

Why does land-use history facilitate non-native plant invasion? A field experiment with *Celastrus orbiculatus* in the southern Appalachians

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Received: 7 January 2012 / Accepted: 21 August 2012 / Published online: 2 September 2012
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Abstract Although historic land use is often implicated in non-native plant invasion of forests, little is known about how land-use legacies might actually facilitate invasion. We conducted a 2-year field seeding experiment in western North Carolina, USA, to compare germination and first-year seedling survival of *Celastrus orbiculatus* Thunb. in stands that had been cultivated and abandoned a century earlier and were dominated by tulip poplar (*Liriodendron tulipifera* L.), and in paired stands that had never been cultivated and were dominated by oaks (*Quercus* spp.). Experiments were conducted at five sites with paired tulip poplar and oak stands by varying litter mass (none, low, or high) and litter type (tulip poplar or oak). We also performed reciprocal soil translocations using pots seeded with *C. orbiculatus*. Soil moisture and temperature were measured throughout the growing season. Germination and survival were highest in the tulip poplar stands. Germination was also higher in plots

with low litter mass. Seedling survival was highest in plots with low litter mass or no litter. Soil moisture was higher in tulip poplar stands and under low-mass litter. Differences in germination and survival among the potted plants were minimal, suggesting that soil type and ambient site conditions were less important than litter conditions for *C. orbiculatus* establishment. Our results suggest that the low litter mass and mesic soil conditions that are characteristic of tulip poplar stands may confer higher invasibility and explain the higher abundance of *C. orbiculatus* in areas with successional overstory communities associated with historically cultivated forests.

Keywords Oriental bittersweet ·
Liriodendron tulipifera · Exotic species · Invasibility ·
Leaf litter · Soil moisture

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Introduction

Invasion of intact forests by non-native plants has generally received less attention than invasion of more open or disturbed habitats, perhaps owing to the comparatively slow rates of invasion and smaller pool of potential forest invaders (Martin et al. 2009). Nonetheless, such species pose a considerable threat to forest ecosystems. They may alter forest structure and composition (Richardson 1998), reduce biodiversity

(Lugo 2004; Stinson et al. 2007), and affect nutrient cycling (Kourtev et al. 1998; Ehrenfeld et al. 2001; Ashton et al. 2005). Invasive plants tend not to spread uniformly in forest landscapes but seem to respond to heterogeneity that makes certain areas more susceptible to invasion than others (Meekins and McCarthy 2000; Chabrierie et al. 2007). By understanding the factors that influence invasibility of forests, we can improve our understanding of the mechanisms underlying the invasion process and increase our ability to predict future spread of non-native plants.

Historic land use can increase invasive plant abundance in forested landscapes (Lundgren et al. 2004; Von Holle and Motzkin 2007; DeGasperis and Motzkin 2007). However, the actual mechanisms related to land-use history that may facilitate plant invasion are poorly understood. Based on previous work at the Bent Creek Experimental Forest (BCEF) in western North Carolina, USA, we found that forested areas that had previously been cultivated and were abandoned roughly a century ago had a considerably higher abundance of non-native invasive plants in their understories than comparable reference sites that had not been cultivated (Kuhman et al. 2011). The overstories of these historic agricultural areas were frequently dominated by tulip poplar (*Liriodendron tulipifera* L.), whereas areas that lacked an agricultural land-use history were typically dominated by oak (*Quercus*) species. There was a strong positive correlation between tulip poplar basal area and the abundance of non-native invasive plants. Tulip poplar dominated stands also had higher cation concentrations, pH, and total nitrogen in their soils, and the leaf litter layer tended to be thinner than in the oak dominated stands.

In this study we investigated the factors influencing invasibility at BCEF using a field seeding experiment with Oriental bittersweet (*Celastrus orbiculatus* Thunb.), a common invader of forests in eastern North America, and the most frequently encountered invasive plant species at the BCEF. *Celastrus orbiculatus* is a woody twining vine that was introduced in the northeastern U.S. from eastern Asia in 1860 and spread rapidly throughout eastern North America (Patterson 1973; Dreyer et al. 1987). Seedlings exhibit a wide tolerance for light conditions and are able to persist for long periods in lowlight conditions (Ellsworth et al. 2004b; Leicht-Young et al. 2007; Leicht and Silander 2006), making it an effective understory invader and a considerable threat

to forests in the eastern U.S. (Patterson 1973; McNab and Loftis 2002).

We set out to address the following overarching question: Why do areas with greater overstory dominance by tulip poplar (historically cultivated areas) have higher abundances of non-native plants (particularly *C. orbiculatus*) than adjacent stands with high oak dominance (areas without an agricultural land-use history)? First, we wished to determine whether the tulip poplar stands actually exhibited greater invasibility. The higher abundance of invasive plants in these historically cultivated areas could instead be related to the time since establishment; for example, higher *C. orbiculatus* abundance could be attributed to greater propagule pressure exerted by localized populations of reproductive individuals (often abundant along roads adjacent to historically cultivated areas) that may have become established around the time of agricultural abandonment. Propagule pressure often plays a major role in determining the success of invasion by non-native plants (Lockwood et al. 2005; Lonsdale 1999). Secondly, if tulip poplar stands were indeed more invulnerable than oak stands, we wished to identify which factors differed between stand types that might explain their disparate invasion success. Specifically, we considered the respective roles of soil (chemistry, texture, and moisture), leaf litter quantity, leaf litter quality (type of litter), and ambient site conditions (e.g., those related to overstory density and leafing phenology) in determining differential germination and survival of *C. orbiculatus* in the tulip poplar and oak dominated stands. We expected to see higher germination and seedling survival in the richer soils from the *Liriodendron* stands. Several studies have noted the positive correlation between abundance of non-native invasive plants and forest soil nutrient concentrations and pH (Cole and Weltzin 2004; Howard et al. 2004; Silveri et al. 2001; Pande et al. 2007). We also expected germination and survival to decrease with increasing litter mass because litter can act as a physical barrier for emergent seedlings (Facelli and Pickett 1991; Ellsworth et al. 2004a). Similarly, we expected germination and survival to be lower in litter from oak stands due to the toughness and more curled structure of oak leaves compared to those of tulip poplar (Abrams 1990; Van Lear 2004), perhaps making the oak litter a more formidable barrier for the germinating seedlings. We did not expect

ambient site conditions unrelated to the forest floor to affect germination and survival.

