Berberis thunbergii* had the smallest belowground biomass. The maximal root lengths for both *B. thunbergii* and *V. dentatum* were significantly shorter than those measured for either *Rubus* species. Only two responses showed a trend in which both exotic species differed from both native species; exotics produced more leaves and greater total fine root length than natives on average.

Species also differed in leaf C:N ratio, leaf ^{15}N enrichment, and ^{13}C fractionation (Table 2; Fig. 1; Fig. S3). Differences among species were more pronounced in the second temporal block as a result of greater growth in all species. *Viburnum dentatum* displayed a significantly lower ^{15}N enrichment in leaf tissue than did the other three species. *Viburnum dentatum* had greater water use efficiency than *B. thunbergii* and *R. allegheniensis*, as indicated by ^{13}C fractionation in the leaves. *Berberis thunbergii* had a lower leaf C:N ratio than the other three species.

EFFECTS OF ROOT COMPETITION ON FOCAL PLANT GROWTH. Belowground competition reduced the growth of *B. thunbergii*, although the effect was dependent on temporal block (Table 3; Fig. 2; Fig. S4, S5). Competition with either *Rubus* species reduced the aboveground biomass and total stem length of *B. thunbergii* more than it did for the other species. *Viburnum dentatum* had an intermediate effect on *B. thunbergii* size, while there was no detectable effect of intraspecific competition. Competitors did not affect belowground biomass, maximal root length, or fine root production of *B. thunbergii*.

For *R. allegheniensis*, intraspecific competition and competition with *R. phoenicolasius* reduced aboveground growth measures similarly, while competition with *B. thunbergii* or *V. dentatum*

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not available for *B. thunbergii* C:N ratio in the second block. Different letters above bars indicate that treatment-level means differ significantly. Error bars indicate ± 1 standard error of the mean.
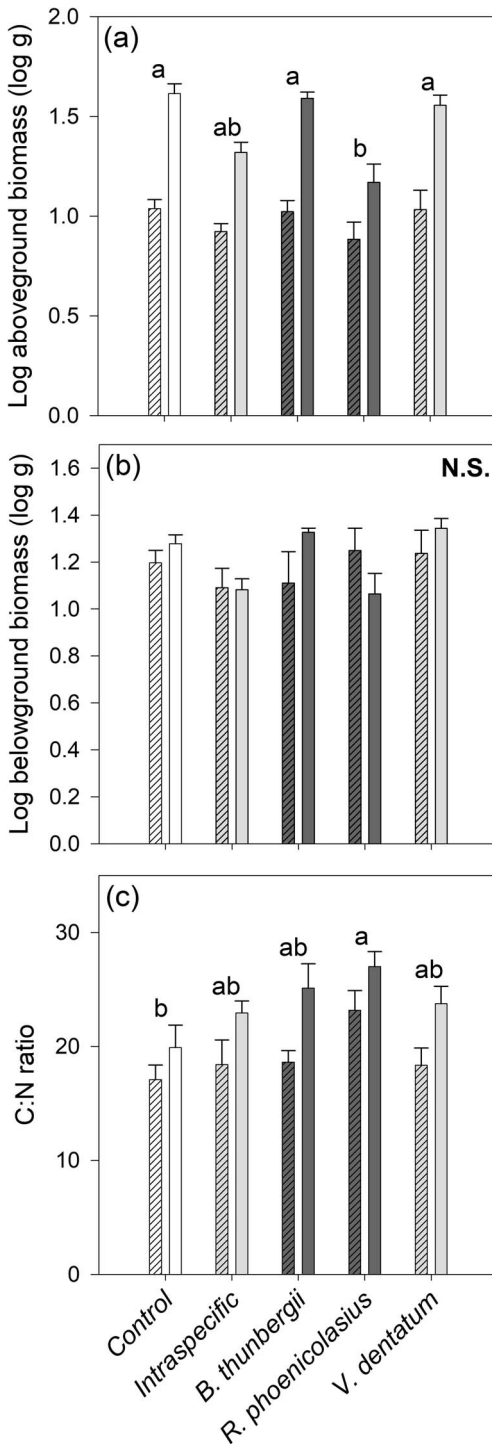
FIG. 3a–c. *Rubus allegheniensis* responses to competitor treatments. Dark gray bars correspond to an exotic competitor, light gray bars to a native competitor, and white bars are plants grown without competitors. Hatched bars indicate the first block and unhatched bars indicate the second block. Different

had no measurable effect on growth; there was also no block by competitor interaction (Table 3; Fig. 3; Fig. S6, S7). We found no differences among treatments on belowground growth metrics in this species.

