Heredity **75** (1995) 1–9
©The Genetical Society of Great Britain

Received 16 June 1994

Comparison of allozyme variability in a native and an introduced species of *Lonicera*

KRISTINA A. SCHIERENBECK*†‡, J. L. HAMRICK§ & RICHARD N. MACK†

†Department of Botany, Washington State University, Pullman, WA 99163, ‡Savannah River Ecology Laboratory, Aiken, SC 29802, and §Departments of Botany and Genetics, University of Georgia, Athens, GA 30602, U.S.A.

Levels of allozyme variation are compared between a diploid invasive plant species, *Lonicera japonica* Thunb. ($2n = 18$) and its polyploid native congener, *Lonicera sempervirens* L. ($2n = 36$). Both are woody perennials and were sampled within the native range of *L. sempervirens* in the south-eastern United States where *L. japonica* has been an invader since the late 19th century. Genetic structure and allozyme diversity were determined for nine and ten populations of *L. sempervirens* and *L. japonica*, respectively. Genetic variation within *L. japonica* is similar to that in other species with similar life history traits (per cent polymorphic loci, $P_s = 75$ per cent, mean alleles per polymorphic locus, $A_{ps} = 2.28$, and total genetic diversity, $H_t = 0.216$); *L. sempervirens* has even higher genetic variation than *L. japonica* ($P_s = 91$ per cent, $A_{ps} = 2.60$ and $H_t = 0.283$). Although both species have high levels of genetic diversity, this may be less important than their life history traits to their success in early successful habitats. However, establishment of a relationship between success in naturalization for woody perennials and levels of genetic diversity is hampered by the paucity of comparable records for other native: alien congeneric pairs.

Keywords: genetic variation, introduced populations, *Lonicera japonica, Lonicera sempervirens,* native populations.

Introduction

Studies of invasive plant species (*sensu* Mack, 1985) have often involved a search for generalizations about these species' life history and genetic characteristics (Baker, 1974, 1986). However, several comprehensive syntheses (see Barrett & Richardson, 1986; Gray, 1986; Barrett & Shore, 1989; Warwick, 1990) have revealed few discernible patterns. Their detection may be hampered, however, by comparisons among invasive species with different modes of reproduction and habits or that occur in different successional stages or in new ranges. This current dilemma is illustrated by the lack of consensus regarding the relation of genetic variability to the invasive ability of plants, i.e. some invasive species maintain low levels of genetic variation whereas others are highly variable (Barrett & Richardson, 1986). Alternatively, grouping species by life history traits and geographical range has been successful in detecting associations between genetic diversity and life history characteristics for plant species in general (Hamrick *et al.*, 1979; Loveless & Hamrick, 1984; Hamrick *et al.*, 1992).

Thus, first categorizing invasive species by life history traits and then looking for patterns through the comparison of taxonomically related noninvasive species may provide new insight. For example, invasive species with low levels of allozyme diversity often share life history traits, e.g. inbreeding and polyploidy (Warwick, 1990) or the annual habit with selfing breeding systems (Barrett & Richardson, 1986).

We examined the genetic structure and diversity of two perennial *Lonicera* (Caprifoliaceae) congeners, one an aggressive invader and the other a common but noninvasive native. These honeysuckles are the diploid ($2n = 18$) *Lonicera japonica* Thunb., native to temperate eastern Asia, and the tetraploid ($2n = 36$) *L. sempervirens* L., native to the eastern United States. *Lonicera japonica* was introduced as an ornamental in the early to mid-19th century (exact date undocumented); its rapid spread was noted in southwest Virginia in 1892, Florida in 1897 and Athens, Georgia in 1900 (Leatherman, 1955). *Lonicera sempervirens* is far more widespread than its native congeners in North America and may be considered a colonizer (Radford

*Correspondence: Department of Biology, California State University, Fresno, CA 93740, U.S.A.

et al., 1968). Parentage of the allopolyploid *L. sempervirens* is not known, but based on morphology its extant native diploid congeners, *L. flava* and *L. dioca*, are good candidates as putative parents (K. A. Schierenbeck, personal observation) and as possible sources of variation.

Lonicera japonica and *L. sempervirens* now occur sympatrically in the southeastern United States; both outcross and also persist clonally to an unknown extent. Although these bird-dispersed species (Snow & Snow, 1988) are common in mid-successional sites, the blanket-like clonal growth of *L. japonica* contributes to its local influence in the reduction of species diversity and alteration of successional patterns (Oosting, 1942; Slezak, 1976; Sasek, 1983). Both *L. japonica* and *L. sempervirens* have similar photosynthetic rates (Schierenbeck, 1992) but different patterns of biomass allocation, both spatially and temporally (Sasek & Strain, 1991; Schierenbeck, 1992).

Natural hybrids between subgenera in *Lonicera* are unknown, and no seeds have been obtained following artificial pollination (Sax & Kribs, 1930). We also found no evidence for hybridization between *L. japonica* (subgenus *Chamaecerasus*) and *L. sempervirens* (subgenus *Pericylmenum*).

