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Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest

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Abstract

Factors contributing to an invasion of the Asian woody vine *Celastrus orbiculatus* in a mesic forested Massachusetts (USA) sanctuary were investigated. Planting germinated *C. orbiculatus* seeds in the field revealed that, although they tolerate a wide range of conditions, seedlings grow largest in moist circumneutral soil under high irradiance. A study of naturally occurring vines in a logged forest suggested that *C. orbiculatus* invaded two years after harvest, and invasion may have been triggered by logging disturbance. Vine stems were more abundant on former logging roads than in surrounding selectively logged areas. Former logging roads had a significantly higher soil pH than surrounding areas and, due to the direction of construction, a significantly more southerly aspect. Fourteen years after harvest, logging roads continued to provide this aggressive exotic with superior habitat for establishment and growth.

Introduction

A general theory of plant community invasibility is in its infancy (Rejmanek 1996; Alpert et al. 2000; Richardson et al. 2000), and ecologists are unable to predict when and where a species will invade a given community. Johnstone (1986) proposed that all plant invasions proceed by removal of a barrier that previously excluded a species, resulting in a temporary 'safe site' (Harper 1977) for establishment. Davis et al. (2000) proposed that plant community invasibility depends on an increase in the amount of unused resources that coincides with the availability of invading propagules. These two hypotheses are not incompatible, as lack of a resource (such as irradiance) may be equivalent to an invasion barrier (such as a closed forest canopy). According to these authors, invasibility is not a permanent attribute, but varies over time and increases following disturbances that increase resource availability and/or remove invasion barriers.

Numerous studies have documented plant invasions in mesic forests following disturbance, either natural (wildfires and hurricanes) or manmade (logging or road construction; see Brothers and Spingarn 1992; Deferrai and Naiman 1994; Robertson et al. 1994; Horvitz et al. 1998). Depending on the severity, disturbance in mesic forests may increase light availability, especially in the understory (Reader and Bricker 1994), remove existing vegetation and litter cover and scarify the soil (Mou et al. 1993), and increase soil nutrients (Bungard et al. 1997). Vines are good invaders of disturbed forests. Hegarty and Caballe (1991) reported that clumps of vines in temperate forests are biological markers of disturbance, and Putz (1984) noted that post-logging suppression of tree regeneration in the tropics due to liana growth is common. Horvitz et al. (1998) reported that, in hurricane-prone North American subtropical forests, both native and introduced vines grow vigorously after disturbance and tend to out-compete other native plants.

Celastrus orbiculatus (Oriental bittersweet: Celastraceae), a deciduous, dioecious round-leaved vine, is one of the most invasive exotic plants in the northeastern United States (Dreyer 1994). Although this twining liana is not considered a forest species in its native Asia (Owhi 1965), it invades early- and late-successional forests in North America (McNab and Meeker 1987). Its fleshy berries are winter food for frugivorous birds (Baird 1980), and its decorative fruiting vines are dispersed by humans (Dreyer 1994). The annual growth rate of *C. orbiculatus* may exceed 3 m (Patterson 1974), allowing plants in open-light habitats to climb a canopy-sized tree in 3–4 growing seasons. Twining vines are generally limited to small-diameter supports (Teramura et al. 1991), but *C. orbiculatus* is able to climb tree trunks with a wide variety of diameters, aided by spiny projections around its bud and leaf scars that lodge in the host's bark (Dunwiddie, personal observation). *C. orbiculatus* kills other vegetation through blanketing and constrictive twining, and halts the succession of young deciduous forests (McNab and Meeker 1987; Dreyer 1994). Due to the negative effects of *C. orbiculatus* on North American forests, and the difficulty of eradication (Dreyer 1988), it is important to identify environmental factors that facilitate invasion. If these are known, high-risk areas can be monitored and invasions can be prevented or contained.

Early growth of seedlings is a critical stage in the establishment of an invasive plant (Baker 1974). Seeds dispersed to a site that is not conducive to seedling growth are unlikely to produce adult plants. Although *C. orbiculatus* has been propagated in the laboratory (Patterson 1974; Dreyer et al. 1987), little information is available on seedling establishment and growth under field conditions. Field observations suggest that preferred habitat includes moist circumneutral soil and high irradiance. To investigate habitat preference of *C. orbiculatus* seedlings, germinated seeds were planted in the field. We consider here the question of how variation in soil pH, soil moisture, and irradiance affect the survival and growth of *C. orbiculatus* seedlings.

