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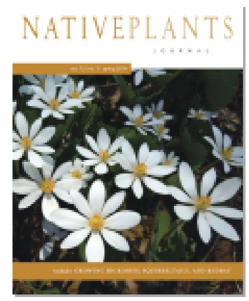

INVASION BIOLOGY *and control of* INVASIVE WOODY PLANTS in Eastern Forests

| Christopher R Webster, Michael A Jenkins, and Shibu Jose

ABSTRACT

Invasive exotic plants are displacing native plants and rapidly degrading native ecosystems. In this paper, we chronicle the sometimes erratic invasion biology of woody plants and review control strategies for some of the most serious woody invaders of eastern forests. Design features of a well-integrated control strategy include early detection, rapid response with the most effective control techniques possible, persistence and continued monitoring, and outreach/education to reduce the number of source populations on neighboring lands. Invasive plants are probably here to stay, but through concerted and diligent effort their spread and impact can be greatly reduced.

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KEY WORDS
alien plants, exotic plants, invasive species, perennial weeds

NOMENCLATURE
USDA NRCS (2006)

Planted for erosion control, kudzu (*Pueraria montana*) completely envelops trees, structures, and abandoned vehicles. Photo courtesy of USDI National Park Service

A growing body of scientific literature suggests that invasive woody plants are fundamentally altering forest ecosystems through the displacement and competitive exclusion of native plants (see Webster and others 2006 for a recent review). Consequently, a basic understanding of the mechanisms and consequences of exotic plant invasions is vital to preserving native biodiversity. Further, control of exotic plant species is essential to the restoration and management of native plant populations and communities.

The loss of native plant diversity sets into motion a cascade of events that diminish the stability and productivity of forest ecosystems. For a plant to become invasive, it has to overcome a host of obstacles, which include effectively dispersing away from its point of origin, establishing in novel environments, and outcompeting and replacing native vegetation (Myers and Bazely 2003). The ability of a species to accomplish these tasks can change over time in response to environmental change, disturbance, and natural and human-mediated adaptation. Consequently, risk assessment is a moving target, with aggressive species sometimes failing to become invasive and seemingly innocuous species eventually emerging as invaders (Rejmánek and Richardson 1996; Williamson and Fitter 1996; Reichard and Hamilton 1997; Sutherland 2004). In fact, recent research suggests that one of the greatest risks associated with long-lived, woody invaders is underestimating the ability of scattered colonists to drastically change the ecological trajectory of a forest (Wangen and Webster 2006).

Nevertheless, while it is difficult to predict with certainty which species will become invasive, some general patterns have emerged. A common characteristic of invasive species is that they are relatively free of natural enemies (for example, pathogens and herbivores) in their introduced ranges. In the absence of host-specific pests and pathogens, there are few checks on growth and reproduction, which may give exotics an upper hand over native species existing with coevolved natural enemies (Keane and Crawley 2002; Carpenter and Cappuccino 2005). While this tendency clearly applies to some invasions, recent research suggests this is not a universal mechanism underlying successful biological invasions as was once believed (Colautti and others 2004). Invasiveness may be more generally described by constellations of traits that interact synergistically with resource availability, disturbance, and the structure of native plant communities (Myers and Bazely 2003; Colautti and others 2004; Muth and Pigliucci 2006). Life history traits that contribute to invasive behavior include, but are not limited to, natural or enhanced (through plant breeding) robustness, higher resource use efficiency than native plants, high reproductive output and (or) propensity for vegetative reproduction, short juvenile period, animal-dispersed seeds, and the ability to form a seedbank. Combinations of the above traits, or even the expression of a single trait in certain contexts ("triggering attribute," Gurvich and others 2005), can facilitate invasive behavior and confer exotics with the ability to competitively exclude native species. The advantages conveyed by various trait syndromes, however, may change over time in response to environmental change or alteration of disturbance regimes.

