

# Celastrus orbiculatus

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## INTRODUCTORY

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FEIS ABBREVIATION:  
CELORB

SYNONYMS:  
*Celastrus orbiculata* Thunb. [[78,179](#)]

NRCS PLANT CODE [[173](#)]:  
CEOR

COMMON NAMES:  
Oriental bittersweet  
Asian bittersweet  
climbing spindleberry  
round-leaved bittersweet

TAXONOMY:  
The scientific name of Oriental bittersweet is *Celastrus orbiculatus* Thunb. It is in the stafftree (Celastraceae) family [[47,70,118,122,138,186,189](#)].

**Hybrids:** Prior to Oriental bittersweet's introduction, American bittersweet (*C. scandens*) was the only North American representative of the stafftree family north of Mexico. Oriental and American bittersweet have the potential to hybridize. Although the current extent of Oriental bittersweet × American bittersweet hybridization in the wild is unknown, the 2 bittersweets are cross-fertile in the laboratory [[136,185,190](#)]. Hybrids are not widely reported in the field; however, this may be due to the difficulty in identifying bittersweet hybrids. Dreyer and others [[29](#)] noted a bittersweet plant in Connecticut that produced 2 distinct types of pollen. Both Oriental and American bittersweet were present in the study area, and the authors speculated that the individual may have been a hybrid. Genetic studies of field specimens are needed to determine levels of hybridization and introgression between Oriental bittersweet and American bittersweet.

LIFE FORM:  
Vine-liana

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## DISTRIBUTION AND OCCURRENCE

**SPECIES:** *Celastrus orbiculatus*

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- [GENERAL DISTRIBUTION](#)
- [HABITAT TYPES AND PLANT COMMUNITIES](#)

GENERAL DISTRIBUTION:  
Oriental bittersweet is native to Korea, China, and Japan [[122](#)]. Its southern limit in southeastern Asia is along the Yangtze River watershed (Cheng and Huang 1999 cited in [[103](#)]). Oriental bittersweet is nonnative in North America [[47,70,78,118,138,179,180,188](#)] and New Zealand [[180,186](#)].

In North America, Oriental bittersweet is sporadically distributed from Ontario and Quebec south through the Great Lakes states, New England, and the Southeast to Arkansas, Tennessee, Florida, Louisiana, and the southeastern edge of the Great Plains [[8,27,52,78](#)]. It was introduced in the United States around 1860 as an ornamental and for erosion control [[140](#)]. It spread to Connecticut by 1916, Massachusetts by 1919, and New Hampshire by 1938 [[114](#)]. By 1974, Oriental bittersweet had spread to 33 states [[102,128](#)] and was considered invasive in 21 [[102](#)]. As of 2011, it was widespread in the Northeast and sporadic [[36](#)] but locally dominant [[27](#)] farther south [[36](#)]. [Plants database](#) provides a distributional map of Oriental bittersweet in the United States.

Oriental bittersweet is most common and invasive in New York, coastal Connecticut, and the southern Appalachian Mountains [27]. In 2008, it covered an estimated 8,960 acres (3,630 ha) in forests of the Southeast and South [116]. Using biogeographical models, Leicht [95] predicted that Oriental bittersweet could increase in New England and spread further north. Based on Oriental bittersweet's native range and habitat preferences, others also expect Oriental bittersweet to expand its range in the United States and Canada [31,89].

#### HABITAT TYPES AND PLANT COMMUNITIES:

In the eastern United States, Oriental bittersweet is most abundant in mesic, mixed-hardwood forests and forest edges [80,112,143,182]. It may also be common in coniferous forests [54,112,123] and in woodland, ([8], fact sheet by [161]), shrubland [165,178], old field [143], duneland, coastal beach (fact sheet by [114]), tidal freshwater [93], and saltmarsh communities (fact sheet by [114]).

**Great Lakes states:** In the Great Lakes states, Oriental bittersweet occurs in mixed-hardwood, pine (*Pinus* spp.), and prairie or prairie-edge communities. In Giant City Park of Carbondale County, Illinois, Oriental bittersweet presence was positively associated with that of yellow-poplar (*Liriodendron tulipifera*) and negatively associated with that of oaks (*Quercus* spp.) ( $P < 0.001$  for both variables). It was present in but not significantly associated with pine communities and was absent from silver maple (*Acer saccharinum*) and baldcypress (*Taxodium distichum*) swamps [125,126]. Although Oriental bittersweet sometimes avoids oak communities, in southern Illinois it was common in mixed-oak-bitternut hickory (*Carya cordiformis*) as well as mixed-deciduous forests [85], and in Delaware Gap National Recreation Area of Pennsylvania and New Jersey, Oriental bittersweet was found only in oak-hickory forests [67]. In Ohio, Oriental bittersweet was a component of wetland prairies dominated by either narrowleaved mountainmint (*Pycnanthemum tenuifolium*) or Dudley's rush (*Juncus dudleyi*) [45].

**New England:** Oriental bittersweet is documented in mixed-hardwood, conifer, shrubland, and old-field communities of New England. In coastal southern New England, Oriental bittersweet was more common in pitch pine/wavy hairgrass (*P. rigida/Deschampsia flexuosa*) forests (2.2% mean Oriental bittersweet cover) than in bear oak/northern bayberry-rose (*Quercus ilicifolia-Myrica pennsylvanica-Rosa* spp.) shrublands (1.4% Oriental bittersweet cover) or on open sites that had <25% woody plant cover (0.6% Oriental bittersweet cover). It did not occur in heathlands (Ericaceae) [178]. In Amherst, Massachusetts, Oriental bittersweet occurred in the understory of a northern red oak-hickory-red maple (*Quercus rubra-Carya* spp.-*Acer rubrum*) forest. Native and nonnative honeysuckles (*Lonicera* spp.) dominated the shrub layer [34]. On riparian floodplain forests of Massachusetts, Oriental bittersweet occurred in the understory of a sugar maple-eastern cottonwood (*Populus deltoides* subsp. *deltoides*) forest. Sycamore (*Platanus occidentalis*) and white ash (*Fraxinus americana*) were occasional in the canopy. Slippery elm (*Ulmus rubra*), hackberry (*Celtis occidentalis*), and boxelder (*A. negundo*) dominated in the subcanopy. Other riparian species occurring with Oriental bittersweet in the understory included staghorn sumac (*Rhus typhina*), nonnative multiflora rose (*Rosa multiflora*), and nonnative Japanese barberry (*Berberis thunbergii*), with Japanese barberry most common. Ostrich fern (*Matteuccia struthiopteris*) dominated the herb layer [80]. In central and western Massachusetts, Oriental bittersweet, multiflora rose, and Japanese barberry were positively associated with one another ( $P < 0.001$ ) [109]. Oriental bittersweet occurred and sometimes codominated in Allegheny blackberry-porcelainberry (*Rubus allegheniensis-Ampelopsis brevipedunculata*) shrublands of Rock Creek National Park, Washington, DC [165].

In the Pennyback Wilderness of southeastern Pennsylvania, Oriental bittersweet occurred in mixed-mesophytic woodland and forest, riparian, and old-field communities. American beech (*Fagus grandifolia*), oaks, yellow-poplar, white ash, red maple, and black walnut (*Juglans nigra*) dominated woodland and forest overstories. Flowering dogwood (*Cornus florida*), black cherry (*Prunus serotina*), sweet cherry (*P. avium*), poison-ivy (*Toxicodendron radicans*), Canadian woodnettle (*Laportea canadensis*), goldenrods (*Solidago* spp.), and nonnative Japanese stiltgrass (*Microstegium vimineum*) were common understory components. Boxelder, sycamore, green ash (*F. pennsylvanica*), and silver maple dominated riparian zones. Blackberries (*Rubus* spp.) dominated old fields. Little bluestem (*Schizachyrium scoparium*), milkweeds (*Asclepias* spp.), and Indianhemp (*Apocynum cannabinum*) were common old-field components. Nonnative Japanese honeysuckle (*L. japonica*) associated with Oriental bittersweet in each of the 4 community types [143].

**Southeast:** In the Southeast, Oriental bittersweet occurs mostly in mixed-hardwood and old-field communities. On

the George Washington Memorial Parkway in Virginia, Oriental bittersweet occurred on the edges of late-successional oak-hickory forests. White oak (*Q. alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), pignut hickory (*Carya glabra*), and mockernut hickory (*C. tomentosa*) dominated interior forest overstories. Forest-edge communities were a mix of nonnative and native lianas and herbs including Oriental bittersweet, Japanese honeysuckle, summer grape (*Vitis aestivalis*), riverbank grape (*V. riparia*), white clover (*Trifolium repens*), Kentucky bluegrass (*Poa pratensis*), common velvetgrass (*Holcus lanatus*), and broomsedge bluestem (*Andropogon virginicus*) [182].

On the Bent Creek Experimental Forest near Asheville, North Carolina, Oriental bittersweet occurred in the understory of a mixed-hardwood forest. Yellow-poplar and sweet birch (*Betula lenta*) dominated on mesic sites, where Oriental bittersweet was most common. Oriental bittersweet was less common on dry sites where scarlet, chestnut, and black (*Q. velutina*) oak mixed with occasional shortleaf pine (*Pinus echinata*). Red maple, hickories, and white oak were scattered throughout the mixed-hardwood community [54,112]. Midstory species included red maple, sourwood (*Oxydendrum arboreum*), and flowering dogwood. Rosebay (*Rhododendron maximum*), blueberries (*Vaccinium spp.*), and huckleberries (*Gaylussacia spp.*) occurred in the shrub layer. Oriental bittersweet did not associate with mountain-laurel (*Kalmia latifolia*), which was common on the Experimental Forest but tended to occupy relatively dry soils [112]. Another survey in Bent Creek Experimental Forest found Oriental bittersweet was mostly associated with yellow-poplar forests that had succeeded from agricultural fields. Oriental bittersweet was less common in mixed-oak forests, which had no known history of agricultural use [87].

English-language literature on Asian plants communities with Oriental bittersweet's was scant as of this writing (2010). Pande [125] reported that Oriental bittersweet is not considered a forest species in its native Asia. In Japan, Oriental bittersweet occurs in lowland and mountainous thickets and on grassy slopes [122].

The following vegetation classifications describe US plant communities in which Oriental bittersweet is dominant.

- autumn-olive-gray dogwood-multiflora rose-eastern redcedar/Oriental bittersweet shrublands in Delaware Water Gap National Recreation Area of Pennsylvania and New Jersey; these are successional old fields [131]
- yellow-poplar/Oriental bittersweet-Japanese honeysuckle forests of Hopewell Furnace National Historic Site, Pennsylvania; Oriental bittersweet and Japanese honeysuckle had  $\geq 60\%$  ground cover and climbed almost 66 feet (20 m) into the subcanopy [133]
- successional scrub-shrub [alliances](#) on powerline rights-of-way of Hopewell Furnace National Historic Site; fox grape, Japanese honeysuckle, and/or multiflora rose may codominate [133]
- sycamore-green ash/spicebush/Oriental bittersweet/Japanese stiltgrass riverine forest of Valley Forge National Historic Site, Pennsylvania [134]
- successional old-field and/or shrubland alliances of Valley Forge National Historic Site; autumn-olive, multiflora rose, and/or Japanese honeysuckle may codominate [134]
- nonnative shrub thickets on Boston Harbor Islands National Park, Massachusetts; Japanese barberry, multiflora rose, Morrow's honeysuckle (*Lonicera morrowii*), and/or glossy buckthorn (*Frangula alnus*) may codominate [32]

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## BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: *Celastrus orbiculatus*

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| <ul style="list-style-type: none"><li>• <a href="#">GENERAL BOTANICAL CHARACTERISTICS</a></li><li>• <a href="#">SEASONAL DEVELOPMENT</a></li></ul> |  |
|--|--|

- [REGENERATION PROCESSES](#)
- [SITE CHARACTERISTICS](#)
- [SUCCESSIONAL STATUS](#)



Split capsules with red arils. Photo by Les Mehrhoff, courtesy of IPANE.

#### GENERAL BOTANICAL CHARACTERISTICS:

- [Botanical description](#)
- [Raunkiaer life form](#)

**Botanical description:** This description covers characteristics that may be relevant to fire ecology and is not meant for identification. These sources: [[47,70,118,122,138,186](#)] provide general identification keys. Oriental bittersweet is commonly mistaken for the rarer, native American bittersweet [[29](#)]. See these sources: [[8,46,97](#)] for keys specifically designed to distinguish Oriental bittersweet from American bittersweet.

