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Corresponding author:
Scott R. Abella; Email: scott.abella@unlv.edu

Increasing invasive liana cover following tree mortality and containment treatments associated with a fungal pathogen

Scott R. Abella[1], Timothy L. Walters[2] and Karen S. Menard[3]

[1]Associate Professor, University of Nevada Las Vegas, School of Life Sciences, Las Vegas, NV, USA; and Founder and Ecologist, Natural Resource Conservation LLC, Boulder City, NV, USA; [2]Senior Technical Expert, Haley & Aldrich, Inc., Portland, OR, USA and [3]Research and Monitoring Supervisor, Metroparks Toledo, Toledo, OH, USA

Abstract

Tree-afflicting pests, such as insects and pathogens, could change forests in ways promoting invasions by non-native plants. After tree death associated with the fungal pathogen oak wilt (*Bretziella fagacearum*) and its attempted containment (severing root connectivity and sanitation removal of infected trees), we examined change in cover of the non-native liana Oriental bittersweet (*Celastrus orbiculatus* Thunb.; hereafter *Celastrus*) at 28 sites in temperate black oak (*Quercus velutina* Lam.) forests, Ohio, USA. During our 5-yr study spanning 2020 to 2024, *Celastrus* cover increased significantly ($P < 0.05$) through time at oak wilt sites but not in untreated reference forest sites without evidence of oak wilt. *Celastrus* cover increased by an order of magnitude, up to an average of 32 times among oak wilt treatments up to 10 yr old. By 2024, *Celastrus* cover ranged from 6% to 22% on average in 5- to 10-yr-old oak wilt treatments, compared with 1% cover in reference forest. Results indicate that non-native plant invasion accelerated following disturbance associated with a fungal pathogen and its attempted containment and, more generally, suggest that tree-afflicting pests can promote invasive plants in forests. Co-management of tree-afflicting pests and non-native plants may become increasingly important to ensure forests recovering from tree mortality are dominated by native plants.

Introduction

Introduced, tree-afflicting pests, such as insects and pathogens, could make forests more invasible by non-native plants (Baron and Rubin 2021; Burnham and Lee 2010; Eschtruth and Battles 2009). Additionally, management attempting to contain or slow the spread of tree-afflicting pests could inadvertently accelerate non-plant invasions (Hausman et al. 2010). However, how these tree-afflicting pests or their attempted containment may be associated with non-native plants is unclear for many pests. The limited research available for three of the most major introduced pests of trees in eastern North American forests exemplifies potential variation in associations of tree pests with non-native plants. After invasion by the beetle emerald ash borer (*Agrilus planipennis*), non-native plants increased after cutting of ash (*Fraxinus* spp.) trees for attempted quarantine of the invading insects (Hausman et al. 2010). However, without attempted cutting for quarantine of this pest, non-native plants have not increased (Abella et al. 2019) or have increased where already present (e.g., Baron and Rubin 2021; Dolan and Kilgore 2018; Hoven et al. 2017). After invasion by the sap-sucking insect hemlock woolly adelgid (*Adelges tsugae*), non-native plants already present increased in one study (Eschtruth and Battles 2009) and not in another, but new invasions occurred (Small et al. 2005). After arrival of beech bark disease (a complex of an invasive insect and fungal pathogen), no non-native plants were recorded in diseased forest sites (Cale et al. 2013). With existing invasions of pests that afflict trees expanding and new introductions accumulating, further understanding their potential associations with invasive plants is a research priority (Gougherty et al. 2023).

We examined change in cover of the non-native liana Oriental bittersweet (*Celastrus orbiculatus* Thunb.; hereafter *Celastrus*) after ongoing death and sanitation removal of black oak (*Quercus velutina* Lam.) trees associated with the fungal pathogen oak wilt (*Bretziella fagacearum*). Oak wilt was first documented in the United States in the 1940s and was reported in 24 eastern states by 2009 (Juzwik et al. 2011). Trees of the red oak group (subgenus *Erythrobalanus*) are most susceptible to oak wilt and can die the first growing season after infection (Juzwik et al. 2011). The pathogen can spread belowground through root grafts and overland via flying beetles transporting it to wounds on trees. A protocol intended to contain the spread of oak wilt includes severing root connectivity with neighboring trees followed by sanitation cutting and removal of infected trees (Juzwik et al. 2010).

