American Journal of Botany 90(10): 1487–1495. 2003.

VEGETATIVE REGENERATION IN INVASIVE *REYNOUTRIA* (POLYGONACEAE) TAXA: THE DETERMINANT OF INVASIBILITY AT THE GENOTYPE LEVEL[1]

Petr Pyšek,[2,6] John H. Brock,[2,5] Kateřina Bímová,[3]
Bohumil Mandák,[2] Vojtěch Jarošík,[2,4] Irena Koukolíková,[2]
Jan Pergl,[2] and Jan Štěpánek[2]

[2]Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic;
[3]Institute of Applied Ecology, Czech Agricultural University Prague, CZ-281 63 Kostelec nad Černými lesy, Czech Republic; and
[4]Department of Zoology, Charles University, Prague, Viničná 7, CZ-128 00 Praha 2, Czech Republic

Vegetative regeneration of individual genotypes of Asian *Reynoutria* taxa, which are invasive in the Czech Republic, was studied in *R. sachalinensis* (five genotypes), *R. japonica* (a single genotype present in the country), and their hybrid *R.* ×*bohemica* (nine genotypes). Identity of genotypes was confirmed by isozyme analysis. Ten rhizome segments of each genotype were planted in a randomized block design. After 30 d, the regeneration rate of each genotype was measured as the proportion of rhizomes that produced shoots. Emergence time and final mass of each shoot were recorded. The regeneration rate and final shoot mass were significantly affected by genotype in *R.* ×*bohemica* but not in *R. sachalinensis*. In *R.* ×*bohemica*, easily regenerating genotypes grew faster. Regeneration characteristics that crucially contribute to the fitness of these vegetatively spreading plants are closely related to each other. In genotypes with a low regeneration rate, early-emerging shoots produced more biomass, while in those with a high regeneration rate, shoot mass was independent of emergence time. Mean clone size recorded in the field was marginally significantly related to emergence time during regeneration; regeneration characteristics might thus affect the extent of *R.* ×*bohemica* invasion at a regional scale. Hybrids genetically intermediate between the parents regenerated better than those closely related to parents. Novel hybrid invasive genotypes may be produced by rare sexual reproduction, fixed by clonal growth, and present a previously unknown threat to native vegetation.

Key words: Czech Republic; emergence time; *Fallopia*; genotype; isozyme analysis; plant invasion; Polygonaceae; regeneration; *Reynoutria*; shoot growth.

Biological invasions have been receiving increasing attention because of their scientific appeal (Rejmánek, 1996, 2000; Lonsdale, 1999; Richardson et al., 2000; Grotkopp et al., 2002) and practical connotations (McNeely et al., 2001; Rejmánek and Reichard, 2001). Vast numbers of species have been translocated over the globe, and these alien taxa contribute remarkably to species numbers of local floras (e.g., Weber, 1997). By competing with native species, invaders may reduce native species diversity (Pyšek and Pyšek, 1995; Higgins et al., 1999), although only a small number of alien species appear to negatively affect native communities (Williamson, 2001; Cronk and Fuller, 1995). For example, only 90 species of the 1378 Czech alien species are classified as invasive (Pyšek et al., 2002), and only a fraction of these can be considered as transformer species that change the character, condition, form, or nature of ecosystems (Wells et al., 1986; Richardson et al., 2000). The low percentage of alien species that interfere with human objectives appears to be typical, described as the ‘‘tens rule’’ (Williamson, 1996; Williamson and Fitter, 1996). Species of the genus *Reynoutria* represent a remarkable example of transformer species not only in central Europe but in a number of regions of the world (Sukopp and Sukopp, 1988; Cronk and Fuller, 1995; Sukopp and Starfinger, 1995).

The mode of reproduction is a crucial determinant of any successful invasion (Daehler and Strong, 1994, 1996). High fecundity and capability of sexual reproduction, which generates genetic variation (Crawley, 1997), has been a common attribute in most lists of characteristics that promote invasion since early attempts to define an ideal invader (e.g., Baker, 1965; Noble, 1989; Roy, 1990; Saxena, 1991; Richardson and Cowling, 1992; Rejmánek, 1995; Crawley et al., 1996). However, vigorous vegetative reproduction can be a similarly effective means of spread (Baker, 1965, 1986; Ashton and Mitchell, 1989; Roy, 1990; Mitchell and Gopal, 1991; Saxena, 1991). Plants that reproduce clonally are, in terms of whole floras, as successful invaders as those relying solely on sexual reproduction (Pyšek, 1997). Clonal plants are common in the central European flora (Klimeš et al., 1997), and their successful invasion can be related to various aspects of plasticity in clonal growth (van Groenendael and de Kroon, 1990; Beerling et al., 1994). Indeed, some highly successful invaders reproduce mainly vegetatively in their introduced geographical range (Room, 1990; Williamson, 1996), including *Reynoutria japonica* (Hollingsworth et al., 1998; Hollingsworth and Bailey, 2000). In such cases, we face an appealing natural experiment because when production of new individuals is limited to vegetative means, genetically identical progeny are produced and vegetative regeneration becomes the necessary condition of successful invasion (Bímová et al., 2003).