**Morphology:** Oriental bittersweet is a deciduous liana [[189](#)]. The stems are woody and twining [[47,96,122,138](#)]. They may reach 66 feet (20 m) in length and 4 inches (10 cm) in width [[8,28,152](#)], depending upon stem age and supporting vegetation [[8](#)]. In surveys along the plain of Lake Michigan (including sites in Illinois, Indiana, and Michigan), Oriental bittersweet stems were likely young, ranging from only 2.4 to 10.5 mm DBH [[96](#)]. The leaves are alternate, oblong, 2 to 5 inches (4-12 cm) long, and 1.4 to 2.0 inches (3.5-5.1 cm) wide [[29,47,70,118,122](#)]. Leaf morphology is highly variable [[35,189](#)], with Oriental bittersweet showing reduced leaf mass per unit leaf area and increased leaf area in shade [[35](#)]. Oriental bittersweet is functionally [dioecious](#) (see [Breeding system](#)). Flowers are sparse, occurring in 3-flowered, axillary cymes [[29,47,70,118,122](#)]. Fruits develop next to the vegetative buds [[29](#)]. Outer vegetative bud scales may be spiny [[27](#)]. A typical plant bears upwards of 370 fruits/year [[186](#)]. Fruits are dehiscent, 3-valved capsules about 0.4 inch (1 cm) in diameter [[47,122,138,161](#)]. The capsules are relatively large [[34,128](#)] and deciduous [[186](#)]. Each valve contains 1 or 2 seeds covered by fleshy, yellowish-red [arils](#) [[47,122,138,161](#)]. In Japan, Fukui [[44](#)] recorded mean sizes of 3.8 mm in seed length, 0.023 mm in seed width, and 7.5 mm in capsule length. Similar capsule sizes occur on plants in the United States (range: 1.5-1.6 mm in width; 6-8 mm in diameter) [[17,27](#)]. Oriental bittersweet roots are deep [[148](#)] and spreading [[103](#)]. They may be as much as 0.8 inch (2.0 cm) thick [[103](#)] and reach deeper than roots of surrounding plant species [[148](#)]. In greenhouse studies, biomass of Oriental bittersweet roots infected with mycorrhizae was less than biomass of uninfected roots ( $P \leq 0.05$ ) [[99](#)].

**Stand structure and age class:** Oriental bittersweet's growth habit is climbing and/or sprawling. It uses woody shrubs and/or trees for structural support, intertwining its branches around support trunks and branches. Branches may eventually overtop or shade out supporting plants. In Rock Creek Park, Washington DC, Oriental bittersweet used other bole-climbing lianas and vines including Virginia creeper (*Parthenocissus quinquefolia*), poison-ivy, and English ivy (*Hedera helix*) for initial structural support. After twining around these lianas, Oriental bittersweet branches grew into and twined around tree crowns. This climbing habit enabled Oriental bittersweet to grow above other lianas and access the tops of the largest trees (3.7 feet (1.1 m DBH)) in the Park [[137](#)]. In red maple, American beech, red oak, and black oak forests on the plain of Lake Michigan, jack pine and white oak were more likely to support Oriental

bittersweet than other overstory species ( $P < 0.02$ ). In general, trees larger than 0.3 inch (10 cm) in DBH were more likely to support lianas than trees of smaller girth ( $P < 0.03$ ), although this varied with liana and host species. Oriental bittersweet's DBH did not significantly increase with increasing DBH of host trees [96].

Oriental bittersweet assumes a sprawling form on open sites. Sprawling Oriental bittersweet branches may form impenetrable thickets [3,29]. On Naushon Island, Massachusetts, Oriental bittersweet spread horizontally in pastures. Grasses and native shrubs in the pastures, including lowbush blueberry (*Vaccinium angustifolium*) and black huckleberry (*Gaylussacia baccata*), were covered to a height of 3 feet (1 m) [135].

On the Pleasant Valley Wildlife Sanctuary, Massachusetts, age of Oriental bittersweet plants was determined 13 years after logging and underbrush removal. Mean basal stem age was 3.4 years (range 1-12 years). Mean plant length was 4.6 feet (1.4 m; range 0.03-6.6 ft (0.01-2 m)). Some Oriental bittersweet plants just outside the Sanctuary (the likely seed sources for the infestation) were 35 years old [152]. In a red maple-American elm forest in West Virginia, Oriental bittersweet individuals (excluding seedlings) ranged from 8 to 23 years old; 15 was the median age [102].

In Pines Hills Campground in southern Illinois, Oriental bittersweet was younger and smaller, but more abundant, in forest-edge than in interior forest communities. Oriental bittersweet averaged 3.3 years of age, 3.9 mm in stem diameter, and 110.5 stems/m<sup>2</sup> in a forest-edge, white oak-black oak-bitternut hickory community. The canopy was 86% closed. In adjacent interior forests with similar overstory composition, Oriental bittersweet averaged 7.7 years of age, 8.7 mm in stem diameter, and 32.2 stems/m<sup>2</sup>. The interior forest canopy was 96% closed [85].

**Raunkiaer [139] life form:**

[Hemicryptophyte](#)

[Geophyte](#)

**SEASONAL DEVELOPMENT:**

Oriental bittersweet starts growth in midspring and flowers soon after [8,28]. Pollen sheds about 2 weeks after flowers open [136]. Leaves abscise in late fall, usually later than the leaves of associated native species [8,166]. Oriental bittersweet in Michigan, for example, retained leaves for a month after the first October frost [166]. Arils and seeds mature in autumn and remain on the plant all winter unless harvested by frugivorous animals. Animals disperse the seeds throughout autumn, winter, and into early spring [34,54,128,152], with most seeds dispersed after leaf drop [54]. Plants are dormant in winter [27]. Phenology of Oriental bittersweet in various locations is given below.

Phenology of Oriental bittersweet by area		
Area	Event	Season
Carolinas	flowers	mostly in May; extends to Aug. or Sept. [138]
	seed disperses	November-January [54]
Connecticut	flowers	May-June
	fruits & arils ripen	September [8]
Illinois	flowers	May-June [118]
Michigan	bud break	late April
	leaf out	mid-May
	flowers	early June [167]
North Carolina	seed disperses	December-March 148
	flowers	May-June

New York	fruits & arils develop	July-October [ <a href="#">17</a> ]
Tennessee	germinates	mid- to late spring
	flowers	May
	arils mature	August-September [ <a href="#">8</a> ]
Blue Ridge Mountains	flowers	May-June [ <a href="#">188</a> ]
China	flowers	May-June
	fruits	July-October [ <a href="#">189</a> ]
Japan	flowers	May-June [ <a href="#">122</a> ]

#### REGENERATION PROCESSES:

- [Vegetative regeneration](#)
- [Breeding system and pollination](#)
- [Seed production](#)
- [Seed dispersal](#)
- [Seed banking](#)
- [Germination](#)
- [Seedling establishment](#)
- [Plant growth](#)



Oriental bittersweet, August root sprouts. Photo by James H. Miller, USDA Forest Service.

Oriental bittersweet regenerates by sprouting and from seed. Its invasiveness is due, in part, to its superior ability to establish from both sprouts and seeds compared to most native lianas and other associated native woody species [[54,105,115,128,138,152](#)]. Based on Oriental bittersweet's ability to spread from both root sprouts and bird-dispersed seed and its use of multiple breeding systems (see the Regeneration Processes links above), Huebner [[68](#)] suggested that Oriental bittersweet may become the fastest spreading invasive species among Oriental bittersweet, Japanese stiltgrass, garlic mustard (*Alliaria officinalis*), tree-of-heaven (*Ailanthus altissima*), and European buckthorn (*Rhamnus cathartica*) [[68](#)].

A comprehensive study of Oriental bittersweet regeneration [[33](#)] is reviewed in [Plant growth](#).

**Vegetative regeneration:** Asexual regeneration is important for Oriental bittersweet spread. Oriental bittersweet sprouts from roots, root fragments, and the root crown [[3,29,34,161](#)]. Damage to the branches, root crowns, or roots encourages sprouting [[8](#)]. An invasive plant guide reports "vigorous" sprouting after damage to Oriental bittersweet

plants [36]. In a greenhouse study using soil samples from a Massachusetts field, no Oriental bitter-sweet seedlings emerged from the soil, but Oriental bitter-sweet root fragments in the soil samples sprouted. Sprouts were distinguished by their lack of cotyledons [34].

**Breeding system and pollination:** Oriental bitter-sweet uses both [dioecious](#) and [perfect](#) breeding systems [68]. This species is typically "functionally dioecious" because early abortion of either male or female organs makes most individual plants unisexual [11]. Plants occasionally develop both unisexual and perfect flowers, becoming [polygamodioecious](#) [47,138], and some plants are reportedly [monoecious](#) [64].

Hymenoptera, especially bees, pollinate Oriental bitter-sweet flowers. Wind pollination also occurs ([8], review by [183]).

Four Oriental bitter-sweet populations from Connecticut were studied for pollen viability. Mean pollen viability across populations was 67%, but viability was significantly different among populations ( $P < 0.05$ ), varying from 17.3% to 74.3%. Oriental bitter-sweet  $\times$  American bitter-sweet hybrids had low pollen viability [29].

**Seed production:** Oriental bitter-sweet typically produces abundant flowers, fruits, and seeds [128,161] (see photo in [Importance to Wildlife and Livestock](#)). In the greenhouse, both male and female plants produced flowers in their second year [190]. Open conditions promote abundant fruiting (Musser 1970 personal communication cited in [183]). For Oriental bitter-sweet plants in forests, fruit production may be sparse until stems reach the overstory [181].

**Seed dispersal:** Animals, water, and humans disperse Oriental bitter-sweet seed [29,114,138]. The seed disperses after the 3-valved capsules split open and expose the arils [138]. The brightly colored, fleshy arils attract birds and small mammals, which disperse most of the seed after ingesting the arils [54,105,115,128,152]. The fruits can float if they fall into water [114]. Undispersed seed falls under or near parent plants. Along the Blue Ridge Parkway, North Carolina, 24% of Oriental bitter-sweet fruits fell to the ground [53].

Frugivorous birds are probably most important for Oriental bitter-sweet seed dispersal because they are highly mobile, travel in flocks, and often eat "voraciously" [28,54,184]. Northern flickers, yellow-rumped warblers, American robins and other thrushes (Turdidae), mockingbirds and catbirds (Mimidae), and European starlings and mynas (Sturnidae) are the primary Oriental bitter-sweet seed dispersers [184]. In an oak forest in North Carolina, small animals removed 75% of the total Oriental bitter-sweet seed crop [54]. Near Asheville, North Carolina, birds and small mammals dispersed Oriental bitter-sweet seeds in "large numbers". Still, more than 80% of Oriental bitter-sweet arils remained on the parent plant until December, and >50% remained until mid-January [54]. Birds likely disperse Oriental bitter-sweet seeds where they perch. In central Japan, where Oriental bitter-sweet is native, Oriental bitter-sweet seed rain was densest under the liana *Smilax china* (10 seeds/1.5 m<sup>2</sup>) and the shrub *Neolitsea sericea* (8 seeds/1.5 m<sup>2</sup>), both of which were used as bird perches [162].

Seed dispersal by birds is an important factor in Oriental bitter-sweet's ability to rapidly colonize a site. Long-distance dispersal of seed by birds may promote faster rates of Oriental bitter-sweet establishment on new sites compared to plant species without bird-mediated seed dispersal, particularly late-successional herbs with seeds that are primarily dispersed by ants [106]. Oriental bitter-sweet seedlings were noted the first year following restoration plantings in a landfill on Staten Island, New York. Minimum mean travel distance to the nearest Oriental bitter-sweet seed source was 430 feet (131 m); the authors surmised that birds dispersed Oriental bitter-sweet seed onto the landfill [144]. Long gut-retention times may result in very long Oriental bitter-sweet dispersal distances when birds migrate. In Japan, Oriental bitter-sweet seed remained in the digestive tracts of brown-eared bulbuls (*Hypsipetes amaurotis*, a native Japanese passerine) for 14 to 42 days ( $\bar{x}$ =27 days). That was one of the longest retention times recorded among 16 bird-dispersed plant species [44].

Roads may act as corridors for seed dispersal. Oriental bitter-sweet is common along roadsides [125], especially interstate highways in New England [29]. It has been used in roadside plantings in the Northeast. Humans using fruiting branches for ornaments may disperse seeds when collecting or disposing of the branches [8,29]. People can facilitate animal dispersal of Oriental bitter-sweet seed by planting Oriental bitter-sweet as an ornamental [28].

