

Greater morphological plasticity of exotic honeysuckle species may make them better invaders than native species¹

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SCHWEITZER, J.A. AND K.C. LARSON (Dept. of Biology, University of Central Arkansas, Conway, AR 72032). Greater morphological plasticity of exotic honeysuckle species may make them better invaders than native species. *J. Torrey Bot. Soc.* 126:15–23. 1999.—In a greenhouse experiment, we measured the morphological plasticity of two congeneric vines, *Lonicera japonica* Thunb., an important invasive species in the U.S. and *L. sempervirens* L., a non-invasive native. We hypothesized that greater morphological plasticity may contribute to the ability of *L. japonica* to occupy more habitat types, and contribute to its invasiveness. We compared the morphology of plants provided with climbing supports with plants that had no climbing supports, and thus quantified their morphological plasticity in response to an important variable in their habitats. The two species responded differently to the treatments, with *L. japonica* showing greater responses in more characters. For example, *Lonicera japonica* responded to climbing supports with a 15.3% decrease in internode length, a doubling of internode number and a 43% increase in shoot biomass. In contrast, climbing supports did not influence internode length or shoot biomass for *L. sempervirens*, and only resulted in a 25% increase in internode number. This plasticity may allow *L. japonica* to actively place plant modules in favorable microhabitats and ultimately affect plant fitness.

Key words: Caprifoliaceae, exotic species, honeysuckle, invasiveness, *Lonicera*, morphological plasticity, plant foraging.

The introduction of exotic plant species into native communities has increased dramatically over the past 200 years. Although many species fail to establish following introduction to a new area, or establish only small, local populations, other species invade established communities and strongly affect native populations (Simberloff 1981; Mack 1985; Richardson and Bond 1991; Rice and Mack 1991; Lodge 1993; Ruesink et al. 1995). The question of what makes a species invasive is complex because character lists of common traits rarely fit all invaders. However the success of any invader depends on the ecological characteristics of the introduced species and the attributes of the invaded habitat (Lodge 1993).

Successful invasion by exotic plants is frequently associated with habitat disturbance (Hobbs 1989; Rejmánek 1989). Disturbed sites are unpredictable, rapidly changing, and heterogeneous, and one plant characteristic likely to be

advantageous in such a habitat is strong phenotypic or morphological plasticity (Zimmerman 1976; Hume and Cavers 1982; Barrett and Richardson 1986; Ashton and Mitchell 1989; Teramura et al. 1991; Bazzaz 1996). Plants with great morphological plasticity have the ability to change the size or shape of vegetative structures under different environmental conditions (Schlichting 1986; De Kroon and Hutchings 1995; Williams et al. 1995).

The goal of our research was to compare the morphological plasticity of an invasive introduced vine, *Lonicera japonica* Thunb. to a native congener, *Lonicera sempervirens* L. These similar species are both twining vines that grow sympatrically in the southeastern United States, where they occupy mid-successional habitats that are heterogeneous with regard to climbing supports and light (Radford, Ahles and Bell 1983). They are strikingly different, however, in abundance within habitats. *Lonicera japonica* is an aggressive invader that often dominates the native vegetation and is considered one of the most important weed species on state and federal lands in the USA: *L. sempervirens* rarely reaches the same density (Hamel and Shade 1985; Robertson, Robertson and Tague 1994; pers. observ.). *Lonicera japonica* is found growing vigorously in a wide range of conditions, including thickets, old fields, riparian zones, and even undisturbed natural communities: *L. sem-*

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pervirens is not found colonizing as many different communities or successional stages (Oosting 1942; Radford, Ahles and Bell 1983; Rejmánek 1989; Robertson, Robertson and Tague 1994; pers. obser.).

Other researchers, while not testing for phenotypic plasticity directly, demonstrated greater morphological plasticity in *L. japonica* than *L. sempervirens* in response to herbivory (Schierenbeck et al. 1994) and CO₂ enhancement (Sasek and Strain 1991). Schierenbeck et al. (1994) have demonstrated that *L. japonica* compensates for herbivory damage by increasing allocation to leaf and stem biomass while *L. sempervirens* does not compensate. Sasek and Strain (1991) found that *L. japonica* responded to CO₂ enrichment with a greater increase in overall biomass due to increased allocation to leaf and branch biomass than *L. sempervirens*. However, no studies that we are aware of have specifically tested for differences in morphological plasticity between these congeners.