To gain a measure of site invasibility, the habitat preferences of naturally established vines were investigated in a forest logged in 1980. Field observations suggested that moderate to severe infestations of *C. orbiculatus* occur mainly in areas with a history of farming or logging. We therefore suspected that disturbance associated with these activities increases site invasibility. In the logged forest we studied (see 'Study site') stems appeared common on former logging roads (skid trails) but rare in intervening areas. Logging roads are the most disturbed parts of a logged forest (e.g. Mou et al. 1993), as they are completely denuded of vegetation at harvest. Because they probably represent more invasible habitat than surrounding logged areas (in which only portions of the canopy are removed and the soil is less disturbed), logging roads may serve as *C. orbiculatus* invasion corridors.

To determine if the 1980 logging facilitated colonization by *C. orbiculatus*, we explored three questions: (1) Was *C. orbiculatus* present prior to the 1980 logging or did it invade afterwards? (2) Are former logging roads more invasible than surrounding selectively logged areas? (3) Do former logging roads provide better *C. orbiculatus* habitat than surrounding selectively logged areas?

Materials and methods

Study site

Research was conducted at the Pleasant Valley Wildlife Sanctuary, located in the Berkshire Mountains in Lenox, Massachusetts (latitude 42°23′ N, longitude 37°18′ W; elevation 371–603 m, mean annual precipitation approximately 110 cm). This 583 ha refuge is covered with rich mesic forest and mesic acidic oak–conifer forest (Rawinski 1983; cited in Weatherbee 1992). *C. orbiculatus* has naturalized on the sanctuary and, although it grows most abundantly in open-light habitats, seedlings are present on the floor of late-successional deciduous and coniferous forests. Weatherbee (1992) divided the sanctuary into 30 management units based on soil type, land use history, and vegetation cover. One unit, a 47 ha mesic forest (439 m altitude; referred to hereafter as 'the study area'), selectively logged in 1980 shortly before acquisition and covered with rich mesic forest grading into mesic acidic oak–conifer forest, was selected as the site of seedling growth experiments and habitat preference studies.

Early growth of seedlings

C. orbiculatus berries were collected from seven Massachusetts locations in the winter of 1993–1994. Berries were air dried, and seeds were extracted and treated with a fungicide (Captan, ICI Americas Inc., Wilmington, Delaware). To break dormancy, seeds were placed in moist sand in plastic bags and stored in the dark at approximately 7 °C. While in storage, the seeds were inspected daily, resulting in brief exposure to light. After 37 days, radicles began to emerge. Indoor germination trials revealed that only radicle-bearing seeds were easily propagated (Silveri, personal observation), so germinating seeds were used in field experiments. Field plots to test the effects of soil pH, soil moisture, and irradiance levels on the early growth of *C. orbiculatus* were established in the southern part of the study area, a location with sparse canopy cover and a history of flooding. We suspected that soil pH was important in determining *C. orbiculatus* habitat quality, so two plots with differing soil pH (roughly 3 m × 15 m each, approximately 100 m apart) were used for experimental plantings. (Plot A: pH = 4.3–5.2; Plot B: pH = 7.1–7.7. For mean pH, Student's t-test, $P < 0.005$. Differences are likely due to local bedrock characteristics and/or flooding. See below for details on pH measurement.)

All surface vegetation was removed from the study plots, and the soil was loosened and cleared of roots to a depth of 10 cm. Due to the labor involved in clearing, it was not possible to provide replicate plots at the two pH treatment levels. To exclude small mammals, the area was fenced with chicken wire. Each plot was divided into five replicate blocks. Each block was divided into four quadrats (1 m × 1 m) separated by a 0.5 m border. Because lower irradiance limits on the survival and growth of *C. orbiculatus* may determine its ability to invade mature forests, we reduced natural irradiance in half of the quadrats by shading them with 60% shadecloth (DeWitt Co., Sykeston, Missouri) suspended 15 cm above the quadrat prior to planting. To investigate the apparent correlation of *C. orbiculatus* abundance with high soil moisture, we raised soil moisture in half of the quadrats by watering them every 3 days with 0.6 cm/m^2 of water drawn from a reservoir. Our experimental design was fully crossed for water and shade treatments, with each of the four possible treatment combinations randomly assigned to one quadrat within each block. One hundred fifteen germinating *C. orbiculatus* seeds (some with shoots of under 1 cm) were planted in each quadrat on 7 June 1994, buried to a depth of 0.5 cm. All quadrats were watered every 3 days for the first 15 days to prevent dehydration of newly germinated seedlings. After 15 days, the experimental watering regimes described above were implemented.