Rubus phoenicolasius growth was also affected only by conspecifics or congeners, irrespective of the temporal block (Table 3; Fig. 4; Fig. S8, S9). Overall, intraspecific competition decreased *R. phoenicolasius* growth most strongly. *Rubus allegheniensis* had a moderately weaker competitive effect than conspecifics on aboveground biomass and total leaf area. *Berberis thunbergii* and *V. dentatum* had no detectable effects on *R. phoenicolasius*.

For *V. dentatum*, temporal block interacted significantly with competitor, but both *Rubus* species reduced *V. dentatum* total stem length and aboveground biomass, while neither *B. thunbergii* nor conspecifics affected its growth (Table 3; Fig. 5; Fig. S10, S11). Belowground growth was unaffected by competition in *V. dentatum*.

EFFECTS OF ROOT COMPETITION ON LEAF TISSUE CHEMISTRY. Competitors significantly reduced ^{15}N enrichment for *B. thunbergii* in all treatments except that of competition with *R. allegheniensis* (Table 4; Fig. S12). Competition did not affect ^{13}C fractionation. C:N ratios were greatest for plants competing with *R. phoenicolasius*, intermediate for plants competing with *R. allegheniensis*, and smallest for plants competing with *V. dentatum* (Fig. 2).

Rubus allegheniensis grown with *V. dentatum* showed significantly greater enrichment with ^{15}N compared to plants grown with conspecifics, but there were no differences among remaining treatments (Table 4; Fig. S13). Carbon-13 fractionation was unaffected by competition; however, competition with *R. phoenicolasius* did result in a significantly greater C:N ratio compared to controls (Fig. 3).

For *R. phoenicolasius*, competition had no effect on ^{15}N enrichment or C:N ratio (Table 4; Fig. 4; Fig. S12). Intraspecific competition significantly enriched *R. phoenicolasius* in ^{13}C relative to controls (Fig. S14).

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letters above bars indicate that treatment-level means differ significantly. Error bars indicate ± 1 standard error of the mean.

Leaf tissue chemistry in *V. dentatum* differed among blocks (Table 4). Leaf ^{15}N enrichment and ^{13}C fractionation were unaffected by root competition (Fig. S15), although root competition with both *Rubus* species significantly increased the leaf C:N ratio of *V. dentatum* plants (Fig. 5). Temporal block did not interact significantly with competitor for any of the four species.

Discussion. Observations of some exotic invasive species in their nonnative ranges suggest that they are superior competitors due to traits that influence nutrient uptake, allelopathy, and growth patterns (Gioria and Osborne 2014). However, we found no consistent difference between native and exotic species in nitrogen acquisition or in their ability to affect nitrogen acquisition in a competitor plant. While the exotic species (*B. thunbergii* and *R. phoenicolasius*) produced more leaves and fine root biomass, there were no origin-specific effects for this pair of species on competitor growth.

Instead, the two *Rubus* species exhibited similar and strong competitive effects, while the distantly related *B. thunbergii* and *V. dentatum* were distinctly different from one another in terms of the measured responses. Both *Rubus* species decreased competitor biomass by at least 50% relative to control plants, although *R. phoenicolasius* appeared to have a slight competitive advantage over the native *R. allegheniensis*. Since interactions with enemies can mediate competition among understory woody plants (Dietz, Wirth, and Buschmann 2004; Ashton and Lerdau 2008; Knapp, Fownes, and Harrington 2008), release from natural enemies may help to confer the greater success of *R. phoenicolasius* compared to *R. allegheniensis* not explained by competition.

