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Fruit fate, seed germination and growth of an invasive vine – an experimental test of 'sit and wait' strategy *

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Abstract

Oriental bittersweet (*Celastrus orbiculatus* Thunb.) is a non-indigenous, invasive woody vine in North America that proliferates in disturbed open sites. Unlike most invasive species, *C. orbiculatus* exhibits a 'sit and wait' strategy by establishing and persisting indefinitely in undisturbed, closed canopy forest and responding to canopy disturbance with rapid growth, often overtopping trees. We compared fruit fates of *C. orbiculatus* and native American holly (*Ilex opaca*). We also explored mechanisms for this 'sit and wait' invasion strategy by testing the effect of *C. orbiculatus* fruit crop density on removal rates and by examining the influence of seed treatment and light intensity on seed germination and seedling growth. More *C. orbiculatus* than *I. opaca* fruits became damaged, and damage occurred earlier. More fruit fell from *C. orbiculatus* than *I. opaca*, but removal rates by frugivores did not differ ($76.0 \pm 4.2\%$ vs $87.5 \pm 3.7\%$, respectively). Density (number of fruits in a patch) of *C. orbiculatus* did not influence removal rates. Scarification (bird-ingestion) of *C. orbiculatus* seed delayed germination but seeds germinated in similar proportion to manually defleshed seeds (sown either singly or all seeds from a fruit). Germination of seeds within intact fruits was inhibited and delayed compared to other treatments. Seed treatment did not affect seedling growth. The proportion of seeds germinating and time until germination was similar among five light intensity levels, ranging from full sun to closed-canopy. Seedlings in >70% photosynthetically active radiation (PAR) had more leaves, heavier shoots, and longer, heavier roots than seedlings at lower PAR levels. Results show that most (>75%) *C. orbiculatus* seeds are dispersed, seedlings can establish in dense shade, and plants grow rapidly when exposed to high light conditions. Control strategies for this highly invasive species should likely focus on minimizing seed dispersal by vertebrates.

Introduction

Invasive, non-indigenous plant species pose a major threat to the conservation and management of natural ecosystems by reducing native plant species richness and potentially altering ecosystem processes, disturbance types, and disturbance regimes (e.g., Vitousek 1990; Gordon 1998). Successful invasion requires effective mechanisms for reproduction, dispersal, establishment, and growth (Gordon 1998). Characteristics that predispose non-indigenous plants as potentially invasive include *r*-selected traits, high dispersal rates, and vegetative reproduction (Lodge 1993). Invasible habitat was traditionally thought to be islands with depauperate floras and unfilled niches (Woodward 1993; Gordon 1998), or disturbed sites with abundant light, disturbed soil, and released

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resources (Fox and Fox 1986; Orians 1986; Drake et al. 1989; Hobbs and Huenneke 1992). However, there are many examples of non-indigenous species that invade relatively undisturbed habitats (e.g., Bazzaz 1986; Hobbs and Atkins 1988; Usher 1988; Huenneke 1991; Lodge 1993).

Oriental bittersweet (*Celastrus orbiculatus* Thunb.) is a highly invasive woody vine (Dreyer 1988) introduced to North America from southeast Asia in 1860 as an ornamental plant. By 1974 it had spread to 33 states (Patterson 1974). It is now becoming a serious threat to many native plant communities in the eastern United States (Dreyer et al. 1987). In the southern Appalachians, *C. orbiculatus* is particularly abundant near Asheville, North Carolina (McNab and Meeker 1987). It proliferates primarily in disturbed, open sites but also establishes and persists indefinitely in low light under closed canopies. It responds to canopy disturbance with rapid vegetative growth that overtops and kills native vegetation at all strata by blocking light (Hutchinson 1992) and increasing the susceptibility of trees to mechanical breakage from wind and ice damage (Patterson 1974).

Shade tolerance, ability to spread by root suckering, rapid vegetative growth under high light conditions, and prolific annual crops of bright orange arillate fruits all contribute to the success of *C. orbiculatus* as an invader. Seeds are dispersed primarily by birds and mammals (Patterson 1974; McNab and Meeker 1987). Humans contribute significantly to seed dispersal by ornamental plantings and by decorating with fruiting stems, then discarding them outside (Dreyer et al. 1987). Clearly, a better understanding of fruit availability and fruit fate, seed germination and growth requirements would benefit land managers in designing control strategies for the dispersal and spread of *C. orbiculatus.*

Patterns of fruit availability and use by vertebrates likely correlate to a plant species' abundance and rate of spread (Willson and Whelan 1993). Therefore, understanding the factors that influence removal of *C. orbiculatus* fruit is important in its management and control. Comparing fruit fate of the non-indigenous *C. orbiculatus* with the similar sized and colored fruit of the native American holly (*Ilex opaca*), could improve our understanding of *C. orbiculatus* dispersal mechanisms.