Two soil pH measurements were recorded for each quadrat at the onset of the study (pH wand model 35624-00, Cole-Parmer, Vernon Hills, Illinois), and their average used in later analyses. The quadrats were checked every 3 days for seedling emergence and mortality. Approximately every 2 weeks, beginning on day 42, light and moisture data for each quadrat were recorded. Irradiance readings (photosynthetically active radiation) were taken at ground level from the center of each quadrat using a Quantum Sensor (LI-COR Inc., Lincoln, Nebraska). If irradiance fluctuated, a median reading was determined after 60 s of exposure. To sample the range of irradiance levels, light readings were taken under varying weather conditions and at different times of day. Moisture readings were taken (prior to any watering treatment) from the center of each quadrat at a depth of 5 cm using a Quickdraw tensiometer (Soil Moisture Equipment Corp., Santa Barbara, California), which measures soil moisture indirectly as centibars (cb) of soil suction. Soil moisture and irradiance readings gathered throughout the study were averaged and the quadrat means were used in later analyses.

Rainfall was heavy during the second half of July through September 1994 (16%, or 3.81 cm, above the annual mean for this period for North Adams, Massachusetts). On 26 July watering treatments were discontinued due to fungi growth in some quadrats. On 17 September (after 102 days of growth) seedlings were harvested by excavating entire plants from the ground. The plants were oven-dried at 80 °C to constant weight and weighed to 0.1 mg using a Mettler AE 163 scale (Mettler Instrument Corp., Heightstown, New Jersey). The effects of measured environmental variables (quadrat means for soil pH, soil moisture, and irradiance, including all possible pairwise interactions) on seedling performance (quadrat means for survival to harvest and dry weight at harvest) were explored using General Linear Modeling (GLM) (SYSTAT 5.2.1). Stepwise multiple regression with backwards elimination was used to determine which variables to retain in the final model. Condition indices were used to verify that collinearity was not significant. To eliminate the inverse relationship between soil suction and soil moisture, soil suction values were transformed for use in the GLM and correlation analyses by the equation $\textit{soil moisture} = (-1)\ \textit{soil suction}$.

Habitat preference and age structure of C. orbiculatus *in a logged forest*

Sample plots

Three 550 m transects, running due east–west and 50 m apart, were established in the northern part of the study area, which was logged in 1980 (30–70% of the canopy removed, depending on site accessibility). Each of the transects was bisected in five locations by old north–south logging roads, still clearly identified by the presence of two parallel ruts and sparse ground cover along the historic roadbed. At each location where a logging road crossed a transect, a 2 × 5 m plot was located east–west (crosswise) on the logging road. In addition to these 15 logging-road plots, 15 additional plots (5 per transect) were located at random along the transects in the same orientation as the logging-road plots. We then looked for differences between the two plot types in physical parameters and in *C. orbiculatus* abundance.

Each plot was censused for the presence of *C. orbiculatus*. If present, stems were counted, and percent cover was estimated. To test for physical differences between the two plot types, we recorded soil pH, soil moisture, slope (estimated with a compass), aspect, and light level. Light readings were taken on an overcast day to collect measurements of average diffuse solar radiation. Diurnal patterns and levels of direct solar radiation were not investigated. Percent exposed mineral soil and percent exposed rock on the ground in a 5 m radius of the plant were estimated. Parametric and non-parametric two-sample tests were used (Statmost 2.5, Datamost, Inc., Salt Lake City, Utah) to identify differences between the two plot types. Because the two measures of *C. orbiculatus* abundance (number of stems per plot and percent plot cover) were not independent of each other, the Bonferroni correction was employed when these variables were used in correlation analyses.