The presence of plant-soil feedbacks that develop over multiple growing seasons (Elgersma *et al.* 2011; Elgersma *et al.* 2012) and selective herbivory in field environments (Eschtruth and Battles 2009a, b) may help to explain why *B. thunbergii* can achieve competitive dominance in natural communities but did not exhibit belowground competitive superiority in our greenhouse experiment. This experiment examined belowground competition among recently established
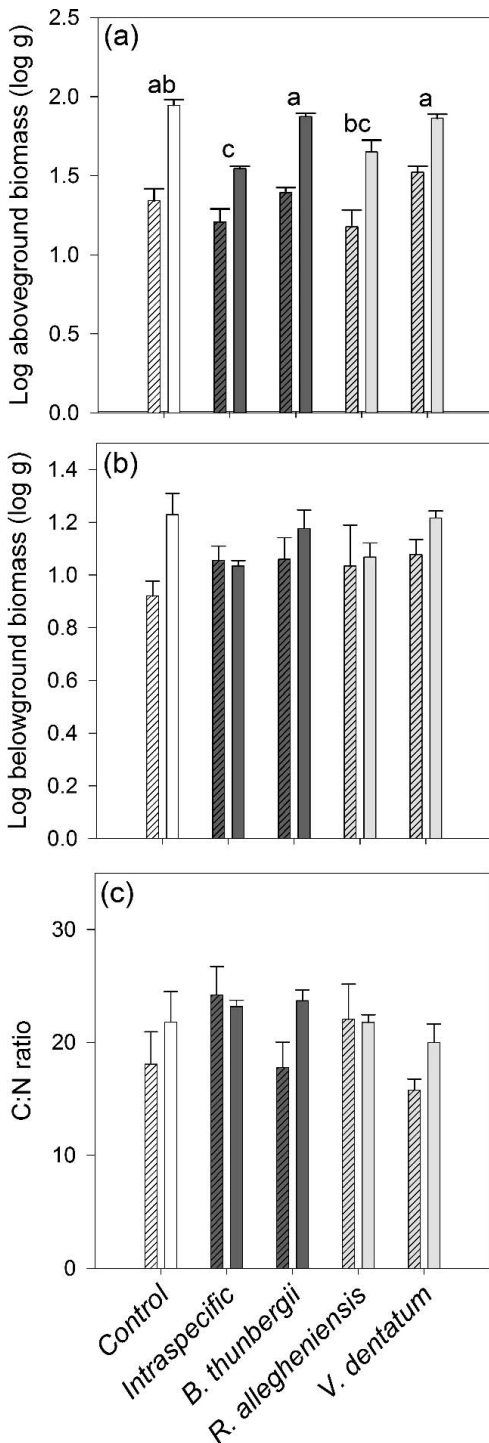
Fig. 4a–c. *Rubus phoenicolasius* responses to competitor treatments. Dark gray bars correspond to an exotic competitor, light gray bars to a native competitor, and white bars are plants grown without competitors. Hatched bars indicate the first block and unhatched bars indicate the second block. Different

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letters above bars indicate that treatment-level means differ significantly. Error bars indicate ± 1 standard error of the mean.

seedlings using field-collected soil that was not preconditioned by any of our species. Our experimental conditions were therefore most representative of the initial stages of invasion rather than of ongoing invasion by established shrubs.

The stronger competitive effects of the two *Rubus* species after reaching relatively large sizes is consistent with other empirical and theoretical work suggesting that larger plants are superior competitors (Goldberg 1987, Gaudet and Keddy 1988, Goldberg and Miller 1990). The roots of larger plants forage through a larger volume of soil, giving them access to a greater resource pool. Both *Rubus* species exerted measurable competitive effects but did not routinely decrease leaf ^{15}N enrichment or root biomass of competitor plants, indicating that they did not consistently prevent competitors from acquiring nitrogen from a nutrient patch. However, the increased leaf C:N ratio of all species except *R. phoenicolasius* when grown with a *Rubus* competitor suggests that the larger *Rubus* plants did decrease the total nitrogen available (but not ^{15}N) to smaller competitor plants. We did not find any consistent effects of competition on water use efficiency (as inferred from ^{13}C data); in fact, only *R. phoenicolasius* measurably increased water use efficiency when grown with an intraspecific competitor relative to controls. This may indicate that there are ecophysiological differences between the two *Rubus* species.