We hypothesized that the capacity of *L. japonica* to occupy more types of plant communities in more stages of succession (Oosting 1942) was possible because of its greater morphological plasticity. In heterogeneous habitats, increased plasticity could lead to a competitive advantage over a less plastic species by increasing survival under varying physical habitats. One alternative hypothesis to explain the capacity of *L. japonica* to colonize a wider range of habitat types is that *L. japonica* is more genetically variable than *L. sempervirens*. This alternative hypothesis was not supported by Schierenbeck, Hamrick and Mack (1995) who found that field populations of *L. sempervirens* had higher allozyme diversity than *L. japonica*.

To test our hypothesis we conducted a greenhouse experiment designed to measure morphological plasticity by comparing the morphology of each species growing under two different physical conditions. We chose to measure plant responses to the presence or absence of climbing supports because both species, as twining vines, encounter habitats that are heterogenous in terms of available supports and regularly must trail when supports are not available.

Methods. RESEARCH ORGANISMS. *Lonicera japonica* (Japanese honeysuckle) is native and common in Japan, China, Korea and Manchuria, where it grows as a trailing or climbing vine in thickets on hills and mountainsides (Ohwi 1965). Following its introduction to the United

States in the early 1800's, this species easily escaped cultivation and became an important naturalized pest in nearly every county of the southeastern USA (Leatherman 1955). Invasion was facilitated by frequent planting for erosion control and as a winter browse for wildlife (Stransky 1984).

Lonicera sempervirens (coral honeysuckle) is native to the southeastern United States, but is much less common and more patchily distributed than the introduced Japanese honeysuckle. It is a trailing or climbing vine that commonly grows in woodlands, thickets and fencerows (Gleason and Cronquist 1991).

COLLECTIONS. To compare growth patterns of climbing and trailing individuals of both Japanese and coral honeysuckle, cuttings were collected from plants in the Ouachita National Forest, Perry County, Arkansas. In June 1995, we took five 10 cm cuttings of each species, from slightly woody, lateral shoots at the first 25 roadside sites where both species could be found together. To prevent collecting multiple cuttings from the same large individual and to increase genetic diversity, all collection sites were separated by at least 500 m. The bottom pair of leaves were removed, and cuttings were treated with the rooting hormone Hormex® (N. Hollywood, CA; Dirr and Hueser 1987). Cuttings were then planted in a peat-based potting soil, given a fungicide drench with Benomyl® (Bonham, TX), and maintained for two weeks under fine mist. Successfully rooted cuttings were transplanted into 20 cm diameter pots with the same substrate.

To maintain uniform size and form of the rooted cuttings, plants were included in the study only if they had reached a stage of 12 nodes within a given time period. In addition, some plants had secondary shoots that were removed. Typically a single meristem would develop into a single shoot on the rooted cuttings. However, on some cuttings (<25%), several meristems would develop into shoots. Because young developing shoots can act as competing sinks for limited resources from storage tissues in the stem (Sachs et al. 1993; Larson and Whitham 1997), we removed any smaller, basal shoots that were produced. Consequently, all cuttings began the experiment with a single shoot of 12 nodes.

GREENHOUSE EXPERIMENT. We set up a two-factor experiment examining the effect of species (*L. japonica* and *L. sempervirens*) and

climbing condition (climbing or trailing) on plant morphology. For each species, rooted cuttings that had reached the size of 12 nodes from the same collection site were haphazardly assigned to either the climbing or trailing treatment. The final sample size was affected by the rooting success of the cuttings; only 54.7% of *L. sempervirens* cuttings rooted successfully, thus only 14 of the original 25 genets were included in this study (14 climbing and 14 trailing plants). Rooting success of *L. japonica* was 93.3% and 20 of the original 25 genets are included in this study (20 climbing and 20 trailing plants).

After assignment to the different treatments, the climbing plants were allowed to grow onto a 12 mm diameter nylon rope suspended 1.5 m from the greenhouse roof and attached to the table adjacent to each pot. Trailing plants were positioned adjacent to the climbing plants but were not allowed to climb any structure. All plants were grown under uniform conditions of regular fertilization and watering as well as the same temperature and humidity in the greenhouse environment.

Several characteristics were measured on each cutting after the plants were grown for 135 days. We counted internodes, measured their diameter, recorded the position of the longest internodes on either the main shoot (score=1) or a lateral shoot (score=2), and measured the length of the three longest and the length of five randomly selected internodes. We measured the length of the longest shoot and recorded its position as either the main shoot (score=1) or a lateral shoot (score=2) as well as counted the total number of secondary and tertiary lateral shoots. Finally, we counted the number of times the climbing shoots coiled around the host rope.