Transect samples

The transects laid out for the sample plot study were also used for this investigation. In late July and early August of 1994, after completion of the sample plot study, all *C. orbiculatus* stems within 1 m of a transect were collected, and their location noted as distance from origin of the transect. To ascertain whether any plants pre-dated the 1980 logging, stems were aged by counting annual rings in cross-sections under a dissecting microscope. (Inspecting annual rings in a small subsample of *C. orbiculatus* roots suggested that they were approximately the same age as attached stems.) Stem length was measured, or estimated to the nearest meter in the case of large individuals attached to trees. We used stem length as a measure of plant size and success, and the early growth experiment later confirmed a strong correlation between stem length and dry mass. Vines exhibit rapid extension growth but slow diameter growth (Putz 1990), making stem length a good predictor of mass for twining vines like *C. orbiculatus*.

The environmental parameters measured for the sample plots were also measured at the location of each stem collected. To determine what environmental characteristics were conducive to *C. orbiculatus* growth, vine length was tested for associations with physical parameters using principal components analysis (PCA) (Statmost 2.5). PCA reduced the number of parameters for testing and produced uncorrelated factors (constructed from one or more measured physical parameters) against which vine length was regressed. The PCA factors were then used in stepwise multiple regression to determine which best predicted vine stem length.

Results

Early growth of seedlings

C. orbiculatus seeds germinated readily in the dark of stratification storage, with germination per bag ranging from 30% to 89%. Although light and moisture in the field were experimentally manipulated to produce two treatment levels, the results of these treatments were not consistent. There was no significant difference in mean soil moisture (measurements collected over the course of the study) between watered and unwatered quadrats. It is likely that high rainfall obliterated the cumulative effects of the watering treatment. Occasional readings of 0 cb (saturated soil) were recorded in both plots. Although unshaded quadrats had, on the average, higher irradiance than shaded quadrats, a few shaded quadrats had substantially higher mean irradiance than some of the unshaded quadrats. Due to this microenvironmental heterogeneity, we employed a regression approach to analyzing these data. Because the results of the treatments were not consistent, the effects of light and moisture on seedling performance were most accurately determined by measurement of plant response to measured field levels of environmental variables.

Survival to harvest was not significantly related to any of the measured physical parameters. However, all physical parameters were significant predictors of plant dry mass at harvest and were retained in the final GLM model (Table 1). Dry mass at harvest increased with increases in soil pH, soil moisture, and irradiance. None of the interaction terms were significant. For the final overall model (total $R^2 = 0.65$), 34% of the variance in dry mass was explained by irradiance, 33% by soil pH, and 8.6% by soil moisture.

Habitat preference and age structure of C. orbiculatus *in a logged forest*

Sample plots

C. orbiculatus was located in 9 of 15 logging-road plots but in only 1 of 15 randomly placed plots ($P < 0.005$, Fisher's exact test). Mean density and mean cover of *C. orbiculatus* were significantly greater in logging-road plots than in randomly placed plots. Of the physical parameters measured, logging roads differed significantly from surrounding areas only in mean soil pH (Table 2) and aspect. Mean soil pH was higher in logging-road plots (5.33, SE = 0.11) than in randomly placed plots (4.96, SE = 0.11, $P = 0.02$, Student's t-test). Logging-road plots were more likely to have a south aspect than randomly placed plots, which were more likely to have an east or southeast aspect ($P = 0.02$, contingency table analysis – this difference is a result of the north–south construction of roads). *C. orbiculatus* density and *C. orbiculatus* cover increased with increasing soil pH (Spearman's rank correlation coefficient = 0.48, $P < 0.025$ for both density and cover). *C. orbiculatus* density also increased with increasing amounts of exposed mineral soil (Spearman's rank correlation coefficient = 0.41, $P < 0.025$). Caution should be exercised when interpreting these correlations, as many of the environmental parameters exhibited significant covariance (Table 3).

Table 1. GLM analysis: effects of physical parameters[a] on harvest size (log dry mass) of *C. orbiculatus* seedlings.[b]

Variable	Coefficient	SE	P
Intercept	0.887	0.052	<0.0001
Soil pH	0.352	0.060	<0.0001
Soil moisture ((-1)cb)	0.063	0.021	0.006
Irradiance (μmol photons/m^2/s)	0.007	0.001	<0.0001

Model $R^2 = 0.646$, $F_{3,36} = 21.88$, $P < 0.0001$.