Comparing a native species growing sympatrically with an invasive congener has been suggested as a means of detecting the attributes that characterize invasive species (Baker, 1965). *Lonicera japonica* and *L. sempervirens* provide a good basis for such a comparison, given their similarities in taxonomy, habitat, successional role, growth form, dispersal mechanism and physiology (Schierenbeck, 1992). Consequently, we employed starch gel electrophoresis to examine genetic diversity within and among populations of these two species. We then compared our data with those for other woody perennial angiosperms and invasive species with similar life history traits.

Materials and methods

Collection sites for this study were chosen in west-central South Carolina and eastern Georgia (Fig. 1). Vegetative cuttings were collected from 10 and nine populations of *L. japonica* and *L. sempervirens*, respectively, in April and May 1991. The number of individuals from each population ranged from six to 14 in *L. sempervirens* and seven to 20 in *L. japonica*. 'Population' as used in this study is defined as a group of individuals separated from other groups of individuals by at least 20 km. This distance is thought to be sufficient to ensure extremely low levels of gene flow between populations through pollination (Handel, 1983; Johnsgard, 1983; Waddington, 1983). We collected cuttings from individuals at least 50 m apart to avoid sampling the same clone twice. The sporadic occurrence of individual clones made collecting larger numbers of individuals per population impractical. Cuttings from each individual were rooted with Rootone™ and cultivated in a greenhouse until sampled for electrophoresis.

Samples were prepared for electrophoresis by first grinding a small amount of mature leaf tissue in liquid nitrogen and extracting the enzymes in phosphate buffer (Soltis *et al.*, 1983). Electrophoresis was performed for all systems using 11 per cent Sigma™ starch. Both species were scored and analysed for 13 enzyme systems (see Table 1 for buffers): aspartate aminotransferase (AAT, EC 2.6.1.1), diaphorase (DIA, EC 1.6.99.-), fluorescent esterase (FE, EC 3.1.1.1), fructose-1,6-diphosphatase (F16, EC 3.1.3.11), isocitrate dehydrogenase (IDH, EC 1.1.1.42), leucine aminopeptidase (LAP, 3.4.11.1), malate dehydrogenase (MDH, EC 1.1.1.37), malic enzyme (ME, EC 1.1.1.40), 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), phosphoglucoisomerase (PGI, EC 5.3.1.9), phosphoglucomutase (PGM, EC 5.4.2.2), shikimate dehydrogenase (SKDH, EC 1.1.1.25) and triose-phosphate isomerase (TPI, EC 5.3.1.1). These enzymes provided 24 and 22 scorable loci for *L. japonica* and *L. sempervirens*, respectively. In both species the number of independent banding zones as well as the banding patterns within each variable zone were largely consistent with expected enzyme substructure and compartmentalization. Thus, with one exception (see below) the banding patterns seen were consistent with diploid inheritance and were treated as such in our analyses. Because sample sizes were small, we concentrated on obtaining the maximum number of scorable loci to gain accurate estimates of genetic variability (Nei, 1978).

Genetic diversity within each species was summarized using percentage polymorphic loci (P_s (subscript s indicates species)), mean number of alleles per locus (A_s) and per polymorphic locus (A_{ps}) and mean gene diversity (H_{es}) per locus, as described by Hamrick & Godt (1989). Equivalent statistics were calculated at the population level (P_p, A_p, A_{pp} and H_{ep} (subscript p indicates population)) following Hedrick (1985). The mean effective number of alleles per locus was calculated within populations (A_{ep}) and species (A_{es}) [$A = 1/(\Sigma p_i^2)$]. H_T is defined as total mean genetic diversity (Nei, 1973). Within each population, each polymorphic locus was examined using Wright's fixation index (F_{IS}) for deviations from expected Hardy–Weinberg genotype frequencies (Wright, 1922; Li & Horvitz, 1953). Genetic differentiation among populations was measured using a χ^2 analysis to test