The invasion biology of exotic woody plants differs from that of most weedy exotics because of the long life span of the invader and the time required for individuals to reach reproductive age. These attributes can produce significant lag periods over the course of an invasion. First, following introduction (for example, establishment of an ornamental planting) several years may be required before a species first begins to invade nearby native plant communities. This initial lag phase is influenced by the reproductive biology of the species, how much horticultural care is given (which can shorten time to first reproduction), and the distance that must be traversed to reach invadable habitat. Species often move progressively as a radiating wave front, but chance long-distance dispersals are usually the drivers of range expansion (Moody and Mack 1988; Neubert and Caswell 2000). Additional lags may occur while the emerging cohort matures and reaches reproductive age (Frappier and others 2003; Wangen and Webster 2006). For shade-tolerant woody shrubs, this may take only a few years. However, many invasive trees (for example, *Acer platanoides*, Bertin and others 2005) and some woody vines (for example, *Celastrus orbiculatus*, Greenberg and others 2001) do not become fully reproductive until they reach the canopy or are released from overhead shade by a canopy disturbance (for example, tree-fall gap). This latter group employs what has been termed a "sit and wait" strategy (Greenberg and others 2001), which can lead to a prolonged lag in the progress of the invasion while these species build up "seedling banks" in the understory (Martin and Marks 2006). Once these suppressed populations are released from overhead shade, they dominate the post-disturbance vegetation community and quickly reach reproductive maturity. The seeds cast from these satellite populations rapidly expand the range of the invading species (Moody and Mack 1988). Consequently, in a few short years, a seemingly innocuous scattering of invasives in the understory can literally explode (Wangen and Webster 2006).

In this article, we review specific treatment techniques that have shown promise for combating some of the most serious woody invaders in the eastern US and provide some general guidelines for the development of effective invasive plant control strategies. A listing of other woody invaders of concern in the eastern US is provided in Table 1, control strategies for most of which can be found through the website resources listed in Table 2.

GENERAL GUIDELINES

By taking some cues from the burgeoning field of invasion biology and aggressively pursuing invasive species with the best control strategies available, it may be possible to greatly reduce the extent and consequences of woody plant invasions. Keep in mind these important fundamentals when combating invasive plants.

1) Not all exotic plants or even invasive species carry the same risks. Consequently, the first steps in devising a control plan should be to inventory existing invasive species, determine which are likely to invade following a disturbance, and prioritize control efforts based on the specific threat that each poses. Additionally, some sites may be more susceptible to invasion than others. For example, several recent studies have found that productive, nutrient-rich sites may be more susceptible to invasion than low-fertility sites (Howard and others 2004).
2) Start with satellite populations and lightly infested areas, and then work back toward heavily invaded areas (Moody and Mack 1988). Satellite populations, like spot fires, greatly accelerate the rate of spread. Early detection and rapid response are key elements of a successful control strategy (do not wait until a species has become a problem to start control efforts).
3) Use the best control strategy available! Some exotic woody plants are very difficult to kill and respond vigorously to cutting, so be prepared to do what it takes to kill the plant, including its roots. Targeted use of herbicides will likely be necessary (see Webster and others 2006 for herbicide recommendations). In most cases, infested sites will need to be visited on an annual basis for several years to re-treat persistent individuals and those recently emerged or missed during earlier passes.

TABLE 1

Major woody invaders of the eastern US. Adapted from Webster and others (2006) (reproduced with permission from Journal of Forestry*).*

Common name	Latin name
TREES	
Norway maple	*Acer platanoides* L. (Aceraceae)
Ailanthus or tree-of-heaven	*Ailanthus altissima* (P. Mill.) Swingle (Simaroubaceae)
Mimosa	*Albizia julibrissin* Durazz. (Fabaceae)
Russian-olive	*Elaeagnus angustifolia* L. (Elaeagnaceae)
Melaleuca or paper-bark tree	*Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae)
Paulownia or empress tree	*Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud. (Scrophulariaceae)
White poplar	*Populus alba* L. (Salicaceae)
Chinese tallow tree	*Sapium sebiferum* (L.) Roxb. (Euphorbiaceae)
SHRUBS AND SMALL TREES	
Japanese barberry	*Berberis thunbergii* DC. (Berberidaceae)
Scotch broom*	*Cytisus scoparius* (L.) (Fabaceae)
Autumn-olive	*Elaeagnus umbellata* Thunb. (Elaeagnaceae)
Winged burning bush	*Euonymus alata* (Thunb.) Sieb. (Celastraceae)
Chinese privet	*Ligustrum sinense* Lour. (Oleaceae)
European privet	*Ligustrum vulgare* L. (Oleaceae)
Amur honeysuckle	*Lonicera maackii* (Rupr.) Herder (Caprifoliaceae)
Morrow's honeysuckle	*Lonicera morrowii* Gray (Caprifoliaceae)
Tatarian honeysuckle	*Lonicera tatarica* L. (Caprifoliaceae)
Bell's honeysuckle (Tatarian x Morrow's)	*Lonicera* x *bella* Zabel (Caprifoliaceae)
Common buckthorn	*Rhamnus cathartica* L. (Rhamnaceae)
Glossy buckthorn	*Rhamnus frangula* L. (Rhamnaceae)
Multiflora rose	*Rosa multiflora* Thunb. ex Murr. (Rosaceae)
WOODY VINES	
Oriental bittersweet	*Celastrus orbiculatus* Thunb. (Celastraceae)
Japanese honeysuckle	*Lonicera japonica* Thunb. (Caprifoliaceae)
Kudzu	*Pueraria montana* (formerly *lobata*) (Lour.) Merr. (Fabaceae)
Wisteria, Japanese and Chinese	*Wisteria floribunda* (Willd.) DC. and *W. sinensis* (Sims) DC. (Fabaceae)

