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10. Browsing by White-Tailed Deer on Invasive Oriental Bittersweet Spreading into Restored Grasslands

Neal Mundahl
Winona State University, nmundahl@winona.edu

Bruno Borsari
Winona State University

Browsing by White-Tailed Deer on Invasive Oriental Bittersweet Spreading into Restored Grasslands

NEAL D. MUNDAHL[1] AND BRUNO BORSARI

Program in Ecology & Environmental Science, Department of Biology, Winona State University, Winona, MN 55987, USA (NDM, BB)

ABSTRACT Non-native oriental bittersweet (*Celastrus orbiculatus* Thunb.) was first detected in southeastern Minnesota in 2010 and has spread from woodlands into adjacent grasslands. Anecdotal evidence suggests that browsing by white-tailed deer (*Odocoileus virginianus*) on young oriental bittersweet slows the growth and spread of this plant. This study assessed the population characteristics of density, age structure, growth rate, and branching morphology of oriental bittersweet in small, restored grasslands (mixed native grasses and forbs) in Winona County, Minnesota, and quantified the browsing damage inflicted by white-tailed deer on bittersweet and native red osier dogwood (*Cornus sericea*) at the end of winter. Bittersweet densities averaged 20 plants/m^2 in grasslands near infested woodlands. Plants ranged in age from 1 to 7 yr, and growth rates (stem length) in plants $\geq$2 yr old averaged only 9 cm/yr but were highly variable. Spread of bittersweet into grasslands from woodland edges averaged 48 m across all transects, but densities declined with increasing distance from woodlands. Winter browsing damage was present on 100% of all bittersweet and dogwood plants, with terminal buds removed from 70% (2,183 of 3,118) of all bittersweet branches and 99% (391 of 392) of all dogwood branches. Browsing seems to have suppressed fruiting in >35% of plants $\geq$2 yr old in the grasslands examined. Overwinter browsing by deer heavily damaged terminal buds and greatly reduced the growth rates of oriental bittersweet in restored grasslands in southeastern Minnesota, but not enough to prevent most plants in the population from maturing and producing fruit and seed.

KEY WORDS browsing, deer, Oriental bittersweet, restored grasslands

Nearly 5,000 species of non-native plants have become established in North America, collectively causing US$20 billion/yr in economic damage to forests, grasslands, residential/commercial landscaping, and agricultural fields (Kaufman and Kaufman 2007). Free of their natural predators, these species can spread quickly over wide geographic areas, often outcompeting the native flora in the process (Invasive Species Advisory Council 2006). Control and management of many of these species have proven to be problematic due to their ever-expanding ranges, good dispersal strategies, and strong competitive abilities (Booth et al. 2010).

Oriental bittersweet (*Celastrus orbiculatus* Thunb.) is an invasive, woody liana that has been expanding its range westward in North America since its introduction from East Asia for horticultural purposes (Albright et al. 2009, U.S. Department of Agriculture [USDA] 2012). It is now one of the most abundant and rapidly increasing invasive species on the continent (Leicht-Young et al. 2007*b*). Although typically a woodland species in the United States (McNab and Meeker 1987), its native habitat is considered to be "thickets and grassy slopes" (Ohwi 1984), and its tolerance of high light levels (Greenberg et al. 2001, Ellsworth et al. 2004, Leicht-Young et al. 2007*b*) allows it to invade grassland habitats (Fike and Niering 1999, Mundahl 2014*a*). Once established, the superior growth rate (Leicht and Silander 2006, Leicht-Young et al. 2007*b*), high seed production (Leicht-Young et al. 2007*a*), and high rates of seed dispersal and germination (Greenberg et al. 2001) of oriental bittersweet is hypothesized to promote its rapid spread.

Grazing or browsing herbivores can have suppressive effects on some invasive plants. Both native (e.g., deer, bison, elk, and antelope) and domesticated (e.g., sheep, goats, and cattle) mammalian herbivores can limit some species of invasive plants and maintain native plant communities through their selective grazing and browsing actions (Frank et al. 1998, Rossell et al. 2007, Ingham and Borman 2010, Kleppel and LaBarge 2011, Kleppel et al. 2011). White-tailed deer (*Odocoileus virginianus*) are abundant or expanding in numbers in many areas of the continental United States and southern Canada, leading to considerable concern about their potential impact on plant communities (Russell et al. 2001). High deer densities (>8.5 deer/km^2) can produce significant, negative organismal-level and population-level effects on plants; shift plant communities among alternative stable states; and ultimately impact ecosystem properties and processes such as nutrient availability and cycling (Rooney 2001, Russell et al. 2001, van der Hoek et al. 2002, Rossell et al. 2007, Knight et al. 2009). However, deer often exhibit distinct feeding preferences for certain species of plants (Russell et al. 2001, Wakeland and Swihart 2009, Batzli and Dejaco 2013),

[1] Corresponding author email address: nmundahl@winona.edu

a behavior that may help limit the spread of some invasive plants (Rossell et al. 2007, Sarver et al. 2008).

