



A review of the biology and ecology of three invasive perennials in New York State: Japanese knotweed (*Polygonum cuspidatum*), mugwort (*Artemisia vulgaris*) and pale swallow-wort (*Vincetoxicum rossicum*)

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Abstract

Terrestrial weeds continue to evolve in association with the rapid global changes in our land-use systems, due to their regenerative strategies, their adaptability to change, and their inherent diversity. Currently, invasive weeds are estimated to cost the United States' economy up to \$35 billion per year, and this total is rapidly increasing, as greater numbers of invasive species become naturalized. Several invasive exotic species have more recently established across New York State, creating difficulties for agricultural producers, roadside and natural areas managers, and homeowners and resulting in millions of dollars expended annually for their control. Three perennials that have become particularly problematic in New York State in recent years in both agricultural and roadside settings include Japanese knotweed (*Polygonum cuspidatum* Sieb. & Zucc.), mugwort (*Artemisia vulgaris* L.), and pale swallow-wort (*Vincetoxicum rossicum* (Kleop.) Barbar.). This review describes their history, biology, ecology, and potential for management and focuses on key characteristics contributing to their spread in New York State and adjacent regions.

Introduction

Weeds have invaded terrestrial and aquatic rural and urban areas across the United States, with some dramatically reducing our productivity and quality of life. They have co-evolved with our systems of land use, and the methods we have developed for their management have proven to be major contributions to modern agriculture. Although these methods have released many from the burden and drudgery of weed control and allowed others to pursue more creative and pleasurable activities, weeds continue to cost the American economy billions of dollars annually (Westbrooks, 1998). Due to their remarkable ability to reproduce and spread, invasive terrestrial weeds are also limiting our ability to preserve and

protect the diversity of native species and landscapes (Levine, 2000; Lonsdale, 1999; Westbrooks, 1998).

Although exact figures are difficult to obtain, Pimentel et al. (2000) have estimated that non-indigenous species cost the United States more than \$138 billion annually, with plants accounting for \$34.7 billion of the total expense. Pimentel et al.'s (2000) report only includes economic damages and control costs, but not environmental and health costs. Even though environmental consequences cannot be accurately estimated, these costs could be potentially great, due to the active displacement of native species following invasion of non-indigenous species and resultant loss of biodiversity (Elton, 1958; Westbrooks, 1998). According to Elton and other ecologists, if

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biological invasions continue as they have over the past 100 years, biological systems will be well homogenized and many native species will decline or disappear altogether.

In the United States, introduced species account for about 65% of the total weed flora (Westbrooks, 1998). About 675 out of nearly 5000 introduced plant species now naturalized are estimated to be highly invasive and problematic. In New York State, about 3000 plant species have been identified, with just over 1100 being non-native (Westbrooks, 1998). As far as invasive species in the Northeast are concerned, over 100 plants are listed as invasive across the Mid-Atlantic region (The Maryland Invasive Species Council, 2004) and 24 in New York State (Invasive Plant Council of New York State, 2004). These recent invasive plant introductions have established themselves across New York State, creating difficulties for agricultural producers, roadside and landscape managers and homeowners and have necessitated the expenditure of millions of dollars annually for their control. Unfortunately, we have limited information about the ecology, biology and management of many of these newly invasive weed species in their introduced range. Therefore, the development of focused ecological research upon selected species is desperately needed.

The study of the establishment, spread and reproductive potential of key invasive species in both managed and natural settings is of high priority. We have selected three perennial weed species that are particularly invasive in New York State and deserving of further study. These include Japanese knotweed (*Polygonum cuspidatum* Sieb. & Zucc.), mugwort (*Artemisia vulgaris* L.), and pale swallow-wort (*Vincetoxicum rossicum* (Kleop.) Barbar.). This review presents an overview of the historical spread and current status of the biology, ecology and potential management of each of these highly aggressive plant species.

Japanese knotweed

Japanese knotweed is a member of the Polygonaceae or knotweed family which originated in Asia, primarily in Japan, Taiwan and Northern China (Child and Wade, 2000; Di Tommaso et al., 2005). This showy plant forms upright, bamboo-like stems that can reach upwards of 5 m in

height. Leaves exhibit morphological variations ranging from triangular to heart-shaped, depending on level of hybridization (Bailey, 1994; Child and Wade, 2000). Stems can be reddish in color and individual plants eventually form dense stands. Flowers are an attractive cream color forming attractive panicles, generally from July through August in North America (Hollingsworth et al., 1998). Knotweed flowers have previously been reported to be mainly male sterile in the UK and on the North American continent, and seed production appeared to be limited or absent (Beerling et al., 1994). In the United Kingdom, although hybrid seed is occasionally formed, no germination has been recorded in the wild (Child and Wade, 2000).

Japanese knotweed is considered to be an invasive exotic species and is recognized as a serious problem in the United Kingdom, parts of Europe, and is increasingly a threat to naturalized areas in the United States (Forman and Kesseli, 2003; Wade et al., 1996). In North America and the UK, this plant establishes in disturbed areas, most commonly by roadsides and along riparian corridors. Invasion results in loss of wildlife habitat, decreased species diversity and reduction in the available water supply and carrying capacity of rivers and streams (Conolly, 1977; Toney et al., 1998). In the US, its range extends throughout much of the Northeast, from Georgia to Maine, with populations naturalized across the central US into the Pacific Northwest (Child and Wade, 2000; Zika and Jacobson, 2003) (Figure 1).