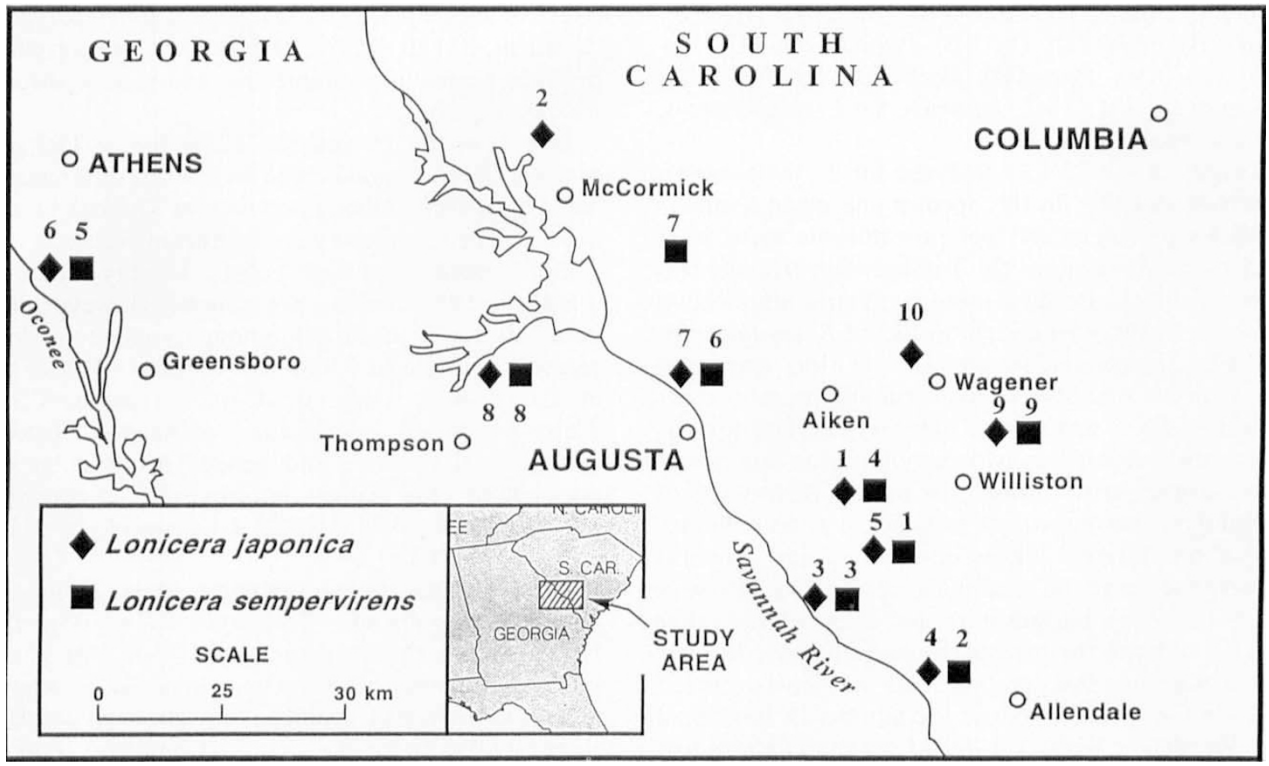

Fig. 1 Locations of nine populations of *Lonicera sempervirens* and 10 populations of *L. japonica* in the southeastern United States from which samples were collected for electrophoretic analysis.

Table 1 Electrode and gel buffers used to resolve 13 enzyme systems in *Lonicera japonica* and *L. sempervirens*

Electrode buffer	Gel buffer	Enzymes	References
0.3 M boric acid 0.1 M NaOH pH 8.6	0.015 M Tris 0.004 M citric acid pH 8.6	LAP, PGM, AAT	Mitton *et al.* (1977)
0.388 M LiOH 0.263 M boric acid pH 8.0	0.006 M citric acid 0.004 M LiOH 0.029 M boric acid 0.033 M Tris pH 7.6	PGI, TPI, FE	Modified from Adams & Joly (1980)
0.22 M Tris 0.085 citric acid pH 7.5	0.008 M Tris 0.003 M citric acid pH 7.5	ME, DIA, 6PGD	Modified from Shaw & Prasad (1970)
0.4 M citric acid (trisodium salt) pH 7.0	0.009 M L-histidine HCl, monohydrate pH 7.0	IDH, MDH, SKDH, F16	Modified from Gottlieb (1981)

Full names of enzymes are given in Material and methods.

for heterogeneity in allele frequencies among populations (Workman & Niswander, 1970) and Nei's gene diversity statistics to assess the partitioning of total genetic diversity within and among populations (Nei, 1973, 1977).

Results

The resolution of 13 enzyme systems provided data for the following loci: *Aat-1*(B), *Aat-2*(B), *Dia-1*(B), *F16-1*(B), *Fe-1*(J), *Fe-2*(B), *Fe-3*(S), *Idh-1*(J), *Lap-1*(B),

Mdh-1(J), *Mdh-2*(B), *Mdh-3*(B), *Me-1*(B), *Me-2*(B), *6Pgd-1*(B), *6Pgd-2*(B), *Pgi-1*(B), *Pgi-2*(J), *Pgi-3*(B), *Pgi-4*(S), *Pgm-1*(B), *Pgm-2*(B), *Skdh-1*(B), *Tpi-1*(B), *Tpi-2*(B) and *Tpi-3*(B) (J = *L. japonica*, S = *L. sempervirens*, B = both species).

Twenty of the 22 loci analysed for *L. sempervirens* were polymorphic. In this species, the mean numbers of alleles per locus and per polymorphic locus were 2.45 and 2.60, respectively. Total genetic diversity was 0.283 (Table 2). Because there is no strict duplication of loci in an allopolyploid, most loci of *L. sempervirens* could be interpreted as diploid loci (loci expressed through only one homologous pair of chromosomes). However, *Pgi-3* was a fixed heterozygote and for this analysis was treated as two monomorphic loci. Fixed heterozygotes arise through the pairing of two sets of homologous chromosomes in which a gene is homozygous for different alleles in each set and a hybrid genotype arises in the resulting allopolyploid (Roose & Gottlieb, 1976). Furthermore, for many of the other enzyme systems, the two species had the same number of loci indicating that gene silencing may have occurred in *L. sempervirens* to reduce the number of functional loci (Weeden & Wendel, 1989). *Lonicera japonica* had 75 per cent of its loci polymorphic, 2.28 alleles per polymorphic locus, 1.96 alleles per locus and total genetic diversity was 0.216 (Table 2).