Oriental bittersweet was first reported in 2010 in southeastern Minnesota (Minnesota Department of Agriculture [MDA] 2012, USDA 2012, Mundahl 2014*a*), a region that also has high densities of white-tailed deer (Minnesota Department of Natural Resources [MN DNR] 2013). Because deer may be able to exert some control over oriental bittersweet when plants are at low densities (Rossell et al. 2007), this study assessed the effects of deer browsing on bittersweet growth, branching, and fruit production within a restored prairie in southeastern Minnesota, on the northwestern fringe of the bittersweet's invasion front. It was hypothesized that browsing by deer would suppress bittersweet growth rates, stimulate increased branching, and suppress fruiting. This study also compared overwinter browsing damage from white-tailed deer on oriental bittersweet with browsing damage on a common, native co-occurring shrub, *Cornus sericea*, hypothesizing that nonnative bittersweet would suffer less damage than would this native plant.

METHODS

Study Area

The study was conducted during early spring 2011 and late fall 2014, near Winona, Minnesota, in a valley where restored grasslands are bordered by deciduous forests. Oriental bittersweet was first officially reported in Winona County in 2010, in another valley ~800 m from the study area (USDA 2012). Large bittersweet stems removed from this first invasion site in 2013 were determined to be 20+ yr old, placing species arrival in the area as early as 1990 (M. Chandler, Minnesota Department of Agriculture, personal communication).

Oriental bittersweet occurred intermittently along the eastern edge of the study area valley for approximately 2,000 m, along and extending outward from a former fence line border between an upland forest and restored grasslands in a valley. Upper hillsides were covered in oak–basswood forests (red oak [*Quercus velutina*], American basswood [*Tilia americana*], black walnut [*Juglans nigra*], and paper birch [*Betula papyrifera*]), with bittersweet, European buckthorn (*Rhamnus cathartica*), tatarian honeysuckle (*Lonicera tatarica*), black locust (*Robinia pseudoacacia*), and boxelder (*Acer negundo*) common in windfall openings and the woodland edge understory. Grassland habitats within the valley floor and lower hillsides were dominated by wild bergamot (*Monardo fistulosa*), common milkweed (*Asclepias syriaca*), Jerusalem artichoke (*Helianthus tuberosus*), big bluestem (*Andropogon gerardii*), smooth brome (*Bromus inermis*), goldenrod (*Solidago* spp.), Queen Anne's lace (*Daucus carota*), and rough bedstraw (*Galium asprellum)*, with small (<5- to 20-m^2) patches of reed canarygrass (*Phalaris arundinacea*). Many occurrences of bittersweet within the grasslands, 40–70 m from the woodland edge habitat, were associated with the presence of nest boxes erected within the grassland for eastern bluebirds (*Sialia sialis*; Mundahl 2014*a*). Smooth sumac (*Rhus glabra*), red osier dogwood (*Cornus sericea*), and wild plum (*Prunus americana*) also were present at scattered locations within and nearby the study area.

The study area was located within the farmland region of southern Minnesota, specifically within the southeastern section of that region where densities of white-tailed deer in 2011 were the highest (7–9 deer/km^2 before fawning; MN DNR 2013). Deer caused US$3.5 million in crop damage in southeastern Minnesota in 2011 (70% of that to corn crops), averaging >$50 in damages/ha across all crop types (Pradhananga et al. 2013). Deer had continuous access to oriental bittersweet and other plants within the study area during winter 2010–2011 and fall 2014 and were observed regularly feeding in the area in groups of four to seven deer (rarely 10 or more; N.D.M., personal observation). Nearby property owners concurrently experienced browse damage to unprotected landscaping shrubs, fruit trees, and young conifers.