Japanese knotweed rhizomes, or underground stems, can extend more than 2 m in depth and 15–20 m in length, and are fleshy to woody with a distinctive orange interior (Child and Wade, 2000; Seiger and Merchant, 1997). Rhizome or stem fragments, the purported means of reproduction in the introduced range, are typically dispersed via water or transported in soil by humans (Brock et al., 1995; Connolly, 1977). Once established, Japanese knotweed is extremely persistent, limiting the amount of light reaching the soil surface and surrounding vegetation (Seiger and Merchant, 1997).

Historically, this plant was first described as *Reynoutria japonica* by Houltuyn in 1777 from dried material brought back from Japan. It was



Figure 1. Photographs (clockwise from left to right) of Japanese knotweed (*Polygonum cuspidatum* Sieb. & Zucc.) invasive growth in riparian habitat, inflorescence, and fruit.

apparently introduced to the UK from China in 1825 by the London Horticultural Society, and was later introduced to Kew Gardens in 1855 as *Polygonum cuspidatum* (Siebold and Zuccarini), possibly from a nursery in the Netherlands (Child and Wade, 2000). Various synonyms for this species have been published in the literature, including *Fallopia japonica* (Houtt.) Ronse Decraene, *Polygonum japonicum* Meissn, *Polygonum zuccarinii* Small, and *Reynoutria japonica* (Houtt.). The plant was billed as a collector's item initially and was later sold exclusively by von Siebold in England in the 1840s and 1850s (Bailey and Conolly, 2000; Child and Wade, 2000).

A dwarf variant of *P. cuspidatum* (var. *compactum*) was also introduced to the UK as a decorative garden plant, many of them male sterile with dark red stem pigmentation (Bailey and Conolly, 2000; Child and Wade, 2000; Mandak et al., 2004). Between 1850 and 1880 variants of this male sterile plant became widely available for cultivation in public and private gardens. An additional species, *Polygonum sachalinense* (syn. *F. sachalinensis*), a male fertile species exhibiting greater genetic diversity than *P. cuspidatum* (Bailey and Conolly, 2000) was introduced in the UK in the mid-1800s from the island of Sakhalin, north of Japan. The hybrid of *P. cuspidatum* and *P. sachalinense* soon became

established in England as well, and is referred to in England as *P. bohemicum* (syn. *Fallopia* × *bohemicum*) (Child and Wade, 2000). In the UK, the majority of established knotweed consists of *P. cuspidatum*, a common invasive throughout all the islands. *P. sachalinense* appears to be associated mainly with old estates in the UK where it was once established as a cover crop for erosion protection or as an ornamental. Hybridization between these species likely occurred numerous times, as shown by the various genotypes identified (Bailey and Conolly, 2000). It has also hybridized in the UK with *P. baldschuanica*, or Russian vine, a creeping relative (Child and Wade, 2000).

In the 1880s, *P. cuspidatum* became naturalized in the US, after it was introduced in the 1870s as an estate planting in the Northeast (Bailey and Conolly, 2000; Child and Wade, 2000). Today, this species is found across New York State as far north as the Adirondack Mountains (Brown et al., 2001), and especially across central and southern NY roadsides where, according to the NY State Department of Transportation, its spread appears to be associated with disturbances along highways and roadsides, and direction of water flow in riparian habitats (Miller, 2004).

In the UK, Japanese knotweed escape from country gardens reportedly increased from the 1880s onward (Conolly, 1977). Today, it is hardy even in the northern latitudes of the UK and achieves spectacular size while producing multiple blooms. By 1905, the invasive nature of Japanese knotweed was already noted and the Journal of the Royal Horticulture Society no longer advised its planting (Child and Wade, 2000). Today, *P. cuspidatum*, along with giant hogweed (*Heracleum mantegazzianum* Som. and Lev.), another invasive perennial, is prohibited from planting in the wild in the UK (Bailey and Conolly, 2000).

In North America, Japanese knotweed is classified as a noxious weed and as highly invasive by the Mid-Atlantic Exotic Pests Plant Council and the New York State Invasive Plant Council. The species is also on the National Exotic Pest Plants list, as well as the Invasive Alien Plants of Ontario list, and many state lists (Child and Wade, 2000; Zika and Jacobson, 2003). *P. sachalinense* is also established across the conti-

nent, and classified as a noxious weed in California and Washington (Kartesz, 1999; Zika and Jacobson, 2003). The hybrid of these two species has been recently renamed by Zika and Jacobson (2003) as *P. bohemicum* (J. Chrték and A. Chrtkova) P.F. Zika and A.L. Jacobson and is widely established in western Washington, and likely across North America, although not often recognized (Zika and Jacobson, 2003). Despite the prolific fruit production now observed in the US in these species and their hybrid, the primary means of reproduction of these gynodioecious perennials remains vegetative (Zika and Jacobson, 2003). Viable seeds are thought to be the result of pollen donation by *P. sachalinense* or *P. bohemicum* (Bailey, 1994), as *P. cuspidatum* is still primarily a male-sterile clone in its introduced range (Zika and Jacobson, 2003) (Table 1).