At the midpoint of the growing period, mean photosynthetic rates were measured using a Licor portable photosynthesis system (Li-6200, Lincoln, NE). Photosynthetic rates from the longest terminal shoot of each plant within both species and treatments were measured. Two measurements each from intact, attached leaves from five randomly selected plants of each species and condition were measured individually, for a total of 10 readings for each species (five genotypes each) under each treatment condition. Specific leaves were chosen using the Plastochron Index which allows selection of similar-aged leaves based on a morphological rather than a chronological scale (Lamoreaux et al. 1978). Readings were taken at peak photosyn-

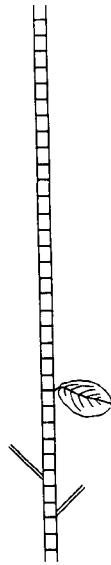
thetic conditions for each species, as determined by a light response curve.

At the end of the growing period, the leaf area of the same leaf used in the photosynthesis reading was taken. Leaf areas were measured using a CID leaf area meter (CID-202, Vancouver, WA). The plants were oven-dried for 24 hours at 65°C and the biomass of above-ground and below-ground structures was measured. Above-ground shoots were divided into main shoots and lateral shoots, and separate weights were taken for leaves and stems of each shoot type.

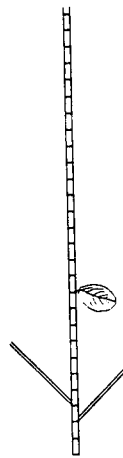
STATISTICAL ANALYSES. To examine the two species under the conditions of climbing and trailing the data were analyzed with a multivariate analysis of variance. Variables accounting for the significant MANOVA were further examined using univariate two-way analysis of variance, followed by one-way analysis of variance for characters with significant species * condition interactions. The results are discussed below.

Results. A multivariate analysis of variance (MANOVA), analyzing all variables simultaneously, indicated that *L. japonica* showed greater variation in more characters than *L. sempervirens*. This was indicated by the significant interaction term ($F=17.53$, $P<0.001$) which shows that the responses to the treatments were not the same for both species and suggests that some traits were showing plastic responses (Schlichting 1986). The MANOVA also indicated a significant difference between species ($F=21.96$, $P<0.001$) and a significant impact of climbing condition on the overall morphology of these vines ($F=53.53$, $P<0.001$). Figure 1 diagrammatically represents a summary of the significant architectural differences between species and for each climbing condition.

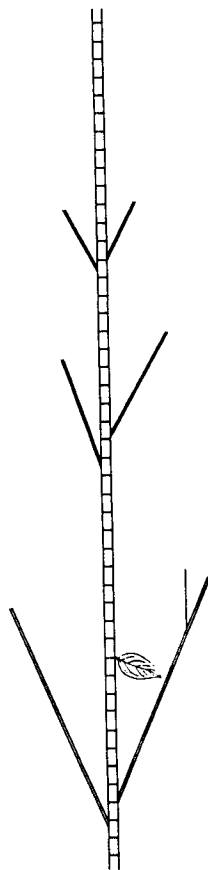
SHOOT BIOMASS AND ROOT/SHOOT RATIO. The significant interaction term for shoot biomass (Table 1) indicates that the two species did not respond in the same way to climbing supports. Contrasts within each condition (species and climbing status), necessary because of the significant interaction term, are shown in Table 1. *Lonicera japonica* had a higher shoot biomass regardless of climbing condition (Table 1). In addition, *L. japonica* increased its size 43% when climbing, while *L. sempervirens* did not show a statistically significant increase in size when climbing. Increased biomass when climbing corresponded with an increased number of



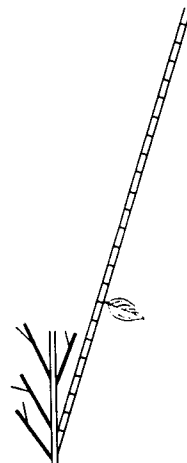
Climbing
L. sempervirens



Trailing
L. sempervirens



Climbing
L. japonica



Trailing
L. japonica

internodes on the longest shoot; *L. japonica* exhibited an increase of 49% when climbing, while the internode number of *L. sempervirens* increased by only 25%.

Lonicera japonica had higher photosynthetic rates than *L. sempervirens* regardless of treatment (Table 1). The photosynthetic rates for *L. japonica* were comparable to rates found by other authors under similar light conditions (Carter and Teramura 1988). However, our PS rates for both species were slightly higher than those recorded by Schierenbeck and Marshall (1993) under similar light levels (PPFD 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$). This difference may be attributed to differences in field vs. greenhouse grown plants, with our values representing maximum PS values under ideal conditions of adequate water, nutrients, etc. Associated with a greater shoot biomass, *L. japonica* had a lower root:shoot ratio than *L. sempervirens* (Table 1).