[a] Mean of all measurements in each 1 × 1 m quadrat.

[b] Mean of plants in each 1 × 1 m quadrat.

Transect samples

One hundred and five *C. orbiculatus* vines were collected from the transects in the study area (Figure 1). Mean age was 3.4 years (SE = 0.2), and mean length was 138.9 cm (SE = 27.0, range 1 cm–approximately 20 m). Length of vines showed significant positive correlations with several physical parameters (including soil pH, soil moisture, and irradiance), but many of these parameters covaried, making their correlations with vine length difficult to interpret. To solve this problem, physical parameters were analyzed with PCA. Two PCA factors, each constructed from two parameters (Table 4), were significant predictors of vine length. Factor 1, constructed mainly from soil pH and soil moisture, was named 'soil quality'. Areas of high soil pH also tended to have high soil moisture. Factor 2 (named 'site quality') was constructed mainly from percent exposed mineral soil and light level. Areas of high light tended to have low percentages of exposed

Table 2. Comparisons of sample plot parameters.

	$\bar{x}$ logging road	$\bar{x}$ randomly placed	P	Test type
Density (stems per plot)	3.07	0.20	<0.005	Mann–Whitney U
Cover (%)	4.73	0.07	<0.005	Mann–Whitney U
Soil pH	5.33	4.96	0.019	Student's t-test
Soil suction (centibars)	4.97	5.40	0.71 (n.s.)	Student's t-test
Exposed rock (%)	4.87	14.07	0.11 (n.s.)	Welch's approximate t
Exposed mineral soil (%)	33.53	21.00	0.11 (n.s.)	Student's t-test
Irradiance (μmol photons/m^2/sec)	16.6	13.3	0.58 (n.s.)	Student's t-test
Slope (degrees)	6.7	9.4	0.10 (n.s.)	Student's t-test

Table 3. Intercorrelations of sample plot environmental parameters.

	Soil moisture	% Exposed rock	% Exposed mineral soil	Irradiance	Slope
Soil pH	0.34	0.06	0.77**	0.18	−0.36
Soil moisture		0.04	0.36*	0.12	−0.45*
% Exposed rock			0.18	−0.15	0.26
% Exposed mineral soil				0.03	−0.35
Irradiance					0.03

$^*P = 0.05$, $^{**}P = 0.01$, Spearman rank correlation (correlation coefficients are not significant unless labeled otherwise).

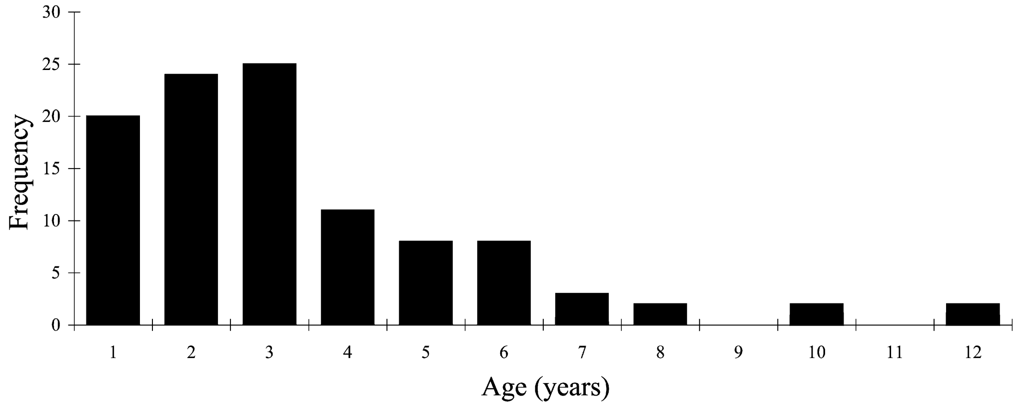

Figure 1. Age distribution of *C. orbiculatus* stems collected from belt transects 14 years after logging.

Table 4. Principal components analysis of belt transect physical parameters: factor loading matrix.