**Seed banking:** Oriental bittersweet has a short-lived soil seed bank. Field [33], and laboratory [34] studies suggest Oriental bittersweet seed does not remain viable for more than one growing season, although some managers report that soil-stored Oriental bittersweet seed remains viable for several years [164]. The small portion of viable seed remaining in seed banks for more than 1 year contributes little to Oriental bittersweet regeneration [34,86]. A 3-year field study in New Jersey showed a 90% establishment rate of Oriental bittersweet seed the 1st spring after a winter planting. There was no "appreciable" Oriental bittersweet germination in the 2nd or 3rd years of the study [174]. In a 2-year study in an Oriental bittersweet-infested Massachusetts field, Oriental bittersweet seedling recruitment was measured after Oriental bittersweet seed was hand-sown onto study plots. Density of Oriental bittersweet seedling recruitment closely matched the density of seeds sown. Seed rain ranged from 14 seeds/m<sup>2</sup> to 826 seeds/m<sup>2</sup> ( $\bar{x}$ =168 seeds/m<sup>2</sup>). Oriental bittersweet seedling emergence from the seed bank averaged 0.9 seedling/m<sup>2</sup>. All seedlings emerged in the 1st year of the study, with seedling recruitment ranging from 11 seedlings/m<sup>2</sup> to 532 seedlings/m<sup>2</sup> ( $\bar{x}$ =107 seedlings/m<sup>2</sup>) [34].

In a green ash-yellow-poplar forest near Philadelphia, Pennsylvania, Oriental bittersweet seedlings emerged from the seed bank following herbicide treatment of Japanese stiltgrass. Oriental bittersweet was a common component of the aboveground vegetation before spraying [51].

Field managers in Great Smoky National Park report substantial Oriental bittersweet seedling recruitment during the first 6 years of a grubbing and herbicide control program involving "complete removal and rootkill" of Oriental bittersweet (Langon 1993 cited in [8]), suggesting that either the seedlings originated from the seed bank or there was an off-site seed source. The authors noted that because Oriental bittersweet is such a prolific seed producer, its seed bank is quickly replenished when seed sources remain on site or nearby [8].

**Germination:** In the field, Oriental bittersweet seeds likely require overwintering to germinate. The embryos are dormant, and seeds require stratification for germination [17,29,53]. (review by [8]). Overall germination rate of Oriental bittersweet seed is high [8,161,174], showing 85% (review by [183]) to 95% [8] germination in the laboratory.

Mechanical or chemical scarification of the seed is not necessary for germination [34,54,128]; however, germination in the laboratory is delayed or reduced when arils remain attached to the seeds [54]. In a laboratory study, Oriental bittersweet seeds that had either been ingested by birds or had the fruits and arils removed manually showed similar, and higher, germination rates ( $\bar{x}$ =82%) than seeds with intact fruits ( $\bar{x}$ =51%). The authors concluded that although animals aid in seed defleshing and dispersal, gastrointestinal scarification is not needed for germination to occur [53]. Near Asheville, North Carolina, seeds that fell beneath the parent plant, and thus were not ingested by animals, showed reduced germination rates (51%) compared to ingested seeds (82%). However, the authors noted that 51% germination was high enough to substantially contribute to Oriental bittersweet recruitment. Seeds still on the plant in February were damaged and unviable [54].

Light is not required for germination [29,152]. Oriental bittersweet germination occurs under a wide range of light intensities [127]. Greenberg and others [53] found Oriental bittersweet seed germination and seedling survival rates in the greenhouse were similar from 20% photosynthetically active radiation to full sunlight ( $P=0.05$  X<sup>2</sup> value). They concluded that the ability to germinate over a wide range of light intensities allows Oriental bittersweet to establish under closed canopies [53]. In the greenhouse, Oriental bittersweet germination rates were not significantly different under 20% sunlight to full sunlight, although seedlings with  $\geq 70\%$  full sunlight had more leaves, more stem and root biomass, and longer roots than seedlings in lower light levels [53]. In contrast, Patterson [128] found best germination occurred under low-light conditions in the greenhouse.

Some water-dispersed seed may germinate on floodplains, although seed that floats may be less viable than seed that cannot float. In Connecticut, Oriental bittersweet seed viability was tested for floating vs. sinking seeds. Mean viability was 41% for floating seeds and 88% for sinking seeds [29].

**Seedling establishment:** Oriental bittersweet seedling emergence is generally high [113,128], but survivorship may vary greatly depending upon field conditions and population differences. Survivorship of field-germinated seedlings in Massachusetts ranged from 0% to 88% ( $\bar{x}$ =17%) [34]. Patterson [128] reported densities of 60

emergents/m<sup>2</sup> for an Oriental bittersweet population in Connecticut; however, seedling density declined over the growing season. He attributed seedling mortality to drought [128]. In the laboratory, seedling emergence rate differed significantly among 2 Oriental bittersweet populations in Connecticut ( $P < 0.001$ ). Percent emergence after 21 days was 59% and 82% [29].

Oriental bittersweet frequently establishes along fencelines and other sites where birds perch and defecate the seeds [49,50,113,113].

Thick litter may retard Oriental bittersweet seedling emergence. A study on the Bent Creek Experimental Forest found Oriental bittersweet was significantly less abundant in oak communities than in yellow-poplar-sweet birch communities ( $P \leq 0.005$ ) [112], which may have been partially due to differences in litter depth. A survey in North Carolina found Oriental bittersweet was associated with yellow-poplar forests that had succeeded from agricultural fields, while Oriental bittersweet was less common in mixed-oak forests. The author concluded that thinner leaf litter layers and moister soils in yellow-poplar forests favored Oriental bittersweet germination, seedling establishment, and growth. Survivorship was greater on plots with thin litter (1 kg litter/m<sup>2</sup>) than with thick (3 kg litter/m<sup>2</sup>) or no litter ( $P \leq 0.01$ ) [87]. A greenhouse study showed that intact oak litter physically impeded Oriental bittersweet seedling emergence, although hypocotyls grew sideways as much as 4 inches (9 cm) to find a point of reduced litter (in this case, the pot edge), and then emerged. Seedlings in deep litter tended to allocate more growth to hypocotyls, while seedlings in shallow litter tended to allocate more growth to cotyledons. The authors concluded that Oriental bittersweet seedlings would probably find litter patches thin enough for emergence in all but the deepest oak litter, but pine litter may be more conducive to Oriental bittersweet establishment than oak litter [34]. A shadehouse experiment showed mixed-deciduous litter loads above 3 Mg/ha lowered Oriental bittersweet seedling emergence ( $P < 0.05$ ), but lesser loads or fine-ground litter had no significant effect on Oriental bittersweet emergence. The author suggested that litter disturbance likely favors Oriental bittersweet establishment [33].

**Plant growth:** Oriental bittersweet shows rapid growth under partial to full sun [3,111], although seedlings grow slower in low than in high light [54,127]. In Massachusetts, artificially shaded Oriental bittersweet transplants showed greatest aboveground biomass gain under 28% of full sunlight. Mean aboveground biomass 1 year after transplanting was significantly different ( $P = 0.002$ ) under 100% full sunlight (0.9 g), 28% of full sunlight (14.4 g), and 2% of full sunlight (0.3 g) [33]. Oriental bittersweet growing in partial to full sun can overtop 3- to 7-foot (1-2 m) tall associated vegetation after one growing season [35]. On mesic sites in full sunlight, Oriental bittersweet may grow 10 to 12 feet (3-3.7 m)/year [111]. In Connecticut, Oriental bittersweet grew 10 feet (3 m)/year [128]. The Tennessee Exotic Plant Pest Council [163] reported annual growth rates of 1 to 12 feet (0.3-3.0 m) in the first 7 years after establishment, with little growth thereafter. Oriental bittersweet may persist in a densely shaded understory for many years, then respond with rapid growth when disturbance opens the canopy [111,128].

Besides having both shade and sun tolerance, other factors contributing to Oriental bittersweet's often rapid growth include tolerance to varying soil moisture and ability to form mycorrhizal associations. In Connecticut, transplanted Oriental bittersweet seedlings showed low mortality and good height and biomass gain across a wide range of soil moisture and light conditions [97]. See [Effects on diversity](#) for further information on this study and [Soils](#) for more information on Oriental bittersweet soil tolerances. In greenhouse studies, Oriental bittersweet with their roots infected with mycorrhizae grew taller than plants with uninfected roots when phosphorus was limiting ( $P \leq 0.05$ ). When phosphorus was added to the soil, mycorrhizae appeared to limit Oriental bittersweet growth [99]. Oriental bittersweet has shown faster growth rates than associated native lianas. In Michigan, Oriental bittersweet plants were younger than native riverbank grapes ( $\bar{x} = 3.7$  vs. 4.2 years, respectively) but stems were 8% thicker [166].

Clonal growth can result in large patches of Oriental bittersweet that originated from a few seedlings [8]. Increased seedling vigor (biomass and growth rates) under high light intensity in the greenhouse and higher cover of Oriental bittersweet on open sites led researchers to suggest that canopy disturbance aids vegetative spread of established seedlings [53]. In Connecticut, Oriental bittersweet cover on 0.1 acre (0.06 ha) increased from 5% to 100% within 5 years [128].

A study by Ellsworth [33] illustrates many Oriental bittersweet characteristics that enhance its invasiveness: abundant seed production, high rates of germination and seedling establishment, and tolerance to a wide range of light

intensities. The study included field, shadehouse, and greenhouse experiments. Across 15 sites in Massachusetts, Oriental bittersweet seed rain averaged 168 seeds/m<sup>2</sup>. Seed rain was highly variable, however, ranging from 13 to 826 seeds/m<sup>2</sup>. In the greenhouse, germination averaged 68%, and emergence averaged 107 seedlings/m<sup>2</sup>. In the field, emergence averaged 1 seedling/m<sup>2</sup>. In the shadehouse, litter biomass greater than 4 Mg/ha reduced seedling emergence. Survival of Oriental bittersweet seedlings in the field varied and was not associated with Oriental bittersweet seedling density. Survival averaged 16.8% by August; summer weather conditions were "extremely dry". In the field and shadehouse, light intensities of 100%, 28%, and 5% of full sunlight had no significant effect on Oriental bittersweet survival or growth in the 1st growing season. In the 2nd growing season, survivorship was similar (68%) under all light intensities, but seedlings in 28% sunlight had greater total stem length (all stems combined: 15.1 feet (4.6 m)) than seedlings in full sun (7 feet (2 m)) or 5% sun (0.7 feet (0.2 m)). The author predicted that given partially shaded to open conditions, seedlings surviving their 1st year would have high survivorship thereafter. He suggested that given Oriental bittersweet's high seedling survivorship in deep shade and growth plasticity under variable light intensities, intact forests are vulnerable to Oriental bittersweet invasion. He predicted that a density of 12 seedlings/m<sup>2</sup> is enough to establish a new Oriental bittersweet population on many sites [33].

#### SITE CHARACTERISTICS:

In the United States, Oriental bittersweet grows on woodland [188] and forest [3,102,106,107] edges; in thickets, woodlands, and forests [3,47,118,138,161,179]; and on coastal wetlands, beaches, and saltmarsh edges [8,161]. Oriental bittersweet is common on disturbed sites such as roadsides [3,125,138], logged forests, and old fields [3,138]. It is also common in urban areas, from which it may disperse onto wildlands. Most Oriental bittersweet specimens in West Virginia herbaria had been collected in open forests [65]:

Collection sites of Oriental bittersweet from herbaria in West Virginia [65]	
Site	Percent of collection ( <i>n</i> =26 plants)
Open forest	31%
Roads	23%
Railroad tracks	11%
Closed forest	6%
Trails	6%
Streamsides	3%
Old fields	3%
Residential	3%
Other	14%

Three studies report site characteristics associated with Oriental bittersweet invasion.

On the Cheat Ranger District of the Monongahela National Forest, West Virginia, site conditions that increased susceptibility of sugar maple forests to invasive species, including Oriental bittersweet, included high overall species richness, north-facing slopes, mesic conditions, and clearcuts ( $P < 0.05$  for all variables). Red oak tended to codominate the sugar maple stands with these characteristics [69].

In a study of mixed-oak and yellow-poplar-sweet birch forests on the Bent Creek Experimental Forest, Oriental bittersweet was significantly associated with wind disturbance, topographical features associated with mesic conditions, bare mineral soil, tree harvest, and canopy gaps. Oriental bittersweet was most common at relatively high elevations ( $\bar{x}$ =2,460 feet (749 m)), on steep slopes ( $\bar{x}$ =36% slope), and on concave landforms. It was significantly associated with mesic soils, soils disturbed by animal scarification, and logged sites. Significant stand structure variables for Oriental bittersweet occurrence were canopy gaps, dense midstories, and hardwood overstories dominated by species other than oak. The 2 variables of strongest significance were lack of an oak overstory ( $P=0.001$ ) and presence of animal-scarified soils ( $P=0.001$ ). Oriental bittersweet was weakly associated with sites where Hurricane Opal had uprooted

trees ( $P < 0.157$ ). McNab and Loftis [112] developed a rapid survey technique and probability-of-occurrence model for hazard rating in areas where Oriental bittersweet is known to occur. Although the study was conducted in western North Carolina, the results may be applicable over a broader area of the Southern Appalachian Mountains with similar environmental conditions [112].

Based on site variables, Pande and others [125,126] provide a model to predict Oriental bittersweet presence across southern Illinois. In their study, best predictors of Oriental bittersweet presence were high elevation, mesic soils, clay soils, proximity to roads, and an overstory other than oak [125,126]. However, Oriental bittersweet is invasive in other oak-hickory forests in southern Illinois [85], Pennsylvania, and New Jersey [67].