SHOOT ALLOCATION. Both species significantly increased allocation to the main shoot when climbing, as might be expected for a climbing vine. However, *L. sempervirens* allocated more biomass to the main shoot than *L. japonica* regardless of climbing condition. *L. japonica* demonstrated a greater allocation to lateral biomass than *L. sempervirens* (Table 1, Fig. 1). For *L. japonica*, 67% of above-ground biomass was in lateral branches, whereas only 36% of above-ground biomass was allocated to laterals for *L. sempervirens*.

Although both species had a similar increase in allocation to the main stem when climbing, their laterals did not respond in a similar way, as indicated by the significant interaction term for the lateral stem dry weight. For *L. sempervirens*, climbing plants shift biomass allocation into main stems, and because overall shoot biomass did not significantly increase when climbing, a reduction in lateral biomass occurred (Table 1). In contrast, climbing *L. japonica* increased overall shoot biomass when climbing, allocating all of the increased biomass to the main stem with no significant change in allocation to biomass of the laterals.

Although the biomass of laterals on trailing *L. japonica* did not differ from climbing plants, trailing plants shifted allocation from the elon-

gation of secondary laterals to the production of tertiary laterals. The number of tertiary shoots increased 167% on trailing *L. japonica*, but the number of secondary shoots was not different between climbing and trailing plants (Table 1; Fig. 1). Although the average length of secondary shoots decreased when trailing in *L. japonica*, a single lateral shoot became the longest shoot on the plant in 60% of the trailing plants. In contrast, the mean length of secondary laterals increased in climbing *L. japonica*, but a single lateral shoot became the longest shoot in only 20% of the plants (Table 1).

INTERNODES. The responses of the internodes of the two species to the presence of climbing supports differed greatly, as indicated by the significant species * condition interaction. The mean length of randomly selected internodes was greater for *L. japonica* than *L. sempervirens*, but a major difference between the species becomes apparent when focusing only on the longest internodes of the shoot. Contrasts within each climbing condition and species indicate that the length of the longest internodes of *L. sempervirens* do not change when climbing, and are not significantly different from those of climbing *L. japonica*. In contrast, *L. japonica* showed a significant increase in the length of the longest internodes when trailing. Thus, despite increased growth when climbing, the average length of the three longest internodes decreased 15% for *L. japonica*, but remained stable for *L. sempervirens* under both conditions (Fig. 1). Shorter internodes for climbing *L. japonica* perhaps conferred greater structural strength and support for the shoot when climbing. The three longest internodes of climbing *L. sempervirens* exhibited a 20% increase in diameter but the mean diameter of *L. japonica* remained nearly constant under both conditions. There was also a significant difference between the two species with regard to the number of times the longest shoot wrapped around the rope. *Lonicera japonica* coiled much more frequently (70% more) and tightly than *L. sempervirens* which coiled infrequently around a rope "host" (Table 1).

Discussion. We found that while both *Lonicera* species demonstrated some morphological

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Fig. 1. Phenotypic diagram of both *Lonicera* species under the conditions of climbing and trailing. Values are to scale from means in Table 1. Variables included are internode number, internode diameter, internode length, number of secondary and tertiary branches, position of longest shoot, branch length and leaf area.

Table 1. Results of the two-way ANOVA on the dependent variables. Means and SE for each species and condition are included. For variables with a significant species * condition interaction (in bold), brackets show the results of one-way ANOVAs.