Physical parameter	Factor 1 'soil quality'	Factor 2 'site quality'
% Exposed mineral soil	−0.259	−0.879
Soil pH	−0.858	0.074
Soil moisture[a]	0.872	0.095
Irradiance	−0.308	0.766

[a] Measured as soil suction.

mineral soil. A multiple linear regression of vine length on the PCA factors 'soil quality' and 'site quality' yielded the equation: vine length = 167.3 − 558.5 'soil quality' + 881.3 'site quality' (for the overall model, adjusted $R^2 = 0.10$, $P < 0.05$ for both independent variables).

Discussion

Early growth of seedlings

In this study, *C. orbiculatus* seeds germinated readily in the near-continuous darkness of stratification storage. Dreyer et al. (1987) also reported that *C. orbiculatus* germinates readily during dark stratification, and Patterson (1974) reported the highest greenhouse germination rates at low (200 ft candles) light intensities. This suggests that increases in light levels due to habitat disturbance may be less important in triggering invasion than other disturbance-related changes, such as removal of existing plant and litter cover, soil scarification, and/or an increase in soil nutrients.

In this field experiment, seedlings grew largest in moist circumneutral soil under high irradiance. However, all plants in this experiment (grown for 102 days) were substantially smaller than unfertilized plants grown in the laboratory for 120 days by Patterson (1974) under varying irradiance levels at 19–30 °C. Plants in the present study reached only 2–42% of the weight of Patterson's plants, and this cannot be attributed to differences in seed source. When we planted seeds from the present study indoors (sunny window, unfertilized, watered liberally, grown for 180 days), the mean weight of the six indoor-grown plants was 80 times the mean weight of field-grown plants. The most likely explanation for the slow growth in our field experiment is low irradiance in the study plots, shaded by adjacent trees (and our shade treatments), and averaging 73–76 μmol photons/m^2/s, approximately 10% of irradiances recorded in a nearby open field on sunny days. This hypothesis is supported by the fact that dry mass at harvest showed a positive relationship to irradiance. Other possible explanations for the small size of field-grown seedlings include pathogens and soil oxygen levels.

Although conditions in the field plots were not conducive to the growth of *C. orbiculatus* seedlings, plants survived well under these adverse conditions. The majority of the seedlings (79.9%) survived until harvest and increased somewhat in size. Possibly because of a wet summer, none of the independent variables (irradiance, soil pH, soil moisture) had a significant effect on seedling survival. Like *C. orbiculatus*, many invasive vines survive and grow under low irradiance. Carter and Teramura (1988) reported low light-compensation points (approximately 20–45 μmol photons/m^2/s) for several exotic vines in the southeastern United States, and Ramco Baars (1998) reported that introduced and native weedy vines in New Zealand have light-compensation points as low as 0.9% of full sunlight.

Dry mass at harvest showed a positive relationship to soil moisture, reinforcing field observations suggesting that preferred habitat for *C. orbiculatus* includes moist soil. Dry mass at harvest also showed a significant positive relationship to soil pH, with plants growing largest in circumneutral soil. There are several possible explanations for this. Availability of many mineral nutrients is maximal in circumneutral soil (Jeffrey 1987a). Plants in acidic soil may encounter toxic levels of metal ions (Grime 1979) and decreased soil microbe activity (Jeffrey 1987b), either of which may slow growth. Note that, because the two plots differing in overall pH could not be replicated, it is possible that differences in seedling size could be caused by other, unquantified factors that covaried with soil pH. However, data collected from the transect samples (see below) also suggested that the growth of *C. orbiculatus* shows a positive relationship to soil pH.

Plots and transect samples

1. Was C. orbiculatus *present prior to the 1980 logging, or did it invade afterwards?* A vegetation survey of Pleasant Valley Wildlife Sanctuary (Weatherbee 1992) revealed an apparent sanctuary-wide relationship between *C. orbiculatus* density and level of past disturbance from farming and/or logging. We classified Weatherbee's forest units as being uninfested, lightly infested (*C. orbiculatus* rare), moderately infested (*C. orbiculatus* common), or heavily infested (*C. orbiculatus* approaching monoculture). Units with a known history of farming and/or logging tended to have moderate to heavy infestations, while other units tended to be uninfested or have light infestations. Of the logged units, those logged with draft animals, which results in less soil damage (Hartshorn 1989), had lighter infestations than those logged with mechanical equipment. The one small undisturbed forest unit located by Weatherbee (approximately 3 ha, soil pH 5.5, mixed hardwoods, with extensive mound and pit topography), apparently never farmed or logged due to a steep slope, did not contain *C. orbiculatus*, although surrounding areas were infested. The study area was acquired after a 1980 logging, so no previous inventory existed of exotics, and it was impossible to ascertain whether *C. orbiculatus* was present before the harvest. However, the failure of our 1994 survey to locate any stems older than 12 years suggests that *C. orbiculatus* invaded the study area after harvest, and invasion may have been triggered by the logging disturbance. Prior to logging, there were probably abundant nearby *C. orbiculatus* seed sources, since large fruiting vines up to 35 years old are located today less than 50 m south of the study area. Robinson and Handel (1993) reported that *C. orbiculatus* was dispersed by natural vectors at least 131 m from woodland fringes to a landfill.