Fruit density can affect removal rates by vertebrates, but results are inconsistent among studies. Sargent (1990) found that fruits in areas with high fruit density and high-density neighborhoods were removed significantly faster than fruits in low-density areas. Willson and Whelan (1993) found that fruits of rough-leaf cornel (*Cornus drummondii*) were removed faster from small than large crops, but Davidar and Morton (1986) found no correlation between the fruit crop size and the proportion of fruits removed. Murray (1987) concluded that although the total proportion of fruit removed was independent of crop size, the probability of visitation by fruit predators increased with crop size. Fruit neighborhood effects and other landscape level factors that influence removal (and presumably dispersal) rates of *C. orbiculatus* fruits could potentially be controlled to reduce its rate of spread, but only with a better understanding of these factors.

Seed germination success also influences the potential of plants to become invasive. Ingestion by birds may increase, decrease, or have no effect on seed germination rates of different species (Murray 1988; Barnea et al. 1990, 1991; Traveset 1998). Seed germination rates are high in *C. orbiculatus* (Patterson 1974; Dreyer et al. 1987; Clement et al. 1991). Although birds are thought to be the primary dispersers of *C. orbiculatus* (Patterson 1974), no one has examined whether gastrointestinal scarification by birds enhances seed germination or seedling growth.

Finally, the influence of light intensity on germination and growth patterns has important implications for establishment and spread of non-indigenous plants in response to forest disturbance. Patterson (1974) reported highest germination rates of *C. orbiculatus* seeds at low light intensities, but greater seedling growth and dry weight at medium and high light intensities. To explore the 'sit and wait' invasion mechanism of *C. orbiculatus*, we hypothesized that root growth would increase proportionately with low light intensities to ensure 'readiness' for light-creating disturbances, whereas shoot growth would increase with full sunlight.

We conducted four experiments to test the mechanisms of this 'sit and wait' invasion strategy. Our hypotheses were: (H_1) fate (removal, damage, and fall rates) of *C. orbiculatus* and *I. opaca* fruits will differ; (H_2) fate of *C. orbiculatus* fruit will differ in high-density vs low-density fruit patches; (H_3) the proportion of seeds germinating, number of days until germination, and seedling growth will differ among seeds that have been ingested and defecated or regurgitated (scarified) by birds, defleshed and sown singly,

defleshed and sown together with all seeds per fruit, and seeds within intact fruits; and (H_4) the proportion of seeds germinating, number of days until germination, and seedling growth will differ among five levels of photosynthetically active radiation (PAR).

Methods

Study area

The Bent Creek Experimental Forest and nearby Blue Ridge Parkway are located in the Asheville basin near Asheville, North Carolina. Average annual precipitation is 120 cm and is distributed throughout the year. Elevation within the study area ranges from 700 to 1070 m. Winters are short and mild, summers are long and warm. Common tree species include scarlet oak (*Quercus coccinea*), chestnut oak (*Q. prinus*), black oak (*Q. velutina*), blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), and occasional shortleaf pines (*Pinus echinata*). Tulip poplar (*Liriodendron tulipifera*) and northern red oak (*Q. rubra*) dominate on moist slopes and coves. Red maple (*Acer rubrum*), hickories (*Carya* spp.), dogwood (*Cornus florida*), and white oak (*Q. alba*) are common throughout (McNab 1996).