Source of Variation	<i>L. sempervirens</i>		<i>L. japonica</i>		P species	P condition	P species*condition
	Climbing	Trailing	Climbing	Trailing			
Internode length (cm-3 longest)	9.46 ± 0.45	9.40 ± 0.29	8.89 ± 0.21	10.49 ± 0.36	0.433	0.024 *	0.015 *
Internode number	34.93 ± 1.45	28.00 ± 2.03	48.0 ± 1.40	24.50 ± 1.53	0.847	0.000 ***	0.054
Internode diameter (mm)	2.67 ± 0.14	2.16 ± 0.06	2.27 ± 0.14	2.21 ± 0.07	0.136	0.014 *	0.053
Mean internode length (cm)	6.09 ± 0.28	6.20 ± 0.31	6.90 ± 0.19	7.40 ± 0.23	0.000 ***	0.263	0.477
Position of longest internodes	1.14 ± 0.10	1.64 ± 0.13	1.30 ± 0.11	1.80 ± 0.09	0.151	0.000 ***	1.000
Main Shoot length (cm)	47.63 ± 11.10	65.20 ± 8.03	95.69 ± 11.03	75.89 ± 6.66	0.003 ***	0.908	0.056
Number of tertiary shoots	0.00 ± 0.00	0.57 ± 0.34	3.0 ± 1.34	8.00 ± 1.15	0.000 ***	0.011 *	0.042 *
Number of secondary shoots	3.50 ± 0.84	3.57 ± 0.47	12.30 ± 1.19	10.65 ± 1.16	0.000 ***	0.465	0.426
Position of longest shoot	1.00 ± 0.00	1.14 ± 0.10	1.20 ± 0.09	1.60 ± 0.11	0.001 ***	0.006 ***	0.185
Shoot biomass (g)	19.34 ± 1.20	16.29 ± 1.48	29.44 ± 1.06	20.59 ± 1.14	0.000 ***	0.000 ***	0.021 *
Lateral shoot dry wt. (g)	4.90 ± 0.95	7.75 ± 0.87	17.47 ± 1.59	16.03 ± 1.02	0.000 ***	0.577	0.093
Main shoot dry wt. (g)	14.44 ± 0.97	8.54 ± 1.09	11.97 ± 1.17	4.56 ± 0.44	0.001 ***	0.000 ***	0.433
Lateral stem dry wt. (g)	2.01 ± 0.43	3.30 ± 0.37	8.22 ± 0.78	6.64 ± 0.40	0.000 ***	0.799	0.015 *
Main stem dry wt. (g)	7.40 ± 0.66	4.36 ± 0.61	6.92 ± 0.72	2.21 ± 0.23	0.028 *	0.000 ***	0.161
Lateral leaf dry wt. (g)	2.85 ± 0.56	4.45 ± 0.59	9.25 ± 0.84	9.41 ± 0.72	0.000 ***	0.243	0.337
Main leaf dry wt. (g)	7.04 ± 0.42	4.19 ± 0.52	5.06 ± 0.48	2.34 ± 0.22	0.000 ***	0.000 ***	0.870
Root dry wt. (g)	18.05 ± 1.66	16.47 ± 2.03	21.98 ± 2.27	16.67 ± 1.82	0.319	0.099	0.368
Internode dry wt. (g-longest shoot)	0.21 ± 0.02	0.16 ± 0.01	0.19 ± 0.01	0.11 ± 0.00	0.007 ***	0.000 ***	0.274
Root:shoot ratio	0.47 ± 0.03	0.49 ± 0.04	0.36 ± 0.03	0.39 ± 0.03	0.003 ***	0.364	0.914
Number of coils	4.36 ± 0.36	0.00 ± 0.00	14.35 ± 0.49	0.00 ± 0.00	0.000 ***	0.000 ***	0.000 ****
Leaf area (cm ²)	16.58 ± 1.57	13.09 ± 0.84	14.55 ± 0.82	12.61 ± 0.64	0.202	0.007 **	0.425
Photosynthetic rate (μmol m ⁻² s ⁻¹)	8.49 ± 0.91	8.89 ± 0.78	10.10 ± 0.83	10.36 ± 0.66	0.011 *	0.578	0.906

* Overall significance level <.05, ** significance level <.01, *** significance level <.001.

¹ All one-way ANOVA interactions were significant due to zero values.

plasticity in response to the presence or absence of climbing support, the introduced honeysuckle *L. japonica* showed much greater morphological plasticity than the native *L. sempervirens*. Our hypothesis that *L. japonica* would be more morphologically plastic than *L. sempervirens* was based on the observation that *L. japonica* not only occupies, but regularly dominates, a wide range of habitats. It can trail across mature forest floors, sprawl over herbaceous vegetation in prairie sites, and twine up young trees and shrubs (Robertson et al. 1994; pers. obser.). In contrast, *L. sempervirens* is usually found climbing in woodlands, thickets and fencerows, where

it is not nearly as ubiquitous as *L. japonica* (Oosting 1942; Radford, Ahles and Bell 1983; Sasek and Strain 1991). Greater plasticity may give Japanese honeysuckle several competitive advantages compared to its native congener, *L. sempervirens*.

First, the disturbed forest edges and gaps where these species are typically found are heterogeneous in both light availability and the presence of climbing supports; thus, species that are morphologically plastic are likely to be favored (Putz and Holbrook 1991; Teramura et al. 1991; Bazzaz 1996). In our study, the plastic responses of *L. japonica* appear to be associated

with significant increases in growth. In response to climbing support, *L. japonica* not only changed its allocation patterns but increased its overall biomass by 43% compared to trailing plants. In contrast, *L. sempervirens* showed fewer morphological changes in response to the climbing condition, and did not significantly increase in biomass when climbing. Overall, *L. sempervirens* under either condition, and trailing *L. japonica*, were all similar in total biomass, while only climbing *L. japonica* was considerably larger. In a habitat heterogeneous with respect to climbing supports, where some shoots are climbing and others are trailing on the ground, as is often observed in the field, *L. japonica* can be expected to perform better than *L. sempervirens*.