If logging created the disturbance necessary for the *C. orbiculatus* invasion, what might account for the apparent two-year post-harvest lag in invasion? Schupp et al. (1989) state that 'most animal seed vectors avoid recently created gaps. New gaps offer few resources and are dangerous sites for birds to perch. . . . We expect lower animal-mediated seedfall in recent gaps than beneath the forest canopy.' In Oregon USA pine forests (USDA-FS 1982) researchers noted that, in the year following harvest, birds were present only at the margins of clear cuts. In addition to a paucity of dispersal agents, it is likely that environmental conditions on a new logging road are not conducive to the seedling survival, with high light and soil disturbance resulting in desiccating conditions. *C. orbiculatus* seedlings germinate best in low light (Patterson 1974) and are prone to desiccation for two weeks after germination (Silveri, personal observation).

2. Are former logging roads more invasible than surrounding selectively logged areas? C. orbiculatus occurred more frequently on former logging roads than in surrounding areas, suggesting that they are (or were in the past) more invasible than their surroundings. This may be due to a higher seed rain, better conditions for seedling establishment, or both. Levels of *C. orbiculatus* seed rain in the study area were not investigated, and little information is available on the dispersal of seeds into forest corridors by avian frugivores. A higher seed rain could occur if frugivorous birds perceive former logging roads as desirable 'edge habitats' or gaps, or preferentially use them as flyways (e.g. Malmborg and Willson 1988; Gates and Griffen 1991; Miller et al. 1998).

Although this study detected no significant difference in percent exposed mineral soil between logging roads and surrounding areas, it is likely that this difference was statistically significant shortly after the logging (e.g. Mou et al. 1993) and was a factor in the initial invasion. Ramco Baars and Sparrow (1998) found that, although direct estimates of site disturbance (such as treefall) were not correlated with New Zealand invasive liana frequency, *inferred past disturbance* (the presence of early successional vegetation) was associated with a higher frequency of introduced vines.

Within the sample plots, *C. orbiculatus* density was positively correlated with percent exposed mineral soil, suggesting that areas with a large amount of exposed soil are more invasible than areas with little exposed soil, whether they exist on or off of former logging roads. Removal of the litter layer may increase invasibility by making it easier for seedlings' roots to penetrate the soil, producing drier conditions unfavorable to pathogens, and/or reducing the incidence of lethal surface temperatures (e.g. Roberts and Dong 1993). In the study area, the altered aspect of logging roads (from east or southeast to south) may increase their invasibility by increasing levels of direct solar radiation and soil temperature. Brothers and Spingarn (1992) found that, in central Indiana (USA) old-growth forests, alien plant frequency was greater on 'warm' south and west plot aspects than on 'cold' north and east ones.

3. Do former logging roads provide better C. orbiculatus *habitat than surrounding selectively logged areas?* The present study suggests that logging roads provide *C. orbiculatus* with habitat that is superior (for establishment and growth) to adjacent selectively logged tracts of land. Fourteen years after being constructed, logging roads in the study area differed from surrounding selectively logged areas in having a higher (closer to circumneutral) soil pH, a difference that promotes the growth of this invading vine. The bedrock underlying the study area is predominately limestone, so the higher pH may be the result of an increase in bedrock exposure and weathering following road construction. Ramco Baars and Sparrow (1998) also reported that, in New Zealand forest remnants, past disturbance was associated with elevated soil pH. In addition to the positive correlation between vine length and soil pH in the study area, two other lines of evidence suggest that circumneutral soil constitutes preferred habitat for *C. orbiculatus* of all ages: (1) Germinated seeds planted in the field produced the largest seedlings in circumneutral soil; and (2) *C. orbiculatus* density and percent cover were positively correlated with soil pH. Many vine species are associated with high soil pH. Ramco Baars and Sparrow (1998) reported that New Zealand sites with introduced lianas generally have high soil pH. Teramura et al. (1991) report that in the tropics high liana abundances are often associated with areas of relatively rich (moist and circumneutral pH) soil. Though *C. orbiculatus* grows most rapidly on circumneutral soils, it is not excluded from acidic soils. In coastal Connecticut, USA, for instance, *C. orbiculatus* grows abundantly in soils with pH ranging from 4.5 to 5.5 (G. Dreyer, personal communication). Like many invasive plants (Baker 1965), *C. orbiculatus* tolerates a wide range of edaphic conditions.