* A recent arrival in the eastern US that has been a successful invader in the western US.

4) Eradication is usually impossible, but control is attainable. Most species will reinvade after treatment so continuous monitoring and a long-term commitment are necessary. Also, working with adjacent landowners to control the exotics on their property can go a long way toward preventing reinvasion.
5) Although it seems obvious, the most important step is to quit planting invasive exotic plants.

TREES

Norway Maple *(Acer platanoides)*

Norway maple (Figure 1) is an aggressive shade-tolerant species that readily invades disturbed sites and the understories of native forests (Webb and others 2000; Webster and others 2005; Fang 2005; Reinhart and others 2005). This species is a prolific sprouter, which makes cutting alone ineffective. Cut stump, basal bark, and hack and squirt application of a systemic herbicide can be effective, but follow-up treatments may be necessary to control sprouts. Small saplings can be hand-pulled when the ground is moist and friable. This species superficially resembles our native sugar maple (*Acer saccharum* Marsh.) but can be easily distinguished by the white milky sap that is exuded at the base of the petiole when a leaf is removed.

TABLE 2

Selected Internet resources for invasive species identification and control. Adapted from Webster and others 2006 (reproduced with permission from Journal of Forestry*).*

http://bugwood.org
  Invasive species profiles and control techniques

http://dnr.state.oh.us/dnap/invasive
  Plant profiles and control techniques

Exotic Pest Plant Councils: profiles and control techniques
  http://www.gaeppe.org
  http://www.fleppe.org
  http://www.ma-eppe.org
  http://www.se-eppe.org
  http://www.tneppe.org

http://www.ndflora.org/publications/invasives.htm
  Control techniques for invasive plants

http://www.newfs.org/nps.htm
  Alternatives to exotics for landscaping and restoration

http://www.invasive.org
  Descriptions and control guidelines for several species

http://www.invasivespeciesinfo.gov/plants
  Species profiles and links to related publications

http://www.na.fs.fed/fhp/invasive-plants/pdfs
  Plant descriptions and identification

http://www.nps.gov/plants/alien/factmain.htm
  Fact sheets and control techniques for several species

http://www.tncweeds.ucdavis.edu/esadoc.htm
  Management guidelines for several species

Ailanthus or Tree-of-Heaven *(Ailanthus altissima)*

Ailanthus (Figure 2) is a rapidly growing, shade intolerant invader of disturbed soils and canopy gaps (Knapp and Canham 2000; Call and Nilsen 2003). Copious production of seeds and allelochemicals in conjunction with clonal establishment (vigorous stump and root sprouting) enables ailanthus to form dense stands and exclude native species (Miller 1990; Lawrence and others 1991). Given the tremendous ability of this species to sprout in response to stem damage, cutting alone is counterproductive and strongly discouraged. Control of this species requires treatment with a systemic herbicide and continued monitoring for root suckers and stump sprouts (Miller 1990, 2003). Foliar, basal bark, cut stump, and hack and thin line herbicide applications can be effective. Because of the high potential for root suckering, however, cut stump applications may be less effective than basal bark and hack and squirt herbicide applications, which result in better translocation of herbicides to the root system (Miller 2003). Cut stump applications may kill the stump but result in vigorous root suckering. Frilling (applying herbicide to a girdle) is not effective since it top-kills the plant and results in poor translocation of herbicide to the root system.