Materials and Methods

Study area

The study was conducted at BCEF, a research station managed by the U.S. Forest Service. BCEF is located 15 km southwest of Asheville, NC, USA, and largely covers the 2,500-ha Bent Creek watershed. Typical of areas in the Blue Ridge physiographic province, BCEF has steep topography and extensive forest cover. The elevation range is 700 to 1100 meters and is predominantly covered by mixed oak and mixed mesophytic forest. Common overstory species include *Quercus coccinea*, *Q. velutina*, *Q. prinus*, *Q. alba*, *Q. rubra*, *Carya* spp., *L. tulipifera*, *Acer rubrum*, *Oxydendrum arboreum*, *Pinus rigida*, *P. echinata*, *P. strobus*, and *Tsuga canadensis* (McNab 1996). The bedrock geology primarily consists of Precambrian gneisses and schists. Soils are ultisols (associated with intermontane basins) and inceptisols on steeper slopes and are relatively deep, with solums commonly >80 cm (Greenberg and McNab 1998).

Settlement of the Bent Creek basin by European immigrants began in the 1790s. By 1900 over 100 homes were constructed and 23 % of the basin (ca. 600 ha) had been cleared for agriculture (Nesbitt and Netboy 1946). Some of the cleared land was used only for pasture, but most was cultivated at some time. Residents practiced low-input subsistence agriculture, primarily growing corn, wheat, and rye in rotation (Nesbitt and Netboy 1946). Much of the basin was purchased between 1900 and 1910 to expand the holdings of the nearby Biltmore Estate, at which time most of the cleared areas were abandoned and have since regrown to forest. The US Forest Service has managed the basin since 1925.

Experimental design

The field experiment was initiated in five sites at BCEF (Fig. 1) in March 2008 and repeated at the same sites beginning in March 2009. Within each site, two forest stands were selected: one stand with oaks (*Quercus* spp.) as the dominant overstory species (hereafter *Q*-stands) and another with tulip poplar

(*L. tulipifera*) as the dominant overstory species (hereafter *L*-stands). All *L*-stands were located in areas that were previously cultivated and abandoned around 1905. The *Q*-stands were located in areas that were not previously cultivated. The paired stands within each site were selected to control for differences in topography to the extent possible (see Table 1). The *Q*-stands were on slightly steeper slopes than the paired *L*-stands (average slope difference = 2.6°, *SE* = 0.36). This small difference in slope probably reflects the selection of gentler slopes by early settlers for agriculture, but does not likely represent an ecologically significant difference given the steep topography of the study region. Paired stands were in close proximity (100–400 m apart) to limit differences in bedrock geology and soil type.

In each stand, a 20 × 20-m experimental area was established. Slope and aspect were recorded in each stand. A terrain shape index (TSI) was calculated by averaging slopes from the center of the experimental area in eight sub-cardinal directions to describe the concavity (a positive TSI) or convexity (a negative TSI) of the local landform (McNab 1989). We identified all trees with stems >5-cm DBH and measured their diameter to compute basal area for each species. Canopy cover was determined using a spherical densiometer by averaging measurements from the center and four corners of the 20 × 20-m area. Soil samples were collected using a 5-cm diameter soil corer. The upper 15 cm of mineral soil were sampled after removal of coarse organic material. Soil cores were taken at the four corners and the center of the 20 × 20-m area and combined as a composite sample. They were dried, sieved, and analyzed at the University of Wisconsin-Madison Soil and Plant Analysis Lab for pH, total nitrogen (organic N, NH₄⁺, NO₃⁻, and NO₂), organic matter content, exchangeable cations (Ca⁺⁺, Mg⁺⁺, and K⁺), and plant-available P. We performed soil particle-size analysis using the hydrometer method (Gee and Bauder 1986). In March 2009, soils were re-sampled as described above, but only to a depth of 5 cm, and were analyzed for organic matter content.

Plots

Twenty-five 1-m² experimental plots were established in each stand within the 20 × 20-m experimental area, arranged in a five-by-five grid with 5-m spacing

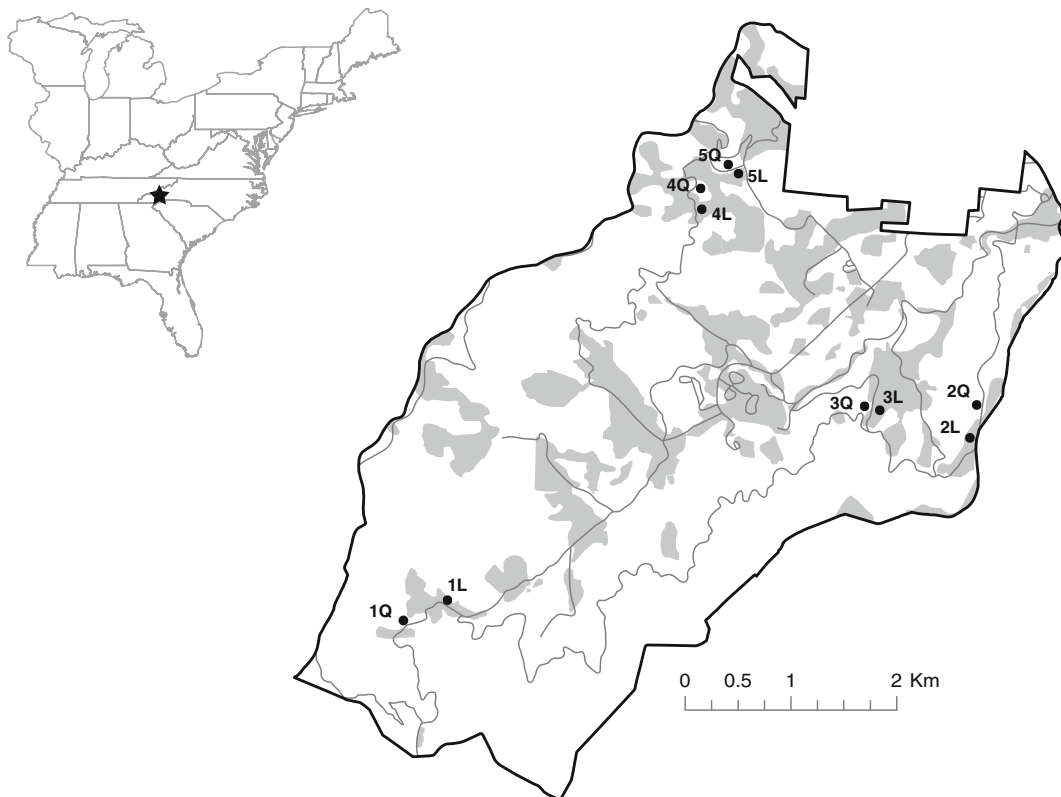


Fig. 1 Map of the study area. The *inset* map on the *left* shows the location of Bent Creek Experimental Forest (BCEF) in western North Carolina, USA. The larger map shows the BCEF boundary and roads. The *gray polygons* represent areas that