Plant Characteristics: Spring

Characteristics of oriental bittersweet plants were examined on a hill slope with a westerly aspect within the grassland habitat. Studies occurred in spring before leaf-out by bittersweet. Three parallel transects (17 m in length) were established extending perpendicularly from the woodland edge out into the prairie. Beginning 1 m from the woodland edge and continuing every 1 m along each transect, all oriental bittersweet plants were counted and measured (heights, nearest centimeter) within 0.25-m^2 plots. Plant heights (or main stem length for leaning plants) and distances from the woodland edge (nearest 0.1 m) were measured for any additional bittersweet plants that were found along these transects. Additional transects ($n = 10$, variable lengths) were established to determine the maximum extent of spread of bittersweet from the woodland edge. Simple linear regression was used to determine whether plant densities or heights varied with distance from the woodland edge.

At the same site, varying numbers ($n = 13$–30) of oriental bittersweet plants were collected from each of seven different distances from the woodland edge (2, 4, 6, 8, 10, 12, and 14 m) for more detailed assessment of bittersweet characteristics. Bittersweet plant heights (nearest centimeter) and stem basal diameters (nearest 0.1 mm) were measured, plant ages determined (basal stem cross section, using ×10 magnification hand lens), and the number of branches were counted on each plant (including branches of branches; anything that should end in a terminal bud).

Linear regression analyses examined possible relationships between 1) distance from forest edge and individual plant characteristics, 2) age versus plant characteristics, and 3) plant height versus stem diameter.

Plant Characteristics: Fall

At the end of the growing season in November 2014, 40 bittersweet plants (20 with fruits, 20 without fruits) were selected randomly from within the grassland habitat to examine possible physical differences between fruiting and non-fruiting plants. Plant heights, basal diameters, plant ages, and branch numbers were assessed as described above. Plant characteristics were compared between fruiting and non-fruiting plants with *t*-tests. Linear regression analyses were used to compare age versus plant characteristics and plant height versus stem diameter.

Deer Browsing

At the same area where bittersweet plant characteristics were assessed, the prevalence of browsing damage to bittersweet caused by white-tailed deer was examined at the end of the winter 2010–2011 (assessed in early spring 2011 before the initiation of new growth) and at the end of the 2014 growing season (assessed in November 2014). Browsing damage caused by deer was differentiated from that caused by other browsers (e.g., rabbits, mice, voles, and squirrels) by using information provided in Pearce (1947). For example, twigs browsed by deer exhibit rough, shredded ends resulting from breaking over only their lower incisors, whereas rodents and lagomorphs produce clean bites by using both upper and lower incisors. The numbers of terminal and lateral shoots that were browsed versus non-browsed were determined on each of the same plants (spring $n = 129$, fall $n = 40$) that were used to determine age, stem diameter, and height (see above). Simple linear regression was used to investigate whether distance from the woodland edge (spring only) had any influence on browsing damage to oriental bittersweet. Single-factor ANOVA was used examine whether the extent of browsing damage was related to plant age. In spring, the level of browsing damage on bittersweet also was compared to browsing damage on stems ($n = 45$) of a nearby (250 m away) population of red osier dogwood, a native shrub. A Mann–Whitney *U* test was used to compare the degree of browsing damage between bittersweet and red osier dogwood. All statistical tests were conducted using an online statistical calculator (VassarStats; http://vassarstats.net).

RESULTS

Plant Characteristics

Oriental bittersweet densities averaged 20 plants/m^2 along transects extending into the prairie habitat from the woodland edge. Bittersweet plants were present as far as 64 m from the woodland edge (48 ± 3 m [mean ± SE]), but most plots >17 m from the forest contained no bittersweet plants (data not shown). Although individual plot densities varied 10-fold, there was a significant (curvilinear regression $F_{2,48} = 6.9$, $P = 0.002$) change in density with increasing distance from the woodland edge (Figure 1). Densities reached peak levels 6–10 m from the edge before declining.