Experiment 1: fate of C. orbiculatus *vs* I. opaca *fruits*

We compared fruit availability and fate (removal, damage, and fall rates) of non-indigenous *C. orbiculatus* and native *I. opaca* fruits at replicate sites ($n = 13$) along roadsides where both *C. orbiculatus* and *I. opaca* occurred $\leq$30 m apart. At each site, 20 ripe fruits of each species were marked with a dot of white paint at the point of attachment to the pedicel, and also on the branch near the fruit (Levey 1987). Only one fruit per cluster was marked to increase independence of samples (McCarty et al., in press). Shadecloth was placed under each plant to catch fallen fruit. From 1 November to 30 May 2000 marked fruits remaining on plants were counted weekly, and categorized as intact or damaged (including damage by insects, microbes, or desiccation). Marked fruits found beneath plants (on shadecloths or nearby) were counted and categorized as fallen (regardless of condition). Missing fruits were assumed eaten by a vertebrate (Willson and Whelan 1993). Sampling continued until nearly all marked fruits were gone. Some fallen fruits may have been subsequently consumed by vertebrates. Further, removed fruits may be overestimated if fallen fruits rolled off the shadecloth. We conducted univariate repeated measures ANOVA to compare the proportion of *C. orbiculatus* and *I. opaca* fruits that were remaining, fallen, removed, or damaged over time (sample dates) and among sites, and to check for a species $\times$ time interaction effect. All proportion data were square-root arcsin transformed for ANOVA's.

Experiment II: effect of C. orbiculatus *fruit crop density on removal rates by vertebrates*

We compared fruit removal rates in 10 high-density and 10 low-density *C. orbiculatus* patches located $\geq$0.2 km apart along roadsides. We defined a low-density patch as having $<$100 fruits per 0.25 m^2 (counted in twenty 0.25-m^2 quadrats) and $<$500 total fruits, and a high-density patch as having $\geq$100 fruits per 0.25 m^2 ($n = 20$) and $\geq$500 total fruits. Fruits were marked and counted weekly, as described above. Univariate repeated measures ANOVA was used to compare the proportion of fruit that were remaining, fallen, removed, or damaged from high- and low-density patches over time, and to check for a treatment $\times$ time interaction effect.

Experiment III: influence of C. orbiculatus *seed treatment on germination and growth*

In a greenhouse we tested whether seed treatment affects the proportion of *C. orbiculatus* seeds germinating, number of days until germination, and growth of seedlings. Fifty fruits from $\geq$10 individual plants were gathered and mixed to avoid fruit-maternity effects and to randomize seed selection. Four seed treatments were selected to determine whether germination is enhanced by avian gut scarification *per se* (as for seeds that are consumed by birds), or simply by removal of the fruit pulp and skin (a control), compared to seeds within intact fruits (as for seeds within fallen fruits). We also tested whether competition among seeds from a fruit influences germination. The four seed treatments were as follows: (1) scarified: fruits were quartered and fed to 31 captive yellow-rumped warblers (*Dendroica coronata*); defecated or regurgitated seeds were sown singly ($n = 43$), (2) defleshed-1seed (DF1): pulp and skin were removed manually; seeds sown singly ($n = 40$), (3) defleshed-all seeds (DFA): pulp and

skin were removed manually; all seeds from the fruit were sown together (4.3 ± 0.2, mean ± SE, sown within approximately 180 cm^2; total n = 173 seeds in 40 pots), and (4) intact: one intact fruit was sown per pot (estimated n = 173 seeds in 40 pots). All seeds in this experiment were stratified in plastic bags at 5 °C for 60 days before planting (USDA Forest Service 1948). Seeds were sown in ca 1-l of potting soil on 28 February 2000 and watered daily. We recorded the germination date of seeds in all treatments until 61 days after sowing, by which point germination rates had reached asymptote in all but the intact treatment, which continued to germinate a very low rate (Figure 3). Root and shoot lengths of seedlings in treatments 1 and 2 (individually sown seeds only) were measured 28 days after germination.

We used chi-square test for independence to determine whether germination rates differed among treatments after 61 days. We applied Analysis of Variance with least squares means comparisons to test for differences in the mean number of days until germination for the four seed treatments using, and Student's t-tests to determine whether seedling root and shoot length differed between scarified and DF1 treatments 28 days after germination.

Experiment IV: influence of PAR on C. orbiculatus *germination and growth*

We tested the effect of five natural light intensities on germination and growth of *C. orbiculatus* in the greenhouse. We manipulated the percentage of PAR with ultraviolet-treated polypropylene shadecloth (Amoco Co.) to simulate light intensities ranging from closed canopy forest to full sun. PAR was measured using a quantum sensor (Licor Corp.). PAR in full sun was approximately 1108 $\mu mol\ m^{-2}\ s^{-1}$. Treatments were full sun (100%) and PAR of 70%, 53%, 37%, and 20%. Defleshed seeds were sown singly on 23 May 2000 (after 150 days stratification at 5 °C) and watered daily. We applied fertilizer (Miracle-Gro Co., standard application) twice over the duration of the experiment.