**Soils:** Oriental bittersweet grows on forest, alluvial, and floodplain [138,143,150], and glacial till [55] soils of all textures but of generally acidic pH. Oriental bittersweet typically grows in loam [102,167], sand, and silt [55,143] soils. In New Hampshire, it was negatively associated with soils having high percent clay content ( $P = 0.05$ ) [76]. However, in Giant City Park, Illinois, Oriental bittersweet presence was positively associated with mesic soils with high clay content ( $\bar{x} = 25\%$  clay,  $P < 0.05$ ) and relatively high pH ( $\bar{x} = \text{pH } 5.02$ ,  $P < 0.001$ ) [125,126]. Parent materials of soils supporting Oriental bittersweet include granite, sandstone, hornblende, and gneiss. Soil pH is generally moderately to mildly acidic (pH 5.6-6.5) [143], although Oriental bittersweet is reported on gneiss- and schist-derived soils that are  $< 5.5$  in pH [112]. Oriental bittersweet occurred on acidic (4.9-5.3 pH) soils in Massachusetts [152], with best establishment and growth on relatively less acidic soils [143]. Transplant experiments conducted 13 years after logging on the Pleasantville Valley Wildlife Sanctuary showed that low pH, high irradiance, and high moisture content were associated with Oriental bittersweet invasion [152].

Oriental bittersweet is most common on mesic soils. It is generally intolerant of saturated or droughty soils [71,152,161,186] but appears tolerant of a range of soil moistures. It may occur on seasonally flooded soils [133] and may establish on some sites despite drought. Oriental bittersweet seedlings in Massachusetts survived a severe summer drought [33] (see [Plant growth](#)). More research is needed on moisture requirements for Oriental bittersweet [112].

Oriental bittersweet apparently prefers nutrient-rich soils [6,183]. In hardwood forests of Connecticut, soils supporting Oriental bittersweet had significantly higher potassium, calcium, and magnesium levels than soils without Oriental bittersweet. Nitrogen mineralization and litter decomposition rates were higher on plots with than without Oriental bittersweet ( $P < 0.001$  for all variables) [96].

**Climate, elevation, and topography:** Oriental bittersweet tolerates a wide range of climatic conditions [71,121,128]. It is native to temperate and tropical regions on southeastern Asia [180]. Its elevational range is from sea level to 4,600 feet (0-1,400 m) in the United States [8,112,144]; 1,500 to 7,200 feet (450-2,200 m) elevation in its native range of southeastern Asia (Cheng and Huang 1999 cited in [103]); and from sea level to 1,800 feet (0-540 m) in New Zealand [186]. In Giant City Park, Illinois, Oriental bittersweet presence was positively associated with relatively high-elevation ( $\bar{x} = 669$  feet (204 m)), flat sites ( $P < 0.001$  for both variables) [125,126].

Topography varies among sites with Oriental bittersweet, although Oriental bittersweet may be most abundant on mesic depressions or slopes. In Piscataway and Fort Washington National Parks, Maryland, Oriental bittersweet occurs on floodplains, lowlands near the Potomac River, streambanks, stream terraces, and in ravine and upland forests [156]. Along the Blue Ridge Parkway, Oriental bittersweet was more common on relatively moist, north-facing slopes than on dry, south-facing slopes, and occurred up to 6,542 feet (1,994 m) elevation [53]. In a red maple-American elm forest in West Virginia, however, Oriental bittersweet was more common on south- than north-facing slopes [102]. In yellow-poplar/spicebush forests of Inwood Park, Manhattan, Oriental bittersweet was most common on ridgetops (mean density = 788 stems/ha) and least common in valleys (36 stems/ha); it was more common on west-facing (589 stems/ha) than east-facing (100 stems/ha) slopes [39].

#### SUCCESSIONAL STATUS:

Oriental bittersweet is sun and shade tolerant and may occur in all stages of succession.

**Light tolerance:** Oriental bittersweet is shade [35,54] and light tolerant at all life stages. In hardwood forests of Connecticut, canopy closure typically ranged from 76% to 100% on sites with Oriental bittersweet [96]. In the

greenhouse, varying light intensities did not produce significant differences in either the number of days Oriental bittersweet took to germinate, its germination rate, root:shoot weight, or its root:shoot length. However, seedlings exposed to 70% or more of full sunlight tended to produce more leaves, heavier leaves, and longer, heavier roots than more shaded seedlings [54]. In a Massachusetts field, artificially shaded Oriental bittersweet transplants showed good survivorship over a large range of sunlight intensities. Survivorship was best with moderate shade [35].

Mean (SD) Oriental bittersweet survivorship from midsummer transplanting in 2000 to field measurements in fall 2001 [35]				
Treatment (% sun)	Transplant survival (%)	Winter survival (%)	Growing season survival (%)	Cumulative survival after 1 year (%)
100	96 (3)	49 (21) <sup>b*</sup>	90 (9) <sup>ab</sup>	43 (20)
28	87 (19)	84 (12) <sup>a</sup>	96 (4) <sup>a</sup>	70 (21)
2	94(7)	60 (12) <sup>ab</sup>	76 (5) <sup>b</sup>	43 (11)
<i>P</i> value	not significant	0.031	0.029	not significant
*Within columns, means with the same letter are not significantly different among treatments ( $P<0.05$ ).				

Oriental bittersweet employs what Greenberg and others [54] call a "sit and wait" strategy: it can establish, grow slowly, and persist in late-seral, closed-canopy communities. When disturbance opens the canopy, it typically responds with rapid growth [54,113]. In the greenhouse, Patterson [128] found Oriental bittersweet seedlings grown under low light nearly doubled their photosynthetic rate after 8 days of exposure to high light. Oriental bittersweet's ability to establish in low light and then climb towards higher light intensity enables it to shade out, overtop, and eventually kill supporting vegetation [3,29]. When dense, Oriental bittersweet plants may replace the successional subcanopy [38] or the canopy [113].

**Disturbance:** Disturbance increases the likelihood of successful Oriental bittersweet establishment [34]. Field studies show Oriental bittersweet is most common near roads [125,152] and on sites disturbed by logging, windthrow, animal foraging [112,152], disease, or insect outbreaks [123]. Oriental bittersweet often establishes on roads, then spreads to adjacent forests [102], reviews by [18,31], [114]. In Giant City State Park, Illinois, for example, Oriental bittersweet presence was positively correlated with proximity to roads ( $P<0.05$ ) [125]. Along the Blue Ridge Parkway in North Carolina, however, Oriental bittersweet cover and density were unrelated to distance from the roadside, although Oriental bittersweet plants were taller along the road than in interior forests [53]. Oriental bittersweet was common in eastern hemlock (*Tsuga canadensis*) forests in Connecticut following deforestation ( $\geq 50\%$  foliar loss) by hemlock woolly adelgids [123].

On the Pleasantville Valley Wildlife Sanctuary, Massachusetts, Oriental bittersweet density was correlated with level of past site disturbance. Sites with a known history of farming or logging tended to have moderate to heavy infestations, with heaviest infestations on logging roads ( $P<0.005$ ). On logged sites, plots where horse logging had been conducted were less infested than plots where mechanized equipment was used. Oriental bittersweet did not occur on undisturbed plots. Pre- and postlogging surveys suggest that Oriental bittersweet seedling establishment on logged plots occurred 2 or more years after logging ceased. The authors speculated that this establishment lag was due to reluctance of bird dispersers to forage or perch in exposed openings and/or initial colonization by other plant species, which created favorable, mesic conditions that promoted Oriental bittersweet germination and establishment. Oriental bittersweet was positively correlated with percent exposed mineral soil ( $P<0.025$ ) and sites with relatively less acidic soil ( $P=0.01$ ), a combination of which was most common on logging roads and least common on undisturbed sites. Although Oriental bittersweet did not occur on undisturbed plots, small but apparently healthy Oriental bittersweet seedlings were present in late-successional deciduous and coniferous forests elsewhere on the Sanctuary, growing through an intact litter layer on a well-shaded forest floor [152].

An invasive plant guide reports that soil disturbance promotes Oriental bittersweet spread [36]. Nutrient flushes, which are often associated with fire and other soil disturbances, may encourage establishment of Oriental bittersweet and

other invasive species. In Massachusetts, a black oak-white oak/black huckleberry-low sweet blueberry forest irrigated with nitrogen-enriched wastewater was initially invaded with old-field herbs including pokeweed (*Phytolacca americana*) and tangled bindweed (*Polygonum concolculus*). Pokeweed was still abundant after 9 years of wastewater irrigation, but Oriental bittersweet had successionaly replaced tangled bindweed. Compared to control plots, bittersweet nightshade (*Solanum dulcamara*), Tatarian honeysuckle (*Lonicera tatarica*), Virginia creeper (*Parthenocissus quinquefolia*), and poison-ivy were also more abundant after 9 years of wastewater fertilization [77].

Land use history and soil chemistry can affect invasibility of a site for Oriental bittersweet and other nonnative plant species. In central Connecticut, Oriental bittersweet was most frequent in recently abandoned (5-year-old) fields (77% frequency), reforested old fields (43%), and sites undergoing residential or commercial development (39%) ( $P < 0.001$ ) [119]. In northeastern Connecticut and southern Massachusetts, land use history was the greatest single predictor of site invasibility. Oriental bittersweet was most abundant on former (1934) residential areas (20% Oriental bittersweet cover, 33% frequency) and old fields (0.46% cover, 28% frequency). In general, Oriental bittersweet cover and frequency were greatest in populated areas ( $> 8$  houses/km; 7.63% cover, 50.0% frequency) and least in remote areas (1-2 houses/km; 0.02% cover, 1.7% frequency). Oriental bittersweet was detected most often near paved roads (26%-46% of total invaded plots), with frequency decreasing along dirt roads (7%-39%), trails (0-30%), and forest interiors (1%-17%). Oriental bittersweet cover increased with road size [100]. In central and western Massachusetts, the carbon:nitrogen ratio was the strongest site factor correlated with Oriental bittersweet presence ( $P < 0.001$ ). Forest interiors were also negatively associated with Oriental bittersweet presence ( $P < 0.07$ ) [109].

**Forests:** Although it occurs in all stages of forest succession, Oriental bittersweet is most common in early-seral deciduous forests and on forest edges ([102], reviews by [18,31], [114]). Oriental bittersweet colonizes forest edges and canopy gaps [31,35] but also grows in very low light conditions such as those found in interior, closed-canopy forests [94]. It may slow or alter succession in young, developing tree stands [134]. After establishing on woodland and forest ecotones in Delaware and Pennsylvania, Oriental bittersweet invaded oak-hickory forests in both second-growth and closed-canopy successional stages [106,107]. Oriental bittersweet was found in communities representing all stages of succession (floodplain riparian forest and old field to mature forest) in mesophytic mixed-oak (*Quercus* spp.)-American beech and riparian communities of southeastern Pennsylvania. It was most frequent in early and late stages (old fields and forests) [143].

Oriental bittersweet frequency by successional stage and community type in Pennsylvania [143]				
Floodplain riparian	Old field	Thicket	Woodland	Forest
24%	41%	37%	26%	39%

Oriental bittersweet sometimes invades mature and old-growth forests [106,107]. Within late-successional forests, however, it may be most common in gaps or where the canopy is relatively thin. In West Virginia, Oriental bittersweet seedlings were more abundant in red maple-America elm forest interiors than on forest edges. Oriental bittersweet cover, however, was negatively associated with tree and shrub cover ( $P < 0.007$ ) [102], suggesting that within forest interiors, Oriental bittersweet establishment was best in openings. Mean Oriental bittersweet seedling density in interior forest sites was 286.9 seedlings/m<sup>2</sup> compared to 186.3 seedlings/m<sup>2</sup> on forest edges. The oldest Oriental bittersweet plants were closest to forest edges [102], so Oriental bittersweet probably spread from forest edges to the interior forest. Oriental bittersweet presence was negatively correlated with forest cover in yellow-poplar and mixed-oak forests on the Bent Creek Experimental Forest [87] and 25 watersheds at other locations in southwestern North Carolina [88].