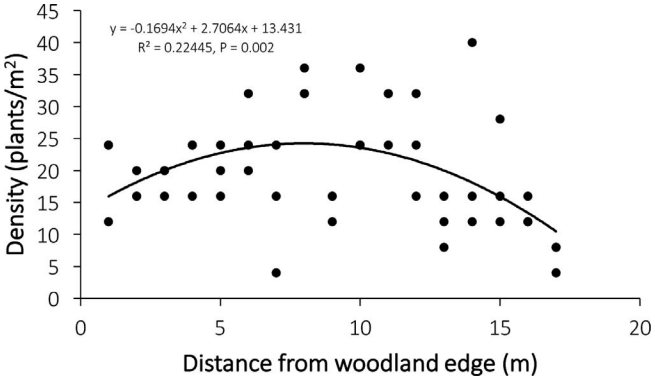

Figure 1. Densities of oriental bittersweet (*Celastrus orbiculatus*) in plots (triplicate at each distance) extending from woodland edge into grassland habitat in Winona, Minnesota, early spring 2011. The best fit curvilinear regression line and equation are included.

Heights (or lengths) of oriental bittersweet plants averaged 92 cm (SE = 7 cm) in all transects extending from the woodland edge, ranging from 52 to 350 cm. Plant heights declined significantly (linear regression $F_{1,53} = 16.3$, $P < 0.001$) with increasing distance from the woodland edge (Table 1). Plants 14 m from the woodland edge were <50% as tall as those nearest the woodland edge (height at 14 m from edge = 69 ± 10 cm [mean ± SE], height at 2 m = 149 ± 26 cm).

Oriental bittersweet plants growing in the prairie ranged in age from 1 to 7 yr, with 2- and 3-yr-old plants representing nearly 50% of the 169 individual plants examined (Figure 2). Both 1- and 2-yr-old plants were underrepresented in the grassland. Mean (±SE) age of plants was 3.3 ± 0.2 yr. Average plant age declined significantly (Table 1; Figure 3) with increasing distance from the woodland edge (0.7 yr decrease every 10 m), but variability was very high and the correlation was weak.

The ages of bittersweet plants were significantly correlated to stem diameter and height during both seasons examined. Basal diameters of 1-yr-old plants averaged 5.5 mm and grew at a rate of approximately 1 mm/yr (Table 1). Diameters ranged from 3.9 to 17.6 mm, averaging 7.8 mm (SE = 0.2 mm). Heights of first-year (1-yr-old) plants averaged 141 cm in late fall, but only 69 cm in early spring (plants measured in spring had been browsed, plants

Table 1. Simple linear regression analyses of oriental bittersweet (*Celastrus orbiculatus*) characteristics at Winona, Minnesota, in early spring 2011 and late fall 2014. Distance was measured from the forest edge.

Season	X Variable	Y Variable	Slope	Y Intercept	r^2	P
Spring	Distance (m)	Height (cm)	−5.46	142.31	0.23	<0.001
Spring	Distance (m)	Age (years)	−0.07	3.79	0.04	0.03
Spring	Distance (m)	% branches browsed	−1.78	85.1	0.1	<0.001
Spring	Age (yr)	Basal diam. (mm)	0.94	4.53	0.45	<0.001
Fall	Age (yr)	Basal diam. (mm)	1.18	4.46	0.51	<0.001
Spring	Age (yr)	Height (cm)	8.77	60.46	0.14	<0.001
Fall	Age (yr)	Height (cm)	1.96	125.70	0.01	0.599
Spring	Basal diam. (mm)	Height (cm)	6.81	37.19	0.17	<0.001
Fall	Basal diam. (mm)	Height (cm)	3.20	104.86	0.05	0.147
Spring	Age (yr)	No. of branches	11.79	−13.54	0.43	<0.001
Fall	Age (yr)	No. of branches	11.67	−7.97	0.57	<0.001

measured in fall had not been browsed). Age–height relationships suggested that bittersweet grew at a rate of 8.8 cm/yr based on early spring 2011 measurements, but only 2.0 cm/yr based on late fall 2014 measurements (Table 1; regression slope shifted by overwinter browsing of first-year plants measured in spring). Plant height and basal stem diameter also were correlated significantly during early spring 2011, but not during late fall 2014 (Table 1).

As oriental bittersweet plants aged, they exhibited greater branching. Most (78%) first-year plants had no lateral branching, although a single, 1-yr-old plant had seven lateral branches. Plants added branches at a rate of approximately 12/yr, based on both spring and fall counts (Table 1). The most branching was observed on a single, 7-yr-old plant with 192 branches. Overall, the 129 bittersweet plants examined in spring each averaged 24 branches (SE = 2 branches), whereas the 40 plants examined in fall averaged 34 branches (SE = 4). Plants within 4 m of the woodland edge in spring had significantly more branching ($t = 4.3$, df = 127, $P << 0.001$) than plants >4 m from the edge (mean number of branches ± SE; <4 m from edge = 41 ± 8, >4 m from edge = 20 ± 1).