Greater morphological plasticity may be augmented by the fact that *L. japonica* grows more vigorously than *L. sempervirens*. In addition to greater plasticity in allocation patterns, the photosynthetic rate of individual, recently matured leaves was 14–16% higher for *L. japonica* than *L. sempervirens*. However, unlike the plastic morphological responses we documented, the photosynthetic responses were not plastic, but likely account for the greater vigor of *L. japonica* when compared to *L. sempervirens* under the same conditions. The increased growth of *L. japonica* when climbing was not associated with increases in individual leaf photosynthetic rates, and appears more likely due to the ability of *L. japonica* to concentrate more photosynthetic organs in favorable areas through the production of shorter internodes when climbing, i.e. photosynthesis can be higher when leaves/propagules are in locations that receive more light.

A second competitive advantage greater morphological plasticity may confer is to allow *L. japonica* to more effectively forage for resources, than *L. sempervirens*. This trait may be important in heterogeneous habitats because for vines a major limiting resource can be the availability of climbing supports (Putz 1984). Both vines and clonal plants are known to show morphological plasticity that may allow selective placement of leaves or ramets in favorable environments (Hutchings 1988; Ray 1992; Putz and Holbrook 1991; Cain 1994; Evans and Cain 1995). Increased branching and decreased internode lengths would enable a plant to concentrate growth in a favorable habitat, while increased internode distance and decreased branching in a non-favorable environment might allow for rapid movement needed when searching for favor-

able habitats (Sutherland and Stillman 1988; Macdonald and Lieffers 1993; Cain 1994; Evans and Cain 1995; Humphrey and Pyke 1997). We found that despite greater growth when climbing, *L. japonica* produced shorter internodes when climbing than when forced to trail. This resulted in more closely spaced leaves on climbing plants, thus allowing climbing plants to concentrate photosynthetic organs in favorable sites (i.e. on supports). In contrast, trailing *L. japonica* produced longer internodes that could allow for more rapid colonization of undiscovered climbing supports. *Lonicera sempervirens* exhibited no significant response in internode lengths between conditions.

Plasticity in foraging vines can allow some responses to be similar to clonal plants, but vines may differ in the responses of lateral branches. Examples of plant foraging from clonally spreading plants have demonstrated greater lateral branching in favorable habitats (de Kroon and Hutchings 1995). However, this response may not apply to vines because increased allocation to lateral branching in favorable environments (i.e., climbing support present) could compete with the main or terminal shoot for resources and thus limit climbing. We found that climbing *L. japonica* produced shorter internodes but did not increase branching, and in fact produced fewer lateral branches than trailing plants. The lateral branches produced by climbing plants were, however, longer than the more numerous but shorter lateral shoots produced on trailing plants. Den Dubbelden and Oosterbeek (1995) also found increased branching on twining vines that were unsupported (trailing), and suggested that increased lateral branching by unsupported plants may increase the potential of vines to find climbing supports. Similarly, Ray (1992) documented foraging behavior in monocot vines in the form of changes in internode shape, but found that the species studied rarely branch laterally, and therefore lateral branching was not an important factor in their foraging behavior.

Vines in general appear to be especially plastic species. For example, Gartner (1991) found that the morphology of poison oak was so plastic that different plants of the same genotype could grow as a shrub or a vine. Interestingly in poison oak, climbing supports resulted in increased internode lengths in the vine growth form, while unsupported plants had shorter internodes and a shrubby form. Other twining vines, however, show a pattern of plasticity in internode length

similar to what we documented for *L. japonica*. Den Dubbelden and Oosterbeek (1995) documented decreased internode lengths and decreased branching in response to climbing supports in several species of herbaceous vines. Additionally, studies with English Ivy (*Hedera helix*) also show plastic morphological responses under variable growth conditions (vertical vs. horizontal) in which vertically grown shoots preferentially partitioned new matter to increase total leaf area (Frey and Frick 1987). The high morphological plasticity we documented for *L. japonica* appears typical for vines, and it is the reduced capacity for plasticity in *L. sempervirens* that appears atypical for vines. However, it is not clear whether the strong plasticity of *L. japonica* carries some cost with it, or if the more conservative growth form of *L. sempervirens* may have some as yet unknown advantages.