In the oak wilt–affected forests of our study area, *Celastrus* was the dominant non-native plant species and the focus of our study. Originally from temperate climates in Asia, *Celastrus* is thought to have been introduced to North America (New York State) by the 1880s as a horticultural plant and has since spread to at least 34 states and 5 Canadian provinces

Management Implications

Insects, pathogens, and other tree-afflicting pests are accumulating and spreading in many forests, often with poorly known effects on invasive plants. In temperate forests in Ohio, USA, we found that cover of the non-native liana *Celastrus orbiculatus* (Oriental bittersweet; hereafter *Celastrus*) proliferated after *Quercus velutina* (black oak) tree mortality associated with the invasive fungal pathogen *Bretziella fagacearum* (oak wilt) and its attempted containment (severing root connectivity and sanitation removal of infected trees). Over 5 yr between 2020 and 2024, *Celastrus* cover increased by an order of magnitude (reaching up to 22% average cover by 2024) in sites with oak wilt, while it remained comparatively low (1%) in reference forest sites without evidence of oak wilt. By 2024, *Celastrus* cover was as high as 60% among oak wilt sites, and the liana formed a mat-like covering on native understory plants. In these forests with spatially and temporally dynamic oak wilt patches, we suggest that *Celastrus* be managed in two contexts: (1) proactively as incipient populations with low cover in understories of non–oak wilt affected patches to potentially suppress the response of *Celastrus* should oak wilt arrive and (2) by reducing established *Celastrus* populations already with high cover in existing oak wilt patches to enable forest recovery from oak wilt to be dominated by native plants. Invasive plant management may need to be increasingly paired with forest management of and adaptation to tree-afflicting pests that may catalyze non-native plant invasions.

(McKenzie-Gopsill and MacDonald 2021). We addressed the following questions: (1) Does cover of *Celastrus* vary among forest sites receiving onetime oak wilt containment treatments 1 to 10 yr prior or change through time spanning our 5-yr study period (2020 to 2024)? (2) Is variation in *Celastrus* cover correlated with tree canopy cover?

Materials and Methods

Study Area and Oak Wilt Treatments

Within the 45,000-ha Oak Openings region in northwestern Ohio, USA, we performed the study in the 200-ha Wildwood Preserve (41.6814°N, 83.6739°W), managed by Metroparks Toledo. Oak forests in the preserve contain overstory trees 80 to more than 120 yr old of mostly *Q. velutina* with some white oak (*Quercus alba* L.). Total live basal area of these *Quercus* species in undisturbed forests is typically 30 to 50 m^2 ha^{-1} with 90% to 97% tree canopy cover. Understories typically contain vascular plants of all growth forms, including native shrubs, tree seedlings, and herbaceous plants with mixtures of forbs, graminoids, and ferns (Abella et al. 2021). The sandy soils are classified as the Ottokee (mixed, mesic Aquic Udipsamments) and Oakville (mixed, mesic Typic Udipsamments) series. Climate is temperate, averaging 86 cm yr^{-1} of precipitation (Toledo Airport weather station, National Centers for Environmental Information, Asheville, NC, USA). Within our 2020 to 2024 study period, early to midsummer (May through July) precipitation was 108% of the 26-cm (1955 to 2024) average, being 92% (2020), 133% (2021), 110% (2022), 87% (2023), and 116% (2024).