We recorded the date of germination and the number of leaves and length and dry biomass of roots and shoots (n = 16–22 per treatment, destructively sampled) 100 days after germination. We used chi-square analysis to test whether germination rates differed among the five light treatments after 100 days. We applied ANOVA with least squares means comparisons to test for differences in mean number of days to germination for the five light treatments, and whether the number of leaves, root, and shoot length or root and shoot dry biomass of seedlings differed among the five light treatments 100 days after germination.

Results

Experiment 1: fate of C. orbiculatus *vs* I. opaca *fruits*

Ilex opaca retained fruit longer (median 15.5 weeks) than *C. orbiculatus* fruits (median 10.5 weeks). By 30 May, significantly more fruit remained on *I. opaca* than on *C. orbiculatus* plants (7.9 ± 4.1% vs none; $F_{1,11}$ = 10.1, P = 0.009; Figure 1). The amount of fruit remaining on plants also differed among sites ($F_{1,11}$ = 38.4, P < 0.0001) and sample dates ($F_{29,638}$ = 164.1, P < 0.0001), and the sample date × species interaction was significant ($F_{29,638}$ = 1.8, P = 0.0081).

Differences in fruit retention between species were due to fruit fall rather than removal. By 30 May significantly more fruit had fallen from *C. orbiculatus* than from *I. opaca* plants (24.0 ± 4.2% vs 4.6 ± 1.8%; $F_{1,11}$ = 23.9, P = 0.0005; Figure 1). The proportion of fallen fruit differed among sites ($F_{1,11}$ = 67.4, P < 0.0001) and sample dates ($F_{29,638}$ = 24.5, P < 0.0001), and the time × species interaction was significant ($F_{29,638}$ = 24.5, P < 0.0001). In contrast, the overall proportion of removed fruit (not found on or beneath plants) did not differ between *C. orbiculatus* and *I. opaca* (76.0 ± 4.2% vs 87.5 ± 3.7% by 30 May; $F_{1,11}$ = 0.1, P = 0.7923; Figure 1). Removal rates differed among sites ($F_{1,11}$ = 54.0, P < 0.0001) and sample dates ($F_{29,638}$ = 123.9, P < 0.0001), and the time × species interaction effect was significant ($F_{29,638}$ = 4.4, P < 0.0001).

Significantly more *C. orbiculatus* fruits than *I. opaca* fruits were damaged ($F_{1,11}$ = 482.2, P < 0.0001; Figure 1). The proportion of damaged fruit also differed among sites ($F_{1,11}$ = 14.7, P < 0.0001) and sample dates ($F_{29,638}$ = 18.7, P < 0.0001), and the time × species interaction effect was significant ($F_{29,638}$ = 14.90, P < 0.0001). *Celastrus orbiculatus* fruits became damaged more rapidly than *I. opaca* fruits. By early February (week 14) virtually