Some *Rubus* species are strong competitors in disturbed areas and under resource limitation (Fotelli, Rennenberg, and Geßler 2002; Caplan and Yeakley 2013), while others are capable of becoming nuisance exotics (Ostertag and Verville 2002; Kosiński, Czarna, and Maliński 2014). Our results demonstrate that both *Rubus* species can have measureable effects on plant performance through belowground competition; however, the mechanism by which they compete remains uncertain. A strong allocation to roots and construction of root tissue with a high energetic return on the investment (Caplan *et al.* 2017) may contribute to their success by enabling more rapid foraging for nutrients in the soil. Allelopathy could be another potential mechanism underlying the
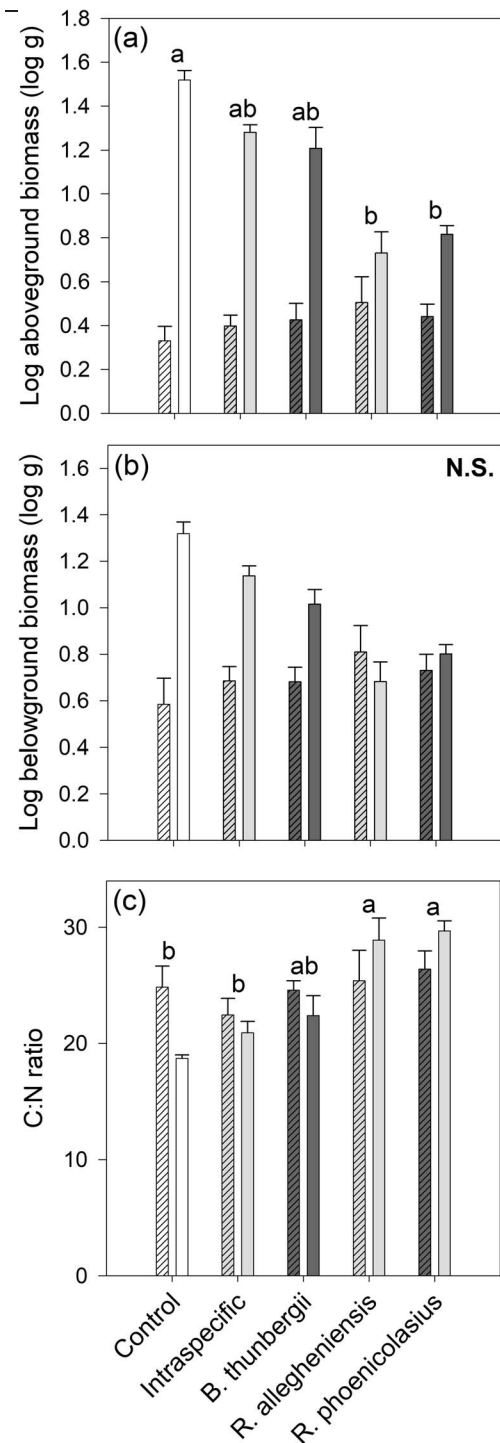
FIG. 5a–c. *Viburnum dentatum* responses to competitor treatments. Dark gray bars correspond to an exotic competitor, light gray bars to a native competitor, and white bars are plants grown without competitors. Hatched bars indicate the first block and unhatched bars indicate the second block. Different

letters above bars indicate that treatment-level means differ significantly. Error bars indicate ± 1 standard error of the mean.

Table 4. MANOVA table for effects of competitors on leaf ^{15}N, ^{13}C, and C:N ratio for *Berberis thunbergii* ($N = 34$), *Rubus allegheniensis* ($N = 43$), *Rubus phoenicolasius* ($N = 40$), and *Viburnum dentatum* ($N = 43$).