Oak wilt was first noted in the preserve after 2010 based on symptoms exhibited by trees, signs of fungal presence on likely infected trees (Juzwik et al. 2011), and on tissue samples collected from symptomatic trees testing positive for oak wilt (C. Wayne Ellett Plant and Pest Diagnostic Clinic, Ohio State University, Reynoldsburg, OH, USA). Thereafter, in scattered sites throughout the preserve, groups of two to three or individual mature trees of the susceptible *Q. velutina* showing oak wilt sign and symptoms began dying, often within the same year that symptoms were detected. In 2015, Metroparks Toledo began implementing an oak wilt containment protocol consisting of: (1) using a vibratory plow blade, mounted on a Ditch Witch RT125Q Quad Ride-On Tractor (Charles Machine Works, Perry, OK, USA), to establish a containment trench line (1.5-m deep and 4-cm wide) in the soil designed to sever root connectivity for 30 m around symptomatic trees and encircling the groups of two to three or individual symptomatic trees, (2) sanitation cutting (using chainsaws with cuts made just above ground level) of symptomatic trees within the containment line, and (3) chipping of wood and slash of the infected trees and removal of the chipped material (Juzwik et al. 2010). Although assessing effectiveness of this attempted containment would require a below- and aboveground fungal distribution and transport investigation beyond the scope of our study, prior research in similar oak forests in Minnesota concluded that the containment protocol slowed the spread of oak wilt from infection centers for at least 4 to 6 yr (Juzwik et al. 2010).

Data Collection and Analysis

We defined an oak wilt treatment site as the canopy gap centered on a single tree or group of two to three trees sanitation cut and encircled by a containment line following the protocol described earlier. We designated oak wilt treatments by their age according to the growing season immediately following the dormant season completion of the onetime treatments. We named these treatments as old (established in 2015; age 6 yr in 2020 when our study began and age 10 yr in 2024 when our study ended), middle-aged (2018; age 3 yr in 2020 and 7 yr in 2024), and young (2020; age 1 yr in 2020 and 5 yr in 2024). Sites containing dead trees consistent with oak wilt symptoms that had not received oak wilt treatments were not available to sample, because managers wished to avoid leaving areas with potentially unabated spread of oak wilt. This situation of unavailability of invaded, untreated sites is common in invasive species science and management but can enable comparison of invaded, treated sites with uninvaded, reference sites (McNair et al. 2024). We used this type of design in our study. Thus, while oak wilt and its attempted containment are an inseparably combined influence in our study, we were able to sample mature oak forest sites without evidence of oak wilt as untreated reference forest. We randomly selected 7 sites for sampling for each of the three oak wilt treatment ages and for reference forests, totaling 28 sites. Sample sites among treatments and reference forests were interspersed across the landscape, averaged 0.3 km apart, had an extent of 1.0 km, and were intermixed on the same soil series (Ottokee and Oakville).

During peak plant cover in June to July, we measured *Celastrus* cover within a circular, 100-m^2 plot centered on the single or central stump of removed *Q. velutina* trees at each of the 21 oak wilt treatment sites. In each of the 7 sites in reference forests, we centered the plot on the bole of the nearest live *Q. velutina* tree to the randomly selected point. In 2020, stump diameters of focal, sanitized trees ranged from 29 to 130 cm in plots within treatment sites and from 45 to 107 cm for live, mature trees in reference forest plots. In all 28 plots in 2020, 2022, and 2024, we visually categorized areal cover of *Celastrus* as 0.1%, 0.25%, 0.5%, and 1%; 1% intervals to 10% cover; and 5% intervals above 10% cover up to the maximum 100% areal cover. Nearly all (typically 99% to 100%) *Celastrus* cover

Figure 1. Example plot showing the increase in cover of the invasive *Celastrus orbiculatus* in a young containment treatment for the fungal pathogen oak wilt, Wildwood Preserve, Ohio, USA. On this plot in June 2020 (the first growing season and 3 mo after oak wilt sanitation treatment), *C. orbiculatus* had 0.25% cover, increasing to 2% in 2022 and 10% in 2024. In the June 2024 photo, *C. orbiculatus* formed a mat-like covering (visible in the foreground and topped with twining *C. orbiculatus*) on native woody and herbaceous understory plants and had also climbed the black cherry (*Prunus serotina* Ehrh.) tree in the foreground on the right. Photos by SRA.