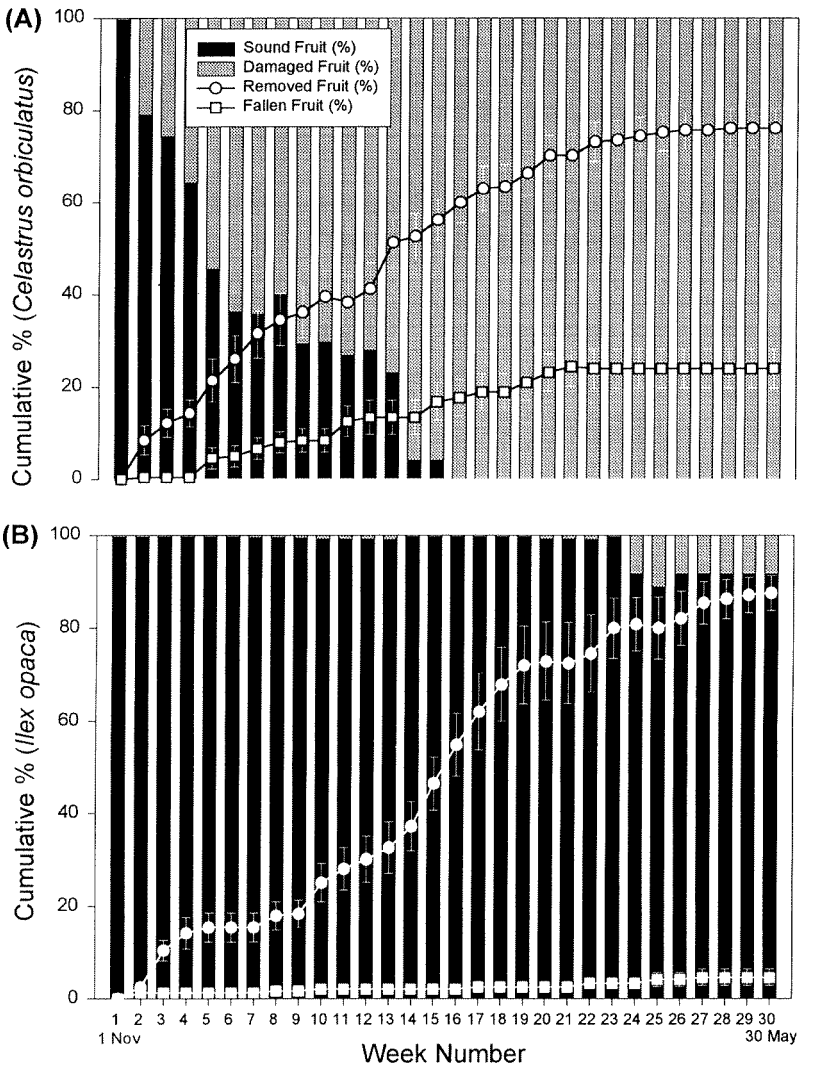

Figure 1. Mean (± SE) cumulative proportion of fallen and removed fruit from 1 November to 30 May 2000 of (A) *C. orbiculatus* and (B) *I. opaca*, represented by lines. Bars indicate the proportion of sound vs damaged fruit remaining on the plant (e.g., by week 16 100% of *C. orbiculatus* fruits remaining on the plant were damaged).

all remaining *C. orbiculatus* fruits were damaged, whereas most *I. opaca* fruits were still sound at the end of May (Figure 1). Continued removal of *C. orbiculatus* fruits after early February suggests that damaged fruits were consumed and dispersed by vertebrates.

The temporal pattern of fruit fall and removal differed between the species. Higher rates of *C. orbiculatus* fruit-fall were apparent beginning in mid-December (Figure 1), possibly because more fruits were damaged. In late February and March, American robins (*Turdus migratorius*) removed a large proportion of *I. opaca* fruit from some sites (L.M. Smith, personal observation) (Figure 1) probably accounting for the previously noted time × species interaction.

Experiment II: effect of C. orbiculatus *fruit crop density on removal rates by vertebrates*

Fruit retention was similar between high- and low-density *C. orbiculatus* fruit patches by 30 May (1.5 ± 0.8% vs none; $F_{1,18} = 0.3$, $P = 0.5796$). However, differences among sample dates were significant ($F_{29,522} = 172.3$, $P = 0.0001$) as was the time × treatment interaction ($F_{29,522} = 2.0$, $P = 0.0023$).

Median fruit retention was identical (8.5 weeks) for both high- and low-density fruit patches.

The amount of fallen fruit was similar between treatments ($F_{1,522} = 0.7$, $P = 0.4258$). However, differences in the amount of fallen fruit among sample dates were significant ($F_{29,522} = 36.9$, $P = 0.0001$) as was the time × treatment interaction ($F_{29,522} = 1.9$, $P = 0.0032$). The amount of fruit removed was also similar between high- and low-density patches ($F_{1,522} = 0.0$, $P = 0.9293$). However, removal rates differed among sample dates ($F_{29,522} = 99.2$, $P = 0.0001$). There was no time × treatment interaction effect ($F_{29,522} = 0.5$, $P = 0.9945$).

By 30 May the proportion of damaged fruit remaining was similar between treatments ($F_{1,332} = 3.1$, $P = 0.0963$). However, differences among sample dates were significant ($F_{29,332} = 27.9$, $P = 0.0001$) as was the time × treatment interaction ($F_{24,332} = 3.9$, $P = 0.0001$). Most fruit was damaged by early February (Figure 1).

Experiment III: influence of C. orbiculatus *seed treatment on germination and growth*

The experiment revealed significant differences in the mean number of days until germination (Figure 2) among the four seed treatments ($F = 52.05$, d.f. = 3294; $P < 0.0001$). Seeds within intact fruits took longer to germinate, followed by scarified seeds. Defleshed seeds took the fewest number of days to germinate regardless of whether they were sown individually (DF1) or with all seeds from a fruit (DFA) (Figure 2). The proportion of seeds germinating within 61 days also differed among treatments ($\chi^2 = 14.78$, d.f. = 3, $P < 0.005$; Figure 3). We found no differences in the proportion of seeds germinating among scarified, DF1, or DFA treatments (total 82.0%; $\chi^2 = 3.67$; d.f. = 2; $P < 0.25$), but significantly fewer (51%) seeds of intact fruits germinated than in other treatments ($P < 0.001$).