**Old fields:** Oriental bittersweet occurs in all stages of old-field succession [3,161,167] and may change old-field successional pathways. In southeastern Connecticut, old-field vegetation surrounded by a late-successional oak-hickory forest was measured approximately every 10 years from 1954 to 1992. The old field burned just prior to the 1954 survey. In 1954, field cover was primarily Kentucky bluegrass (*Poa pratensis*), redtop (*Agrostis gigantea*), and wrinkleleaf goldenrod (*Solidago rugosa*). Allegheny blackberry (*Rubus allegheniensis*) and northern bayberry (*Morella pennsylvanica*) had scattered occurrence. By 1960, black cherry (*Prunus serotina*) and black oak had established. By the 1970s, a thicket of shrubs and trees had developed; important new woody species included

common greenbrier (*Smilax rotundifolia*) and flameleaf sumac (*Rhus copallinum*). Nonnative Oriental bittersweet, Morrow's honeysuckle, and multiflora rose and native Virginia creeper were noted for the first time. By the early 1980s, 2 distinct plant communities were described. The eastern portion of the field was a young hardwood forest dominated by black cherry, red maple, and black tupelo (*Nyssa sylvatica*). Southern arrowwood (*Viburnum dentatum*), Morrow's honeysuckle, and common greenbrier dominated the midstory. Woody vines <2.0 feet (0.5 m) tall, including Oriental bittersweet, Virginia creeper, and poison-ivy, dominated the lowest strata. The western portion of the old field was an "almost impenetrable" woody vine community dominated by Oriental bittersweet. Fox grape (*Vitis labrusca*) was increasing in cover and spreading into the canopy by using Oriental bittersweet for support. Scattered woody species on the western field were covered by nonnative and native lianas. Host trees were suffering branch breakage and low reproduction; shrubs were suppressed or killed. The authors speculated that the initial Oriental bittersweet invasion was facilitated by an Oriental bittersweet plant at the edge of the field, which provided perching support and arils (with seeds) for frugivorous birds. This field-edge Oriental bittersweet plant was 2 inches (5 cm) in basal diameter by 1992. Oriental bittersweet did not invade sites where common greenbrier dominated the initial community [38].

In Connecticut, Goslee [49] reported that Oriental bittersweet, and to a lesser extent, Japanese honeysuckle and grape (*Vitis* spp.), had invaded an old field, creating a liana-dominated field that excluded other woody species. This probably "dramatically altered" the successional path the old field would otherwise have followed [49].

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## FIRE EFFECTS AND MANAGEMENT

SPECIES: *Celastrus orbiculatus*

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- [FIRE EFFECTS](#)
- [FUELS AND FIRE REGIMES](#)
- [FIRE MANAGEMENT CONSIDERATIONS](#)

FIRE EFFECTS:

- [Immediate fire effect on plant](#)
- [Postfire regeneration strategy](#)
- [Fire adaptations and plant response to fire](#)

**Immediate fire effect on plant:** As of this writing (early 2011), there was no published information on the effects of fire on Oriental bittersweet. It is likely that fire top-kills Oriental bittersweet but does not damage the root crown and roots, which are insulated by soil.

**Postfire regeneration strategy** [158]:

[Geophyte](#), growing points deep in soil

[Initial off-site colonizer](#) (off site, initial community)

[Secondary colonizer](#) (on- or off-site seed sources)

**Fire adaptations and plant response to fire:**

Fire adaptations: Oriental bittersweet sprouts from the root crown and roots [3,29,34,161]. Additionally, it produces abundant, animal-dispersed seed and shows rapid growth on open sites [28,54,68,144,161,184] (see [Regeneration Processes](#)). Although there is no literature suggesting that these regeneration strategies evolved in response to fire disturbances in southeastern Asia, sprouting, bird dispersal of off-site seed, and rapid growth would likely favor Oriental bittersweet regeneration in postfire environments of North America.

Plant response to fire: Published accounts of Oriental bittersweet's response to fire were sparse as of this writing (2011); however, since Oriental bittersweet can sprout from the root crown and roots and establishes from animal-

dispersed seed following other types of disturbance, it would likely establish from sprouts and/or seed after fire. Dibble and others [25] inferred that species like Oriental bittersweet, which persist in closed canopies and spread after the canopy opens, may spread and become dominant in early postfire environments. Both Oriental bittersweet sprouts and seedlings respond to canopy release with rapid growth [54,113] (see [Successional Status](#) and [Plant growth](#)). Oriental bittersweet may increase after nutrient flushes (see [Disturbance](#)), which often occur after fire [1,2,77]. It may also establish later in postfire succession. In southeastern Connecticut, portions of an old field that was burned and abandoned 40 years prior to the study were dominated by Oriental bittersweet, with Japanese and Morrow's honeysuckle also establishing around postfire year 40 [23].

**Seedling establishment:** New burns may provide favorable sites for Oriental bittersweet establishment. Field and laboratory studies suggest that open conditions [34,102,125,152] and exposed mineral soil [112,152] favor Oriental bittersweet seedling establishment on mesic sites. Plants with bird-dispersed seed have good opportunities for short- and long-distance seed transport after fire [92]. Birds are known to disperse Oriental bittersweet seeds from nearby seed sources onto old fields and other disturbed sites [38,113,144], so they would likely disperse Oriental bittersweet seed onto burns as well. Long gut-retention times for Oriental bittersweet seed may result in long-distance dispersal by birds [44]. Greenberg and others' [53] [germination](#) study suggests that seed scarification by fire or animals does not enhance Oriental bittersweet germination rates.

Because most Oriental bittersweet seed remains viable in the seed bank for only 1 year [34,174], fire that kills a year's cohort of Oriental bittersweet seedlings, and any seeds remaining on plants, would remove most of the Oriental bittersweet seed bank. Even with severe fire, however, it is unlikely that a single fire would kill all Oriental bittersweet seed sources on or near a site. Because Oriental bittersweet is a prolific seed producer, its seed bank can be quickly replenished by on-site, unburned plants or nearby seed sources [8].

**Sprouting:** Plants that can sprout from the roots, such as Oriental bittersweet (see [Vegetative regeneration](#)), can be powerful competitors for space, light, and nutrients in early postfire environments [79,82,108,145]. Roots are less susceptible to fire damage, and often capable of greater carbohydrate storage, than rhizomes and root crowns [81,82]. Although many of Oriental bittersweet's associates in eastern mixed-hardwood forests can sprout from their root crowns (for example, [9,40]), Oriental bittersweet may have a competitive edge over associated species that cannot root sprout. Huebner [66] speculates that growing-season fire may increase Oriental bittersweet abundance by promoting Oriental bittersweet root sprouting.

On Naushon Island, Massachusetts, the effectiveness controlling Oriental bittersweet by mowing followed by either spring or fall prescribed burning was compared with the effectiveness of mowing followed by either 1) spring mowing, 2) fall mowing, 3) spring herbicide (triclopyr), or 4) fall herbicide treatments. The management objective was to reduce encroachment of nonnative Oriental bittersweet, nonnative Scotch broom (*Cytisus scoparius*), and native common greenbrier (*Smilax rotundifolia*) onto a remnant little bluestem-indiangrass (*Sorghastrum nutans*) prairie. Initially, all plots except the untreated controls were mowed to reduced standing woody vegetation. Early-season (spring) plots were mowed in early May, with follow-up spot burning, mowing, or spraying in July. Late-season (fall) plots were mowed in July, with follow-up spot burning, mowing, or spraying in mid-October. Oriental bittersweet cover was less on fall-burned plots than on unburned control plots, although the difference was not statistically significant. Spring prescribed fire had no appreciable effect on Oriental bittersweet cover compared to controls. In both spring and fall treatments, herbicide reduced Oriental bittersweet the most [135].

Mean percent difference (SD) in Oriental bittersweet cover (%) on early- and late-season treatments from cover on control treatments on Naushon Island [135]		
Treatment	Early season	Late season
Control	6.3 (11.6)	14.6 (6.0)
Burn	-8.3 (6.7)	-25.0 (5.9)
Mow	-8.3 (9.7)	+8.3 (6.8)
Herbicide	-50.0 (6.4)	-72.9 (9.0)

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Native graminoids had positive responses to fall fire or herbicide application, averaging 20.8% higher cover on burned or sprayed plots than on control plots. Spring burning had no effect on graminoid cover compared to control plots, while early-season herbicide plots averaged 31.3% greater graminoid cover than control plots [[135](#)].

#### FUELS AND FIRE REGIMES:

- [Fuels](#)
- [Fire regimes](#)

#### Fuels:



Oriental bittersweet liana using a tree for structural support.  
Photo by Carrie S. Miller, Univ. of Tennessee,  
<http://tenn.bio.utk.edu>.

Oriental bittersweet may alter fuel structure and loads (review by [[25](#)], communication by [[142](#)]), although quantitative data of Oriental bittersweet fuel loads were lacking as of early 2011. Oriental bittersweet may act as a ladder fuel by growing up and over supporting shrubs and trees [[38,66](#)], which increases the chance that a fire will crown [[25](#)]. Oriental bittersweet can also support other lianas and vines [[38](#)], possibly enabling other twining species to become ladder fuels as well. It also contributes to understory fuel loads. In total, it contributes substantial biomass to forests of the Northeast [[54](#)]. Oriental bittersweet sometimes attains heavy understory cover in hardwood and coniferous communities, such as yellow-poplar, that historically had sparse understories (for example, [[133](#)]). Forest understories with Oriental bittersweet or a mix of Oriental bittersweet and other nonnative invasive woody shrubs, such as Japanese honeysuckle and Japanese barberry, can have substantially greater overall cover than uninvaded forests( [[23](#)], review by [[25](#)]). On opens sites where host plants are scarce, Oriental bittersweet's sprawling habit may also increase fuel continuity and loads over historic levels. Studies are needed on how Oriental bittersweet affects fuel characteristics.

In the laboratory, Oriental bittersweet's mean heat of combustion was near average for northeastern nonnative and native lianas and shrubs [22,24].

**Fire regimes** differ across Oriental bittersweet's North American range. In northeastern maple-birch-beech (*Acer-Betula-Fagus*) forests, historic fire return intervals were highly variable, depending upon microclimate, topography, and soil. Fires were mostly of mixed severity. Stand-replacing, medium-interval (~ 80-year) fires were most common in forests dominated by birches, while long-interval ( $\geq 300$  years), mixed-severity or stand-replacing fires occurred in forests dominated by maple and/or beech [37,42,59,147]. Oak-hickory, oak-pine, and pine forests of the Northeast and Southeast had mostly short-return interval, surface fires [160]. Oriental bittersweet was not present in these forests while historic fire regimes were still operating. See the [Fire Regime Table](#) for further information on fire regimes of vegetation communities in which Oriental bittersweet may occur.

A dearth of fire studies makes it unclear how Oriental bittersweet may affect or alter fire regimes in plant communities where it is present. Oriental bittersweet's climbing habit can alter forest structure [29,38,101] and may carry fire into the canopies of forests that historically did not experience crown fires. The fire ecology of Oriental bittersweet is poorly understood [141], and research is needed to determine Oriental bittersweet's impact on fire behavior and fire regimes.

#### FIRE MANAGEMENT CONSIDERATIONS:

Given the potential for rapid Oriental bittersweet growth in early postfire environments, prescribed fire alone seems unlikely to control and would probably increase Oriental bittersweet. An invasive plant guide stated that Oriental bittersweet is not a fire hazard, but speculated that Oriental bittersweet is likely to sprout after prescribed fire and that a nutrient flush and increased light availability after fire might promote Oriental bittersweet spread. The authors concluded that prescribed fire was not an option for Oriental bittersweet control [36].

**Preventing postfire establishment and spread:** More research is needed to determine fire tolerance and postfire response of Oriental bittersweet on specific sites and ecosystems in which it occurs. The [Guide to noxious weed prevention practices](#) [172] provides several fire management considerations for weed prevention in general that apply to Oriental bittersweet. Guidelines for determining burn severity, revegetation necessity, and establishing and managing competitive plants are also available [5,48].

Fire suppression activities may inadvertently promote Oriental bittersweet establishment. On scrub oak sandplains of Martha's Vinyard, Oriental bittersweet established along firelines [129].

Preventing invasive plants from establishing in weed-free burned areas is the most effective and least costly management method. This may be accomplished through early detection and eradication, careful monitoring and follow-up, and limiting dispersal of invasive plant propagules into burned areas. General recommendations for preventing postfire establishment and spread of invasive plants include:

- Incorporate cost of weed prevention and management into fire rehabilitation plans
- Acquire restoration funding
- Include weed prevention education in fire training
- Minimize soil disturbance and vegetation removal during fire suppression and rehabilitation activities
- Minimize the use of retardants that may alter soil nutrient availability, such as those containing nitrogen and phosphorus
- Avoid areas dominated by high priority invasive plants when locating firelines, monitoring camps, staging areas, and helibases
- Clean equipment and vehicles prior to entering burned areas
- Regulate or prevent human and livestock entry into burned areas until desirable site vegetation has recovered sufficiently to resist invasion by undesirable vegetation
- Monitor burned areas and areas of significant disturbance or traffic from management activity
- Detect weeds early and eradicate before vegetative spread and/or seed dispersal
- Eradicate small patches and contain or control large infestations within or adjacent to the burned area
- Reestablish vegetation on bare ground as soon as possible

- Avoid use of fertilizers in postfire rehabilitation and restoration
- Use only certified weed-free seed mixes when revegetation is necessary

For more detailed information on these topics, see the following publications: [[5,12,48,172](#)].