were previously cultivated and abandoned around 1910. The five pairs of experimental stands are represented by *black circles* (*L* *Liriodendron tulipifera* stands, *Q* *Quercus* spp. stands)

between plots. All coarse leaf litter was removed and a 15-cm high fence was erected around each plot to minimize movement of leaf litter into or out of the plots. Litter treatments were then randomly assigned to each of the plots. In each stand, five plots had no litter returned following the litter removal. Ten plots were designated as low-litter plots in which 1 kg of leaf litter was added to each plot. The remaining ten plots were designated as high-litter plots in which 3 kg of leaf litter were added. Litter mass was measured in the field (without drying first), and was done during a dry period when moisture in the litter was minimal. The two litter masses approximated the low and high ends of the range of litter quantities encountered throughout BCEF, based on preliminary measurements. The low litter mass was more representative of conditions in *Liriodendron* stands whereas the high litter mass was more similar to those in oak-dominated stands. In half of the low litter plots and half of the high litter plots, leaf litter from the *L*-stand within that site

was used. In the other half of the litter plots, leaf litter from the *Q*-stand within the site was used. This design resulted in five litter treatments: “no litter,” “low *L*-litter,” “low *Q*-litter,” “high *L*-litter,” and “high *Q*-litter.”

For each treatment within a stand, three of the five plots were sown with 100 Oriental bittersweet (*Celastrus orbiculatus*) seeds each ($N = 1,500$ seeds per stand; $N = 15,000$ seeds total). The other two plots in each treatment were left unseeded to determine the frequency of establishment by bittersweet seedlings due to seed inputs from parent plants in the vicinity and to offer a means of correcting germination rates of seeded plots to account for such inputs if necessary. The bittersweet seeds sown in experimental plots were collected from several locations at BCEF in November 2007. The fruits were dried at 20 °C for several weeks before removing the seeds. Seeds were then placed in plastic bags with moist sand and cold stratified for 3 months at 5 °C before sowing in March

Table 1 Experimental site/stand characteristics

Site	Stand type	<i>L. tul.</i> BA (m ² ha ⁻¹)	<i>Q.</i> spp. BA (m ² ha ⁻¹)	Total BA (m ² ha ⁻¹)	Canopy cover (%)	Elev. (m)	Slope (°)	Aspect (°)	TSI
1	L	26.7	0.0	33.6	87.2	782	17	160	0.00
	Q	0.0	35.7	48.3	88.4	842	19	160	-0.38
2	L	20.2	0.9	34.8	90.4	759	16	290	0.13
	Q	0.2	30.2	43.1	89.8	751	20	295	1.38
3	L	39.8	0.8	44.3	89.6	713	19	110	1.13
	Q	0.0	23.1	36.8	88.8	720	20	110	-0.75
4	L	31.7	1.1	38.5	90.6	744	17	80	1.00
	Q	11.7	30.9	51.9	91.6	747	20	60	-0.63
5	L	20.1	0.8	34.9	91.8	720	13	160	0.63
	Q	0.3	22.6	32.0	90.8	720	16	150	1.63
Paired-t		6.55***	10.66***	1.18	0.09	1.02	5.10**	1.12	0.51

Site	Stand type	Clay (%)	Sand (%)	pH	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Total N (mg/L)	O.M. 15 cm (%)	O.M. 5 cm (%)
1	L	23.6	52.8	4.9	7	50	220	33	0.17	7.2	11.4
	Q	23.4	55.3	4.6	4	34	63	18	0.11	6.6	8.6
2	L	14.1	62.6	5.0	2	38	185	46	0.09	4.8	7.8
	Q	15.1	59.8	4.6	3	24	88	19	0.09	4.2	5.3
3	L	18.0	55.0	5.4	5	74	419	78	0.15	5.7	10.0
	Q	20.3	48.1	4.4	6	29	58	15	0.10	6.5	10.0
4	L	17.2	54.4	5.6	3	54	569	72	0.15	5.4	8.5
	Q	19.1	53.6	4.5	3	34	42	17	0.10	5.2	6.3
5	L	17.3	60.3	4.7	3	38	165	56	0.09	4.3	7.5
	Q	17.2	59.4	4.4	3	34	29	14	0.05	4.5	5.5
Paired-t		1.89	1.15	3.5*	0.27	2.90*	3.12*	4.59*	3.81*	0.30	3.85*

Stand type refers to stands dominated by *L. tulipifera* (L-stands) or *Quercus* spp. (Q-stands), respectively. L-stands were all in areas that were previously cultivated, and Q-stands were in areas with no agricultural disturbance history. Total basal area (BA) includes all trees with stems >5-cm DBH. The terrain shape index (TSI) measures the concavity (positive values) or convexity (negative values) of the local landform. Soil texture and chemistry were measured in soil cores sampled to a depth of 15 cm. Organic matter (O.M.) was measured in both the top 15 and 5 cm of soil. Results of the paired t tests are based on differences between paired stands within the five sites

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

2008. The seeds were sown by scattering them evenly across the surface of the plot (on top of the leaf litter where it was present). Seed germination was measured in late June 2008. Bittersweet seedlings were identified by their cotyledons, and a small wire was inserted beside each seedling to mark its location. First-year survival of the seedlings was determined in June 2009.

Soil moisture and temperature were measured for all plots in March, May, June, July, and October 2008. Soil temperature was measured at 5 cm depth in the center of each plot with a digital thermometer. Four soil measurements were recorded, as volumetric water content of the top 12 cm of soil (Hydrosense Portable Soil Moisture System, Campbell Scientific, Australia), and averaged for each 1-m² plot.

Due to low germination rates in 2008 (a drought year), the field experiment was reinitiated in March 2009 using the same set of experimental plots. Leaf litter that had fallen on plots since the previous year was removed from all plots without disturbing any established bittersweet seedlings. Although some decomposition of the original litter undoubtedly occurred, relative differences between low and high litter mass treatments were maintained; all litter was again removed from the no-litter plots. We added a soil scarification treatment in 2009 by establishing five additional plots (three of which were seeded) within each existing experimental grid. As in the no-litter plots, all coarse leaf litter was removed, but in this “scarification” treatment, the surface was then scraped using a hand cultivator to remove any partially decomposed organic layer (common in oak-dominated stands) and to scarify the surface of the mineral soil. Seeds for the 2009 planting were collected in November 2008 and processed just as they had been the previous year. The seeds were treated with a fungicide (Captan 50) prior to cold stratification in response to small amounts of mold observed in bags the previous year. Again, 100 seeds were sown in each of the seeded treatment plots (N = 1,800 seeds per stand; N = 18,000 seed total). Surviving seedlings from the 2008 planting were small enough and in low enough density as to not warrant concern regarding competition with new seedlings. Seed germination rates were assessed in June 2009.