Seedlings from the DF1 and scarified treatments showed no differences in root length (mean (cm) ± SE) (12.4 ± 1.0 vs 12.2 ± 0.8; $t = 0.15$, d.f. = 59, $P = 0.8812$), shoot length (3.7 ± 0.2 vs 3.4 ± 0.2; $t = 1.36$, d.f. = 59, $P = 0.1789$), or total length (16.1 ± 1.0 vs 15.6 ± 0.9; $t = 0.38$, d.f. = 59, $P = 0.7089$).

Experiment IV: influence of PAR on C. orbiculatus *germination and growth*

Varying light treatments did not produce significant differences in the proportion of seeds germinating (55.0 ± 2.9%; range 45–65%; $\chi^2 = 1.54$, d.f. = 4,

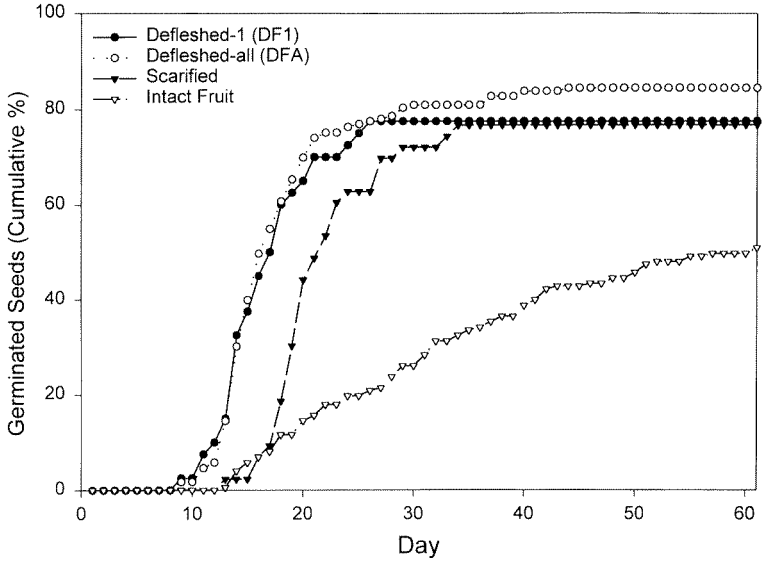

Figure 2. Mean (±SE) number of days in a greenhouse until germination of *C. orbiculatus* seeds following four treatments: defleshed and sown singly (DF1); defleshed and sown together with all seeds from fruit (DFA); ingested by birds (scarified) and sown singly; and intact fruit (with all seeds). Different letters above bars indicate significant differences among treatments.

$P < 0.9000$), the number of days until germination ($F_{4,105} = 1.8$, $P = 0.1328$) (Table 1), the root : shoot weight ratio ($F_{4,90} = 1.6$, $P = 0.1867$), or the root : shoot length ratio ($F_{4,90} = 0.4$, $P = 0.8168$). In general, seedlings in full sun or 70% PAR had more leaves, heavier shoots, and longer, heavier roots, although there was some overlap between measurements of seedlings in 70% PAR and lower PAR levels (Table 1). Significantly more defleshed (including scarified) seeds that were sown in late February for Experiment III (stratified 60 days) germinated compared to those sown in late May for this experiment (stratified 150 days) (total 82%, $n = 256$ vs 55%, $n = 200$; $\chi^2 = 18.65$, d.f. $= 1$, $P < 0.001$).

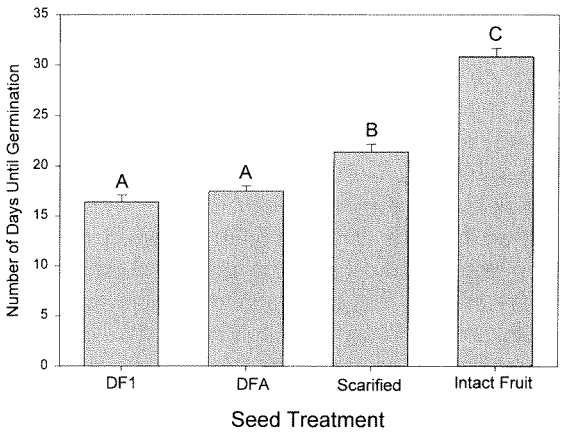

Figure 3. Cumulative number of *C. orbiculatus* seeds germinated in a greenhouse over a 61-day period following four treatments: defleshed and sown singly (DF1); defleshed and sown together with all seeds from fruit (DFA); ingested by birds (scarified) and sown singly; and intact fruit (with all seeds).