Studies of these congeners (Schierenbeck et al. 1994; Sasek and Strain 1991), plus our own, consistently indicate that *L. japonica* has a greater capacity than *L. sempervirens* to respond to a variety of environmental conditions through a plastic morphology. Strong morphological plasticity of the introduced *L. japonica* appears to make one important contribution to its strongly invasive nature, allowing individual plants or shoots to rapidly produce more leaves under favorable conditions, such as when climbing. Overall, greater morphological plasticity in response to environmental parameters, as well as to herbivores (Schierenbeck et al. 1994), and a greater annual carbon gain (Schierenbeck and Marshall 1993) together may act to make *L. japonica* successful as an invasive species.

Literature Cited

- ASHTON, P. J. AND D. S. MITCHELL. 1989. Aquatic plants: Patterns and modes of invasion, attributes of invading species and assessment of control programmes, pp. 111–154. In J. A. Drake and H. A. Mooney [eds.], *Biological Invasions: A global perspective*, John Wiley and Sons, Chichester, England.
- BARRETT, S. C. H. AND B. J. RICHARDSON. 1986. Genetic attributes of invading species pp. 21–33. In R. H. Groves and J. J. Burdon [eds.], *Ecology of Biological Invasions*, Cambridge University Press, Cambridge, MA.
- BAZZAZ, F. A. 1996. Plants in Changing Environments: Linking Physiological, Population, and Community ecology. Cambridge University Press, Cambridge, MA. 320 p.
- CAIN, M. L. 1994. Consequences of foraging in clonal plant species. *Ecology* 75: 933–944.
- CARTER, G. A. AND A. H. TERAMURA. 1988. Vine photosynthesis and relationships to climbing mechanics in a forest understory. *Am. J. Bot.* 75: 1011–1018.
- DE KROON, H. AND M. J. HUTCHINGS. 1995. Morphological plasticity in clonal plants: the foraging concept reconsidered. *J. Ecol.* 83: 143–152.
- , AND J. KNOPS. 1990. Habitat exploration through morphological plasticity in two chalk grassland perennials. *Oikos* 59: 39–49.
- DEN DUBBELDEN, K. C. AND B. OOSTERBEEK. 1995. The availability of external support affects allocation patterns and morphology of herbaceous climbing plants. *Funct. Ecol.* 9: 628–634.
- DIRR, M. A. AND C. W. HUESER, JR. 1987. *The Reference Manual of Woody Plant Propagation*. Varsity Press, Athens, GA. 239 p.
- EVANS, J. P. AND M. L. CAIN. 1995. A spatially explicit test of foraging behavior in a clonal plant. *Ecology* 76: 1147–1155.
- FREY, D. AND H. FRICK. 1987. Altered partitioning of new dry matter in *Hedera helix* L. (Araliaceae) induced by altered orientation. *Bull. Torrey Bot. Club* 114: 407–411.
- GARTNER, B. L. 1991. Is the climbing habit of poison oak ecotypic? *Funct. Ecol.* 5: 696–704.
- GLEASON, H. A. AND A. CRONQUIST. 1991. *Manual of Vascular Plants of the Northeast United States and Adjacent Canada*. Hafner Publishing Company, Inc. New York, NY. 810 p.
- HAMEL, D. R. AND C. I. SHADE. 1985. Weeds, trees, and herbicides: A public forest and rangelands survey. USDA Forest Service, Washington, DC. 52 p.
- HOBBS, R. J. 1989. The nature and effects of disturbance relative to invasions, pp. 389–406. In J. A. Drake and H. A. Mooney [eds.], *Biological Invasions: A Global Perspective*, John Wiley and Sons, Chichester, England.
- HUME, L. AND P. B. CAVERS. 1982. Geographic variation in a widespread perennial weed, *Rumex crispus*. The relative amounts of genetic and environmentally induced variation among populations. *Can. J. Bot.* 60: 1928–1937.
- HUMPHREY, L. D. AND D. A. PYKE. 1997. Clonal foraging in perennial wheatgrass: A strategy for exploiting patchy soil nutrients. *J. Ecol.* 85: 601–610.
- HUTCHINGS, M. J. 1988. Differential foraging for resources and structural plasticity in plants. *Trends Ecol. Evol.* 3: 200–204.
- LAMOREAUX, R. J., W. R. CHANEY, AND K. M. BROWN. 1978. The Plastochron index: A review after two decades of use. *Am. J. Bot.* 65: 586–593.
- LARSON, K. C. AND T. G. WHITHAM. 1997. Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling. *Oecologia* 109: 575–582.
- LEATHERMAN, A. D. 1955. *Ecological life history of Lonicera japonica* Thunb. PhD. Dissertation. University of Tennessee, Knoxville, TN.
- LODGE, D. M. 1993. Biological invasions: Lessons for ecology. *Trends Ecol. Evol.* 8: 133–137.
- MACDONALD, S. E. AND V. J. LIEFFERS. 1993. Rhizome plasticity and clonal foraging of *Calamagrotis canadensis* in response to habitat heterogeneity. *J. Ecol.* 81: 769–776.
- MACK, R. N. 1985. Invading plants: Their potential contribution to population biology, pp. 127–142. In James White [ed.], *Studies on Plant Demography:*