Pots

To test for independent effects of soils and site conditions, we performed a reciprocal soil translocation.

At each of five locations in the 20 × 20-m grid described above (the four corners and the center), we filled two one-gallon plastic pots with soil. After removing the organic layer, soil was extracted as a single core and placed in a pot to maintain stratigraphy and structure. For each pair of pots, one was left in that location and the other was moved to the paired stand within the site so that at each of the five locations in a stand, there was one *L*-soil pot and one *Q*-soil pot. All pots were placed in holes so that the soil surface in the pots was even with the ground surface to maintain ambient soil temperature and avoid excessive drying. All pots were sown with 20 *C. orbiculatus* seeds in March 2008, and germination rates were assessed in late June. Soil moisture and temperature measurements were taken in pots prior to sowing seeds in March and again in October 2008 after seedlings were established to avoid disturbance by the instrument probes.

Beginning in March 2009 we repeated the reciprocal soil experiment. A 5-cm wide strip of mesh window screen was affixed to the rim of each pot in 2009 to avoid possible flushing of seeds due to overflow in heavy rain events (a suspected problem in 2008). We also doubled the number of seeds sown in 2009 to 40 seeds per pot in response to low germination rates in 2008. Seed germination rates in the pots were assessed in June 2009.

Data analysis

Differences in stand characteristics (topography, overstory composition, canopy cover, soil texture, and soil chemistry) between *L*-stands and *Q*-stands were analyzed using paired *t* tests. *C. orbiculatus* germination rates and first-year seedling survival were analyzed using ANOVA with PROC GLM (SAS Institute 2002). For the 2008 seed germination in plots, we first considered the effects of site, stand type, and litter versus no-litter treatments. Stand type was nested within sites to account for differences among the sites. We then analyzed those plots with litter added to determine effects of litter mass and litter type, with stand type again nested within sites. Germination rates (% of seeds that germinated) were arcsine square root transformed prior to analyses. For the 2009 seed germination, analyses were repeated as for the 2008 data, but the plots without litter were subsequently analyzed for an effect of the scarification treatment. Survival rates (% of seedlings present in June 2008

that were still alive in June 2009) were arcsine square root transformed and analyzed using ANOVA with PROC GLM. Soil moisture and temperature data were analyzed using repeated measures ANOVA with PROC GLM. For the plots, March data were excluded since they were collected at the time of experimental setup and therefore were not expected to reflect treatment effects due to litter manipulation. For all analyses involving only those plots with litter or without litter, respectively, we used a Bonferroni procedure to correct significance levels. Germination, and seedling survival in the pots were similarly analyzed using ANOVA to test for effects of site, stand type, and soil type. Again, stand type was nested within site to account for differences among sites. Soil moisture and temperature in pots was also analyzed using repeated measures ANOVA.

Results

Stand characteristics

With respect to their physiographic characteristics, total basal area, and canopy cover, the paired sites only differed significantly in their slopes ($T = 5.1$, $P = 0.007$), with slightly steeper slopes in the *Q*-stands (Table 1). Soil texture (clay, silt, and sand content) did not differ between stand types. Several soil chemical properties were significantly different between stand types: pH ($T = 3.5$, $P = 0.025$), potassium ($T = 2.9$, $P = 0.044$), calcium ($T = 3.1$, $P = 0.035$), magnesium ($T = 4.6$, $P = 0.010$), and total nitrogen ($T = 3.8$, $P = 0.019$) were all significantly higher in *L*-stands. Although soil organic matter content did not differ in the upper 15 cm of soil ($T = 0.30$, $P = 0.78$), it was significantly greater in the top 5 cm of soil in *L*-stands ($T = 3.9$, $P = 0.018$).

Plots

In 2008 (a below-average rainfall year), the mean germination rate across all seeded plots was 3.1 % ($SE = 0.43$, range = 0–39 %, $N = 150$ plots). The most variation in germination rates was explained by stand type ($F = 11.5$, $P < 0.0001$, $df = 5$), with higher germination in *L*-stands (Fig. 2a). There was also higher germination in plots with litter than those without

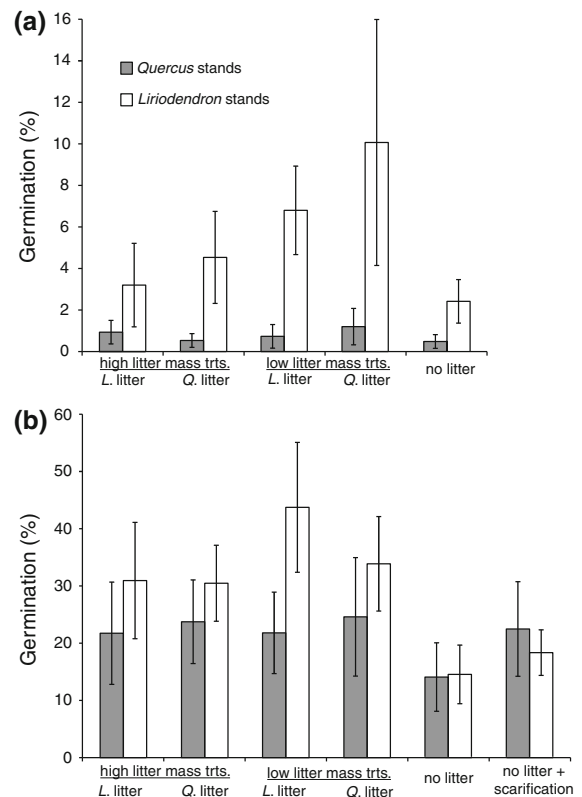


Fig. 2 Germination rates in plots sown with *Celastrus orbiculatus* seeds in 2008 (a) and 2009 (b). Note the different scales for germination rates in a and b. Mean percent germination is shown for the respective treatments. Treatments were the same in 2008 and 2009, with the exception of an additional scarification treatment in 2009. There were significant differences in germination between stand type, no litter versus litter treatments, and litter mass for both years. There was also a significant effect of scarification among plots without litter in 2009. 95 % confidence intervals are shown

($F = 6.6$, $P = 0.012$, $df = 1$). Among plots with litter ($N = 120$), the importance of stand type was even more pronounced ($F = 31.0$, Bonferroni-corrected $P < 0.0001$, $df = 5$). There was no significant effect of litter type ($F = 1.4$, Bonferroni-corrected $P = 0.48$, $df = 1$). However, plots with low litter mass treatments had significantly higher germination rates than those with high litter mass treatments ($F = 12.7$, Bonferroni-corrected $P < 0.001$, $df = 1$). Among the plots that were not seeded ($N = 100$), only seven plots had first-year *C. orbiculatus* seedlings in 2008, with an average of only 0.19 seedlings per plot. Given this minimal seed input from local sources, germination data for the seeded plots were not adjusted prior to analysis.