Melaleuca or Paper-bark Tree *(Melaleuca quinquenervia)*

Melaleuca (Figure 3) is a serious problem in southern Florida where it was introduced as an ornamental and for "swamp drying." This flood- and drought-tolerant evergreen forms impenetrable thickets, accelerates the loss of groundwater, and has converted wetlands and marshes into melaleuca forests (Sebersoff-King 2003). This species is extremely difficult to control. Herbicide application results in the release of millions of cached seeds. Cutting or pushing over followed by the application of a systemic herbicide to the stumps and subsequent sprouts is recommended. Control of this species requires a long-term commitment of time and resources. Seedlings can be hand-pulled. On a positive note, biocontrol efforts for this species are starting to show some promise (Dray and others 2004).

Paulownia or Empress Tree *(Paulownia tomentosa)*

Paulownia (Figure 4) is a fast-growing, pioneer species that readily invades following fire or site disturbances (Carpenter and others 1983) and frequently invades rock outcrop and cliff line communities (Langdon and Johnson 1994). This species is widely planted as an ornamental (very showy purple flowers), and its lumber has been promoted as a high-value export crop (Tang and others 1980). Cut stump, basal bark, and hack and squirt application of systemic herbicides have proven effective against this species (Miller 2003). Repeated cutting may also be effective but is labor intensive. Regardless of the technique employed, follow-up treatments will be necessary to control sprouting. Young seedlings can also be hand-pulled if the soil is moist and (or) friable.

Chinese Tallow Tree *(Sapium sebiferum)*

Chinese tallow (Figure 5) is an aggressive invader of both open and shaded environments across a range of habitat types, from brackish swampy areas to upland forests (Jones and McLeod 1990; Jones and Sharitz 1990). This species has tremendous reproductive potential; copious seed crops are spread by birds and water (Jubinsky and Anderson 1996), and stumps and roots sprout readily. Once established, the species displaces native species, reduces species diversity, and alters habitat (Bruce and others 1997). Over the past 25 y, habitat loss due to tallow tree invasion has drastically reduced populations of grassland and savanna birds (Knopf 1994). Cut stump, basal bark, and frill application of a systemic herbicide during late summer and early fall are typically most effective (Miller 2003; Burns and Miller 2004).

SHRUBS

Privet *(Lingustrum* spp.*)*

Privets (Figure 6) are shade-tolerant, tall shrubs that were introduced as ornamentals from China and Europe in the mid-1800s (Chinese privet [*Ligustrum sinense*]; European privet [*Ligustrum vulgare*]). These species have invaded upland and bottomland forests from Florida to southern New England, and pockets of invasion stretch as far west as eastern Kansas, Oklahoma, and Texas. Privets form dense stands in the understory and exclude most native plants, drastically altering habitat structure and function (Brown and Pezeshki 2000; Merriam 2003; Harrington and

Figure 1. Norway maple (*Acer platanoides*) sapling growing in full sun and a dense monotypic stand of saplings along a forest edge. Photo by CR Webster

Figure 2. Ailanthus (*Ailanthus altissima*) saplings and near pure stand of ailanthus in North Carolina. Photo courtesy of USDI National Park Service

Figure 3. Dense stand of melaleuca (*Melaleuca quinquenervia*). Photo by Randy Westbrooks, US Geological Survey, www.forestryimages.org

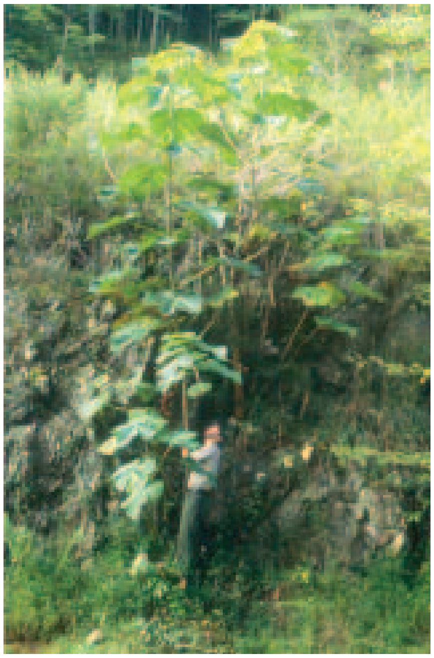

Figure 4. Paulownia (*Paulownia tomentosa*) frequently invades cliff lines and road cuts. Photo courtesy of USDI National Park Service

Figure 5. Fall foliage of Chinese tallow (*Sapium sebiferum*). Photo by James H Miller, USDA Forest Service, www.forestryimages.org

Miller 2005). Vigorous sprouting from root suckers and the ability to produce huge amounts of seeds that are dispersed by birds (Strong and others 2005) have contributed to the success of privet invasions. Spring or fall foliar application of systemic herbicides can provide effective control (Miller 2003; Harrington and Miller 2005). If stems are too tall for foliar sprays, a cut surface or basal bark herbicide application is recommended.