Several recent studies have shown that viable seeds can be produced in several Japanese knotweed populations in the northeastern US (Bram and McNair, 2004; Forman and Kesseli, 2003). However, these studies characterized the seed source as *P. cuspidatum sensu lato* (including *P. cuspidatum*, *P. sachalinense* and *P. bohemicum*), leaving some remaining uncertainty regarding seed production. In the study published by Bram and McNair (2004), seed collected from established Japanese knotweed plants in the Philadelphia, PA park system proved to be highly viable. Collected seed exhibited high germination rates (>90%) when planted subsequently in either greenhouse or field settings. Amazingly, plants at this Philadelphia site were able to generate up to an estimated 127,000 seeds per stalk, with many being viable. This study did not attempt to characterize recruitment rates in the wild, or characterize the pollen source for the seeds collected, but the authors suggest that hybridization or genetic diversity could be responsible for the ability to produce viable seed in these plantings.

Attempts to genetically characterize knotweed species in the UK have used molecular markers, including RAPDs and ISSRs to evaluate genotypic diversity in invasive *Polygonum* germplasm. In the UK, a single genotype of *P. cuspidatum* was detected, suggesting all individuals were ramets of a single clone. Two genotypes of *P. sachalinense* were detected with

Table 1. Common growth and reproductive characteristics of three North American exotic invasive species, currently spreading throughout New York State

Character	Japanese knotweed ^{a,b,c}	Mugwort ^{d,e,f}	Pale swallow-wort ^g
Floral sexuality	Dioecious, gynodioecious, subdioecious	Monoecious	Monoecious
Primary mode of reproduction	Vegetative, but hybridizes with <i>P. sachalinense</i> and <i>P. × bohemicum</i>	Vegetative	Sexual (seed)
Seed viability	High in native range, variable in naturalized range; high viability within hybrids	Variable in naturalized range	High in naturalized range
Seed production yr ⁻¹ plant ⁻¹	127,000–192,000	200,000–450,000	Open habitats: 85 seeds/ramet (or 2090 seeds/m ²); shaded sites: 15 seeds/ramet (or 1330 seeds/m ²)
Rhizome characteristics	Large diameter; orange to red	Fragile, 0.2–1.5 cm diameter, branching at nodes, few to many adventitious roots	No rhizomes produced
Rhizome length	Reaching 1 m deep, length yr ⁻¹ unknown	~3 km yr ⁻¹ ; 114 km ha ⁻¹	–
Area infested	Single clones can increase several m ² yr ⁻¹	9 m ² after 3 yrs	No data available

^aBeerling et al. (1994).

^bForman and Kesselli (2003).

^cBram and McNair (2004).

^dBarney and DiTommaso (2003).

^ePawłowski et al. (1967).

^fGarnock–Jones (1986).

^gDiTommaso et al. (2005a).

one genotype predominating. Five genotypes of the hybrid were recovered, and *P. bohemicum* was the only male fertile taxon recorded. It is likely that some, if not most, of the genetic variation is attributable to hybrid fertility. Both ISSR and RAPD techniques provided data that were broadly congruent (Hollingsworth et al., 1998). Similar studies are now underway to assess genetic interrelatedness among North American Japanese knotweed populations (Bram and McNair, 2004), including one study in our laboratory using a modified RAPD approach. Preliminary results suggest that significant genetic diversity exists among local populations of Japanese knotweed (Weston, data not presented).

Japanese knotweed also exhibits the ability to produce and release a series of novel secondary products from its living root system, including a close relative of the antioxidant resveratrol,

methyl resveratrol (Vastano et al., 2000). Interestingly, the amount of stilbenes, including resveratrol, within the roots of *P. cuspidatum* was much higher than concentrations reported in red grapes and wine. In addition, other unique compounds have been reported in rhizomes of *Polygonum* spp., perhaps having value as medicinals (Kimura et al., 1983), and also possibly contributing to potential allelopathic properties of Japanese knotweed. Although Japanese knotweed forms dense monocultural stands, and its decomposing litter and rhizomes are thought to interfere with surrounding plant growth and diversity (Child and Wade, 2000), its allelopathic properties have not been thoroughly evaluated to date. This is another relevant ecological area that deserves further scrutiny.

Knotweed management has proven to be extremely difficult, if not impossible, in both the UK and the US (Child and Wade, 2000; Figueroa, 1989). Mechanical control by mowing

or cutting knotweed stems is possible, especially when the plant is small (Baker, 1988). The ultimate goal of repeated mowing involves depletion of root reserves over time so the plant is less able to regenerate successfully after cutting. In the vast majority of cases, repeated mowing, even on a monthly basis, failed to eradicate even small patches of knotweed, unless it was performed over a number of years (Baker, 1988). Uprooting the plant after three successive years of digging has also resulted in control of smaller patches, but is not recommended for larger patches. When cutting vegetation, it is recommended to rake and remove all vegetative parts because stem fragments, as well as rhizomes, can resprout (Brock et al., 1995; Hollingsworth and Bailey, 2000; Seiger and Merchant, 1997). The New York State Department of Transportation recommends deep burial, burning or enclosure in multiple layers of plastic until decomposition is ensured (Miller, 2004). In the UK, soil infested with knotweed rhizomes is considered to be an environmental hazard and must be buried to a depth of 3 m after collection (Bailey and Conolly, 2000). If cutting back the stems, it is suggested that stems be trimmed to the ground at least every three weeks from April through August. Care must be taken to prevent movement of plant parts onto moist adjacent sites or into nearby streams (Seiger and Merchant, 1997).