In 2009 (an above-average rainfall year), the mean germination rate was 25.0 % ($SE = 1.3$, range = 0–81 %, $N = 180$ plots). As in 2008, there was a strong effect of stand type ($F = 10.84$, $P < 0.0001$, $df = 5$), with higher germination in the *L*-stands, though relative differences between stand types were not as great as in 2008 (Fig. 2). Germination was also still significantly higher in the plots with litter added than in the no-litter plots ($F = 43.14$, $P < 0.0001$, $df = 1$). Among plots with litter, there was not a significant effect of litter mass at the $\alpha = 0.05$ level following the Bonferroni correction ($F = 4.37$, Bonferroni-corrected $P = 0.078$, $df = 1$); although germination was slightly higher in the low-litter-mass plots, the effect was not as strong as in 2008. There was again no effect of litter type on germination rates in 2009 ($F = 0.18$, Bonferroni-corrected $P = 1$, $df = 1$). Among the plots with no litter, those with the scarification treatment had significantly higher germination than those in which the soil surface was not disturbed ($F = 11.54$, Bonferroni-corrected $P = 0.0028$, $df = 1$). The difference between scarification and no-scarification treatments was greater in the *Q*-stands than in the *L*-stands (Fig. 2b). Among the plots that were not seeded in 2009 ($N = 120$), 16 plots had *C. orbiculatus* seedlings, with an average of only 1.3 seedlings per plot. Seventy-three percent of those seedlings observed in the non-seeded plots occurred in just two plots that were positioned below a mature *C. orbiculatus* vine. With the exception of that single location, seed inputs from local sources were low and did not warrant adjustments to the germination data from the seeded plots.

Mean first-year seedling survival across all plots in which seedlings were present in June 2008 was 34.4 % ($SE = 3.6$, $N = 99$ plots). Survival was significantly higher in *L*-stands ($F = 4.8$, $P = 0.0006$, $df = 5$) (Fig. 3). Survival was also higher in no-litter plots than those with litter, though the difference was only marginally significant ($F = 3.7$, $P = 0.057$, $df = 1$). Among plots with litter treatments, there was a significant effect of litter mass ($F = 12.3$, Bonferroni-corrected $P = 0.0016$, $df = 1$), with higher survival in the low litter mass treatments. There was no effect of litter type on seedling survival ($F = 0.35$, Bonferroni-corrected $P = 1$).

Soil temperatures varied significantly between stand types (repeated measures ANOVA, $F = 7.9$, $P < 0.001$, $df = 5$), but the direction of effect changed among sites and sampling dates with no clear

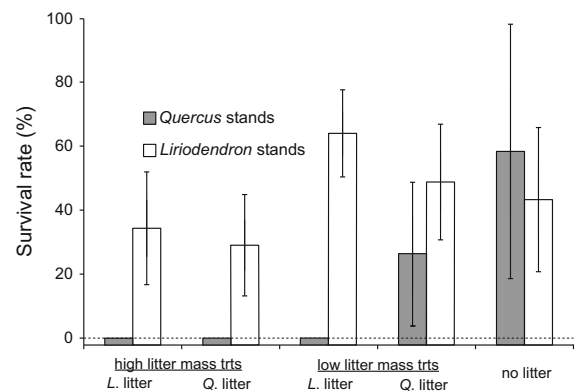
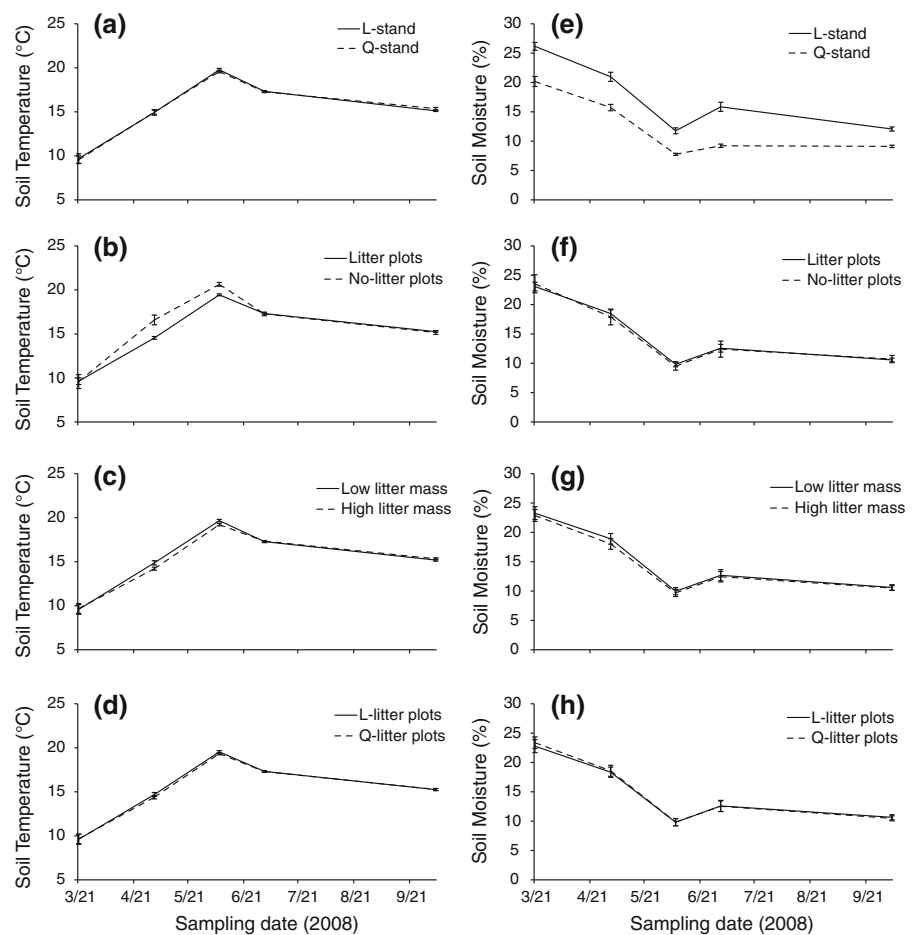