Species	Factor	Wilks' lambda	F value	Num DF	Den DF	$Pr > F$
B. thunbergii	Competitor	0.2235	2.02	20	70.599	0.0166
	Block	0.1598	22.08	5	21	< 0.0001
	Competitor × Block	0.5326	1	15	58.373	0.4701
R. allegheniensis	Competitor	0.3532	1.79	20	97.132	0.0323
	Block	0.0877	60.34	5	29	< 0.0001
	Competitor × Block	0.6225	0.75	20	97.132	0.7688
R. phoenicolasius	Competitor	0.3848	1.45	20	87.182	0.1196
	Block	0.0507	97.37	5	26	< 0.0001
	Competitor × Block	0.5693	0.81	20	87.182	0.6989
V. dentatum	Competitor	0.3094	2.06	20	97.132	0.0105
	Block	0.2677	15.87	5	29	< 0.0001
	Competitor × Block	0.3785	1.65	20	97.132	0.0555

competitive ability of these *Rubus* species, as allelopathic potential has been documented in several other species in the genus (Del Moral and Cates 1971, Coté and Thibault 1988, Baležentienė and Šėžienė 2010). Multiple root competition mechanisms may be important in diverse biological communities and may simultaneously interact in complex or species-specific ways to determine competitive outcomes.

The interaction between the temporal block and competition treatment suggests that competition between plants was more intense in the second temporal block, when soil nutrient availability was greater and plants were actively growing (Grime 1977; Li *et al*. 2010; Li *et al*. 2015). Our results indicate that woody shrubs can exert measurable competitive effects belowground even when nutrients are not scarce. Studies examining interspecific interactions among shrubs should therefore consider the possible implications of belowground competition regardless of soil nutrient status.

The interaction between temporal block and competition may also result from the seasonality of the species' growth patterns. Both *Rubus* species continued to grow actively throughout the autumn and winter, suggesting that they are capable of extended autumn leaf phenology. On the other hand, *B. thunbergii* and *V. dentatum* remained dormant for several months despite our summer-like greenhouse temperature and light settings. Also, responses to belowground competition by both *Rubus* species were unaffected by block (no interaction effect), while *B. thunbergii* and *V. dentatum* responded to belowground competition more strongly in the second temporal block. Thus, it is possible that seasonal growth patterns may drive competitive outcomes, having important

implications for communities in which some shrub species exhibit plastic phenology. In warm autumns, such plants could gain a competitive advantage through an extended growing season compared to competitors (Fridley 2012), a situation possibly exacerbated by global climate change in plant communities in temperate climates (Willis *et al*. 2010; Wolkovich *et al*. 2013; Caplan *et al*. 2015).

Conclusions. Belowground competitive abilities contribute to plants' total competitive effects and may influence competitive outcomes in systems in which light is limited. Root competition occurred in our study system, but our results indicated that competitive outcomes were determined by plant size rather than origin. Specifically, both *Rubus* species grew to larger sizes and were superior competitors than *B. thunbergii* and *V. dentatum*. The strong competitive ability of *Rubus* species demonstrated here, coupled with their ability to grow and spread rapidly via multiple reproductive mechanisms (Lambrecht-McDowell and Radosevich 2005; Caplan and Yeakley 2006; Bennett *et al*. 2011; Caplan *et al*. 2017), likely contributes to their weedy and invasive tendencies in many habitats. Plant species that exhibit plastic growth phenology, such as those in the genus *Rubus*, may gain a competitive advantage during years with warmer autumn months by extending their growing seasons.

Literature Cited

ASHTON, I. W. AND M. T. LERDAU. 2008. Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. Divers. Distrib. 14: 169–178.

BALEŽENTIENĖ, L. AND V. ŠĖŽIENĖ. 2010. Biochemical impact of dominant extracts of Scots pine cuttings on germination. Pol. J. Environ. Stud. 19: 35–42.

BELCHER, J. W., P. A. KEDDY, AND L. TWOLAN-STRUTT. 1995. Root and shoot competition intensity along a soil depth gradient. J. Ecol. 83: 673–682.

BENNETT, J. R., E. J. YOUNG, D. E. GIBLIN, P. W. DUNWIDDIE, AND P. ARCESE. 2011. Avian dispersal of exotic shrubs in an archipelago. Écoscience 18: 369–374.

CAPLAN, J. S. AND J. A. YEAKLEY. 2006. *Rubus armeniacus* (Himalayan blackberry) occurrence and growth in relation to soil and light conditions in western Oregon. Northwest. Sci. 80: 9–17.