Discussion

Patterson (1974) reported that *C. orbiculatus* fruits remain on plants until spring when they are taken by birds and mammals (observations of L.H. Bradley, National Audubon Nature Center, North Greenwich Connecticut). Our data indicate that >80% of *C. orbiculatus* fruits remained on plants until December, and >50% remained until mid-January. By early March >80% of *C. orbiculatus* fruits were gone. *Ilex opaca* fruits were more persistent than *C. orbiculatus*, with >50% remaining on plants until mid-February and >20% remaining until April. By late May new flowers were observed on *I. opaca* trees that still retained marked, sound fruit from the previous year. *C. orbiculatus* fruits fell more rapidly, and fruits became damaged much earlier than *I. opaca* fruits. In contrast, *I. opaca* fruits were more likely to be removed by vertebrates than to fall. Clearly, fruits of both species more often eaten by vertebrates in winter than in fall or spring.

Although temporal patterns of removal differed between *C. orbiculatus* and *I. opaca*, differences in total fruit retention were due to fruit fall. Fruit removal rates differed among sites and sample dates, but total fruit removed did not differ between the two species. Studies of other species report high variation in fruit removal rates (e.g., Denslow 1987; Sargent 1990; Willson and Whelan 1993; McCarty et al. in press). That can be attributed to differences in fruit nutrient content (e.g., Stiles 1993; Fuentes 1994; Witmer and VanSoest 1998), differences in fruit preference by individual birds (e.g., Jung 1992; Willson and Comet 1993; Willson 1994), and effects of habitat, fruit density, and fruit neighborhood (e.g., Levey et al. 1984; Moermond and Denslow 1985; Howe 1986; Sargent 1990; Whelan et al. 1998).

Table 1. Results (mean ± SE) of greenhouse experiment on germination and growth of *C. orbiculatus* under five levels of PAR to simulate full sun (100% PAR; approximately 1108 μmol m^{-2} s^{-1}) to closed canopy (20% PAR) light conditions.

	PAR (%)					
	100	70	53	37	20	*P*-value
Days until germination	16.3 ± 1.5	15.1 ± 1.2	12.8 ± 0.5	14.6 ± 0.8	14.4 ± 0.8	0.1328
Number of leaves	18.6 ± 1.2^{a}	$17.8 \pm 1.2^{a,b}$	$13.3 \pm 0.9^{c,d}$	$15.7 \pm 0.8^{b,d}$	12.9 ± 0.6^{c}	<0.0001
Shoot length (cm)	8.1 ± 0.4	8.2 ± 0.4	7.0 ± 0.4	8.2 ± 0.5	7.5 ± 0.4	0.1606
Shoot weight (g)	0.31 ± 0.06^{a}	$0.27 \pm 0.02^{a,b}$	0.16 ± 0.01^{c}	$0.19 + 0.02^{b,c}$	0.13 ± 0.01^{c}	0.0004
Root length (cm)	27.8 ± 0.4^{a}	27.8 ± 0.3^{a}	25.6 ± 0.8^{b}	$26.5 \pm 0.6^{a,b}$	25.2 ± 0.7^{b}	0.0107
Root weight (g)	$0.20 + 0.04^{a}$	$0.13 + 0.02^{b}$	$0.08 + 0.01^{b,c}$	$0.09 + 0.01^{b,c}$	$0.04 + 0.00^{c}$	<0.0001

Different letters within rows indicate significant differences among treatments.

Our results indicate that fruit density did not affect removal rates of *C. orbiculatus* fruits. However, we observed high spatial and temporal variation in fruit removal. Willson and Whelan (1993) suggest that fruit removal patterns are better explained by avian biology such as flocking and social behavior than by fruit or fruiting plant characteristics. We never observed vertebrates eating *C. orbiculatus* fruits in the field. In late December we found several *I. opaca* fruit fragments in the shadecloth beneath a study tree, suggesting that birds had partially eaten fruits. In late February we observed a flock of American Robins eating *I. opaca* fruits from one of our study trees and from others within the vicinity. These observations suggest that flocks of overwintering birds target specific fruit patches, resulting in pulses of fruit removal over space and time.