Management of Japanese knotweed with herbicides is also feasible, but can be laborious and expensive, especially when plants are large and well-established. Herbicides with an active ingredient of glyphosate, triclopyr, 2,4-D, picloram or imazapyr have been shown to have variable efficacy in controlling knotweed either separately or in combinations (Child and Wade, 2000). Many of these are not suggested for use in riparian areas, thereby complicating the issue of control along streams and rivers. Some can only be used where complete vegetation control is desirable, and herbicide persistence can be tolerated. However, successful control is generally based on the ability of herbicides to translocate effectively from foliar treatments into the extensive rhizome system (Child and Wade, 2000).

Impacts of herbicides on non-target organisms or lack of selectivity can also be problematic in naturalized areas (Conolly, 1977; Seiger and Merchant, 1997). Many herbicides require repeated

applications to achieve moderate control. Glyphosate, glyphosate plus picloram, and imazapyr have proven somewhat effective in suppressing established stands of knotweed along roadsides (Child and Wade, 2000; Figueroa, 1989). The ideal time to apply an herbicide for greatest translocation is when flower buds are developing. However, this may not be practical in terms of height of the established plants. Younger, rapidly growing shoots may be more easily treated in fact. In particular, stem injection of glyphosate also appears to be effective in controlling knotweed, although repeated injections may be needed to achieve full control (Child and Wade, 2000). Application is made with undiluted product, injecting approximately 5 mL of glyphosate per 1–5 cm diameter stem. The municipality of Ithaca, New York is currently evaluating this technique for prevention of Japanese knotweed spread in riparian areas, as is the Nature Conservancy throughout naturalized areas in the Northeast (Weston, personal communication, 2005). Wicking concentrate on cut stems is also possible, but requires several repeated applications for reasonable control (Child and Wade, 2000).

Due to the difficulties associated with chemical or mechanical means for management of Japanese knotweed, biological control would be an obvious choice for future selective control. The Japanese Knotweed Alliance, an organization devoted to the study and management of knotweed, is currently investigating the use of host specific beetles and pathogens for biocontrol. A chrysomelid beetle and a rust fungus that are highly specific to Japanese knotweed have been identified as potential agents for biocontrol in the UK and North America, but biocontrol research on this species remains in its preliminary stages (<http://www.cabi-bioscience.org/Html/Japanese-knotweed.doc>. 2004)

Mugwort

Mugwort (*Artemisia vulgaris* L.) is a rhizomatous perennial weed that commonly infests roadsides, waste areas, agronomic settings and landscapes (Di Tommaso et al., 2005; Henderson and Weller, 1985; Holm et al., 1997). Mugwort is a broadleaf perennial that spreads quickly upon introduction via an extensive rhizome system, and is difficult at

best, to control chemically or culturally (Barney and DiTommaso, 2003; Bing, 1983; Foy, 2001; Henderson and Weller, 1985; Neal and Adkins, 2001). Mugwort is easily identifiable by the woolly abaxial surface of the leaves, its highly dissected leaf margins (giving it an appearance similar to that of a chrysanthemum) as well as the pungent odor released from crushed foliage. Rhizomes, up to 1 cm in diameter, are light brown in color and remain in the upper 20 cm of soil, often forming an extensive underground network. The inflorescence is green and rather unremarkable, with some flower heads sessile or peduncled (Barney and DiTommaso, 2003). *Artemisia vulgaris*

exhibits great morphological variation, both in its native and introduced range (Holm et al., 1997; Barney and DiTommaso, 2003) (Figure 2).

With very few effective strategies for control, this aggressive weed has rapidly colonized new areas in the eastern US. Mugwort is most troublesome, often forming dense mono-specific stands along roadsides, in turfgrass and rights-of-way, and in nursery and landscape settings. Mugwort is also noted as one of the major weeds in the US nursery industry where it strongly interferes with ornamental growth. Its rhizome pieces can be transported by the replanting of nursery stock (Holm et al., 1997). USDA and



Figure 2. Photographs (clockwise from left to right) of mugwort (*Artemisia vulgaris* L.) individual rhizome, clump of rhizomes taken from soil surface beneath monocultural stand of mugwort, and monocultural stand in an agronomic setting.

NY State inspection of nursery stock is now conducted to prevent transport of infested rootstock from New York State, a major site of mugwort infestation in the Northeast (NY State Department of Agriculture and Markets, personal communication).

Following mugwort colonization, species diversity of native flora in many habitats has declined, especially early successional species (Barney and DiTommaso, 2003; Holm et al., 1997). With the displacement of native colonizers, succession in natural ecosystems can be altered following mugwort invasion. Habitats that generally support diverse stands of native ruderals or stress-tolerators are being displaced by monospecific stands of the weedy mugwort (Barney and DiTommaso, 2003). This active displacement is most prominent along heavily traveled urban corridors, especially in the New York City metropolitan area (Barney, data not presented).