Fig. 3 Mean first-year seedling survival in plots with the respective treatments. Survival rate is based on the percent of seedlings present in plots ($N = 99$) in June 2008 that were still present in June 2009. Three of the treatments in the *Quercus* stands (high *L*-litter, high *Q*-litter, and low *L*-litter) had no surviving seedling in 2009. Seedling survival was significantly higher in *L*-stands than in *Q*-stands, in no-litter plots than those with litter, and in low-litter plots than high-litter plots. 95 % confidence intervals are shown

trend in stand effect (Fig. 4a). Far more variation in soil temperature was explained by differences among sites ($F = 77.2$, $P < 0.0001$, $df = 4$). The presence or absence of litter had the strongest effect on soil temperature ($F = 244.5$, $P < 0.0001$, $df = 1$), with higher temperatures in the no-litter plots early in the growing season, and slightly lower temperatures in no-litter plots in October (Fig. 4b). Among the plots with litter treatments, there were also significant effects of litter mass ($F = 34.0$, Bonferroni-corrected $P < 0.001$, $df = 1$) and litter type ($F = 11.0$, Bonferroni-corrected $P = 0.001$, $df = 1$); soil temperature was higher in low litter mass treatments and *L*-litter treatments earlier in the growing season and switched directions in October, though differences in mean sampling temperature between treatments at any given sampling date were < 0.67 °C (Fig. 4c, d).

Soil moisture was consistently and significantly higher in the *L*-stands than in *Q*-stands (repeated measures ANOVA, $F = 135.6$, $P < 0.0001$, $df = 5$). Volumetric water content was on average 5.0 percentage points higher in *L*-stands than in *Q*-stands (Fig. 4e). There was not a significant difference in soil moisture between the litter and no litter treatments ($F = 1.3$, $P = 0.26$, $df = 1$) (Fig. 4f). Litter mass had a minimal effect on soil moisture, and was not significant at the $\alpha = 0.05$ level following the Bonferroni correction ($F = 4.4$, Bonferroni-corrected

Fig. 4 Mean soil temperature (*left panel*) and soil moisture (*right panel*) for plots with the respective treatments: stand type (**a, e**), litter versus no litter (**b, f**), low versus high litter mass (**c, g**), and litter type (**d, h**). Measurements were taken on March 21 (at the time of experimental setup), May 2, June 7, July 2, and October 5, 2008. Soil temperature was recorded at a depth of 5 cm. Soil moisture was measured as volumetric water content in the upper 12 cm of soil. Error bars show $\pm 2 SE$. There was a significant difference in soil temperature between stand types and temperatures were significantly higher in no-litter plots than those with leaf litter. Soil moisture was significantly higher in *L*-stands and there was also a significant effect of litter mass



$P = 0.074$, $df = 1$); moisture was consistently higher in the low-litter-mass plots, but mean differences were modest ($<0.89\%$) and became less pronounced throughout the growing season (Fig. 4g). There was no effect of litter type on soil moisture ($F = 0.01$, Bonferroni-corrected $P = 1$, $df = 1$) (Fig. 4h).

Pots

In 2008 the mean germination rate across all pots was 2.6 % ($SE = 0.51$, $N = 100$). There was a weak significant effect of stand type ($F = 2.6$, $P = 0.028$, $df = 5$), with germination rates slightly higher in the *Q*-stands (Fig. 5a), but this trend only held for stand pairs in two of the five sites. More of the variation in germination rates was explained by differences among the sites ($F = 3.7$, $P = 0.009$, $df = 4$). There was no significant effect of soil type ($F = 0.99$, $P = 0.32$, $df = 1$). In 2009 the mean germination rate for pots

was 20.4 % ($SE = 1.4$, $N = 100$). Germination was significantly higher in *Q*-stands than in *L*-stands ($F = 6.12$, $P < 0.0001$, $df = 5$), though the mean difference between stand types was driven largely by site 2 in which germination was 34.5 % in the *Q*-stand and only 8.0 % in the *L*-stand. Germination was also slightly higher in pots with soil taken from the *L*-stands in 2009 ($F = 4.62$, $P = 0.034$, $df = 1$) (Fig. 5b).

Mean first-year seedling survival for pots in which seedlings were present in June 2008 was 69.8 % ($SE = 7.7$, $N = 29$ pots). Seedling survival did not differ between stand types ($F = 2.45$, $P = 0.081$, $df = 4$) or soil types ($F = 0.02$, $P = 0.88$, $df = 1$) (Fig. 6).

Mean soil temperature in the pots was higher for those in *Q*-stands (repeated measures ANOVA, $F = 27.2$, $P < 0.0001$, $df = 5$) (Fig. 7a). However, differences among sites explained far more variation

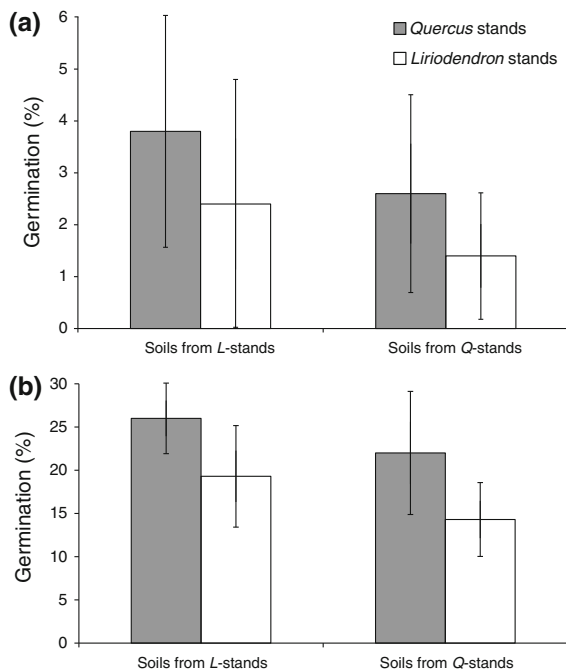


Fig. 5 Germination rates in pots sown with *Celastrus orbiculatus* seeds ($N = 100$ pots) in 2008 (a) and 2009 (b). Mean percent germination is shown for pots placed in either *Q*-stands (gray bars) or in *L*-stands (white bars), and in pots with soil taken from either *Q*-stands or *L*-stands. There was a significant effect of stand type on germination rates in both 2008 and 2009. There was also a significant effect of soil type in 2009. 95 % confidence intervals are shown