There were more differences than similarities between oriental bittersweet plants with fruit and those without fruit (Table 2). Although fruiting and non-fruiting plants had similar heights, they differed in all other characteristics assessed. Plants with fruits were 2 yr older, had greater basal diameters, had nearly twice as many branches, and exhibited twice the browsing damage as their non-fruiting conspecifics. All fruiting plants were 2 yr old or older, indicating that only first-year plants were not capable of reproducing in this grassland habitat. Sixty percent of non-fruiting plants were ≥2 yr old, ranging in age from 2 to 6 yr (3.8 ± 0.4 yr [mean

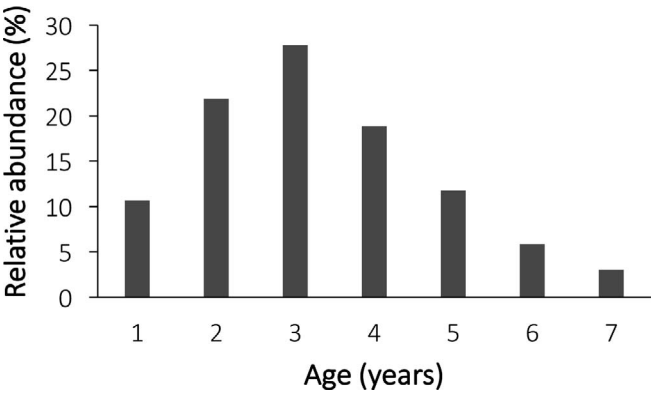

Figure 2. Age distribution of oriental bittersweet (*Celastrus orbiculatus*) in a grassland in Winona, Minnesota, early spring 2011. $n = 129$.

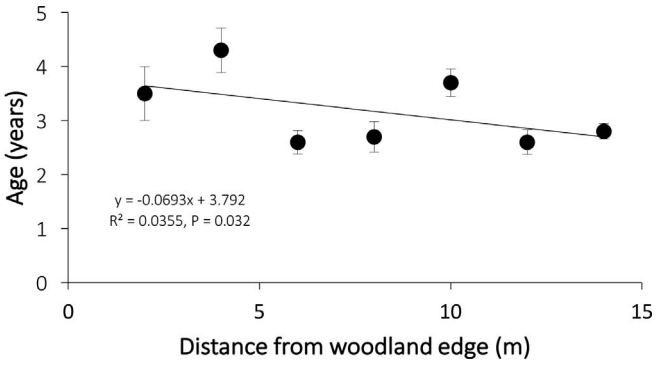

Figure 3. Relationship between plant age and distance from woodland edge in oriental bittersweet (*Celastrus orbiculatus*) in a grassland in Winona, Minnesota, early spring 2011. Values are means ± SE. The regression line and equation are included.

Table 2. Comparisons of physical characteristics of oriental bittersweet (*Celastrus orbiculatus*) plants with and without fruits at Winona, Minnesota, fall 2014. Results of *t*-tests between groups are included. Values in parentheses represent ± 1 SE.

Variable	With Fruit	Without Fruit	*t* Value	*P*
Age (yr)	4.5 (0.3)	2.7 (0.4)	3.39	0.002
Diameter (mm)	9.7 (0.8)	7.7 (0.5)	2.20	0.035
Height (cm)	134 (10)	132 (9)	0.13	0.897
No. of branches	43 (6)	24 (6)	2.25	0.030
% branches browsed	20 (2)	10 (3)	2.92	0.006

± SE]). Of all 2-yr-old or older plants examined in late fall, 37% lacked fruits.

Deer Browsing

Deer browsed heavily on oriental bittersweet plants during winter 2010–2011, with groups of two to seven deer observed frequently feeding in the grassland. Every plant observed had sustained some degree of browsing damage (Figure 4). More than 99% (128 of 129) of all terminal shoots had been browsed, along with 70% (2,183 of 3,118) of all lateral shoots (branches) (Table 3). Although only 10% (13 of 129) of plants examined had browsing damage to every shoot, 88% (113 of 129) of the plants suffered damage to more than 50% of their shoots. Browsing intensity (both percent of shoots browsed/plant and number of shoots browsed/plant) declined significantly (Table 1) with increasing distance from the woodland edge (Figure 5), with the average level of damage declining from >80% to 60% over a distance of 12 m. In addition, first-year plants, with far fewer branches, suffered significantly (ANOVA: $F_{4,124} = 6.6$; $P < 0.0001$) more browsing damage (based on percentage of branches browsed) than that observed for most older bittersweet plants (Figure 6).