- A festschrift for John L. Harper, Academic Press, London, England.
- OHWI, J. 1965. Flora of Japan. Smithsonian Institution, Washington, DC. 1126 p.
- OOSTING, H. J. 1942. An ecological analysis of the plant communities of the Piedmont, North Carolina. *Am. Mid. Nat.* 28: 1-126.
- PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713-1724.
- , AND N. M. HOLBROOK. 1991. Biomechanical studies of vines, pp. 73-97. *In* F. E. Putz and H. A. Mooney [eds.], *The Biology of Vines*, Cambridge University Press, Cambridge, MA.
- RADFORD, A. E., H. E. AHLES, AND C. R. BELL. 1983. *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, Chapel Hill, NC. 1183 p.
- RAY, T. S. 1992. Foraging behavior in tropical herbaceous climbers (Araceae). *J. Ecol.* 80: 189-203.
- REJMÁNEK, M. 1989. Invasibility of plant communities, pp. 369-488. *In* J. A. Drake et al. [eds.], *Biological Invasions: A Global Perspective*, John Wiley and Sons, Chichester, England.
- RICE, K. J. AND R. N. MACK. 1991. Ecological genetics of *Bromus tectorum*. II. Intraspecific variation in phenotypic plasticity. *Oecologia* 88: 84-90.
- RICHARDSON, D. M. AND W. J. BOND. 1991. Determinants of plant distribution: Evidence from pine invasions. *Am. Nat.* 137: 639-668.
- ROBERTSON, D. J., M. C. ROBERTSON, AND T. TAGUE. 1994. Colonization dynamics of four exotic plants in a northern Piedmont natural area. *Bull. Torrey Bot. Club* 121: 107-118.
- RUESINK, J. L., I. M. PARKER, M. J. GROOM, AND P. M. KAREIVA. 1995. Reducing the risks of non-indigenous species introductions. *Bioscience* 45: 465-477.
- SACHS, T., A. NOVOPLANSKY, AND D. COHEN. 1993. Plants as competing populations of redundant organs. *Plant, Cell, Environ.* 16: 765-770.
- SASEK, T. W. AND B. R. STRAIN. 1991. Effects of CO₂ enrichment on the growth and morphology of a native and an introduced honeysuckle vine. *Am. J. Bot.* 78: 69-75.
- SCHIERENBECK, K. A. AND J. D. MARSHALL. 1993. Seasonal and diurnal patterns of photosynthetic gas exchange for *Lonicera sempervirens* and *L. japonica* (Caprifoliaceae). *Am. J. Bot.* 80: 1292-1299.
- , R. N. MACK, AND R. R. SHARITZ. 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75: 1661-1672.
- , J. L. HAMRICK, AND R. N. MACK. 1995. Comparison of allozyme variability in a native and an introduced species of *Lonicera*. *Heredity* 75: 1-9.
- SCHLICHTING, C. D. 1986. The evolution of phenotypic plasticity in plants. *Annu. Rev. Ecol. Syst.* 17: 667-693.
- SIMBERLOFF, D. 1981. Community effects of introduced species, pp. 53-81. *In* Matthew H. Nitecki [ed.], *Biotic Crises in Ecological and Evolutionary Time*, Academic Press, London, England.
- STRANSKY, J. J. 1984. Forage yield of Japanese honeysuckle after repeated burning or mowing. *J. Range Manag.* 37: 237-238.
- SUTHERLAND, W. J. AND R. A. STILLMAN. 1988. The foraging tactics of plants. *Oikos* 52: 239-244.
- TERAMURA, A. H., W. G. GOLD, AND I. N. FORSETH. 1991. Physiological ecology of mesic, temperate woody vines, pp. 245-285. *In* F. E. Putz and H. A. Mooney, [eds.], *The Biology of Vines*, Cambridge University Press, Cambridge, MA.
- WILLIAMS, D. G., R. N. MACK, AND R. A. BLACK. 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: The role of phenotypic plasticity. *Ecology* 76: 1569-1580.
- ZIMMERMAN, C. A. 1976. Growth characteristics of weediness in *Portulaca oleracea* L. *Ecology* 57: 964-974.