Bush Honeysuckle *(Lonicera* spp.*)*

Amur (*Lonicera maackii*) and Tatarian honeysuckle (*Lonicera tatarica*) (Figure 7) are aggressive invaders of eastern forest understories, forming dense thickets that exclude most species of native trees and herbs (Woods 1993; Collier and others 2002). Both species produce fleshy fruits that are attractive to birds, expand their leaves earlier in the spring and retain them later in the fall than do native deciduous species, and grow rapidly with relatively few pests in their introduced range (Woods 1993; Luken and Thieret 1996). Tatarian honeysuckle can hybridize with another invasive bush honeysuckle (*Lonicera morrowii*), and the resulting hybrid (*L.* x *bella*) is also invasive (Woods 1993). The most widely recommended treatment is a cut surface application of a systemic herbicide (Luken and Mattimiro 1991; Nyboer 1992). Foliar herbicide applications can also be effective, especially if timed to take advantage of late leaf-fall in this species, which reduces damage to surrounding vegetation (Rathfon 2006). As a general rule, don't cut these species without a subsequent herbicide application because patches will come back more dense and vigorous following a single cutting. Repeated cutting, while labor intensive, can provide effective control of small invasions growing in densely shaded environments (Luken and Mattimiro 1991). Small bushes can be pulled by hand.

Buckthorn *(Rhamnus* spp.*)*

Glossy (*Rhamnus frangula*) and common buckthorn (*Rhamnus cathartica*) (Figure 8), are aggressive invaders of both open areas and forest understories where they form dense thickets that reduce the cover and diversity of native herbs and inhibit overstory tree regeneration (Frappier and others 2003; Fagan and Peart 2004). Both species grow quickly, produce large numbers of fleshy seeds that are dispersed by birds, leaf out earlier and hold their leaves longer than do native deciduous species, and vigorously stump and root sprout following cutting or burning (Harrington and others 1989). Cutting alone is not recommended because of the tremendous sprouting capabilities of these species. Cut surface, basal bark, and frill applications of systemic herbicide are recommended (Reinartz 1997). Herbicide should also be applied immediately following cutting. Avoid cut surface treatments during the spring when the sap is flowing since the flow will flush out the herbicide. Follow-up treatments and repeated herbicide applications are usually necessary to control sprouting.

VINES

Oriental Bittersweet *(Celastrus orbiculatus)*

Oriental bittersweet (Figure 9) readily invades edge environments, woodlots, abandoned agricultural fields, and hedgerows (Greenberg and others 2001). It often employs a "sit and wait" strategy by establishing and persisting under undisturbed forest canopies, and then following canopy disturbance grows rapidly, often overtopping and girdling trees (Greenberg and others 2001). Because canopy disturbance promotes oriental bittersweet reproduction, the species presents a serious problem for forest management (Silveri and others 2001; McNab and Loftis 2002). The seeds of oriental bittersweet are distributed by birds (McNab and Loftis 2002). Cut stem application of herbicide is recommended for this species (Hutchinson 1992). Small vines may be hand-pulled but should be removed from the site to avoid rooting.

Japanese Honeysuckle *(Lonicera japonica)*

Japanese honeysuckle (Figure 10) has proved to be an aggressive colonizer of forest edges, openings, and understories. After disturbance, it is an aggressive competitor with seedlings of native woody species and often turns forests into vine thickets (Schierenbeck 2004). Japanese honeysuckle may also disrupt fire regimes; the species is encouraged by fire suppression but resprouts vigorously following all but the most intense fires (Schierenbeck 2004). This evergreen to semi-evergreen, moderately shade-tolerant, woody vine employs both vegetative and sexual reproduction (Schierenbeck 2004). In open fields, this species can form dense mats, but it is even more productive if supports, such as young trees, are present (Schweitzer and Larson 1999). Mesic sites are most susceptible to invasion. Repeated burning, mowing, and (or) cutting can be used to control infestations (Evans 1984). Foliar herbicide application is effective and can be done during the dormant season in warmer climates to reduce damage to native vegetation (Evans 1984).