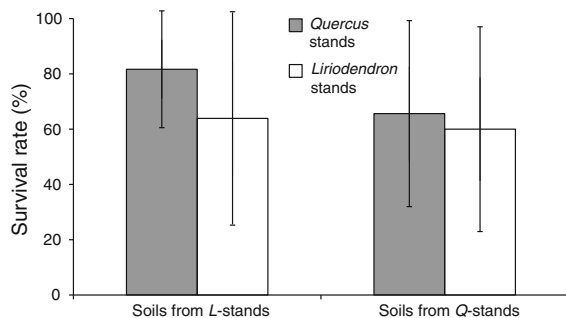


Fig. 6 Mean first-year seedling survival in pots placed either in *Quercus* or *Liriodendron* stands and filled with soil from either *Quercus* or *Liriodendron* stands. Survival rates are based on the percent of seedlings present in pots ($N = 29$) in June 2008 that were still present in 2009. There were no significant effects of stand type or soil type on seedling survival. 95 % confidence intervals are shown

in soil temperature ($F = 732.2$, $P < 0.0001$, $df = 4$). There was no effect of soil type on temperature ($F = 0.04$, $P = 0.84$, $df = 1$) (Fig. 7b). Soil moisture

was higher in *L*-stands ($F = 2.8$, $P = 0.021$, $df = 5$) (Fig. 7c), though the effect was only moderately significant and far more variation was explained by differences among sites ($F = 25.5$, $P < 0.0001$, $df = 4$). There was a strong effect of soil type ($F = 16.7$, $P < 0.0001$, $df = 1$), with higher soil moisture in *L*-soils than in *Q*-soils, and this trend held for both the March and October sampling dates (Fig. 7d).

Discussion

In general, *C. orbiculatus* germination and survival rates were higher in stands dominated by *L. tulipifera* than those dominated by *Quercus* spp., supporting the notion that higher abundance of *C. orbiculatus* previously observed in tulip poplar stands is due at least in part to greater invasibility and not propagule pressure alone. The higher germination and survival rates in tulip poplar stands may be influenced by a number of factors, but our results suggest that higher soil moisture levels in these stands may play an important role. Soil moisture was consistently higher in tulip poplar stands than in oak stands. Others have noted the positive correlation between soil moisture and invasion by non-native plants in general (Rejmánek 1989; Huebner and Tobin 2006; Gelbard and Belnap 2003; Chytry et al. 2008), and *C. orbiculatus* in particular (McNab and Loftis 2002; Silveri et al. 2001; Leicht-Young et al. 2007). The importance of soil moisture may have been exacerbated during the 2008 growing season due to drought conditions experienced throughout the region. Spring rainfall (total for March–May) at BCEF was 11.6 cm below historic (1971–2000) averages in 2008 and 13.3 cm above historic averages in 2009 (BCEF weather station 31-0724, National Climate Data Center 2002).

Although variation in soil moisture is typically attributed to differences in local topography (e.g., slope, aspect, terrain shape, and landform position), topographic differences between the paired stands in this study were minimal. Although the *L*-stands had slightly gentler slopes (likely as a result of preferential selection by early settlers as sites for agricultural use) than *Q*-stands, the differences were modest and not likely to explain the observed differences in soil moisture. The more mesic conditions in the tulip poplar stands may at least in part be a result of the overstory community's effect on soil and litter

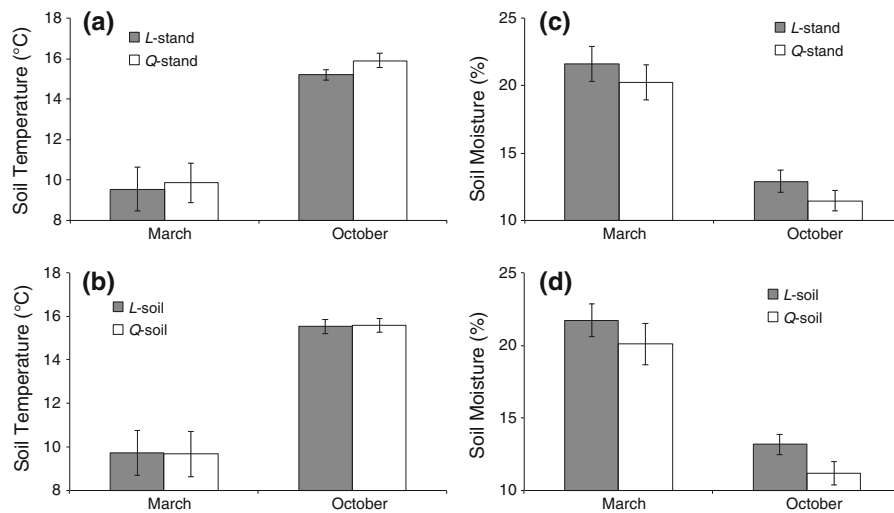


Fig. 7 Mean soil temperature (*left panel*) and soil moisture (*right panel*) for pots placed either in *Quercus* or *Liriodendron* stands (**a, c**) and with soil from either *Quercus* or *Liriodendron* stands (**b, d**). Measurements were taken on March 21 (at the time of the experimental setup) and October 5, 2008. Soil

temperature was recorded at a depth of 5 cm. Soil moisture was measured as volumetric water content in the upper 12 cm of soil. *Error bars* show ± 2 SE. There was a significant effect of stand type on soil temperature. There was a significant effect of both stand type and soil type on soil moisture in the pots

properties. Tulip poplar leaves have low C:N and decompose quickly (Mudrick et al. 1994; Adams and Angradi 1996; Kominoski et al. 2007), likely resulting in a thinner leaf litter layer, rapid turnover of nutrients, and elevated levels of organic matter in the A horizon. Although there were no detectable differences in soil texture (sand, silt, and clay content) that might explain differences in water holding capacity between the stand types, soil in tulip poplar stands had significantly higher organic matter content in the top 5 cm than in oak stands. Soil moisture measured in the pots was also higher in soils from tulip poplar stands both in March and in October regardless of whether the pots resided in *L*-stands or *Q*-stands during the intervening period, suggesting that the physical properties of the soils (e.g., higher organic matter content) may be responsible for higher soil moisture in the tulip poplar stands. Similar effects on forest floor conditions caused by shifts in overstory composition have been noted throughout the eastern U.S., where increasing abundance of shade-tolerant tree species in formerly oak-dominated communities (due largely to fire suppression) have resulted in more mesic understory conditions (Nowacki and Abrams 2008; Rogers et al. 2008).