In central Europe, the genus *Reynoutria* is represented by

---

[1] Manuscript received 30 January 2003; accepted 9 May 2003.

The authors thank Curtis Daehler for comments on the manuscript and Ivan Ostrý and Šárka Jahodová for logistic support. The work was funded by grant no. A6005805/1998 from the Grant Agency of the Academy of Sciences of the Czech Republic, and by grant no. AV0Z6005908 from the Academy of Sciences of the Czech Republic. V. J. was supported by the MŠMT grant No. J13/98113100004.

[5] Present address: Environmental Resources Program, 7001 E. Williams Field Road, Arizona State University East, Mesa, Arizona 85212 USA. E-mail: john.brock@asu.edu.

[6] E-mail: pysek@ibot.cas.cz.

R. japonica Houtt var. *japonica*, *R. japonica* Houtt. var. *compacta* Moldenke, *R. sachalinensis* (F. Schmidt) Nakai, and a hybrid between *R. sachalinensis* and *R. japonica* var. *japonica*, i.e., *R.* ×*bohemica* Chrtek and Chrtková. The situation of two parental species and their hybrid, which are all invasive, creates a challenging opportunity to study the effect of hybridization on plant invasions (Abbott, 1992; Ellstrand and Schierenbeck, 2000; Vila et al., 2000; Daehler and Carino, 2001). The fitness of hybrid progeny affects genetic structure of populations in particular taxa, and such studies contribute to assessing the role of natural hybridization in adaptive ecology and post-invasion evolution (Arnold, 1997; Ellstrand and Schierenbeck, 2000; Lee, 2002).

Previous studies on invasive *Reynoutria* congeners in the Czech Republic focused on the history of introduction and spread (Pyšek and Prach, 1993), the effect of meadow management on their establishment in the wild (Brabec and Pyšek, 2000), long-term persistence of clones in the landscape (Pyšek et al., 2001), possibilities for control (Bímová et al., 2001), and vegetative regenerative capability (Bímová et al., 2003). Because the latter work studied differences in vegetative regeneration from rhizome and stem fragments between the taxa, in the present paper we focus on the genotype level and raise the following questions: Do particular genotypes of the *Reynoutria* taxa that exhibit genetic diversity in the Czech Republic differ in their regenerative potential? If so, is this difference related to the early growth immediately after the establishment (do more successfully regenerating genotypes also grow faster?), and are these differences manifested at the regional level (are easily regenerating genotypes more widely distributed and more abundant than those with low regenerative ability?)? The taxon *R. japonica* var. *compacta* was not considered in the present study because it is rare in the Czech Republic (Pyšek et al., 2002).

MATERIALS AND METHODS

Study species—Representatives of the genus *Reynoutria* Houtt. (syn. *Fallopia* Adans., Polygonaceae) were introduced into Europe as garden ornamentals from eastern Asia and Japan in the 19th century (Conolly, 1977; Sukopp and Sukopp, 1988; Pyšek and Prach, 1993; Sukopp and Starfinger, 1995). They are stout, vigorously growing, clonal perennials that produce a large amount of biomass (Brock, 1995) in vast stands. They are most invasive in riparian and various humanmade habitats and often spread into seminatural vegetation (Pyšek and Prach, 1993). The spread of *Reynoutria* taxa in central Europe is mainly vegetative, through regeneration from rhizome and stem segments. A new plant can originate from a rhizome segment as small as 0.7 g (Brock and Wade, 1992; Brock et al., 1995), and the regeneration rate is generally very high (Child, 1999; Bímová et al., 2003). New shoots have been reported to arise from both rhizome and stem nodes (Brock and Wade, 1992; Beerling et al., 1994; Brock et al., 1995), where lateral buds are located (Adachi et al., 1996).

Members of the genus *Reynoutria* were originally reported not to reproduce sexually within the secondary geographical range because of their almost complete incapability to produce viable seed and/or its inefficient seedling establishment (Bailey et al., 1995). However, genetic variability found in *R.* ×*bohemica*, the hybrid between *R. japonica* var. *japonica* and *R. sachalinensis*, indicates that occasional hybridization might occur (Hollingsworth et al., 1998; Hollingsworth and Bailey, 2000). The species differ in their ecology, establishment success (Brabec and Pyšek, 2000; Bímová et al., 2003), response to control measures (Bímová et al., 2001), and genetic variation (Hollingsworth et al., 1998).