Kudzu *(Pueraria montana)*

Originally introduced to the US from Asia around 1876, kudzu (see photo on page 97) was planted throughout the southeast for erosion control and livestock forage between 1920 and 1950 (Mitich 2000). Kudzu blankets millions of hectares in the southern US and is spreading at a rate of 50000 ha (123 550 ac) per year (Mitich 2000), making it one of the most aggressive perennial weeds in North America. Several of the traits that made this semi-woody, nitrogen-fixing vine desirable for erosion control have contributed to its success as an invader of forest openings and edges. Kudzu grows rapidly (up to 30 cm [12 in] per day and 20 to 30 m [66 to 98 ft] per year), quickly overtops existing vegetation, reproduces vegetatively but rarely by seed, and colonizes poor sites due to its ability to fix atmospheric nitrogen (Forseth and Innis 2004). Kudzu disrupts native forests by overtopping all sizes of trees and eventually shading them to death and (or) crushing them. This species can be controlled, and its spread has been arrested in many areas through the use of effective control techniques; however, continued monitoring and maintenance are required. Successful treatments focus on depleting or destroying this species' extensive root system (Miller and Edwards 1983; Harrington and others 2003; Forseth and Innis 2004). Systemic herbicide applications, either foliar, soil, or immediate applications to cut surfaces, are recommended. Repeated close annual mowing may be used to exhaust carbohydrate stores in the root system.

CONCLUSIONS

Invasive woody plants are probably here to stay, but through concerted and diligent effort their impact and spread can be greatly reduced. The first and arguably most important and difficult step is to stop planting these species. Second, control activities should begin in earnest immediately following the identification of an invasive exotic. Early detection and rapid response are key elements of a successful control program. Activities should be prioritized based on the risks posed by the suit of invaders found on-site as well as those

Figure 6. Privet (*Ligustrum* spp.) with developing fruit. Photo courtesy of USDI National Park Service

Figure 7. Tatarian honeysuckle (*Lonicera tatarica*) and control of Amur honeysuckle (*Lonicera maackii*) in a heavily invaded woodlot. Photo by CR Webster

Figure 8. Glossy buckthorn (*Rhamnus frangula*). Photo by LM Nagel

Figure 9. Oriental bittersweet (*Celastrus orbiculatus*) completely enshrouding the crown of an open-grown tree. Photo courtesy of USDI National Park Service.

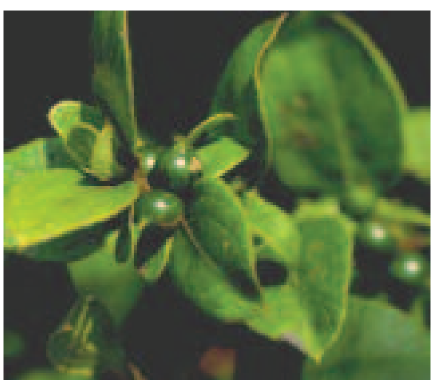

Figure 10. The fruits of Japanese honeysuckle (*Lonicera japonica*) are readily distributed by birds and other animals. Photo courtesy jof USDI National Park Service.

on adjacent properties. As a general rule, however, if a species has exhibited invasive tendencies elsewhere in the introduced range, don't wait for it to become a problem before initiating control activities. Third, use the most effective control technique available and monitor sites, re-treating as needed following initial control activities. Finally, whenever possible, native plants should be given preference in place of exotics for ornamental, wildlife, and erosion control plantings.

REFERENCES

Bertin RI, Manner ME, Larrow BF, Cantwell TW, Berstene EM. 2005. Norway maple (*Acer platanoides*) and other non-native trees in urban woodlands of central Massachusetts. Journal of the Torrey Botanical Society 132:225–235.

Brown CE, Pezeshki SR. 2000. A study on waterlogging as a potential tool to control *Ligustrum sinense* populations in western Tennessee. Wetlands 20:429–437.

Bruce KA, Cameron GN, Hocombe PA, Jubinsky G. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Natural Areas Journal 17:255–260.

Burns JH, Miller TS. 2004. Invasion of Chinese Tallow (*Sapium sebiferum*) in the Lake Jackson area, Northern Florida. American Midland Naturalist 152:410–417.

Call LJ, Nilsen ET. 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robina pseudoacacia*). American Midland Naturalist 150:1–14.

Carpenter D, Cappuccino N. 2005. Herbivory, time since introduction and the invasiveness of exotic plants. Journal of Ecology 93:315–321.