In contrast with browsing damage to oriental bittersweet quantified in early spring 2011, damage assessed in late fall 2014 was much lower. Although 80% of all plants exhibited browsing damage, only 22% of all branches (294 of 1,350) had been browsed, and no plant had >40% of its branches browsed. No first-year plants had been browsed, and all other plant age groups exhibited far less browsing damage (60–83% less) than did plants of similar ages examined in early spring (Figure 6).

Deer also browsed heavily on red osier dogwood plants nearby the oriental bittersweet site during winter 2010–2011. Nearly every plant ($n = 45$) sustained browsing damage to every shoot (browsing damage to 45 of 45 terminal shoots and 346 of 347 lateral shoots; Table 3). Dogwood plants sustained significantly (Mann–Whitney $U = 5{,}476$, $P < 0.0001$) more browsing damage than did bittersweet plants.

Figure 4. Browsing damage to oriental bittersweet (*Celastrus orbiculatus*) branches caused by white-tailed deer (*Odocoileus virginianus*) in a grassland in Winona, Minnesota, early spring 2011.

Table 3. Characteristics of oriental bittersweet (*Celastrus orbiculatus*) and red osier dogwood (*Cornus sericea*) plants browsed by white-tailed deer at Winona, Minnesota, following winter 2010-2011. Values in parentheses represent ± 1 SE.

Characteristic	Oriental Bittersweet	Red Osier Dogwood
No. of plants	129	45
Branches/plant	25.6 (2.1)	8.7 (0.7)
Plants browsed (%)	100	100
Terminals browsed (%)	99.2	100
Laterals browsed (%)	69.9 (1.8)	99.8 (0.2)

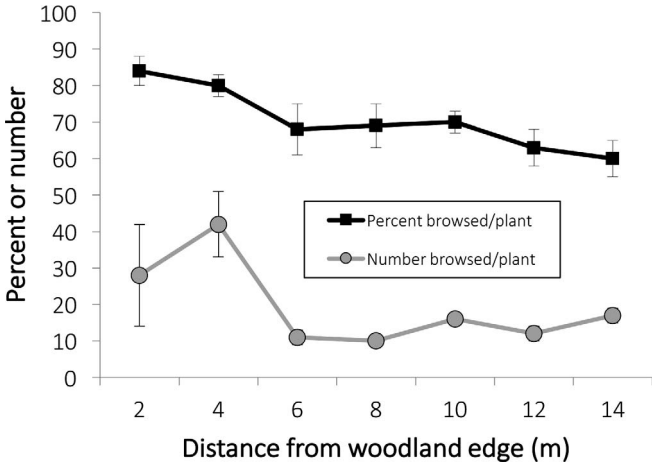

Figure 5. Browsing damage (percentage of branches browsed/plant and number of branches browsed/plant) to oriental bittersweet (*Celastrus orbiculatus*) plants caused by white-tailed deer (*Odocoileus virginianus*) versus distance from woodland edge in a grassland in Winona, Minnesota, late spring 2011. Values are means ± SE.

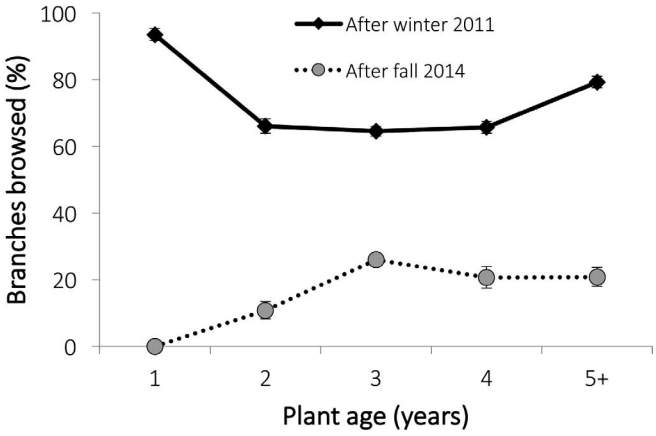

Figure 6. Browsing damage (percentage of branches browsed/plant) to oriental bittersweet (*Celastrus orbiculatus*) plants caused by white-tailed deer (*Odocoileus virginianus*) versus plant age in a grassland in Winona, Minnesota, after winter 2011 and after fall 2014. Values are means ± SE (most error bars are obscured by mean symbols).