Further differences in genetic diversity were also apparent within populations of these two species. Within *L. sempervirens* populations, on average there were 67.7 (range 50–82) per cent polymorphic loci, 2.31 (2.18–2.44) alleles per polymorphic locus, 1.51 (1.41–1.66) effective alleles per locus and an expected heterozygosity of 0.250 (0.205–0.303). *Lonicera japonica* populations had on average 53.8 (range 33.3, 50–62.4) per cent polymorphic loci, 2.20 (2.07–2.33) alleles per polymorphic locus, 1.34 (1.21–1.44) effective alleles per locus, and expected heterozygosity of 0.189 (0.120–0.226). There was no correlation between population sample size and genetic diversity for either species.

Based on the χ^2 analysis, 12 of the 18 loci polymorphic for *L. japonica* had significant differences in allele frequencies among populations whereas 11 of 22 loci for *L. sempervirens* were significant (Table 3).

Both species had high genetic identity indices (I) (Hedrick, 1985) among populations. However, more variation for I occurred among populations in *L. sempervirens* (range 0.826–0.972, mean = 0.904) than in *L. japonica* (range 0.902–0.987, mean = 0.960). There was no significant correlation between geographical distance and genetic distance between populations for either species (*L. sempervirens*, $r = 0.296$, d.f. = 35, $P < 0.2$; *L. japonica*, $r = 0.212$, d.f. = 44, $P < 0.2$).

On a population-by-population basis, *L. japonica* displayed significant deviations ($P < 0.05$) from Hardy–Weinberg expectations in 27 of 240 χ^2-tests (twice the number expected by chance alone), whereas *L. sempervirens* had significant deviations in 24 of 189 χ^2-tests (also twice the expected number). *Lonicera sempervirens* had negative fixation indices, indicating an excess of heterozygotes and significant deviations from Hardy–Weinberg expectations for *Aat-1* (four populations) and *Lap-1* (one population). The remaining deviations, although significant, indicated a lack of heterozygotes, a result predictable for the number of χ^2-tests. The mean F_{IS} value for *L. sempervirens* was 0.081 and was not significant ($\chi^2_1 = 0.55$; $P < 0.50$). In general, *L. japonica* conformed to Hardy–Weinberg expectations; all the significant deviations were for an excess of homozygous individuals, but the overall frequency of deviations was low. F_{IS} values varied widely across loci for both species, but were generally

Table 2 Percentage polymorphic loci, mean number of alleles per locus and per polymorphic locus, and total genetic diversity within *Lonicera japonica* and *L. sempervirens* compared with the mean for 196 species with similar life history characters

Percentage polymorphic loci (P_s)	Mean number of alleles/locus (A_s)	Alleles per polymorphic locus (A_{ps})	Total genetic diversity (H_t)
Lonicera sempervirens			
90.91	2.45	2.60	0.283
Lonicera japonica			
75.00	1.96	2.28	0.216
Other woody perennial angiosperms†			
65.00	2.22	2.88	0.177

†From Hamrick *et al.* (1992).

Table 3 Gene diversity statistics for 20 and 18 polymorphic loci in *Lonicera sempervirens* and *L. japonica*, respectively