The high germination rate (total 82%) of defleshed (including scarified) *C. orbiculatus* seeds indicates that seeds without fruit pulp or skin have a high probability of germinating. Other studies also report germination rates ranging from 71% to 95% (Patterson 1974; Dreyer et al. 1987; Clement et al. 1991). Patterson (1974) reported lower germination of older seeds. In our study, lower germination rates of *C. orbiculatus* seeds sown in late May than in late February also suggest that viability decreases with age or prolonged stratification.

Results of this study indicate that the presence of fruit pulp or skin on *C. orbiculatus* fruit inhibits germination by reducing the proportion of seeds that germinate and by delaying germination. However, a 51% germination rate of seeds within intact *C. orbiculatus* fruits indicates that even fruits that are not consumed or dispersed by vertebrates may contribute to the spread of *C. orbiculatus*.

Scarified seeds showed delayed germination relative to defleshed seeds, but the overall proportion of seeds germinating by day 61 was similar among all seed treatments where fruit pulp and skin were removed (asymptote reached by 26–44 days for scarified, DF1, and DFA treatments). The similar number of days until germination between DF1 and DFA treatments suggests that competition among seeds does not impede the rate of germination. Seedling growth was unaffected by seed treatment.

Clearly, mechanical and chemical abrasion of *C. orbiculatus* seeds by ingestion did not confer any germination or growth advantage. Traveset (1998) reported that seed dispersers enhance seed germination in about 50% of the plant species they consume. Our results indicate that birds probably enhance *C. orbiculatus* seed dispersal, but their contribution to germination is limited to removing the pulp and skin, and not to gastrointestinal scarification.

Several studies report high germination rates of *C. orbiculatus* under low light levels (Patterson 1974; Dreyer et al. 1987). Patterson (1974) reported highest germination at low light intensities or in the dark. In contrast, our results indicate that light intensity does not affect the proportion of seeds germinating, the time until germination, or seedling survival. This high level of germination over a wide range of conditions likely facilitates the establishment of seedling banks under closed canopy conditions. Patterson (1974) reported a high capacity for photosynthetic light acclimation by *C. orbiculatus* seedlings. Seedlings grown in low light conditions nearly doubled their photosynthetic rate within 8 days of exposure to high light. Patterson (1974) also reported greater height growth and dry weight of seedlings in high and medium light than in low light. In our study, seedlings exposed to full sun or 70% PAR had more leaves and greater shoot and root length and dry biomass than seedlings exposed to lower light levels. However shoot length did not significantly differ among light level treatments.

Most invasive species exploit disturbed sites with abundant light, reduced competition, and altered availability of resources such as nutrients and water (e.g., Orians 1986; McIntyre and Lavorel 1994). In contrast, *C. orbiculatus* uses a 'sit and wait' invasion strategy by establishing under closed canopy forest conditions and persisting indefinitely until it is released by a disturbance that creates conditions optimal for rapid growth.

Our experimental results clarify the mechanisms by which *C. orbiculatus* employs this 'sit and wait' strategy for invading undisturbed temperate forest. Most fruits (>75% by 30 May) are apparently removed by vertebrates, and presumably dispersed. Most defleshed seeds (including scarified seeds or seeds with fruit pulp and skin manually removed) germinate (82%), although viability decreased to 55% after 150 days of stratification. Seeds within intact fruits also have a moderate germination rate (51%), suggesting that even fallen fruits (24%) contribute substantially to the viable seed pool. Seed germination and seedling survival is similar under lighting intensities ranging from full sun (as in disturbed, open environments) to 20% PAR (as in closed canopy forest), allowing establishment of a seedling bank under a wide range of light

conditions. However, the number of leaves, and root and shoot mass of seedlings is greater under high light conditions, suggesting that canopy disturbance aids the vegetative and clonal spread of established seedlings.

Our results show that viable *C. orbiculatus* seeds are dispersed in large numbers, are capable of successful establishment under closed canopy conditions, and grow rapidly when exposed to high light conditions. This 'sit and wait' invasion strategy allows *C. orbiculatus* to invade intact forest and await a canopy disturbance for the opportunity to proliferate. In this manner *C. orbiculatus* is becoming an increasingly serious threat to plant communities across the eastern United States. Control strategies for this highly invasive species should likely focus on minimizing seed dispersal by vertebrates.

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