Carpenter SB, Immel MJ, Smith ND. 1983. Effect of photoperiod on the growth and photosynthetic capacity of *Paulownia* seedlings. Castanea 48:13–18.

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Collier MH, Vankat JL, Hughes MR. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. American Midland Naturalist 147:60–70.

Dray FA Jr, Bennett BC, Center TD, Wheeler GS, Madeira PT. 2004. Genetic variation in *Melaleuca quinquenervia* affects the biocontrol agent *Oxyops vitiosa*. Weed Technology 18:1400–1402.

Evans JE. 1984. Japanese honeysuckle (*Lonicera japonica*): a literature review of management practices. Natural Areas Journal 4:4–10.

Fagan ME, Peart DR. 2004. Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. Forest Ecology and Management 194:95–107.

Fang W. 2005. Spatial analysis of an invasion front of *Acer platanoides*: dynamic inferences from static data. Ecography 28:283–294.

Forseth IN, Innis AF. 2004. Kudzu (*Pueraria montana*): history, physiology, and ecology combine to make a major ecosystem threat. Critical Reviews in Plant Sciences 23:401–413.

Frappier B, Lee TD, Olson KF, Eckert RT. 2003. Small-scale invasion pattern, spread rate, and lag-phase behavior of *Rhamnus frangula* L. Forest Ecology and Management 186:1–6.

Greenberg CH, Smith LM, Levey DJ. 2001. Fruit fate, seed germination and growth of an invasive vine—an experimental test of the “sit and wait” strategy. Biological Invasions 3:363–372.

Gurvich DE, Tecco PA, Díaz S. 2005. Plant invasions in undisturbed ecosystems: the triggering attribute approach. Journal of Vegetation Science 16:723–728.

Harrington RA, Brown BJ, Reich PB, Fownes JH. 1989. Ecophysiology of exotic and native shrubs in southern Wisconsin: II. Annual growth and carbon gain. Oecologia 80:368–373.

Harrington TB, Miller JH. 2005. Effects of application rate, timing, and formulation of glyphosate and triclopyr on control of Chinese privet (*Ligustrum sinense*). Weed Technology 19:47–54.

Harrington TB, Rader-Dixon LT, Taylor JW Jr. 2003. Kudzu (*Pueraria montana*) community responses to herbicides, burning, and high-density loblolly pine. Weed Science 51:965–974.

Howard TG, Gurevitch J, Hyatt L, Carreiro M, Lerdau M. 2004. Forest invasibility in communities in southeastern New York. Biological Invasions 6:393–410.

Hutchison M. 1992. Vegetation management guidelines: round-leaved bittersweet (*Celastrus orbiculatus* Thunb.). Natural Areas Journal 12:161.

Jones RH, McLeod KW. 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallowtree and Carolina ash seedlings. Forest Science 36:851–862.

Jones RH, Sharitz RR. 1990. Effects of root competition and flooding on growth of Chinese tallow tree seedlings. Canadian Journal of Forest Research 20:573–578.

Jubinsky G, Anderson LC. 1996. The invasive potential of Chinese tallow-tree (*Sapium sebiferum* Roxb.) in the Southeast. Castanea 61:226–231.

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164–170.

Knapp LB, Canham CD. 2000. Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. Journal of the Torrey Botanical Society 127:307–315.

Knopf FL. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247–257.

Langdon KR, Johnson KD. 1994. Additional notes on invasiveness of *Paulownia tomentosa* in natural areas. Natural Areas Journal 14:139–140.

Lawrence JG, Colwell A, Sexton OJ. 1991. The ecological impact of allelopathy in *Ailanthus altissima* (Simaroubaceae). American Journal of Botany 78:948–958.

Luken JO, Mattimiro DT. 1991. Habitat specific resilience of the invasive shrub Amur honeysuckle (*Lonicera maackii*) during repeated clipping. Ecological Applications 1:104–109.

Luken JO, Thieret JW. 1996. Amur honeysuckle, its fall from grace. BioScience 46:18–24.

Martin PH, Marks PL. 2006. Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). Journal of Ecology 94:1070–1079.

McNab HW, Loftis DL. 2002. Probability of occurrence and habitat features for oriental bittersweet in an oak forest in the southern Appalachian mountains, USA. Forest Ecology and Management 155:45–54.

Merriam RW. 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. Journal of the Torrey Botanical Society 130:283–291.