Locus	No. of alleles	H_T	H_S	D_{ST}	G_{ST}	χ^2 (d.f.)	
Lonicera sempervirens							
Aat-1	2	0.4625	0.4084	0.0541	0.1169	19.64*	(8)
Aat-2	2	0.2098	0.1914	0.0184	0.0875	14.71	(8)
Lap-1	2	0.4762	0.3701	0.1061	0.2228	34.76**	(8)
Pgm-1	2	0.4711	0.3645	0.1066	0.2263	35.76**	(8)
Pgm-2	2	0.0973	0.0915	0.0058	0.0591	9.23	(8)
Fe-2	3	0.6005	0.4813	0.1192	0.1985	72.07**	(8)
Fe-3	4	0.6835	0.5664	0.1171	0.1713	179.94**	(24)
Pgi-1	2	0.2616	0.2442	0.0174	0.0665	11.17	(8)
Tpi-1	3	0.0582	0.0541	0.0041	0.0700	24.57	(16)
Tpi-2	2	0.3170	0.2657	0.0513	0.1618	26.21**	(8)
Tpi-3	3	0.1039	0.0955	0.0084	0.0809	22.44	(16)
F16-1	5	0.7690	0.7046	0.0643	0.0837	51.10*	(32)
Mdh-2	2	0.0713	0.0646	0.0068	0.0951	15.40	(8)
Mdh-3	3	0.0912	0.0771	0.0141	0.1550	33.11**	(16)
Skdh-1	3	0.5446	0.4023	0.1423	0.2613	124.62**	(16)
6Pgd-1	2	0.1327	0.1262	0.0064	0.0486	8.17	(8)
6Pgd-2	2	0.2449	0.2244	0.0205	0.0837	14.05	(8)
Dia-1	2	0.4974	0.3332	0.1643	0.3302	55.47**	(8)
Me-1	2	0.1544	0.1445	0.0099	0.0644	10.69	(8)
Me-2	4	0.5878	0.4962	0.0916	0.1558	43.95**	(24)
Mean		0.3107	0.2594	0.0513	0.1651		
Lonicera japonica							
Aat-1	2	0.1036	0.0888	0.0148	0.1431	41.79**	(9)
Aat-2	2	0.1457	0.1402	0.0055	0.0379	11.98	(9)
Pgm-1	2	0.2228	0.2050	0.0178	0.0801	21.94**	(9)
Pgm-2	2	0.0778	0.0672	0.0106	0.1365	40.40**	(9)
Fe-1	3	0.5357	0.4493	0.0864	0.1614	64.51**	(18)
Pgi-2	2	0.4907	0.4841	0.0066	0.0134	4.12	(9)
Pgi-3	3	0.5369	0.4929	0.0439	0.0818	51.81**	(18)
Tpi-2	2	0.5000	0.4540	0.0460	0.0921	28.72**	(9)
Tpi-3	3	0.0129	0.0124	0.0005	0.0370	15.21	(18)
F16-1	2	0.3940	0.3681	0.0259	0.0658	18.29*	(9)
Idh-1	2	0.1927	0.1808	0.0119	0.0617	15.41	(9)
Mdh-2	2	0.4966	0.4131	0.0835	0.1682	45.98**	(9)
Mdh-3	3	0.0283	0.0263	0.0019	0.0690	25.84	(9)
Skdh-1	2	0.3876	0.3483	0.0393	0.1014	27.39**	(9)
6Pgd-1	2	0.1295	0.1209	0.0087	0.0670	21.17*	(9)
6Pgd-2	2	0.0126	0.0120	0.0006	0.0495	15.65	(9)
Dia-1	2	0.4960	0.4233	0.0727	0.1467	46.05**	(9)
Me-2	3	0.4160	0.3599	0.0561	0.1350	64.23**	(18)
Mean		0.2878	0.2581	0.0296	0.0915		

Key to abbreviations for genetic diversity statistics: H_T, total genetic diversity; H_S, mean genetic diversity within populations; D_{ST}, gene diversity among populations; G_{ST}, proportion of total variation resulting from differences among populations.
Enzyme abbreviations are found in Materials and methods.
χ^2 values test the hypothesis that there are no significant differences among populations.
$^*P \leqslant 0.05$, $^{**}P \leqslant 0.01$.

more positive for *L. japonica*, indicating slightly more heterozygote deficiencies (mean $F_{IS} = 0.118$, $\chi^2_1 = 2.20$; $P < 0.10$).

Among-population variation was higher for *L. sempervirens* ($G_{ST} = 0.165$) than for *L. japonica* ($G_{ST} = 0.092$) (see Table 3). On a per locus basis, G_{ST} values for *L. japonica* ranged from 0.0134 to 0.1682. Thus, most of the variation (90 per cent) for *L. japonica* occurs within populations. For *L. japonica*, D_{ST} and G_{ST} showed similar patterns for most loci.

Lonicera sempervirens had G_{ST} values ranging from 0.0486 to 0.3302 and most of the total variation (83 per cent) occurs within populations. The higher G_{ST} for *L. sempervirens* could be caused to some degree by the higher proportion of populations with sample sizes below 10 individuals. When those *L. sempervirens* populations with sample sizes >10 were analysed the G_{ST} was 0.102, confirming that sample size *per se* did have some effect on the value of G_{ST}.

Discussion

Among the populations sampled in South Carolina and Georgia, *L. sempervirens* has higher genetic variability than *L. japonica* as measured by per cent polymorphic loci, mean number of alleles/locus and total genetic diversity. Values of per cent polymorphic loci (P_s) for both species are consistently higher than those for previously reported species of similar taxonomic status (dicots, $P_s = 44.8$), geographical range (widespread, $P_s = 58.9$), mating system (outcrossing, via animals, $P_s = 50$), mode of reproduction (sexual, $P_s = 51.6$; sexual and asexual, $P_s = 43.8$), and habitat (mid-successional, $P_s = 47.6$) (Hamrick & Godt, 1989; Hamrick *et al.*, 1992).

Long-lived perennial species have a mean within-population variation of 49.3 per cent polymorphic loci, 1.76 alleles per locus and a mean total genetic diversity of 0.148 (Hamrick *et al.*, 1992); all values are lower than for either *L. japonica* or *L. sempervirens*.

The proportions of total diversity among populations (G_{ST}) for *L. japonica* (0.092) and *L. sempervirens* (0.165) are comparable to the G_{ST} values found in other long-lived species (0.084) (Hamrick & Godt, 1989); however, the values for these *Lonicera* spp. may be affected partially by the small sample sizes (increasing G_{ST}), the comparatively small geographical area sampled (decreasing G_{ST}) and differences in pollination systems and distance of seed dispersal. Naturalized outbreeding species that maintain large populations are likely to have little differentiation (Brown & Marshall, 1981). The levels of genetic variation among the *L. japonica* populations we sampled are consistent with the prediction that these are large outbreeding populations.