occurred as plants growing unsupported or mat-like on other understory plants or subcanopy tree saplings, rather than as climbing plants on overstory trees (Figure 1). Taxonomic identification of *Celastrus* in the study area included collecting and depositing two specimens (T.L. Walters #4077 and #4535) in a herbarium (Cleveland Museum of Natural History, Department of Botany, Cleveland, OH, USA). We also recorded tree canopy cover (defined as live foliage on stems above a height of 3 m) averaged per plot from sighting tube measurements (densitometer manufactured by Geographic Resource Solutions, Arcata, CA, USA) at the center and four cardinal directions along the perimeter of each plot.

We analyzed $\log_{10}$-transformed *Celastrus* cover using a generalized linear mixed model including oak wilt treatment (three treatment ages and reference forest), sample year (2020, 2022, and 2024), their interaction, and plot as the repeated-measures subject. We performed the analysis in SAS v. 9.4 (SAS Institute, Cary, NC, USA) using PROC GLIMMIX with autoregressive structure and Tukey tests for multiple comparisons. We then examined association between tree canopy cover and *Celastrus* cover through time using repeated-measures correlation (Marusich and Bakdash 2021).

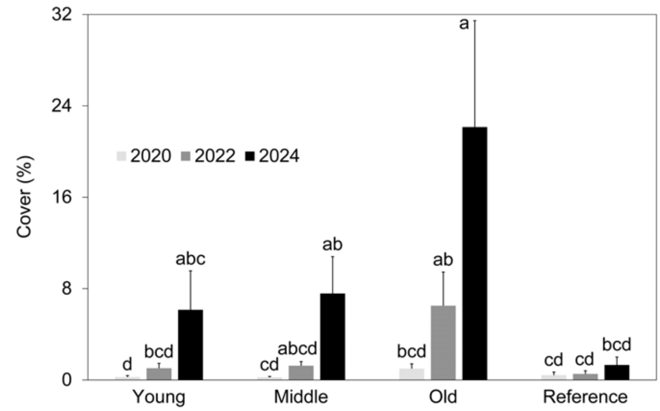

Figure 2. Variation in mean cover of invasive *Celastrus orbiculatus* across oak wilt containment treatments and study years, Wildwood Preserve, Ohio, USA. Error bars are +1 standard error of the mean. Means without shared letters differ at $P < 0.05$. Ages of oak wilt treatments during the 2020–2024 study period were 1–5 (young), 3–7 (middle), and 6–10 yr (old). Plots in reference forest did not display evidence of oak wilt and were untreated for oak wilt.

Results and Discussion

When our study began in 2020, *Celastrus* inhabited nearly all plots (25 of 28, 89%), being absent from only one young oak wilt treatment plot and two reference forest plots without evidence of oak wilt. By 2024, all 28 plots contained *Celastrus*. Mean *Celastrus* cover varied with the main effects of oak wilt treatment ($F(3, 24) = 4.0$, $P = 0.019$), study year ($F(2, 48) = 57.7$, $P < 0.001$), and their interaction ($F(6, 48) = 3.3$, $P = 0.009$; Figure 2). In 2020, among different-aged oak wilt treatments, mean *Celastrus* cover ranged from 0.3% (young treatments: 1 yr old in 2020) to 1.0% (old treatments: 5 yr old in 2020), compared with 0.4% in reference forest. Subsequently, *Celastrus* cover increased sharply through time between 2020 and 2024. The increase was disproportionately high in oak wilt sites, increasing on average by 22 times (old treatments) to 32 times (middle-aged treatments), compared with 3 times in reference forest. By 2024, *Celastrus* mean cover ranged from 6% (young) to 22% (old) among oak wilt treatments, compared with 1% in reference forest. Maximum covers among plots (all of which were in old oak wilt treatments) increased sharply from 3% in 2020 to 20% in 2022 and 60% in 2024.