Mugwort is native to Eurasia and has been naturalized in North America for over 400 years, after reportedly being introduced by Jesuit clergy as a medicinal herb (Fernald, 1900). It is widely known for its medicinal properties in Asian medicine, relieving stomach, gastrointestinal and gynecological problems, and was an early substitute for hops in beer brewing (Holm et al., 1997). Mugwort is now widely distributed across the world, being naturalized in regions from the Himalayan mountains to the warm temperate regions of southern North America, exhibiting wide variation in morphology (Barney and DiTommaso, 2003; Holm et al., 1997). Seed production and recruitment has been documented in its native range of Europe and Asia, but few, if any, seedlings have been observed in North America (Barney and DiTommaso, 2003; Holm et al., 1997). However, seed harvested from naturalized mugwort stands across New York State shows varying degrees of viability (Barney, data not presented). However, this species tolerates most chemical and cultural management strategies, due to its extensive network of underground rhizomes (Bing, 1983; Henderson and Weller, 1985). Due to its rapidly expanding geographic range and more recent invasion of natural and urban areas, mugwort is also gaining

attention in North America as a noxious invasive species.

Mugwort populations across the world vary widely in their general morphology, leaf chemistry, and resource allocation patterns (Barney, 2003; Barney and DiTommaso, 2003; Holm et al., 1997), suggesting that this may be a highly plastic species. We observed that plants from one Ithaca, New York-based population had densely pubescent (woolly) stems and light green leaves with relatively few deeply lobed margins. Conversely, plants from another population also collected in Ithaca exhibited nearly glabrous stems and dark green leaves with numerous deeply lobed margins (Barney, 2003). In 3 years of field and greenhouse studies, we did not observe production of viable seeds with any mugwort phenotype collected; however, one mail order seed house provided viable seed of a North American mugwort biotype.

A remarkable number of secondary compounds have been isolated from mugwort tissue, many of these being terpenes (Banthorpe and Brown, 1989; Milhau et al., 1997; Misra and Singh, 1986; Pino et al., 1999). It has been suggested that mugwort exhibits strong allelopathic properties, either by foliar-produced phytotoxins or those released by living rhizomes (Barney, 2003; Hale, 1982; Melkania et al., 1982). Other studies have indicated that decomposing mugwort foliage and rhizomes were potentially allelopathic to red clover (*Trifolium pratense* L.) seedling growth (Inderjit and Foy, 1999; Inderjit et al., 2001). It has been reported that mugwort rhizomes contain large quantities of 1,8-cineole, ascorbic acid, quercetin and vulgarin, a sesquiterpene lactone (Duke et al., 2002; <http://dreampharm.com/garlic/mugwort.asp>, 2004). In any case, the diversity of compounds produced may contribute to strong potential for allelopathy in this species.

Recent work in our laboratory showed considerable interspecific variation existed in mugwort populations evaluated within Tompkins County, NY with respect to leaf surface chemistry. Volatile compounds stored in leaf surface trichomes were examined for inhibitory effects through indirect (atmospheric) exposure to several test species. Allelopathic effects were observed with as few as three leaves, and were shown to be slightly

more toxic to dicots than monocots. The allelopathic effects of the fresh leaves could not be reproduced with individual volatile isolates (monoterpenes), suggesting that toxicity results from a combination of monoterpenes or an as yet unidentified compound (Barney et al., 2005b).

Not surprisingly, other *Artemisia* species also produce a broad range of terpenoid allelochemicals, including *A. absinthium* L. (Funke, 1943), *A. californica* Less. (Muller, 1966; Muller et al., 1964), *A. princeps* var. *orientalis* (Yun and Kil, 1992), and *A. tridentata* Nutt. ssp. *vaseyana* (McCahon et al., 1973; Weaver and Klarich, 1976, 1977). The antimalarial drug artemisinin, a sesquiterpenoid synthesized in annual wormwood (*A. annua* L.), was found to be extremely inhibitory to the growth of several broadleaf weeds and crops, but its specific mode of action is currently unknown (Duke et al., 1987; Lydon et al., 1997).

Despite the potential role of allelopathy in mugwort interference, the rapid proliferation of mugwort in introduced settings suggests that competition for resources may play an even more important role in mugwort interference. In a recent field study, we investigated resource allocation patterns and the spatial distribution of ramets originating from two local (Ithaca, NY) mugwort populations over a 3-year period (Barney, 2003). These two populations were transplanted into two contrasting habitats; a fallow field with all vegetation removed and a ryegrass turf lawn. An additional factor of mowing was applied to evaluate the ability of mugwort to withstand biomass removal at the colonization stage of invasion.

Interestingly, the turfgrass lawn habitat was more resistant to mugwort spread and proliferation, with 10-fold fewer ramets per plot occupying one tenth the area compared with the fallow field. This can potentially be attributed to differences in community structure, competition for available resources, disturbance, and invasive characteristics of mugwort itself. In addition, a monthly defoliation by mowing above ground foliage reduced mugwort ramet production by 10–90%, while reducing the area of infestation by 30–95%, in the fallow field or turfgrass habitats, respectively. This study demonstrated that variation exists between habitat invasibility, and that intra-specific variation in growth

patterns exists in mugwort. This variation may prove valuable for land managers establishing control strategies, as well as researchers investigating invasion success (Barney et al., 2005a).