Miller JH. 1990. *Ailanthus altissima* (Mill.) Swingle Ailanthus. In: Burns RM, Honkala BH, technical coordinators. Silvics of North America. Vol. 2. Hardwoods. Washington (DC): USDA Forest Service. Agriculture Handbook 654.p 461–465.

Miller JH. 2003. Nonnative invasive plants of southern forests: a field guide for identification and control. Washington (DC): USDA Forest Service. General Technical Report SRS-62. 93 p.

Miller JH, Edwards B. 1983. Kudzu, *Pueraria lobata*, where did it come from and how can we stop it? Southern Journal of Applied Forestry 7:165–169.

Mitich LW. 2000. Intriguing world of weeds: kudzu (*Pueraria lobata* [Wild.] Ohwi.). Weed Technology 14:231–235.

Moody ME, Mack RN. 1988. Controlling the spread of plant invasions: the importance of nascent foci. Journal of Applied Ecology 25:1009–1021.

Muth NZ, Pigliucci M. 2006. Traits of invasives reconsidered: phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. American Journal of Botany 93:188–196.

Myers JH, Bazely DR. 2003. Ecology and control of introduced plants. Cambridge, UK: Cambridge University Press. 313 p.

Neubert MG, Caswell H. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81(6):1613–1628.

Nyboer R. 1992. Vegetation management guideline: bush honeysuckles, tatartian, Morrow's, Belle, and Amur honeysuckle (*Lonicera tatarica* L., *L. morrowii* Gray, *L.* x *belle* Zabel, and *L. maackii* [Rupr.] Maxim.). Natural Areas Journal 12:218–219.

Rathfon R. 2006. Asian bush honeysuckle: an exotic invasive plant threatening Indiana's forests. The Woodland Steward 15(3):5–6, 11, 14.

Reichard S, Hamilton C. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology 11:1993–1203.

Reinartz JA. 1997. Controlling glossy buckthorn (*Rhamnus frangula* L.) with winter herbicide treatments of cut stumps. Natural Areas Journal 17:38–41.

Reinhart KO, Greene E, Callaway RM. 2005. Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the northern Rocky Mountains. Ecography 28:573–582.

Rejmánek M, Richardson DM. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1661.

Schierenbeck KA. 2004. Japanese honeysuckle (*Lonicera japonica*) as an invasive species; history, ecology, and context. Critical Reviews in Plant Sciences 23:391–400.

Schweitzer JA, Larson KC. 1999. Greater morphological plasticity of exotic honeysuckle species may make them better invaders than native species. Journal of the Torrey Botanical Society 126:15–23.

Sebersoff-King K. 2003. Melaleuca in Florida: a literature review on the taxonomy, distribution, biology, ecology, economic importance and control measures. Journal of Aquatic Plant Management 41:98–112.

Silveri A, Dunwiddie PW, Michaels HJ. 2001. Logging and edaphic factors in the invasion of an Asian vine in a mesic North American forest. Biological Invasions 3:379–389.

Strong CM, Brown DR, Stouffer PC. 2005. Frugivory by wintering hermit thrush in Louisiana. Southeastern Naturalist 4:627–638.

Sutherland S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia 141:24–39.

Tang RC, Carpenter SB, Wittwer RF, Graves DH. 1980. *Paulownia*—a crop tree for wood products and reclamation of surface-mined land. Southern Journal of Applied Forestry 4:19–24.

[USDA NRCS] USDA Natural Resources Conservation Service. 2006. The PLANTS database, version 3.5. URL: http://plants.usda.gov. Baton Rouge (LA): National Plant Data Center.

Wangen SR, Webster CR. 2006. Potential for multiple lag phases during biotic invasions: reconstructing an invasion of the exotic tree *Acer platanoides*. Journal of Applied Ecology 43:258–268.

Webb SL, Dwyer M, Kaunzinger CK, Wyckoff PH. 2000. The myth of the resilient forest: case study of the invasive Norway maple (*Acer platanoides*). Rhodora 102:332–354.

Webster CR, Jenkins MA, Jose S. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. Journal of Forestry 104:366–374.

Webster CR, Nelson K, Wangen SR. 2005. Stand dynamics of an insular population of an invasive tree, *Acer platanoides*. Forest Ecology and Management 208:85–99.

Williamson M, Fitter A. 1996. The varying success of invaders. Ecology 77: 1661–1666.

Woods KD. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England Forests. American Midland Naturalist 130:62–74.

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