Celastrus cover was not correlated with tree canopy cover across all years and plots (repeated-measures $r = 0.14$, $P = 0.316$, $df = 55$) nor across only oak wilt plots (repeated-measures $r = 0.15$, $P = 0.334$, $df = 41$). Nearly all or all (99% to 100%) of the *Celastrus* cover was in understories as a shrub- or mat-like growth form rather than as climbers on tree boles.

Results suggest that *Celastrus* was present at low cover in reference forest, and the inseparable influence in our study of oak wilt and its attempted containment acted as a catalyst for a major increase in *Celastrus* cover. As an influence of oak wilt was killing mature oaks to create canopy gaps, it may seem surprising that *Celastrus* cover was not correlated with tree canopy cover. Average tree canopy cover narrowly ranged from 51% to 60% among oak wilt treatments (compared with 91% in reference forest) and changed little (by |2–9|%) between 2020 and 2024. The lack of correlation between tree canopy cover and *Celastrus* cover could result from the qualitative presence of a canopy gap serving as a release event stimulating *Celastrus* growth, then *Celastrus* cover continuing to increase under minimally temporally varying canopy cover, resulting in little correlation. As mentioned previously, our study is not intended to partition the potential relative influences of

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oak wilt–related tree mortality from disturbance associated with its attempted containment, but prior research with *Celastrus* and its traits suggest that the appearance of canopy gaps in the presence of *Celastrus* seedlings was likely a major contributor to *Celastrus*'s increase (Pavlovic and Leicht-Young 2011). Although *Celastrus* may not form persistent soil seedbanks, the species' shade tolerance enables persistence of seedlings in shaded, forest understories (Ellsworth et al. 2004). These seedlings grow slowly in shade but can initiate rapid growth if light increases (McNab and Meeker 1987). As *Celastrus* fruits are dispersed by animals (e.g., birds), which may be attracted to oak wilt openings, the increase in *Celastrus* cover we observed could stem from accelerated growth of existing seedlings as well as new recruitment (Greenberg et al. 2001; McNab and Loftis 2002).

To what extent oak wilt as a disturbance is unique in facilitating *Celastrus* invasion is not clear. Prior research has reported increases in *Celastrus* after logging (Silveri et al. 2001) and wind disturbance (Berg et al. 2023). A potential difference between these typically more discrete disturbance types and oak wilt is that oak wilt apparently kills trees on a more continual basis across the landscape (Juzwik et al. 2011). As these oak wilt–created canopy gaps form, *Celastrus* cover can keep increasing within them for at least 10 yr based on our results and similar to continued increases across two decades observed after tree windthrow in North Carolina (Berg et al. 2023). In our study, this temporal pattern resulted in persistently increasing *Celastrus* cover in existing oak wilt sites, as well as *Celastrus* increasing as new oak wilt sites continually formed, cumulatively increasing the amount of *Celastrus* cover across the landscape.

Celastrus can negatively affect native plant communities by reducing growth or killing trees that the liana climbs and by shading and outcompeting native understory plants (McNab and Meeker 1987). The sharp increase in *Celastrus* we observed at oak wilt sites suggests that treating *Celastrus* could aid forest adaptation to oak wilt. Treating *Celastrus* (e.g., using herbicide; McKenzie-Gopsill and MacDonald 2021) proactively in reference forests where it occurred at low cover could potentially temper the increase that would otherwise occur if or when oak wilt arrived. Although treating *Celastrus* mats that have already formed on top of other understory plants following oak wilt presence may be more challenging, large-diameter stems of *Celastrus* can be controlled by cutting (McKenzie-Gopsill and MacDonald 2021). As *Celastrus* cover increased sharply through time in oak wilt treatments, co-managing oak wilt and *Celastrus* may help favor native plants in oak wilt patches. Our study highlights how forest changes from a tree-afflicting pest and its attempted containment were followed by acceleration of non-native plant invasion.

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