CAPLAN, J. S. AND J. A. YEAKLEY. 2013. Functional morphology underlies performance differences among invasive and non-invasive ruderal *Rubus* species. Oecologia 173: 363–374.

CAPLAN, J. S., R. N. HAGER, J. P. MEGONIGAL, AND T. J. MOZDZER. 2015. Global change accelerates carbon assimilation by a wetland ecosystem engineer. Environ. Res. Letters 10:115006.

CAPLAN, J. S., B. W. STONE, C. A. FAILLACE, J. J. LAFOND, J. M. BAUMGARTEN, T. J. MOZDZER, J. DIGHTON, S. J. MEINERS, J. C. GRABOSKY, AND J. G. EHRENFELD. 2017. Nutrient foraging strategies are associated with productivity and population growth in forest shrubs. Ann. Bot. 119: 977–988.

COOMES, D. A. AND P. J. GRUBB. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecol. Monogr. 70: 171–207.

COTÉ, J.-F. AND J.-R. THIBAULT. 1988. Allelopathic potential of raspberry foliar leachates on growth of ectomycorrhizal fungi associated with black spruce. Am. J. Bot. 75: 966–970.

DEHLIN, H., D. A. PELTZER, V. J. ALLISON, G. W. YEATES, M. C. NILSSON, AND D. A. WARDLE. 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. N. Z. J. Ecol. 32: 67–79.

DEL MORAL, R. AND R. G. CATES. 1971. Allelopathic potential of the dominant vegetation of western Washington. Ecology 52: 1030–1037.

DIETZ, H. R., L. WIRTH, AND H. BUSCHMANN. 2004. Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. Biol. Invasions 6: 511–521.

DORNING, M. AND D. CIPOLLINI. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. Plant Ecol. 184: 287–296.

EHRENFELD, J. G. 1999. Structure and dynamics of populations of Japanese barberry (*Berberis thunbergii* DC.) in deciduous forests of New Jersey. Biol. Invasions 1: 203–213.

ELGERSMA, K. J., J. G. EHRENFELD, S. YU, AND T. VOR. 2011. Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. Oecologia 167: 733–745.

ELGERSMA, K. J., S. YU, T. VOR, AND J. G. EHRENFELD. 2012. Microbial-mediated feedbacks of leaf litter on invasive plant growth and interspecific competition. Plant Soil 356: 341–355.

ESCHTRUTH, A. K. AND J. J. BATTLES. 2009a. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol. Monogr. 79: 265–280.

ESCHTRUTH, A. K. AND J. J. BATTLES. 2009b. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv. Biol. 23: 388–399.

FARGIONE, J. AND D. TILMAN. 2006. Plant species traits and capacity for resource reduction predict yield and abundance under competition in nitrogen-limited grassland. Funct. Ecol. 20: 533–540.

FARQUHAR, G., K. HUBICK, A. CONDON, AND R. RICHARDS. 1989. Carbon isotope fractionation and plant water-use efficiency, pp. 21–40. *In* P. W. Rundel, K. T. Hubick, A. G. Condon, and K. A. Nagy [eds.], Stable Isotopes in Ecological Research. Springer, New York, NY.

FOTELLI, M., H. RENNENBERG, AND A. GEßLER. 2002. Effects of drought on the competitive interference of an early successional species (*Rubus fruticosus*) on *Fagus sylvatica* L. seedlings: 15N uptake and partitioning, responses of amino acids and other N compounds. Plant Biol. 4: 311–320.

FRIDLEY, J. D. 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions. Nature 485: 359–362.

GAIRE, R., C. ASTLEY, M. UPADHYAYA, D. CLEMENTS, AND M. BARGEN. 2015. The biology of Canadian weeds. 154. Himalayan blackberry. Can. J. Plant Sci. 95: 557–570.

GAUDET, C. L. AND P. A. KEDDY. 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334: 242–243.

GILLIAM, F. S. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. J. Ecol. 94: 1176–1191.

GIORIA, M. AND B. A. OSBORNE. 2014. Resource competition in plant invasions: Emerging patterns and research needs. Front. Plant Sci. 5: 501–XXX.