DISCUSSION

This study revealed several important relationships between oriental bittersweet and white-tailed deer in southeastern Minnesota. First, deer browsed heavily on oriental bittersweet during the winter, consuming terminal buds from nearly every plant examined within a grassland. Browsing damage also occurred during the growing season, but at a much lower rate. Second, the heavy browsing damage (60–80% loss of terminal buds) sustained by bittersweet plants was less than that experienced by native red osier dogwood plants. Finally, growth and fruiting of bittersweet seemed suppressed by deer browsing, but not enough to prevent most plants from reproducing.

Deer were observed frequently feeding in the study site during winter 2010–2011, browsing on oriental bittersweet shoots exposed above the snowpack (N.D.M., personal observation). White-tailed deer are opportunistic browsers (Rooney 2001), consuming a mix of woody and herbaceous plants. When a variety of plants foods are available, deer may exhibit distinct feeding preferences (Rossell et al. 2007, Wakeland and Swihart 2009). In woodland and grassland habitats, food plants preferred by deer can include oaks (*Quercus* spp.), cherries and plums (*Prunus* spp.), *Trillium* spp., dogwoods (*Cornus* spp.), sumacs (*Rhus* spp.), and a variety of other trees, woody shrubs, and forbs (van der Hoek et al. 2002, Rossell et al. 2007, Knight et al. 2009, Wakeland and Swihart 2009). Woody plants (shrubs and young trees) are browsed most heavily during winter, when forbs are largely unavailable (Dahlberg and Guettinger 1956, Rogers et al. 1981). Oaks, plums, sumacs, and dogwoods all were present either within or nearby the study site and were available to deer.

The heavy browse damage to bittersweet within the grassland, even when other, preferred foods were available, suggests that deer may actively select bittersweet terminal buds as browse during the winter. Selective browsing by deer on oriental bittersweet has been suggested previously (Rossell et al. 2007, Sarver et al. 2008), even though oriental bittersweet's native congenor, American bittersweet (*Celastrus scandens*), is categorized as "seldom susceptible" to deer browsing (U.S. Department of Agriculture, Natural Resources Conservation Service [USDA-NRCS] 2007). Bittersweet plants in their typical habitat may be largely inaccessible to deer once they climb into the woodland canopy, but those plants within the study grassland were entirely accessible to browsing deer, lacking any large trees or shrubs to climb. Only along the old fence line at the woodland edge were trees tall enough to allow bittersweet to grow out of reach of feeding deer. This is the first report of heavy browse damage by deer to oriental bittersweet, likely because of the unique, deer-accessible habitat that bittersweet had invaded.

Oriental bittersweet within the study area had lost 22% of their terminal buds to browsing deer by late fall (2014), but when examined at the end of winter (2011), 60–80% of terminal buds had been cropped by feeding deer. By comparison, nearby dogwood plants experienced a loss of 99% of terminal buds during the winter months. Deer have been reported to produce highly variable levels of browsing damage to plants in various habitats; for example, 4–19% of the standing crop of various forb stems in a state park prairie in Illinois (Anderson et al. 2001), 38% of seedling eastern

white pine (*Pinus strobus*) in a forest in northern Minnesota (Saunders and Puttman 1999), 0–49% of shrub branches in a tallgrass prairie in Nebraska (van der Hoek et al. 2002), 0–77% of reproductive-age *Trillium grandiflorum* in woodlands in Pennsylvania and Minnesota (Augustine et al. 1998, Knight et al. 2009), and approximately 12% of *Baptisia lactea* flower racemes in restored grasslands in Minnesota (Mundahl 2014*b*). Heavy browsing by deer can damage and weaken plants, leading to development of multiple leaders, increased susceptibility to frost damage, weakened branching, poor form, a pathway for disease or insect infestation, suppressed seedling height, and increased mortality (USDA-NRCS 2007).