Although mowing was investigated as a means of mugwort control, both our recent studies and those of others (Bing, 1983; Bradley and Hagood, 2002) suggest that mowing by itself does not result in complete eradication of mugwort, even if mowing is performed on a routine basis for more than two years. The application of systemic herbicides, therefore, may prove effective in eradication of mugwort especially if coupled with timely mowing (Rogerson and Bingham, 1971). Past studies with glyphosate, picloram and triclopyr have shown reasonable levels of control could be achieved, especially if appropriate surfactants were applied (Foy, 2001). A recent study in densely established mugwort stands in western New York has shown that only partial control may be expected from glyphosate applications alone; whereas good to excellent control was obtained with spot applications of triclopyr plus clopyralid when conditions were favorable for herbicide translocation. Further studies are now underway in an effort to obtain a 24 (C) special local needs label for eradication of this noxious weed in infested nursery settings in western New York State (Weston, data not presented). New technology for enhanced translocation of herbicide concentrates in woody plants for powerline management may have excellent applications to management of invasive perennials with extensive rhizome systems, including mugwort and Japanese knotweed. The use of lipid based carriers, ultra low volumes, and herbicide mixtures has resulted in enhanced translocation and improved control in difficult terrain (Lentz, 2004). Currently, we are unaware of any biocontrol efforts underway with respect to mugwort in North America.

Pale swallow-wort

Pale swallow-wort (*Vincetoxicum rossicum* (Keopow) Barbar.) (syn. *Cynanchum rossicum* (Kleopow) Borhidi) is a perennial herb or small vine in the Asclepiadaceae family that was first introduced into North America some 120 years

ago from the Ukraine region of Eastern Europe (DiTommaso et al., 2005a). The species is currently expanding its range in northeastern North America at an alarming rate, threatening primarily natural and semi-natural forested habitats although no-till cropping systems are also at risk. (Di Tommaso et al., 2005). Plants reproduce both sexually and vegetatively, although seed production appears to be the main method for range expansion (Christensen, 1998). Plants have a horizontal woody rootstalk and extensive somewhat fleshy, fibrous roots. Numerous perennating buds are produced at the root crown which can give rise to tillers. These tillers assist the plant in maintaining its perennial habit, but are apparently not the primary method for the spread of this species. If the main aerial stem is damaged, the buds readily sprout to produce multiple axillary tillers. The stems can attain a length of up to 250 cm and are more or less erect, with a twining or climbing growth habit. Leaves are opposite, ovate to elliptic, with smooth margins, and pubescence on the margins and major veins underneath. Multiple flowers are produced in the axils of the leaves in umbelliform cymes. The corolla is pink or reddish-brown. Fruits are slender (fusiform) follicles, smooth and often two are formed per flower, containing multiple seeds. The light to dark brown seeds are obovoid to oblong, flattened or concave on one side and convex on the other, with a membranous marginal wing up to 0.25 mm wide and an apical tuft of hairs (coma) 2–3 cm long (Cronquist, 1988). Seeds are generally polyembryonic, meaning that more than one (as high as six) genetically identical seedlings can be produced from an individual seed (Cappuccino et al., 2002; DiTommaso et al., 2005a). Seeds are wind-borne, facilitating long-distance dispersal and seedling establishment (Cappuccino et al., 2002) (Figure 3).

Within the lower Great Lakes basin, pale swallow-wort is most widely distributed in central NY, US and southern Ontario, Canada. Examination of herbarium specimens in the US by Sheeley (1992) documented this species' presence in New York, Massachusetts, Pennsylvania, New Jersey, Indiana, Connecticut, New Hampshire and Michigan (DiTommaso et al., 2005a; Sheeley and Raynal, 1996). It has also been collected in Missouri (Kartesz, 1999). It was

likely introduced to this region in the 1890's when the first collections in North America were noted in Monroe and Nassau counties in New York State (Sheeley and Raynal, 1996).

Pale swallow-wort is primarily of concern on natural and semi-natural lands (DiTommaso et al., 2005a). Dense populations tend to cover substantial areas, out-competing other vegetation and reducing faunal and floral biodiversity in affected areas of southern Ontario and more recently in New York State. In North America, it invades gardens, lawns, shrubberies, hedgerows, fencerows, shrubby thickets, a variety of deciduous and mixed forest types, and pastures (DiTommaso et al., 2005a). Small trees in restoration sites have been frequently smothered by its twining vines (Christensen, 1998; Pringle, 1973). Christmas tree growers in central New York State report increased pressure by pale swallow-wort in plantations, especially during the last decade. Recent reports in August 2004 from the Rochester Democrat and Chronicle newspaper document the spread of this weed around Ontario County, and the difficulties in eradication experienced by local land managers. Moreover, the New York State Forest Owners' Association has expressed concern that infestations in central NY may be negatively impacting forest regeneration (DiTommaso et al., 2005a). Pale swallow-wort has been recently observed in no-till corn and soybean fields in several central and western New York State counties and thus may pose a severe management problem in these cropping systems in the future. Some landowners in New York State have gone so far as to abandon their horse pastures after control efforts against swallow-wort over a 5–10 year span were largely unsuccessful (DiTommaso, personal observation).

Managers of natural areas in both Ontario and New York State are also very concerned about pale swallow-wort, which is beginning to invade alvar communities in eastern Ontario (Canada) and Jefferson County (NY). Near-shore islands of eastern Lake Ontario, especially Grenadier Island (NY) and Galloo Island (NY), support large, dense infestations. These sites are southwest and upwind of prevailing winds from the New York alvar systems. Habitats of Hart's tongue fern, *Phyllitis scolopendrium* var. *americanum* Fernald, a species listed on the



Figure 3. Photographs (clockwise from left to right) of pale swallow-wort (*Vincetoxicum rossicum* (Kleop.) Barbar.) flower, tillers re-sprouting from crown buds, and typical invasive growth in the understory of a New York woodlot.

federal endangered species list, in Onondaga County (NY) are also under threat (Lawlor, 2000).