Invasion strategy

The present study and the literature suggest that *C. orbiculatus* possesses a suite of characteristics making it well adapted to invade mesic temperate forests with varying disturbance levels. These characteristics include: (a) wide distribution by avian and human vectors; (b) wide tolerance of edaphic conditions; (c) extensive powers of photosynthetic acclimation (Patterson 1975); (d) rapid extension growth; (e) ability to climb supports of varying sizes. Although resource enrichment (such as increased irradiance) and/or removal of barriers (such as an intact canopy or litter layer) following disturbance increase the odds of invasion into temperate forests, these are apparently not a prerequisite for invasion. Several late-successional deciduous and coniferous forests on the sanctuary contained small but apparently healthy seedlings, growing through an intact litter layer on a well-shaded forest floor (see also McNab and Meeker 1987).

It appears that in the absence of significant disturbance, *C. orbiculatus* is able to invade forested habitat but not reproduce sexually. Of the 105 stems collected in the logged forest, the only fruiting plants were two 12-year-old stems that had reached canopy level, growing in a gap produced by the death of a single tree. However, *C. orbiculatus* stems in open-light habitats produce fruit by their fourth year (Silveri, personal observation) and possibly earlier. This suggests that, in the absence of disturbance, *C. orbiculatus* invades forested habitat using a strategy similar to the 'advance regeneration' of some canopy trees. Like these shade-tolerant species (Philips and Shure 1990; White 1991), *C. orbiculatus* seedlings may persist for long periods on the forest floor but require creation of a gap to reach the canopy and reproduce sexually. Putz (1984) found that lianas on Barro Colorado Island in Panama employ a comparable strategy, and observed that many of the small woody plants on the forest floor were liana rather than tree seedlings. Horvitz et al. (1998) reported that 'advance regeneration into forest communities by non-indigenous species [including vines] is common in tropical and subtropical forests.' Our data suggest that a window for control of *C. orbiculatus* in forested habitat may occur in the early stages of invasion, when population spread is slow because plants are light limited and unable to reproduce sexually. After the initiation of sexual reproduction, *C. orbiculatus* may spread rapidly and, in the presence of sufficient disturbance, become the dominant canopy species.

Because only 3/56 (5%) of the *C. orbiculatus* stems found in the sample plots were in randomly placed plots and 53/56 (95%) were in logging-road plots, the correlations of *C. orbiculatus* abundance with environmental parameters are a result of the vine being associated with certain environmental conditions within former logging roads. While former logging roads provide favorable habitat for *C. orbiculatus*, not all parts of the roads are equally conducive to invasion. Although the effects of microhabitat on *C. orbiculatus* germination were not explored in the present study (planted seeds had been germinated indoors under uniform conditions), this suggests that *C. orbiculatus*, like many species (Harper 1977), may be highly sensitive to microhabitat differences during germination. Collins and Wein (1993) found that microhabitat was important in predicting the distribution of 11 temperate vine species in a mixed hardwoods forest, with density of vines being highest in plots of medium elevation and medium soil moisture. Bungard et al. (1997) reported that germination (and therefore distribution) of the invasive vine *Clematis vitalba* in New Zealand was determined by light levels and increases in plant-available nitrogen following soil disturbance.

In conclusion, the ability of *C. orbiculatus* to invade North American forests and halt succession makes it an invasive exotic plant of the highest management priority. Attention should be given to an investigation of control methods, particularly biological control, that have potential to limit the spread of this exotic invader on a large scale.

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