Although species and population levels of genetic variability in *L. japonica* are high, they may still reflect genetic sampling, immigration and subsequent persistence of a subset of the variation present in its home range. Even with the likelihood of multiple introductions of *L. japonica* (Mack, 1991), the levels of variation found in the southeastern United States may be lower than variation in its native range because of founder effects. To our knowledge, there are no published studies on the allozyme variation in Asian populations of *L. japonica*.

An allopolyploid origin for *L. sempervirens* (Ammal & Saunders, 1952) is supported to some degree by the allozyme patterns we observed, chromosome pairing patterns observed during meiosis in squashes of immature anthers (K. A. Schierenbeck, personal observation) and higher levels of variation (Brown & Marshall, 1981). Although Hamrick *et al.*, (1979) did not compare the levels of genetic variation observed in species with different ploidy levels, they did find that species with higher chromosome numbers had higher levels of genetic diversity. The distribution of *L. sempervirens* supports the hypothesis that a higher genetic variability in polyploids can result in a more widespread distribution than their native diploid congeners (Stebbins, 1971).

In another perennial species that has escaped from cultivation, *Lathyrus latifolius*, the mean genetic diversity is 0.207, 81 per cent of the loci are polymorphic and the mean number of alleles per polymorphic locus is 2.29 (Godt & Hamrick, 1991). These values are high compared with those for other plant species (Hamrick & Godt, 1989) and with values for other naturalized species with similar life history traits. Low levels of allozyme diversity are often found within weedy species but many of these are annual grasses and dicots that reproduce primarily by self-fertilization (Brown & Marshall, 1981; Warwick, 1990). Hamrick *et al.* (1979) found that weedy and early successional species are less variable than species of mid-and late-successional stages. However, many of the weedy species in their review were selfing annuals and may not be directly comparable to long-lived outcrossing species such as these two *Lonicera* species.

Reviews of the allozyme literature have found that among 196 long-lived woody species for which genetic variation has been measured, only nine are for invasive angiosperms (Hamrick *et al.*, 1979, 1992). All nine records report genetic variation in the species' home range. In these studies, all except one species (*Acacia dealbata*, for which data were collected from only one population) show higher levels of variation than expected for species with similar life history traits (Table 4). It should also be noted that all of these species except *Eucalyptus obliqua* are nitrogen fixers, a trait that is associated with the ability to invade new ranges rapidly (Vitousek, 1986). Rapid invasion through only a few introduction events may result in lower levels of genetic variability in the new range, but we lack historical confirmation of this scenario for *L. japonica*. Although most species with broad distributions have higher levels of genetic variability (Hamrick & Godt, 1989), we found levels of polymorphism for

Table 4 Summary of levels of variation within eight species of invasive woody angiosperms

Species	No. of populations	No. of loci	P_s	A_s	A_{es}	H_{es}	Reference
Robinia pseudoacacia	23	40	97.5	2.92	1.52	0.344	a
Eucalyptus obliqua	4	3	—	—	—	0.489	b
Prosopis glandulosa	1	13	61.5	1.92	—	—	c
Prosopis pallida	1	13	15.4	1.15	—	—	c
Casuarina cunninghamiana	6	21	77.7	2.00	1.17	0.145	d
Casuarina cunninghamiana	20	19	100.0	2.79	1.40	0.287	e
Acacia dealbata	1	16	—	—	—	0.085	f
Acacia melanoxylon	1	19	—	—	—	0.300	f
Acacia decurrens	1	26	—	—	—	0.156	f

Key to abbreviations: P_s, percentage polymorphic loci; A_s, mean number of alleles per locus; A_{es}, effective number of alleles per locus; H_{es}, genetic diversity.
References: [a]Surles *et al.* (1989); [b]Brown *et al.* (1975); [c]Paneida & Carstairs (1989); [d]Moore & Moran (1989); [e]Moran *et al.* (1989a); [f]Moran *et al.* (1989b).

these two *Lonicera* species that are higher than expected for invasive species in general. We are unaware of any other studies of the genetic diversity of introduced perennial woody species in their new ranges. Consequently, comparisons remain tenuous.

Life history characteristics that are associated with high genetic variability are also traits characteristic of many invasive woody perennials. High levels of genetic variability may allow species to invade diverse habitats, but quantitative growth characters might provide the adaptations necessary for the invasive species to outcompete native species (Sasek & Strain, 1991; Schierenbeck, 1992). The identification of a particular combination of characteristics important to the success of an individual in any environment is best achieved through comparative studies of species with similar life history categories. *Lonicera* contains both aggressive alien and nonaggressive native woody species in North America. For example, *L. maackii* and *L. tartarica* are widespread alien weeds whereas *L. dioica* and *L. flava* are referred to as rare natives (Radford *et al.*, 1968). Further investigation of native and nonindigenous species in this genus may elucidate differences that will help to explain their differential ability as invaders.

Patterns among the genetic characteristics of invasive species are gradually emerging, but certainly more information is needed. Consistent patterns among the genetic attributes of invaders may cease to be elusive if the examination of genetic variability is correlated with life history traits. Such correlations may eventually allow us to understand the relative importance of genetic variability in relation to other characteristics in the invasion process.