GOLDBERG, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68: 1211–1223.

GOLDBERG, D. E. AND T. E. MILLER. 1990. Effects of different resource additions of species diversity in an annual plant community. Ecology 71: 213–225.

GORCHOV, D. L., E. THOMPSON, J. O'NEILL, D. WHIGHAM, AND D. A. NOE. 2011. Treefall gaps required for establishment, but not survival, of invasive *Rubus phoenicolasius* in deciduous forest, Maryland, USA. Plant Species Biol. 26: 221–234.

GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169–1194.

JO I., FRIDLEY J.D., FRANK D.A. 2015. Linking above- and belowground resource use strategies for native and invasive species of temperate deciduous forests. Biol. Invasions 17: 1545–1554.

KIAER, L. P., A. N. WEISBACH, AND J. WEINER. 2013. Root and shoot competition: A meta-analysis. J. Ecol. 101: 1298–1312.

KNAPP, L. B., J. H. FOWNES, AND R. A. HARRINGTON. 2008. Variable effects of large mammal herbivory on three

non-native versus three native woody plants. For. Ecol. Manag. 255: 92–98.

Kosiński, P., A. Czarna, and T. Maliński. 2014. *Rubus occidentalis* (Rosaceae)—A new naturalized raspberry species in the Polish flora. Dendrobiology 71: 159–165.

Lamb, E. G., A. C. Stewart, and J. F. Cahill. 2012. Root system size determines plant performance following short-term soil nutrient pulses. Plant Ecol. 213: 1803–1812.

Lambrecht-McDowell, S. and S. Radosevich. 2005. Population demographics and trade-offs to reproduction of an invasive and noninvasive species of *Rubus*. Biol. Invasions 7: 281–295.

Li, W., S. Wen, W. Hu, and G. Du. 2010. Root-shoot competition interactions cause diversity loss after fertilization: A field experiment in an alpine meadow on the Tibetan Plateau. J. Plant Ecol. 4: 138–146.

Li, W., J. Cheng, K. Yu, H. E. Epstein, and G. Du. 2015. Short-term responses of an alpine meadow community to removal of a dominant species along a fertilization gradient. J. Plant Ecol. 8: 513–522.

Ostertag, R. and J. H. Verville. 2002. Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. Plant Ecol. 162: 77–90.

Perry, L., D. Blumenthal, T. Monaco, M. Paschke, and E. Redente. 2010. Immobilizing nitrogen to control plant invasion. Oecologia 163: 13–24.

Ricard, J. P., C. Messier, S. Delagrange, and M. Beaudet. 2003. Do understory sapling respond to both light and below-ground competition? A field experiment in a north-eastern American hardwood forest and a literature review. Ann. For. Sci. 60: 749–756.

Roumet, C., C. Urcelay, and S. Diaz. 2006. Suites of root traits differ between annual and perennial species growing in the field. New Phytol. 170: 357–368.

SAS Institute. 2011. The SAS system for Windows. SAS Institute, Cary, NC.

Schenk, H. J. 2006. Root competition: Beyond resource depletion. J. Ecol. 94: 725–739.

Silander, J. A. and D. M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biol. Invasions 1: 189–201.

von Wettberg, E. J. and J. Weiner. 2003. Larger *Triticum aestivum* plants do not preempt nutrient-rich patches in a glasshouse experiment. Plant Ecol. 169: 85–92.

Warren, C. R., J. F. McGrath, and M. A. Adams. 2001. Water availability and carbon isotope discrimination in conifers. Oecologia 127: 476–486.

Webster, C. R., M. A. Jenkins, and S. Jose. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J. For. 104: 366–374.

Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species' success in Thoreau's Woods. PLoS ONE 5: e8878.

Wilson, J. B. 1988. Shoot competition and root competition. J. Appl. Ecol. 25: 279–296.

Wolkovich, E. M., T. J. Davies, H. Schaefer, E. E. Cleland, B. I. Cook, S. E. Travers, C. G. Willis, and C. C. Davis. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. Am. J. Bot. 100: 1407–1421.

Xu, C.-Y., K. L. Griffin, and W. Schuster. 2007. Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. Oecologia 154: 11–21.