**Use of prescribed fire as a control agent:** As of early 2011, there was only one study on using fire to control Oriental bittersweet, so possible effects of prescribed fire use in areas with Oriental bittersweet were speculative. Based upon Oriental bittersweet's patterns of [regeneration](#) and [succession](#), prescribed fire alone is more likely to increase than control Oriental bittersweet due to postfire sprouting and rapid growth under an open canopy. A Virginia fact sheet noted that merely top-killing Oriental bittersweet, and not killing the roots, results in "vigorous regrowth" [[176](#)]. If burning is prescribed to meet management objectives other than control of Oriental bittersweet, burning could be done either very early or very late in the burning season to decrease risk of postfire Oriental bittersweet spread. Because Oriental bittersweet sprouts and establishes from seed, postfire follow-up control, such as grubbing or spraying, and monitoring will be needed (see [Control](#)). Either early spring burning or late fall burning, when most associated plant species have gone dormant but Oriental bittersweet is still green, may lower Oriental bittersweet's carbohydrate reserves [[141,161](#)]. Polatin's [[135](#)] study (see [Plant response to fire](#)) suggests that fall prescribed fire is more likely to reduce Oriental bittersweet cover than spring prescribed fire. Small fires and an adaptive approach would allow managers to assess Oriental bittersweet's response over a small area, where it would be relatively easy to monitor Oriental bittersweet's postfire seedling and sprout production.

**Altered fuel characteristics:** Oriental bittersweet may increase fuel loads and provide ladder fuels, although as of early 2011, studies were lacking on Oriental bittersweet's effects on fuel loads and structure. See [Fuels](#) for further details.

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## MANAGEMENT CONSIDERATIONS

**SPECIES:** [Celastrus orbiculatus](#)

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- [FEDERAL LEGAL STATUS](#)
- [OTHER STATUS](#)
- [IMPORTANCE TO WILDLIFE AND LIVESTOCK](#)
- [OTHER USES](#)
- [IMPACTS AND CONTROL](#)

FEDERAL LEGAL STATUS:

None

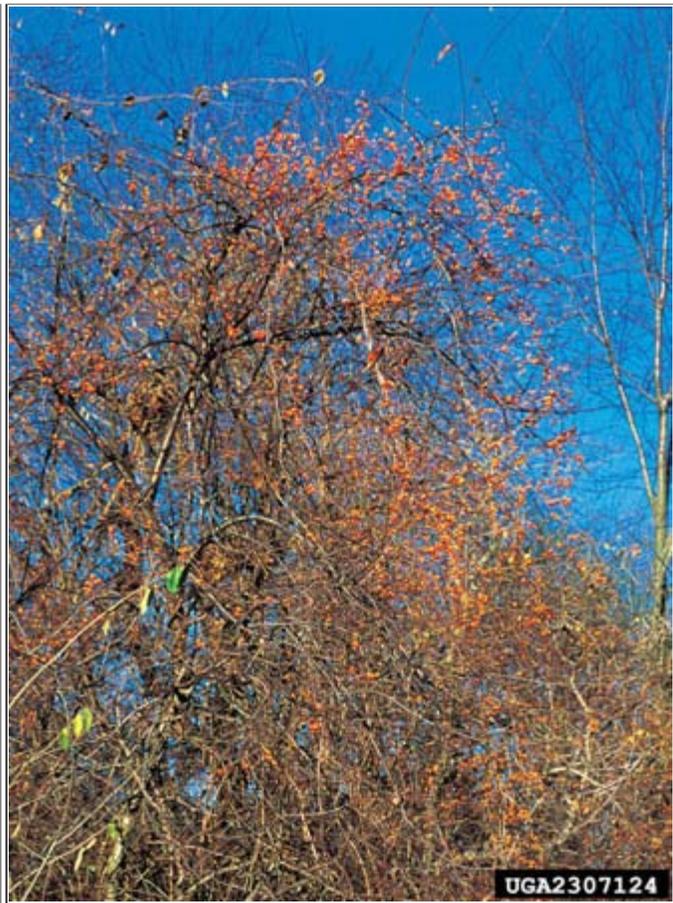
OTHER STATUS:

Information on state-level noxious weed status of plants in the United States is available at [Plants Database](#).

IMPORTANCE TO WILDLIFE AND LIVESTOCK:

Birds and mammals eat Oriental bittersweet arils. Birds that consume and [disperse](#) Oriental bittersweet arils include black-capped chickadees, eastern bluebirds, northern mockingbirds, European starlings, blue jays, northern bobwhites, ruffed grouse, ring-necked pheasants, [[8,132,159,183](#)], and wild turkeys (Poole 2005 personal communication in [[25](#)]). However, it is unclear how important Oriental bittersweet arils are as an avian food source [[85](#)]. Frugivorous mammals that eat the arils include fox squirrels and eastern cottontails (review by [[183](#)]). White-tailed deer may browse the foliage, although the foliage may not be preferred. In Rock Creek Park, Washington DC, Oriental bittersweet was more frequent in enclosure plots than in control plots that were accessible to white-tailed deer [[146](#)].





Oriental bittersweet with abundant arils. Photo by James H. Miller, USDA Forest Service.

**Palatability and nutritional value:** Oriental bittersweet browse is apparently unpalatable to herbivores. Although cattle, white-tailed deer, and lagomorphs browse Oriental bittersweet's congener, American bittersweet [20], browsing animals do not similarly utilize Oriental bittersweet [30].

Oriental bittersweet arils are nutritious. Arils collected on Block Island, Rhode Island had higher protein (8.6% dry weight) and carbohydrate (89.1% dry weight) content than fruits of 8 associated woody species [153]. Fresh Oriental bittersweet arils are 71% water [44]; seed oil content is about 50% [189]. The arils may be toxic to humans (review by [183]).

**Cover value:** Information on wildlife use of Oriental bittersweet for cover was sparse as of early 2011. Because Oriental bittersweet can alter forest [structure](#), it probably favors thicket- and understory-dwelling animals at the expense of animals using other strata. On a Nature Conservancy Preserve on Long Island Sound, Connecticut, Oriental bittersweet threatened sand dunes providing nesting areas for the piping plover, a state-threatened bird. Managers were concerned that Oriental bittersweet would either spread onto and overtake nesting areas or alter dune erosion and formation dynamics (Lapin 1992 cited in [8]). In an American beech-yellow-poplar forest in Delaware, veeries selected nesting areas with nonnative vegetation cover significantly more than areas with native vegetation cover ( $P=0.05$ ). Oriental bittersweet was among the nonnative vegetation providing cover near nests, although multiflora rose was usually selected as the actual nest shrub [62].

#### OTHER USES:

**Medicine and other products:** Oriental bittersweet is an Asian folk medicine used for treating rheumatoid arthritis and bacterial infections. Medical and pharmacological studies show that Oriental bittersweet derivatives have antitumor, antiinflammatory, antioxidant, antibacterial, and insecticidal properties [72,74,117]. One Oriental bittersweet derivative shows ability to reverse multidrug resistance of cancer cells to cancer-treatment drugs [83,84].

Oriental bittersweet bark is used as a fine fiber in China [189]. Enzymes in Oriental bittersweet leaves clot milk. These leaf extracts may provide an alternative to calf rennet enzymes used in making cheese [124].

**Ornamental and rehabilitation:** In the United States, Oriental bittersweet is commercially available and widely planted and harvested as an ornamental [114]. Wreaths and other ornaments are made from fruiting stems; Oriental bittersweet seeds may disperse if these ornaments are discarded on favorable germination sites. Oriental bittersweet was once widely planted in highway and "conservation" plantings, but it is not currently recommended for wildland plantings [56,60,111].

Alternative native lianas recommended for ornamental and restoration plantings include American bittersweet, trumpet honeysuckle (*Lonicera sempervirens*), trumpet-creeper (*Campsis radicans*), yellow passionflower (*Passiflora lutea*), pipevine (*Aristolochia macrophylla*), and American wisteria (*Wisteria frutescens*) [161]. For wildlife plantings, American bittersweet arils can provide food for frugivorous animals [111]. Oriental bittersweet is sometimes mistaken for, mislabeled, and/or planted as American bittersweet in wildlife cover and erosion projects. Correct identification of American bittersweet is needed to meet restoration goals [8].

#### IMPACTS AND CONTROL:

**Impacts:** Oriental bittersweet is considered a "severe" pest plant in the Northeast and Southeast [161]. In the Northeast, it is listed as a high threat in deciduous, coniferous, and mixed conifer-deciduous forests, old fields, grasslands, riparian areas, and fresh wetlands; and an unknown threat in tidal wetlands [25]. On the west end of Long Island, for example, Oriental bittersweet was the most abundant nonnative species on Jamaica Bay Wildlife Refuge, where it invaded old fields, thickets, and woodlands [155]. Invasion traits of Oriental bittersweet include:

- ability to regenerate by cloning
- abundant seed production
- wide-ranging seed dispersal by animals and humans [54,105,115,128,138,152]
- ability to germinate under a wide range of light conditions
- ability to acclimate photosynthetic capacity and persist a wide range of light conditions [127,128]
- rapid growth after release [3,111]
- ability to climb supports of varying sizes [3,29,137]



Oriental bittersweet twining around a trunk. Photo by Leslie Mehrhoff.

Reports of Oriental bittersweet's invasiveness vary. Some classify it as invasive [43] to highly invasive [8]. Voss [179] describes it as "sometimes aggressive" when escaped from cultivation in Michigan. On the Energy Oak Ridge National Environmental Research Park, Tennessee, Oriental bittersweet was ranked the 5th most invasive nonnative dicot and the 9th most invasive nonnative plant species overall [26]. In Farmington, Maine, surveyors of invasive nonnatives in

mixed hardwood-spruce (*Picea* spp.) forests ranked Oriental bittersweet as intermediate in abundance, behind Japanese knotweed (*Polygonum cuspidatum*), Morrow's honeysuckle, Tatarian honeysuckle (*Lonicera tatarica*), and hybrids of the 2 honeysuckles [7].

The ease of seed dispersal and horticultural interest in Oriental bittersweet in the East and elsewhere in the United States creates a potentially large area for Oriental bittersweet invasion [8]. The southern Appalachians are particularly affected by new invasions [8,89]. In southwestern North Carolina, for example, Oriental bittersweet was one of the most commonly encountered nonnative species, occurring at 53% mean frequency on all of 25 watersheds sampled [88]. Available data and climate models suggest that Oriental bittersweet is likely to benefit from warming temperatures and increasing precipitation in the Northeast, where it is likely to increase and spread northward (review by [31]).

Oriental bittersweet presence may alter soil chemistry, plant succession, and stand structure; threaten native plant diversity; and reduce productivity in silvicultural and agricultural systems.

- [Effects on soils](#)
- [Effects on succession and stand structure](#)
- [Effects on diversity](#)
- [Effects on silvicultural and agricultural systems](#)

Effects on soils: Oriental bittersweet may alter soil pH and nutrient levels [96], and Oriental bittersweet's relatively deep roots may allow it to outcompete surrounding vegetation for soil resources [148]. In hardwood forests of Connecticut, Oriental bittersweet litter contained 3 times more calcium than red oak litter, and its leaf pH was higher. The authors concluded that these factors led to the higher soil pH on plots with than on plots without Oriental bittersweet [96]. See [Soils](#) for further information.

Effects on succession and stand structure: Oriental bittersweet may outcompete native vegetation for light and modify stand structure, altering historic patterns of plant succession ([8,10,177], review by [161]). Photosynthesis of host and understory plants can be reduced or prevented by Oriental bittersweet. Patterson [128] noted the scarcity of other plant species beneath Oriental bittersweet canopies in Pennsylvania and attributed it to shading by Oriental bittersweet. Oriental bittersweet's growth habit (blanketing and shading out support species) negatively affects the health of host plants and increases continuity of vegetation among forest strata [29,38,53,101] (see [Fuels](#)). Twining Oriental bittersweet stems may girdle support vegetation, restricting sap and water flow and damaging or killing host plants. Damaged hosts are at risk for stem breakage and uprooting from ice- and windstorms [8,28,29,101,113,161]. Oriental bittersweet may overtop other plant species in all strata. It may also inhibit or facilitate growth of other lianas. In Connecticut, Oriental bittersweet altered hardwood forest succession by inhibiting reproduction and growth of native shrubs and trees and facilitating growth of fox grape, a late-successional native liana, into the canopy (see [Old fields](#)) [38]. Conversely, Oriental bittersweet interfered with growth of native grapes (*Vitis* spp.) on the Pisgah National Forest, North Carolina [113]. See [Successional Status](#) and [Stand structure](#) for more information.

