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*) is a vertebrate-dispersed exotic, invasive woody vine in the USA. Using a "sit and wait" strategy, it establishes in closed-canopy forest, and responds to canopy disturbance with rapid growth, often overtopping trees. We studied bittersweet's distribution, abundance, and effect on native plant diversity along the Blue Ridge Parkway (BRP) in relation to topographic characteristics, elevation, distance from Asheville, NC and distance from roadside. We also experimentally tested its mechanisms for dispersal and establishment. The occurrence of bittersweet along the BRP decreased with elevation, which also corresponded with distance from Asheville; we observed it as high as 1,994 m elevation. Bittersweet cover and number of stems were unrelated to distance from the roadside, but growth height was greater along roads than in the forest. It occurred more often on moist, north-facing than on drier, south-facing slopes, and percent cover was negatively related to native plant diversity. Seventy-six percent of marked fruits were removed; 24% fell to the ground. Fruit crop density did not affect removal rates. Seeds that were scarified by bird ingestion exhibited delayed germination, but seeds germinated in similar proportion to manually defleshed seeds. Germination of seeds within intact fruits was also delayed, and fewer germinated compared to other treatments. The amount of photosynthetically active radiation (PAR) received (20, 37, 53, 70, or 100%) did not affect the proportion of seeds germinating or germination rates. However, seedlings in ≥70% PAR had more leaves, heavier shoots, and longer, heavier roots than seedlings at lower PAR levels. Results show that bittersweet appears to be spreading outward from Asheville, and it reduces native plant diversity. Most (>75%) seeds are dispersed, seedlings can establish in dense shade, and plants grow rapidly when exposed to high light conditions. Control strategies should focus on minimizing seed dispersal.

Invasive, exotic plant species can reduce native plant species diversity and alter ecosystem processes such as disturbance types and regimes (Vitousek 1990). Many invasive species are associated with disturbed sites, where competition is reduced and greater resources are often available. Some can invade undisturbed habitats, presumably posing a more serious threat than invasive species that are restricted to disturbed areas.

Oriental bittersweet (*Celastrus orbiculatus*) was introduced to North America from southeast Asia in 1860 (Dreyer 1988). By 1974 it had spread to 33 states (Patterson 1974); in the southern Appalachians, it is particularly abundant near Asheville, North Carolina. It is highly shade tolerant, and can spread by root suckering. It grows rapidly in response to high light conditions, such as canopy openings from disturbance. It annually produces prolific crops of orange fruits that are dispersed by birds and mammals. When released, bittersweet overtops and kills native vegetation at all strata by blocking light.

We report here on a series of studies that address (1) the distribution of bittersweet in relation to its local primary source (Asheville), distance from the roadside, and topographic variables (Konopik 2002); (2) the effect of bittersweet on native plant diversity (Konopik 2002); (3) mechanisms for seed dispersal (Greenberg et al. 2001); and (4) conditions required for seed germination, establishment, and seedling growth (Greenberg et al. 2001). The studies were conducted at the Bent Creek Experimental Forest and nearby Blue Ridge Parkway (BRP), located in the Asheville basin near Asheville, North Carolina. Statistical significance indicates $P<0.05$.

Distribution of bittersweet in relation to Asheville and topographic variables, and impact on native plant diversity: We established three, 1 X 5-m plots parallel to and at three distances from the roadside on both sides of the BRP, where possible, at each milepost from mile 388-407. Our plots ranged from about 671 to 1,474 m in elevation. Distances from the roadside were: 1-3 m (edge); 9-12 m (transition), and > 30 m (interior). We counted the number of bittersweet stems and growth height in all plots. Aspect, elevation, slope, canopy cover, and percent cover of all vascular plant species were also recorded.

Logistic regression indicated that bittersweet was negatively associated with elevation. However, increasing elevation corresponded with increasing distance from Asheville. We noted its occurrence at the Mt. Pisgah parking area, elevation 1,994 m, indicating that distance from Asheville, rather than elevation, is most important in governing the distribution of bittersweet along that stretch of the BRP. Its occurrence in the parking lot of this highly visited hiking trail also suggests that humans may facilitate bittersweet dispersal. The occurrence, percent cover, and number of bittersweet stems were not related to distance from the roadside. Growth height was greater along the roadside edge (where canopy cover was high - averaging 80%), yet significantly lower than in the transition or interior zones. Bittersweet was more likely to occur on north-facing (90% probability) than on south-facing (30% probability) slopes. We also found a significant, negative relationship between bittersweet cover (>20%) and native plant species diversity (H').