Interestingly, old-field sites colonized by pale swallow-wort in Ontario have significantly lower arthropod diversity than old-field sites with

largely native vegetation (Ernst and Cappuccino, 2005). The decline in arthropod diversity will likely continue if greater displacement of native old-field plants also continues. This species may also have a negative impact on monarch butterfly (*Danaus plexippus* L.) populations because of

displaced oviposition and larval mortality, although a greater threat may be the decline in host plant availability through competitive displacement (DiTommaso and Losey, 2003; Mattila and Otis, 2003). Pale swallow-wort plants also serve as hosts for various insect pests of crops and as alternate hosts for *Cronartium* Fr. rusts attacking *Pinus* L. species (DiTommaso et al., 2005a).

Roots of members of the closely related *Cynanchum* contain the haemolytic glycoside vincetoxin and are considered poisonous to humans and mammals (Haznagy and Toth, 1971; Wiegrebe et al., 1970). The same is likely true for other species in the subgenus *Vincetoxicum* (Alex, 1992). In the past, the closely related congener *Vincetoxicum nigrum* (black swallow-wort) has been widely used in European traditional medicine as a laxative, diaphoretic, diuretic, emetic and anti-tumor agent (Duke et al., 2002; Nowak and Kisiel, 2000; Uphof, 1968). Phenanthroindolizidine alkaloids are characteristic constituents of some genera of Asclepiadaceae, including the subgenus *Vincetoxicum* (Capo and Saa, 1989; Liede, 1996; Staerk et al., 2000), and are strongly cytotoxic. However, biochemical studies focusing specifically on these species have not been performed. Although no published study has investigated the allelopathic properties of pale swallow-wort, this mode of interference could help to explain the formidable success of this species in open areas where no supporting woody vegetation is present. This aspect of competition should be examined further, given the complex secondary chemistry *Vincetoxicum* species are known to produce.

The presence of pale swallow-wort is typically associated with calcareous soils. In Ontario and western Canada, it occurs primarily on shallow soils over limestone bedrock, deep loams of upland woods and rocky or clay loam based ravines. In central NY State, its habitats range from dry and sunny to moist and shaded. Populations are found on shallow soils over limestone bedrock to deep moderate or well-drained silt-loam soils in wooded ravines, calcareous cliff and talus slopes, alluvial woods, pastures and grasslands (Lawlor, 2000). In North America, pale swallow-wort is often also associated with disturbed and waste areas and readily invades

sunny open areas, shrubby habitats and hedges. Once established, it tends to move readily into nearby, less disturbed habitats. Plant densities are usually considerably lower in shaded habitats under forest canopies than in sunny locations (DiTommaso et al., 2005a; Lawlor, 2000; Reschke, 1990; Sheeley, 1992). In forested areas, plants may persist in a non-reproductive state for many years until favorable light conditions for successful reproduction occur (Sheeley, 1992).

Pale swallow-wort plants from old-field and forested sites in central NY State establish symbiotic associations with resident arbuscular mycorrhizal fungal (AMF) populations (Greips-son and DiTommaso, 2002; Smith et al., 2005-03-30). Soils from areas colonized by pale swallow-wort had greater mycorrhizal inoculum potentials (MIP) than soils from adjacent non-colonized areas. It is speculated that the effect of this species on the composition and diversity of the soil microbial community may contribute to the displacement of the resident vegetation. Research is now focused on determining the role that AMF play in mediating the invasion of different habitats by this aggressive weed.

Seed production in pale swallow-wort is affected by the amount of light received. Shoots in a shaded site in New York were found to produce less viable seed than those shoots in an open, sunny site (Sheeley, 1992). In North America, some swallow-wort seeds lack dormancy and will germinate without stratification; however, greater germination percentages are obtained when seeds are subjected to stratification (DiTommaso et al., 2005a). Seeds of pale swallow-wort collected from several central NY sites maturing later in the season (e.g., November) were more likely to be dormant and exhibit a greater germination response after stratification than seeds harvested in late August (DiTommaso et al., 2005b).

Control of this highly aggressive invasive vine using currently available tactics has been difficult and no single strategy has emerged as most promising. Lawlor and Raynal (2002) compared the effectiveness of two systemic herbicides, glyphosate and triclopyr, to control populations of pale swallow-wort in central NY as either foliar sprays or when applied to cut stems. Foliar-spray applications were more effective

than cut-stem applications in reducing cover and biomass. Plots treated with glyphosate ($10.4 \text{ kg ai ha}^{-1}$) at the early flowering stage and triclopyr ($2.6 \text{ kg ai ha}^{-1}$) at early fruit formation showed a 73% reduction in cover compared with untreated control plots. There were no significant differences in reduction of measured plant parameters among the foliar-spray treatments and effective long-term control using either of these herbicides at recommended field rates required repeated applications. Cut-stem applications of glyphosate (4.1 and $8.3 \text{ kg ai ha}^{-1}$) were found to be significantly more effective than similar treatments with triclopyr (1.9 , 3.9 and $7.8 \text{ kg ai ha}^{-1}$) at all concentrations tested (Lawlor and Raynal, 2002).