Germination rates of *C. orbiculatus* were higher in the low leaf litter mass treatments than in either the no

litter treatments or the high litter mass treatments. First-year seedling survival was also lowest in the high litter mass treatments. These results may reflect a tradeoff between the importance of litter in creating appropriate microsite conditions related to moisture and its influence as a physical barrier limiting seedling establishment. Although soil moisture in the litter and no litter treatments were not significantly different, plots with litter did have slightly higher mean soil moisture in the upper 12 cm of soil early in the growing season, and these differences were likely more pronounced at the soil surface. Particularly given the dry conditions during the 2008 growing season, the surface of the no-litter plots may have been too dry for germination of the *C. orbiculatus* seeds. The soils under high litter mass treatments were drier than low litter mass plots early in the growing season, perhaps due to interception of precipitation by the thicker leaf litter layer. While leaf litter often promotes infiltration and reduces evaporation from the soil surface, thus maintaining moister soil conditions (Sayer 2006; Facelli and Pickett 1991), dense leaf litter can have the opposite effect by intercepting incoming moisture and reducing infiltration of the soil beneath it (Facelli and Pickett 1991; Walsh and Voigt 1977). The thicker litter layer may also act as a physical barrier (Facelli and Pickett 1991; Sayer 2006; Sydes and Grime 1981),

requiring the emergent *C. orbiculatus* seedlings to devote substantial energy stores to hypocotyl growth, as noted by Ellsworth et al. (2004a). Low seedling survival in the high litter mass treatments indicates that many of those that did germinate in 2008 were unable to become established, perhaps owing to the high energy demand required to become established in the thicker litter layer and/or the desiccating conditions within the litter. The no-litter plots, on the other hand, had the lowest germination rate but had the highest seedling survival rate. Given the competing roles of litter in creating conditions conducive for germination on one hand, and obstructing seedling growth and reducing survivorship on the other, areas with modest amounts of litter may provide the most appropriate balance between these tradeoffs that results in the highest establishment by *C. orbiculatus*.

Oak-dominated stands in the study region are often characterized by moder (or “duff mull”) humus forms (McNab 1995), which have thick organic layers and a well-developed layer of fine, partially-decomposed litter material (“F horizon”) between the coarse litter and the mineral soil (Green et al. 1993; Ponge 2003). Litter layers in tulip poplar stands, on the other hand, tend to be thin and lack an F horizon, typical of the mull humus form. The presence of an F horizon may also contribute to drier soil conditions in oak stands by intercepting precipitation, and it may act as an additional physical barrier for seedling establishment. Results from the scarification treatment are consistent with such a role of the F horizon in conferring resistance to invasion by *C. orbiculatus*. Plots with the scarification treatment had higher germination than the no-litter plots that lacked a scarification treatment, and these differences were most pronounced in the *Q*-stands where the non-scarified plots were more likely to have an F horizon present. McNab and Loftis (2002) noted a higher probability of *C. orbiculatus* occurrence in areas that had experienced scarification of the forest floor (perhaps from foraging by wild turkeys), underscoring the importance of the organic layer for invasion resistance.

Soils in the tulip poplar stands had higher nutrient levels (especially exchangeable cations and total N), pH, and organic matter (in the upper 5 cm). Nonetheless, soil type had little or no effect on germination and seedling survival of *C. orbiculatus*, as indicated by the potted soil translocation experiment. Although mean germination and survival was slightly higher in soils

taken from the *L*-sites, the only (moderately) significant difference between soil types was for seed germination in 2009. Seed germination in the pots was actually higher in the *Q*-stands than in the *L*-stands, perhaps owing to the later leaf-out of oaks and therefore higher early-season light levels in the *Q*-stands. Regardless of the reason for this relationship, it suggests that site conditions related to the forest canopy and midstory do not explain the higher abundance of *C. orbiculatus* typically observed in *L*-stands. The minimal differences in germination and survival between soil types and stand types in the translocated pot experiment (where litter was excluded) underscores the important role of litter in explaining establishment success by *C. orbiculatus*.

Although soil temperature can have a strong influence on germination (Vandelook et al. 2008; Vleeshouwers et al. 1995; Vegis 1964), the differences between treatments that we observed did not generally correspond to observed differences in seed germination. We expected a positive correlation between spring soil temperature and germination rates. Though soil temperature was higher in no-litter plots early in the growing season, *C. orbiculatus* germination rates were lowest in those plots, perhaps owing to drier surface soil conditions. Furthermore, there were no differences in mean soil temperatures between the *L*-stands and *Q*-stands that could explain the large differences in germination. Mean soil temperatures in the low litter mass treatments were higher than in the high litter mass treatments early in the growing season and could have contributed to the higher germination rates observed in those plots, though mean differences between treatments were small (<1 °C). Overall, our results suggest that soil moisture and litter conditions may be playing a more important role than temperature in determining invasibility.

Although several studies have noted a relationship between land-use history and invasion by non-native plants (Lundgren et al. 2004; Von Holle and Motzkin 2007; DeGasperis and Motzkin 2007), there has been little effort to elucidate the specific factors related to land-use history that facilitate invasion. At BCEF land-use history appears to be influencing invasion indirectly via successional changes in the overstory community (particularly increased dominance by tulip poplar) that in turn affect forest floor conditions, increasing invasibility in such areas. It is noteworthy that areas that have experienced non-agricultural,

large-scale disturbances such as clear-cuts or wind-throw events in the study region also often experience increased tulip poplar dominance (Elliott et al. 2002; Clinton and Baker 2000). High abundance of *C. orbiculatus* have been observed in such areas at BCEF (McNab and Loftis 2002, personal observations), suggesting that the conditions conducive for its invasion are not exclusively associated with agricultural land-use history, but may be more likely in areas with any large-scale disturbance history and associated successional forest communities.

The results from our field experiment suggest that forest management strategies for controlling the spread of *C. orbiculatus* should be context dependent. For example, forest stands that are particularly susceptible to invasion, such as those dominated by tulip poplar, may warrant special treatment at the time of a timber harvest and/or shortly thereafter to eradicate *C. orbiculatus* seedlings that are already present or may become established due to harvesting activities. In the case of oak dominated stands, our results suggest that measures should be taken to minimize disturbance of the leaf litter layer that may confer resistance to *C. orbiculatus* invasion. By understanding the specific factors that influence non-native plant invasion in forests, we might be better suited to predict their spread, determine which forest communities are most at risk, and implement control methods to minimize their detrimental effects.

Acknowledgments This study was funded by the Long-term Ecological Research (LTER) Program of the National Science Foundation (DEB-0823293, Coweeta LTER). We thank Henry McNab and the staff at the BCEF for their assistance with permissions and logistics. We also thank Matthew Hutchins and Nicholas Fabina for their assistance with fieldwork. Finally, thanks to Anthony Ives, Donald Waller, Volker Radeloff, and James Bockheim for valuable comments on the manuscript.

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