Mechanisms for seed dispersal, and conditions required for seed germination, establishment, and seedling growth: In Experiment I we compared removal, damage, and fall rates of non-indigenous bittersweet and native American holly (*Ilex opaca*) fruits by marking fruits at replicate sites (n = 13) along roadsides where both species occurred ≥30 m apart. Both species produce bright orange fruits that ripen in late fall. We conducted univariate repeated measures ANOVA to compare disappearance rates. American holly retained fruit longer (median 15.5 weeks) than bittersweet fruits (median 10.5 weeks). The amount of fruit remaining on plants also differed among sites and sample dates, and the sample date X species interaction was significant. More bittersweet fruits than holly fruits fell, and more were damaged; damaged fruits were apparently consumed and dispersed by vertebrates. The temporal pattern of fruit fall and removal differed between the species due to more bittersweet fruits falling beginning in mid-December, and because American robins (*Turdus migratorius*) removed much holly fruit from some sites in March. Fruits of both species were consumed most during winter. In Experiment II we compared marked fruit removal rates in high- vs. low-density bittersweet patches (n=10) located ≥0.2 km apart along roadsides. ANOVA detected similar fruit retention between high- and low-density bittersweet fruit patches.

In Experiment III we tested in a greenhouse whether seed treatment affects the proportion of bittersweet seeds germinating, number of days until germination, and growth of seedlings. The four seed treatments were: (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-1 seed (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 (ca. 4.3 seeds per fruit), and (4) intact: one intact fruit was sown per pot. The mean number of days until germination differed among the four seed treatments (Chi-square test). 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). The proportion of seeds germinating within 61 days also differed among treatments (ANOVA). We found no differences in the proportion of seeds germinating among scarified, DF1, or DFA treatments (total 82.0%), but significantly fewer (51%) seeds of intact fruits germinated than in other treatments. Seedlings from the DF1 and scarified treatments showed no differences in root length, shoot length, or total height (Student's t-test). The high germination rate (total 82%) of defleshed (including scarified) bittersweet seeds indicates that seeds without fruit pulp or skin have a high probability of germinating, and that the presence of fruit pulp or skin inhibits germination; birds probably disperse bittersweet seeds, but do not aid in germination by gastrointestinal scarification.

In Experiment IV we tested the effect of 5 natural light intensities on germination and growth of bittersweet in the greenhouse by manipulating shadecloth. Treatments were full sun (100%) and photosynthetically active radiation (PAR) of 70%, 53%, 37%, and 20%. We recorded the date of germination, number of leaves and length and dry biomass of roots and shoots (n = 16 to 22 per treatment, destructively sampled) 100 days after germination. Varying light treatments did not produce significant differences in the proportion of seeds germinating (Chi-square test), the number of days until germination, the root:shoot weight ratio, or the root: shoot length ratio (ANOVA). Seedlings in ≥70% PAR generally had more leaves, heavier shoots, and longer, heavier roots. 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). Light intensity did 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.

Our experimental results clarify the mechanisms by which bittersweet employs this "sit and wait" strategy for invading undisturbed temperate forest. Most fruits (>75%) are apparently removed by vertebrates, and presumably dispersed. Most (82%) defleshed seeds, including scarified seeds germinate, although viability decreased with time. Many (51%) seeds within intact fruits also germinate. Thereby, fallen fruits also contribute to the viable seed pool. Seed germination and seedling survival is similar across a wide range of light intensities allowing establishment of a seedling bank even under closed canopy. However, seedling "vigor" is greater under high light conditions, suggesting that canopy disturbance aids the vegetative and clonal spread of established seedlings.

Our results show that viable bittersweet 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 bittersweet to invade intact forest and await a canopy disturbance for the opportunity to proliferate. In this manner bittersweet 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.

References

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