Although non-native oriental bittersweet experienced heavy browsing damage from deer, native dogwood plants suffered significantly greater browsing losses. Rossell et al. (2007) have suggested that non-native plants as a group may not be browsed by deer to the same extent as native plants, even though deer may suppress some non-natives. Native herbivores either may not recognize non-native plants as suitable foods (Daehler 2003, Lankau et al. 2004), or non-native plants may have reduced palatability (e.g., reduced nutritional value, spines or thorns, bitter or toxic chemicals) relative to native plants (Rogers and Siemann 2004, Caño et al. 2009). Although both of the above-mentioned possibilities may be true in some situations, in this study we found strong evidence for deer browsing on introduced bittersweet.

Both native and non-native plants span the entire range of palatability to deer (Dahlberg and Guettinger 1956) and susceptibility to browsing damage (Ward 2000). For example, native plants such as sunflowers (*Helianthus* spp.), oxeye (*Heliopsis* spp.), northern white cedar (*Thuja occidentalis*), oaks (*Quercus* spp.), and Canadian yew (*Taxus canadensis*), as well as non-native hostas (*Hosta* spp.), tulips (*Tulipa* spp.), daylilies (*Hemerocallis* spp.), and apples (*Malus* spp.) all are highly palatable to deer and suffer significant browsing damage (Dahlberg and Guettinger 1956, Ward 2000, Wakeland and Swihart 2009). Conversely, native goldenrods (*Solidago* spp.), Virginia creeper (*Parthenocissus quinquefolia*), boxelder, and common prickly-ash (*Zanthoxylum americanum*), and non-native honeysuckles (*Lonicera* spp.) and barberries (*Berberis* spp.) all experience little damage from browsing deer (Dahlberg and Guettinger 1956, Ward 2000). Plants containing toxic or poisonous chemicals may be avoided by deer (e.g., Virginia creeper) or browsed heavily (e.g., Canadian yew) (Dahlberg and Guettinger 1956, Ward 2000). Consequently, the heavier browsing damage observed on dogwood relative to bittersweet in this study and by others (Ward 2000) likely is simply a difference in plant-to-plant deer preference rather than an indicator of a broader, native versus non-native preference.

Densities of oriental bittersweet within the grassland were low ($\sim$20 plants/m^2) compared to densities reported in other, more established populations of bittersweet. Forest edge populations in Michigan and Illinois have densities three to five times higher (65–110 plants/m^2; Kordecki 2004, Tibbetts 2000) than those observed in southeastern Minnesota. Although low densities may be the result of the young age of the Minnesota population and limited seed sources on the northwestern edge of the invasion front, browsing deer may crop bittersweet seedlings (Rossell et al. 2007), reducing plant survival rates (Russell et al. 2001) and resulting in reduced bittersweet densities.

Growth rates of oriental bittersweet can vary widely depending on environmental conditions, but changes in height (or length) of 0.4–3.7 m/yr have been reported previously (Patterson 1973, McNab and Meeker 1988, Silveri et al. 2001, Ellsworth et al. 2004, Leicht and Silander 2006). First-year bittersweet plants averaged 78 cm in height within the grassland at the end of winter but increased at a rate of only 9 cm/yr thereafter. Only one of the 129 plants measured in early spring exceeded 200 cm in height, even though plants ranged from 1 to 7 yr old. Although plants were measured after winter browsing had occurred and therefore were shorter than immediately after the growing season, even first-year plants have the potential to exceed 200 cm in height when growing in full sun (Leicht and Silander 2006), as plants within the grassland experienced. In fact, two first-year plants in the study grassland were 214 and 215 cm in height in late fall. Repeated winter browsing by deer has slowed the growth rate of bittersweet within our study grassland, keeping the plants much smaller than normal for several years.

Despite heavy browsing by deer, $>$60% of oriental bittersweet plants in a grassland in southeastern Minnesota were able to reach sexual maturity and produce fruits and seeds. Those bittersweet plants that entwined a rare shrub or small tree, or those that grew into an impenetrable mass (Fike and Niering 1999) escaped most herbivory and produced fruits and seeds. Others that grew singly within the grassland, within reach of browsing deer, were browsed heavily, but many still managed to produce fruits. Because oriental bittersweet growing in open conditions can mature in as little as 2 yr (Fryer 2011), most of the bittersweet plants within the grassland were old enough to produce fruit. In the study grassland, browsing by deer suppressed fruiting in approximately 37% of reproductive-age bittersweet plants, potentially limiting the reproductive potential of this introduced population. In other regions with higher densities of deer, browsing impacts on bittersweet could be even greater (Russell et al. 2001).

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