Effects on diversity: Oriental bittersweet can displace native species. Its thickets [113] and climbing stems cast too much shade for many native plant species to establish and grow. For example, Oriental bittersweet canopies inhibited establishment of understory spring ephemerals in Illinois [71]. Along the Blue Ridge Parkway in North Carolina, Oriental bittersweet cover was negatively associated with native plant diversity [53]. On Plummer's Island in the Potomac River of Maryland, a 1912 survey documented presence of American bittersweet and common hop (*Humulus lupulus*), but in 1980, surveyors concluded that those species "appear to have been replaced entirely by the aliens" Oriental bittersweet and Japanese hop (*H. japonicus*) [150].

Oriental bittersweet is apparently expanding its range at the expense of American bittersweet [136,157,161]. Partially as a consequence of Oriental bittersweet competition, American bittersweet has protection status in several areas [173]. For example, Connecticut lists American bittersweet as a "species of special concern", and Great Smoky Mountains National Park lists American bittersweet as a "nonreproducing rare plant" [8]. The same characteristics that make Oriental bittersweet often preferred over American bittersweet as an ornamental: faster growth, greater fecundity, and

a higher tolerance to varying environmental conditions, are the same characteristics that have enabled Oriental bittersweet to become a successful invader [89]. A field study showed Oriental bittersweet increased its photosynthetic rate with increasing light intensity, while American bittersweet's photosynthetic rate tended to saturate under low light conditions [19]. In a common garden study, Oriental bittersweet showed significantly higher photosynthetic rates and faster growth, aboveground biomass gain, and survivorship than American bittersweet in both sun and shade. Oriental bittersweet showed a positive growth response to presence of neighbors, while American bittersweet's response to neighbors was neutral ( $P=0.05$  for all variables) [95]. In the greenhouse, Oriental bittersweet showed increased height, aboveground biomass, and total leaf mass compared to American bittersweet when both species were grown under reduced red:far red light conditions. The authors concluded that Oriental bittersweet's superior ability to grow under these conditions allows it to persist in the understory and "forage" for gaps and sunflecks, whereas American bittersweet's relative inability to gain height and biomass growth under a canopy ensures its decline unless a canopy gap occurs. Further, Oriental bittersweet's ability to detect far red light, which is transmitted and reflected by neighboring plants, may confer ability to "detect" and grow toward neighboring plants that could potentially provide support for Oriental bittersweet's stems [94].

Surveys generally show that Oriental bittersweet is more adaptable and prolific than its native congener. In Connecticut, very wet sites were the only sites where transplanted American bittersweet seedlings outperformed transplanted Oriental bittersweet seedlings (58% vs. 18% mortality for Oriental and American bittersweet, respectively). Oriental bittersweet averaged higher survival (90% vs. 68%) and about 3 times more aboveground biomass (1.93 g vs. 0.67 g) than American bittersweet in low light ( $\leq 6.4\%$  transmittance) [98]. A New Jersey study showed a 90% germination rate for first-year, soil-stored Oriental bittersweet seed compared to a 65% germination rate for first-year, soil-stored American bittersweet seed [174]. In a Connecticut study, Dreyer and others [29] found Oriental bittersweet showed significantly higher pollen and seed viability than American bittersweet ( $P<0.001$ ). While recognizing that many environmental and genetic factors affect seedling establishment, the authors stated that such viability could favor Oriental bittersweet over American bittersweet [29].

American bittersweet is further threatened by potential hybridization and introgression with Oriental bittersweet. Greenhouse studies confirm that the 2 bittersweets are cross-fertile [136,185,190] (see [Taxonomy](#)). In a preliminary greenhouse study, interspecific pollination between the bittersweets was more successful than intraspecific pollination, with 1 seedling/flower resulting from hybridization and 0.6 seedling/flower resulting from intraspecific crosses. Although not statistically significant due to small sample sizes [136], these results show the need for field studies documenting the extent of Oriental bittersweet  $\times$  American bittersweet hybridization.

Effects on silvicultural and agricultural systems: Oriental bittersweet may smother or kill timber trees and understory vegetation [134]. Girdling and stem damage from Oriental bittersweet stems lowers the value of timber trees that host Oriental bittersweet. Where it was present before tree harvest, Oriental bittersweet can rapidly overtake a site after harvest. Its sprouts may overtop understory species and overstory trees. On the Pisgah National Forest, Oriental bittersweet covered sapling-sized hardwood and eastern white pine (*Pinus strobus*) regeneration on small clearcuts [113]. In a Massachusetts clipping experiment, Oriental bittersweet growth ranged from 6.9 to 15 feet (2.1-4.7 m) in 1 year. In contrast, bigtooth aspen (*Populus grandidentata*) sprouts grew from 3.0 to 5.9 feet (0.9-1.8 m) in 1 year, and yellow-poplar sprouts averaged 4.6 feet (1.4 m) in 1 year (review by [35]). On the Bent Creek Experimental Forest, a high-quality stand of upland oaks was clearcut in the summer of 1977. Oak site index before harvest was above 80, with a basal overstory area of 120 feet<sup>2</sup> (11 m<sup>2</sup>). Preharvest Oriental bittersweet density was 830 seedlings/acre and 27 saplings/acre (seedlings were  $<0.6$  inch (2.0 cm) DBH; saplings were  $>0.6$  inch DBH). Seven years after tree harvest, the canopy was nearly 100% Oriental bittersweet [113].

Oriental bittersweet is an alternate host for *Xylella fastidiosa*. This bacterium vectors several crop diseases including Pierce's grapevine (*Vitis*) disease, periwinkle (*Vinca*) wilt, plum leaf scorch and phony peach (*Prunus*) disease, and variegated chlorosis (affects several genera including oaks, elms, sycamores, citrus (*Citrus*), and mulberries (*Morus*)) [110].

**Control:** The Southeast Exotic Pest Plant Council [8] recommends that Rank 1 and Rank 2 species such as Oriental bittersweet be controlled and managed in the early stages of infestation whenever possible. Because Oriental bittersweet appears to build only a short-term seed bank [34], there are better opportunities for control and a higher

probability of success than if seeds were longer-lived. If established plants and nearby seed sources are killed before arils mature, subsequent seedling establishment may primarily come from off-site seed sources, with little seedling emergence from the seed bank [8,34]. Monitoring and early control of new outbreaks can then help control Oriental bittersweet [8,27]. Greenberg and others [53] recommend preventing seed dispersal. This implies treating on- and off-site plants before fruiting, whatever control method is used.

Since Oriental bittersweet resembles the native and rare American bittersweet, it is important to correctly identify Oriental bittersweet before control measures begin [161]. See [General Botanical Characteristics](#) for information on identification keys.

**Prevention:** The most efficient and effective method of managing invasive species such as Oriental bittersweet is to prevent their invasion and spread [149]. Preventing the establishment of nonnative invasive plants in wildlands is achieved by maintaining native communities and surveying, monitoring, and controlling new infestations. Dreyer [27] recommends preventing the introduction of Oriental bittersweet into uninfested areas and making early control of small infestations a priority. Inventories to establish Oriental bittersweet presence and densities are needed before control programs, or any silvicultural treatment that opens the canopy, begin. McNab [111] cautions that if Oriental bittersweet is present in the understory, canopy disturbance will probably stimulate its growth.

**Monitoring** is an important part of an integrated program for Oriental bittersweet control [152]. Monitoring efforts are best concentrated on the most likely sites of Oriental bittersweet invasion: disturbed soil, roadsides, old fields, woodlands, and waterways. Survey uninvaded sites periodically to detect new invasions [27]. Because Oriental bittersweet retains its leaves longer than most associated native species, its yellow leaves are easy to spot in late fall, even from a distance. Consistent fall monitoring can identify new infestations, allowing managers to implement control programs and prevent new infestations from spreading. Managers in Great Smoky Mountains National Park recommend scouting for infestations every 2 weeks after most native species have dropped their leaves, which is approximately November 10th in the Park. [8]. Discouraging nurseries from stocking Oriental bittersweet [61] and encouraging plantings of alternative native ornamentals (see [Ornamental and rehabilitation](#) use) can reduce new introductions [61]. The [Center for Invasive Plant Management](#) provides an online guide to noxious weed prevention practices.

**Monitoring** may be more efficient if areas at high risk for Oriental bittersweet invasion are identified. See [Site Characteristics](#) for further information on Oriental bittersweet site preferences. For mountainous terrain in the southern the Appalachians, McNab and Loftis [112] describe a rapid survey technique for Oriental bittersweet hazard rating, and they provide a model for estimating probability of Oriental bittersweet occurrence for similar environments based on environmental, competitive, and disturbance factors.

**Fire:** See [Fire Management Considerations](#) for information on using prescribed fire to control Oriental bittersweet.

**Cultural control:** No information is available on this topic.

**Physical or mechanical control:** Frequent cutting, mowing, or grubbing helps control Oriental bittersweet. Any portion of stems or roots left on site may sprout [102]; grubbed roots usually sprout unless they are completely removed [8,30,112,161]. Small plants can be hand-pulled, but they need to be moved off site to prevent rooting [181]. Climbing or trailing stems must be cut as close to the root crown as possible [8]. When grubbing, roots need to be bagged and either removed from the site or allowed to sit in the sun until the bagged plants and seeds have died [8,161]. To prevent posttreatment seedling establishment, mechanical treatments are best implemented before Oriental bittersweet is in fruit [161]. Occasional mowing, cutting, or grubbing only encourages root sprouting and is not recommended. Unless the entire root system is completely removed, treatments must be frequent enough to eventually exhaust the underground carbohydrate supply. That may be accomplished by cutting or mowing every 2 weeks [8,30,112,161]; however, that is usually not practical in wildlands.

**Biological control:** As of early 2011, pathogens from Oriental bittersweet's native range had not been approved for use in the United States [8,102,161]. A leaf spot fungus (*Marssonina celastri*) causes defoliation of Oriental

bittersweet in Korea, where Oriental bittersweet is native [151]. Oriental bittersweet has no known pathogens in North America [161]. This may be a factor in Oriental bittersweet's invasiveness in the United States [125].

**Chemical control:** Oriental bittersweet can be controlled with herbicides, using either cut-stem or foliar applications. Systemic herbicides (for example, triclopyr or glyphosate) are recommended [8,161].

Effective use of herbicides requires appropriate herbicide concentration, application technique, and timing. For cut-stem treatments, best Oriental bittersweet control occurs when the herbicide is applied soon after stems are cut or mowed [8,161]. Cut the stems about 2 inches (5 cm) above the root crown. A second treatment may be needed to control sprouts [161]. Polatin [135] found mid-October application of triclopyr gave better control of Oriental bittersweet than spring application. Herbicide applications in early spring, before native herbs have emerged, or in late fall when natives are dormant but Oriental bittersweet is still green, can minimize effects to nontarget plants [161].

In red pine (*Pinus resinosa*) forests in Connecticut, late-summer (17-18 September) herbicide treatments gave fair to good control of Oriental bittersweet. Fourteen treatments involving four different herbicides, used alone or in combination, were used, with various application rates. One year after treatments, imazapyr and triclopyr gave best results with low concentrations. See Ahrens [3] for details of herbicide combinations, concentrations, and other treatment results.

See these sources: [8,15,21,36,102,135,161] for more information on chemical control of Oriental bittersweet.

Herbicides may provide initial control of a new invasion or a severe infestation, but used alone, they are rarely a complete or long-term solution to invasive species management [15]. Herbicides are most effective on large infestations when incorporated into long-term management plans that include replacement of weeds with desirable species, careful land use management, and prevention of new infestations. Control with herbicides is temporary, as it does not change the conditions that allowed the invasion to occur (for example, [191]). See The Nature Conservancy's [Weed control methods handbook](#) [168] for considerations on the use of herbicides in Natural Areas and detailed information on specific chemicals.

**Integrated management:** No single treatment provides effective, long-term control of Oriental bittersweet. Integrated management includes early detection, assessment, and containment of infestations before they spread. Factors to be addressed before a management decision is made also include assessment of nontarget vegetation, soil types, climatic conditions, important water resources, and an evaluation of the benefits and limitations of all control methods [120]. Hobbs and Humphries [63] advocate an integrated approach to the management of plant invasions that includes "a focus on the invaded system and its management, rather than on the invader" and "identification of the causal factors enhancing ecosystem invasibility" as an effective approach to controlling invasive species. This emphasizes removing the ecological stressors that may be underlying the causes of invasion rather than focusing on direct control of invasive species [63].

Few studies to date (2011) investigated using multiple control methods for managing Oriental bittersweet. Compared with mowing alone or mowing and prescribed fire combined, Polatin [135] found a combination of mowing and triclopyr was "by far the most effective treatment for controlling bittersweet and allowing for grass establishment". See [Plant response to fire](#) for details of this study. Hutchison [71] recommends either grubbing or a combination of cutting and herbicide treatment. When practical, he recommends uprooting and removing individual Oriental bittersweet stems from infested sites. In other situations he recommends hand cutting after the first killing frost, then spot-treating cut stems with glyphosate. To maintain control, he advocates immediately pulling and removing invading individuals off site [71].