Acknowledgements

This research was supported under Contract No. DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia, NSF doctoral dissertation improvement grant BSR-8914717 to K.A.S. and R.N.M., Sigma Xi, the Hardman Foundation and The Nature Conservancy. The authors thank M. Rodgers and J. W. Eckert for help with collecting plant samples, D. E. and P. S. Soltis for the use of their laboratory during preliminary data collection, S. Sherman-Broyles, E. Berg, J. Tyrell, L. Manning and S. Dillard for laboratory assistance, M. D. Loveless and A. Schnabel for the use of the computer program for data analysis, and D. E. Soltis, A. Schnabel and S. Warwick for comments on the manuscript.

References

ADAMS, W. T. AND JOLY, R. J. 1980. Genetics of allozyme variants in loblolly pine. *J. Hered.*, **71**, 33–40.

AMMAL, E. K. J. AND SAUNDERS, B. 1952. Chromosome numbers in species of *Lonicera. Kew Bull.*, **4**, 539–541.

BAKER, H. G. 1965. Characteristics and modes of origin of weeds. In: Baker, H. G. and Stebbins, G. L. (eds) *The Genetics of Colonizing Species*, pp. 147–172. Academic Press, New York.

BAKER, H. G. 1974. The evolution of weeds. *Ann. Rev. Ecol. Syst.*, **5**, 1–24.

BAKER, H. G. 1986. Patterns of plant invasion in North America. In: Mooney, H. A. and Drake, J. A. (eds) *Ecology of Biological Invasions of North America and Hawaii*, pp. 44–57. Springer Verlag, New York.

BARRETT, S. C. H. AND RICHARDSON, B. J. 1986. Genetic attributes of invading species. In: Groves, R. H. and Burdon, J. J. (eds) *Ecology of Biological Invasions*, pp. 21–33. Cambridge University Press, Melbourne, Australia.

BARRETT, S. C. H. AND SHORE, J. S. 1989. Isozyme variation in colonizing plants. In: Soltis, D. E. and Soltis, P. S. (eds) *Isozymes in Plant Biology*, pp. 106–126. Dioscorides Press, Portland, OR.

BROWN, A. H. D. AND MARSHALL, D. R. 1981. Evolutionary changes accompanying colonization in plants. In: Scudder, G. C. E. and Reveal, J. L. (eds) *Colonization, Succession and Stability*, pp. 351–363. Blackwell Scientific Publications, Oxford.

BROWN, A. H. D., MATHESON, A. C. AND ELDRIDGE, K. G. 1975. Estimation of the mating system of *Eucalyptus obliqua* L'Heret by using enzyme polymorphisms. *Aust. J. Bot.*, **23**, 931–949.

GODT, M. J. W. AND HAMRICK, J. L. 1991. Genetic variation in *Lathyrus latifolius* (Leguminosae). *Am. J. Bot.*, **78**, 1163–1171.

GOTTLIEB, L. D. 1981. Gene numbers in species of Asteraceae that have different chromosome numbers. *Proc. Natl. Acad. Sci. U.S.A.*, **78**, 3726–3729.

GRAY, A. J. 1986. Do invading species have definable genetic characteristics? *Phil. Trans. R. Soc. B*, **314**, 655–674.

HAMRICK, J. L. AND GODT, M. J. W. 1989. Allozyme diversity in plant species. In: Brown, A. H. D., Clegg, M. T., Kahler, A. L. and Weir, B. S. (eds) *Plant Population Genetics, Breeding and Genetic Resources*, pp. 43–63. Sinauer, Sunderland, MA.

HAMRICK, J. L., GODT, M. J. W. AND SHERMAN-BROYLES, S.L. 1992. Factors influencing levels of genetic diversity in woody plant species. *New Forests*, **6**, 95–124.

HAMRICK, J. L., LINHART, Y. B. AND MITTON, J. B. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Ann. Rev. Ecol. Syst.*, **10**, 173–200.

HANDEL, S. N. 1983. Pollination ecology, plant population structure and gene flow. In: Real, L. A. (ed) *Pollination Biology*, pp. 163–211. Academic Press, New York.

HEDRICK, P. W. 1985. *Genetics of Populations*. Jones and Bartlett, Boston.

JOHNSGARD, P. A. 1983. *The Hummingbirds of North America*. Smithsonian Institution Press, Washington, DC.

LEATHERMAN, A. D. 1955. *Ecological Life-history of* Lonicera japonica *Thunb*. Ph.D. Thesis, University of Tennessee, Knoxville, TN.

LI, C. C. AND HORVITZ, D. G. 1953. Some methods of estimating the inbreeding coefficient. *Am. J. Hum. Genet.*, **5**, 107–117.

LOVELESS, M. D. AND HAMRICK, J. L. 1984. Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.*, **15**, 65–95.

MACK, R. N. 1985. Invading plants: their potential contribution to population biology. In: White, J. (ed.) *Studies on Plant Demography: J. L. Harper Festschrift*, pp. 127–142. Academic Press, London.

MACK, R. N. 1991. The commercial seed trade: an early disperser of weeds in the United States. *Econ. Bot.*, **45**, 257–273.