In a study on Grenadier Island, NY, glyphosate ($1.79 \text{ kg ai ha}^{-1}$) was found to be more effective than triclopyr ($2.24 \text{ kg ai ha}^{-1}$) in controlling swallow-wort. Both were significantly more effective than a mix of triclopyr and 2,4-D ($1.12: 2.24 \text{ kg ai ha}^{-1}$) and a mix of dicamba and 2,4-D ($1.12: 1.07 \text{ kg ai ha}^{-1}$). Dicamba ($2.24 \text{ kg ai ha}^{-1}$) and two levels of 2,4-D (2.13 or $3.19 \text{ kg ai ha}^{-1}$) alone were not significantly different from the untreated control. Treatments were applied in late June 2003. Mean swallow-wort cover in late May 2004 was 96% in the control and 23, 45, 63, 73, 84, 83 and 89% respectively, for the above herbicide treatments (F. Lawlor, unpublished data).

Cultural controls have had limited impact upon further establishment or control of pale swallow-wort infestations in New York or Ontario, Canada. Repeated mowing provided some reduction in plant height, but no effect on overall cover provided by this species (Christensen, 1998). Cultivation will likely not kill established plants as root crown pieces remaining after cultivation can re-root, even in dry soil conditions. Grazing and trampling can stimulate sprouting in pale swallow-wort, from stem leaf axis or from root crown buds. When comparing efficacy of glyphosate treatment with digging and hand pulling methods for control, digging was most effective in controlling swallow-wort growth (S. Bonanno, personal observation, NY Nature Conservancy). Manual removal of seed pods from established plants may also assist in prevention of further seed dissemination, but

multiple harvests may be necessary (F. Lawlor, personal observation).

Although there are several insects that feed on pale swallow-wort foliage or seeds, most insects specializing on pale swallow-wort in Europe appear to feed infrequently or ingest only small amounts of plant parts, perhaps because of the toxins present in the plant foliage (Leimu, 2004). Several of these insect feeders are also polyphagous. Therefore, the possibility of effective biological control by a particular insect species is not clear at this time (DiTommaso et al., 2005a). The possibility also exists for discovery of an effective plant pathogen which may limit swallow-wort establishment or spread, but research findings are preliminary at this stage. *Vincetoxicum* species, especially pale swallow-wort, are important alternate hosts for the widespread European rust fungus, *Cronartium flaccidum* (Alb. & Schwein.) G. Winter. This fungus causes cronartium rust and resin-top on various species in the genus *Pinus* (Moriondo, 1980). Currently, a thorough evaluation of the impact of various rust pathogens on *Vincetoxicum* species has not been performed (DiTommaso et al., 2005a).

Summary

Many introduced species currently classified as invasive, including *Polygonum cuspidatum*, *Artemisia vulgaris* and *Vincetoxicum rossicum*, have exhibited a long lag time after initial arrival before becoming widespread in North America (Kowarik, 1995). It is not currently understood what factors have resulted in their recent and rapid ability to become highly invasive. In the case of Japanese knotweed, hybridization between species or populations that represent disparate sources of germplasm may potentially have served as a stimulus for production of viable seed and the evolution of greater invasive potential (Ellestrand and Schierenbeck, 2000). Further research needs to be conducted to address this possibility as inherent variation for production of viable seeds clearly exists among North American populations of Japanese knotweed, as well as morphological variation among populations (L.A. Weston, personal observation). In the case of mugwort, which also

exhibits great morphological diversity and differences in invasibility among local mugwort populations, inherent phenotypic plasticity may have contributed in allowing this species to successfully adapt and proliferate across North America. Pale swallow-wort, in comparison, does not clearly exhibit morphological variance among populations observed in New York State and Ontario, despite a broad area of severe infestation. Currently, genetic diversity among North American populations of mugwort or pale swallow-wort has not been closely evaluated. These studies, however, are currently being performed with North American populations of Japanese knotweed, and we plan to evaluate genetic distance among populations of both mugwort and pale swallow-wort in the future, and implications of these findings with respect to invasibility will be considered.

Mugwort and Japanese knotweed both produce considerable quantities of below ground biomass due to extensive rhizome generation, which makes chemical or cultural management in these species particularly difficult. Pale swallow-wort reproduces vegetatively by root crown buds which give rise to multiple tillers. However, it generates large quantities of viable polyembryonic seeds which readily disperse into surrounding areas, resulting in large monospecific stands which develop rapidly. Further studies on the ability of these species to invade new sites, either by vegetative or sexual means, are warranted. Determining the potential rate of spread of each species in typical environments encountered across their northeastern US introduced range would better allow us to predict their invasion potential over time.

Interestingly, Japanese knotweed, mugwort and pale swallow-wort also appear to produce potentially allelopathic secondary products either in their foliage or from their living root systems. The impact of allelochemical release into the rhizosphere by invasive species has received increasing attention in the recent plant ecological literature (Callaway and Aschehoug, 2000; Callaway et al., 2003). Although numerous authors have noted that establishment of invasive species can result in rapid reductions in biodiversity among locally associated species and potential long-term changes in the soil rhizosphere, more studies need to be conducted to assess the

impact of invasive species on local soil properties, microbial diversity and long-term impacts on co-existing populations within the same ecosystem.

Successful management strategies must also be developed in order to prevent future spread of these and other invasive species across New York State and North America. Although chemical and cultural management strategies for these species have been attempted with limited success, new technologies to enhance herbicide translocation throughout extensive underground rhizome systems as well as above ground biomass, coupled to the development of effective biocontrol strategies, may have greatest potential for reducing populations and the deleterious impact of these three noxious perennial weeds in their introduced North American range.

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