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## APPENDIX: FIRE REGIME TABLE

**SPECIES:** *Celastrus orbiculatus*

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The following table provides fire regime information that may be relevant to Oriental bittersweet habitats. Follow the

links in the table to documents that provide more detailed information on these fire regimes. Precise distribution information is unavailable for all locations where Oriental bittersweet may be invasive. The following list is not exhaustive, and Oriental bittersweet may be present and possibly invasive in vegetation communities not listed below. If you are interested in fire regimes of plant communities not listed here, see the [Expanded FEIS Fire Regime Table](#).

Fire regime information on vegetation communities in which Oriental bittersweet may occur. This information is taken from the [LANDFIRE Rapid Assessment Vegetation Models \[91\]](#), which were developed by local experts using available literature, local data, and/or expert opinion. This table summarizes fire regime characteristics for each plant community listed. The PDF file linked from each plant community name describes the model and synthesizes the knowledge available on vegetation composition, structure, and dynamics in that community. Cells are blank where information is not available in the Rapid Assessment Vegetation Model.

[Northern Great Plains](#)                      [Great Lakes](#)                      [Northeast](#)                      [South-central US](#)  
[Southern Appalachians](#)                      [Southeast](#)

**Northern Great Plains**

- [Northern Plains Grassland](#)
- [Northern Plains Woodland](#)

Vegetation Community ( <a href="#">Potential Natural Vegetation</a> Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)

Northern Plains Grassland

<a href="#">Northern tallgrass prairie</a>	Replacement	90%	6.5	1	25
	Mixed	9%	63		
	Surface or low	2%	303		
<a href="#">Oak savanna</a>	Replacement	7%	44		
	Mixed	17%	18		
	Surface or low	76%	4		

Northern Plains Woodland

<a href="#">Oak woodland</a>	Replacement	2%	450		
	Surface or low	98%	7.5		
<a href="#">Northern Great Plains wooded draws and ravines</a>	Replacement	38%	45	30	100
	Mixed	18%	94		
	Surface or				

	low	43%	40	10	
<a href="#">Great Plains floodplain</a>	Replacement	100%	500		
<b>Great Lakes</b>					
<ul style="list-style-type: none"> <li>• <a href="#">Great Lakes Grassland</a></li> <li>• <a href="#">Great Lakes Woodland</a></li> <li>• <a href="#">Great Lakes Forested</a></li> </ul>					
Vegetation Community ( <a href="#">Potential Natural Vegetation</a> Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Great Lakes Grassland					
<a href="#">Mosaic of bluestem prairie and oak-hickory</a>	Replacement	79%	5	1	8
	Mixed	2%	260		
	Surface or low	20%	2		33
Great Lakes Woodland					
<a href="#">Great Lakes pine barrens</a>	Replacement	8%	41	10	80
	Mixed	9%	36	10	80
	Surface or low	83%	4	1	20
<a href="#">Northern oak savanna</a>	Replacement	4%	110	50	500
	Mixed	9%	50	15	150
	Surface or low	87%	5	1	20
Great Lakes Forested					
<a href="#">Northern hardwood maple-beech-eastern hemlock</a>	Replacement	60%	>1,000		
	Mixed	40%	>1,000		
<a href="#">Conifer lowland (embedded in fire-prone ecosystem)</a>	Replacement	45%	120	90	220
	Mixed	55%	100		
<a href="#">Conifer lowland (embedded in fire-resistant ecosystem)</a>	Replacement	36%	540	220	≥1,000
	Mixed	64%	300		
<a href="#">Great Lakes floodplain forest</a>	Mixed	7%	833		
	Surface or				

	low	93%	61		
<a href="#">Maple-basswood</a>	Replacement	33%	≥1,000		
	Surface or low	67%	500		
<a href="#">Maple-basswood mesic hardwood forest (Great Lakes)</a>	Replacement	100%	>1,000	≥1,000	>1,000
<a href="#">Maple-basswood-oak-aspen</a>	Replacement	4%	769		
	Mixed	7%	476		
	Surface or low	89%	35		
<a href="#">Northern hardwood-eastern hemlock forest (Great Lakes)</a>	Replacement	99%	>1,000		
<a href="#">Oak-hickory</a>	Replacement	13%	66	1	
	Mixed	11%	77	5	
	Surface or low	76%	11	2	25
<a href="#">Pine-oak</a>	Replacement	19%	357		
	Surface or low	81%	85		
<a href="#">Red pine-eastern white pine (frequent fire)</a>	Replacement	38%	56		
	Mixed	36%	60		
	Surface or low	26%	84		
<a href="#">Red pine-eastern white pine (less frequent fire)</a>	Replacement	30%	166		
	Mixed	47%	105		
	Surface or low	23%	220		
<a href="#">Great Lakes pine forest, eastern white pine-eastern hemlock (frequent fire)</a>	Replacement	52%	260		
	Mixed	12%	>1,000		
	Surface or low	35%	385		
<a href="#">Eastern white pine-eastern hemlock</a>	Replacement	54%	370		
	Mixed	12%	>1,000		
	Surface or low	34%	588		

## Northeast

- [Northeast Woodland](#)
- [Northeast Forested](#)

Vegetation Community ( <a href="#">Potential Natural Vegetation</a> Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
<b>Northeast Woodland</b>					
<a href="#">Eastern woodland mosaic</a>	Replacement	2%	200	100	300
	Mixed	9%	40	20	60
	Surface or low	89%	4	1	7
<a href="#">Pine barrens</a>	Replacement	10%	78		
	Mixed	25%	32		
	Surface or low	65%	12		
<b>Northeast Forested</b>					
<a href="#">Northern hardwoods (Northeast)</a>	Replacement	39%	≥1,000		
	Mixed	61%	650		
<a href="#">Eastern white pine-northern hardwood</a>	Replacement	72%	475		
	Surface or low	28%	>1,000		
<a href="#">Northern hardwoods-eastern hemlock</a>	Replacement	50%	≥1,000		
	Surface or low	50%	≥1,000		
<a href="#">Northern hardwoods-spruce</a>	Replacement	100%	≥1,000	400	>1,000
<a href="#">Appalachian oak forest (dry-mesic)</a>	Replacement	2%	625	500	≥1,000
	Mixed	6%	250	200	500
	Surface or low	92%	15	7	26
<a href="#">Beech-maple</a>	Replacement	100%	>1,000		
<a href="#">Southeastern red spruce-Fraser fir</a>	Replacement	100%	500	300	≥1,000
<b>South-central US</b>					
<ul style="list-style-type: none"> <li>• <a href="#">South-central US Grassland</a></li> <li>• <a href="#">South-central US Woodland</a></li> <li>• <a href="#">South-central US Forested</a></li> </ul>					

Vegetation Community ( <a href="#">Potential Natural Vegetation</a> Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
South-central US Grassland					
<a href="#">Southern tallgrass prairie</a>	Replacement	91%	5		
	Mixed	9%	50		
<a href="#">Oak savanna</a>	Replacement	3%	100	5	110
	Mixed	5%	60	5	250
	Surface or low	93%	3	1	4
South-central US Woodland					
<a href="#">Oak-hickory savanna</a> (East Texas)	Replacement	1%	227		
	Surface or low	99%	3.2		
<a href="#">Interior Highlands dry oak/bluestem woodland and glade</a>	Replacement	16%	25	10	100
	Mixed	4%	100	10	
	Surface or low	80%	5	2	7
<a href="#">Oak woodland-shrubland-grassland mosaic</a>	Replacement	11%	50		
	Mixed	56%	10		
	Surface or low	33%	17		
<a href="#">Interior Highlands oak-hickory-pine</a>	Replacement	3%	150	100	300
	Surface or low	97%	4	2	10
<a href="#">Pine bluestem</a>	Replacement	4%	100		
	Surface or low	96%	4		
South-central US Forested					
<a href="#">Interior Highlands dry-mesic forest and woodland</a>	Replacement	7%	250	50	300
	Mixed	18%	90	20	150
	Surface or low	75%	22	5	35
	Replacement	2%	190		

<a href="#">Gulf Coastal Plain pine flatwoods</a>	Mixed	3%	170		
	Surface or low	95%	5		
<a href="#">West Gulf Coastal plain pine (uplands and flatwoods)</a>	Replacement	4%	100	50	200
	Mixed	4%	100	50	
	Surface or low	93%	4	4	10
<a href="#">West Gulf Coastal Plain pine-hardwood woodland or forest upland</a>	Replacement	3%	100	20	200
	Mixed	3%	100	25	
	Surface or low	94%	3	3	5
<a href="#">Southern floodplain</a>	Replacement	42%	140		
	Surface or low	58%	100		
<a href="#">Southern floodplain (rare fire)</a>	Replacement	42%	≥1,000		
	Surface or low	58%	714		

## Southern Appalachians

- [Southern Appalachians Grassland](#)
- [Southern Appalachians Woodland](#)
- [Southern Appalachians Forested](#)

Vegetation Community ( <a href="#">Potential Natural Vegetation</a> Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)

## Southern Appalachians Grassland

<a href="#">Bluestem-oak barrens</a>	Replacement	46%	15		
	Mixed	10%	69		
	Surface or low	44%	16		
<a href="#">Eastern prairie-woodland mosaic</a>	Replacement	50%	10		
	Mixed	1%	900		
	Surface or low	50%	10		

## Southern Appalachians Woodland

	Replacement	4%	125		
	Mixed	4%	155		

<a href="#">Appalachian shortleaf pine</a>					
	Surface or low	92%	6		
<a href="#">Table Mountain-pitch pine</a>	Replacement	5%	100		
	Mixed	3%	160		
	Surface or low	92%	5		
<a href="#">Oak-ash woodland</a>	Replacement	23%	119		
	Mixed	28%	95		
	Surface or low	49%	55		
Southern Appalachians Forested					
<a href="#">Bottomland hardwood forest</a>	Replacement	25%	435	200	≥1,000
	Mixed	24%	455	150	500
	Surface or low	51%	210	50	250
<a href="#">Mixed mesophytic hardwood</a>	Replacement	11%	665		
	Mixed	10%	715		
	Surface or low	79%	90		
<a href="#">Appalachian oak-hickory-pine</a>	Replacement	3%	180	30	500
	Mixed	8%	65	15	150
	Surface or low	89%	6	3	10
<a href="#">Eastern hemlock-eastern white pine-hardwood</a>	Replacement	17%	≥1,000	500	>1,000
	Surface or low	83%	210	100	>1,000
<a href="#">Red pine-eastern white pine (frequent fire)</a>	Replacement	38%	56		
	Mixed	36%	60		
	Surface or low	26%	84		
<a href="#">Eastern white pine-northern hardwood</a>	Replacement	72%	475		
	Surface or low	28%	>1,000		
<a href="#">Appalachian Virginia pine</a>	Replacement	20%	110	25	125
	Mixed	15%	145		
	Surface or low	64%	35	10	40
	Replacement	6%	220		

<a href="#">Appalachian oak forest (dry-mesic)</a>	Mixed	15%	90		
	Surface or low	79%	17		

**Southeast**

- [Southeast Woodland](#)
- [Southeast Forested](#)

Vegetation Community ( <a href="#">Potential Natural Vegetation</a> Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)

**Southeast Woodland**

<a href="#">Longleaf pine/bluestem</a>	Replacement	3%	130		
	Surface or low	97%	4	1	5
<a href="#">Longleaf pine (mesic uplands)</a>	Replacement	3%	110	40	200
	Surface or low	97%	3	1	5
<a href="#">Longleaf pine-Sandhills prairie</a>	Replacement	3%	130	25	500
	Surface or low	97%	4	1	10

**Southeast Forested**

<a href="#">Sand pine scrub</a>	Replacement	90%	45	10	100
	Mixed	10%	400	60	
<a href="#">Coastal Plain pine-oak-hickory</a>	Replacement	4%	200		
	Mixed	7%	100		
	Surface or low	89%	8		
<a href="#">Maritime forest</a>	Replacement	18%	40		500
	Mixed	2%	310	100	500
	Surface or low	80%	9	3	50
<a href="#">Mesic-dry flatwoods</a>	Replacement	3%	65	5	150
	Surface or low	97%	2	1	8
	Replacement	7%	476		

<a href="#">Loess bluff and plain forest</a>	Mixed	9%	385		
	Surface or low	85%	39		
<a href="#">Southern floodplain</a>	Replacement	7%	900		
	Surface or low	93%	63		

\*Fire Severities—

**Replacement:** Any fire that causes greater than 75% top removal of a vegetation-fuel type, resulting in general replacement of existing vegetation; may or may not cause a lethal effect on the plants.

**Mixed:** Any fire burning more than 5% of an area that does not qualify as a replacement, surface, or low-severity fire; includes mosaic and other fires that are intermediate in effects.

**Surface or low:** Any fire that causes less than 25% upper layer replacement and/or removal in a vegetation-fuel class but burns 5% or more of the area [[58,90](#)].

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