MITTON, J. B., LINHART, Y. B., HAMRICK, J. L. AND BECKMAN, J. S. 1977. Observations on the genetic structure and mating system of ponderosa pine in the Colorado front range. *Theor. Appl. Genet.*, **51**, 5–13.

MOORE, N. J. AND MORAN, G. F. 1989. Microgeographic patterns of allozyme variation in *Casuarina cunninghamiana* within and between the Murrumbidge and coastal drainage systems. *Aust. J. Bot.*, **37**, 181–192.

MORAN, G. F., BELL, J. C. AND TURNBULL, J. W. 1989a. A cline in genetic diversity in River she-oak (*Casuarina cunninghamiana*). *Aust. J. Bot.*, **37**, 169–180.

MORAN, G. F., MUONA, O. AND BELL, J. C. 1989b. Breeding systems and genetic diversity in *Acacia auriculiformis* and *A. crassicarpa*. *Biotropica*, **21**, 250–256.

NEI, M. 1973. Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. U.S.A.*, **70**, 3321–3323.

NEI, M. 1977. *F*-statistics and analysis of gene diversity in subdivided populations. *Ann. Hum. Genet.*, **41**, 225–233.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, **89**, 583–590.

OOSTING, H. J. 1942. An ecological analysis of the plant communities of the Piedmont, North Carolina. *Am. Midl. Nat.*, **28**, 1–126.

PANEIDA, F. D. AND CARSTAIRS, S. A. 1989. Isozymic discrimination of tropical Australian populations of mesquite (*Prosopis* spp.); implication for biological control. *Weed Res.*, **29**, 157–165.

RADFORD, A. E., AHLES, H. E. AND BELL, C. R. 1968. *Manual of the Vascular Flora of the Carolinas*. The University of North Carolina Press, Chapel Hill.

ROOSE, M. L. AND GOTTLIEB, L. D. 1976. Genetic and biochemical consequences of polyploidy in *Tragopogon*. *Evolution*, **30**, 818–830.

SASEK, T. W. 1983. *Growth and Biomass Allocation Patterns of* Lonicera japonica *Thunb. and* Lonicera sempervirens *L. under Carbon Dioxide Enrichment*. M.S. Thesis, Duke University, Durham, NC.

SASEK, T. W. AND STRAIN, B. R. 1991. Effects of CO_2 enrichment on the growth and morphology of a native and an introduced honeysuckle vine. *Am. J. Bot.*, **78**, 69–75.

SAX, K. AND KRIBS, D. A. 1930. Chromosomes and phylogeny in Caprifoliaceae. *J. Arnold Arbort.*, **11**, 147–153.

SCHIERENBECK, K. A. 1992. *Comparative Ecological and Genetic Studies Between a Native* (Lonicera sempervirens *L.*) *and an introduced vine* (L. japonica *Thunb.*). Ph.D. Thesis, Washington State University, Pullman, WA.

SHAW, C. R. AND PRASAD, R. 1970. Starch gel electrophoresis of enzymes — a comparison of recipes. *Biochem. Genet.*, **4**, 297–320.

SLEZAK, W. F. 1976. Lonicera japonica *Thunb., an Aggressive Introduced Species in a Mature Forest Ecosystem*. M.S. Thesis, Rutgers University, New Brunswick, NJ.

SNOW, B. AND SNOW, D. 1988. *Birds and Berries, A Study of an Ecological Interaction*. T. and A. D. Poyser, Calton, U.K.

SOLTIS, D. E., HAUFLER, C. H., DARROW, D. C., AND GASTONY, G. J. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. *Am. Fern J.*, **73**, 9–27.

STEBBINS, G. L. 1971. *Chromosomal Evolution in Higher Plants*. Edward Arnold, London.

SURLES, S. C., HAMRICK, J. L. AND BONGARTEN, B. C. 1989. Allozyme variation in black locust (*Robinia pseudoacacia*). *Can. J. Forest Res.*, **19**, 471–479.

VITOUSEK, P. 1986. Biological invasions and ecosystem properties: can species make a difference? In: Mooney, H. A. and Drake, J. A. Drake (eds) *Ecology of Biological Invasions of North America and Hawaii*, pp. 163–176. Springer-Verlag, New York.

WADDINGTON, K. D. 1983. Foraging behavior of pollinators. In: Real, L. A. (ed.) *Pollination Biology*, pp. 213–239. Academic Press, New York.

WARWICK, S. I. 1990. Allozyme and life-history variation in five northwardly colonizing North American weed species. *Pl. Syst. Evol.*, **169**, 41–54.

WEEDEN, N. F. AND WENDEL, J. F. 1989. Genetics of plant isozymes. In: Soltis, D. E. and Soltis, P. S. (eds) *Isozymes in Plant Biology*, pp. 46–72. Dioscorides Press, Portland, OR.

WORKMAN, P. L. AND NISWANDER, J. D. 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Pagayo. *Am. J. Hum. Genet.*, **22**, 24–49.

WRIGHT, S. 1922. Coefficients of inbreeding and relationship. *Am. Nat.*, **56**, 330–338.