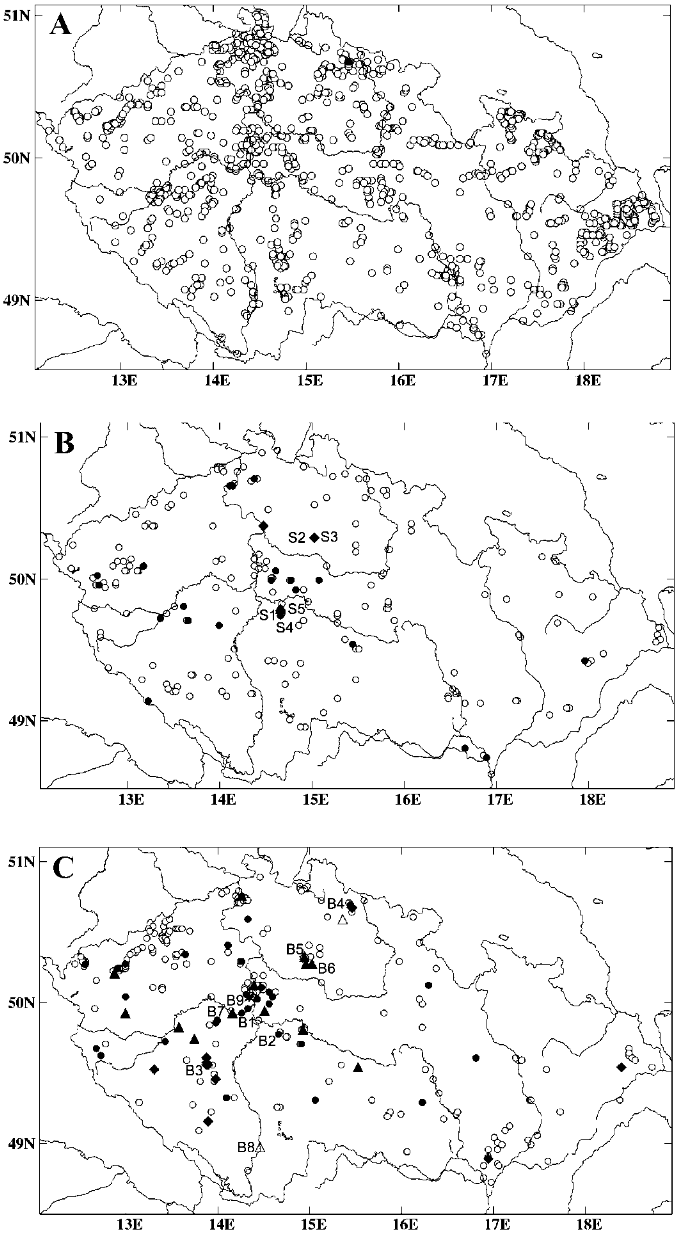

Fig. 1. Distribution of *Reynoutria* taxa and genotypes selected for the present study in the Czech Republic. Different symbols are used for particular genotypes; empty circles are used where the genotypes were not identified. Genotypes used in the study are indicated by their codes (see Table 1 for coordinates of sites where they were sampled). (A) *R. japonica*. Note that this taxon does not exhibit genetic variation in the study territory. (B) *R. sachalinensis*. (C) *R.* ×*bohemica*.

Regeneration experiment—The identity of particular genotypes was confirmed by isozyme analysis performed on clones sampled within the territory of the Czech Republic in 1998–2001 and brought to cultivation in the experimental garden of the Institute of Botany, Academy of Sciences of the Czech Republic, in Průhonice, near Prague (49°59′41″ N, 14°33′56″ E). This research provided an overall picture of the genetic variation within the studied complex of taxa and yielded information about the number of genotypes present in the region and their frequency (Fig. 1). Genotypes used in the present study were chosen on the basis of this knowledge.

Clones representing genotypes used in the study were then sampled in their original localities in the field on 28–29 May 2001 (Table 1). In total, 15 genotypes were obtained (*R.* ×*bohemica*, nine; *R. sachalinensis*, five; *R. japonica*, the single genotype present in the country). Because a previous study

TABLE 1. Source localities of genotypes used in the study. Where the sex was known, *Reynoutria* ×*bohemica* plants were male-fertile (2, 3, 5, 6, 7, 8, 10); among *R. sachalinensis*, nos. 3 and 5 were male-fertile and 1, 2, 4 male-sterile. Number of clones recorded during the field sampling and their mean size are given for genotypes of *R.* ×*bohemica* when the distribution in the landscape was analyzed. See Fig. 2 for regeneration rate of particular genotypes. Stand size and number of clones are not given for *R. sachalinensis* because the results from the experiment were not related to the landscape characteristics for this taxon (the number of genotypes was not sufficient to permit statistical analysis).

Taxon	Genotype	Locality	Latitude	Longitude	Stand size (m²)	Number of clones in the field
R. ×*bohemica*	B1	Černošice (distr. Praha), rubbish dump	49°57′86″	14°19′60″	179.9	24
R. ×*bohemica*	B2	Konopiště (distr. Benešov), along a park road	49°47′12″	14°39′66″	503.8	5
R. ×*bohemica*	B3	Bezděkov (distr. Příbram), 200 m N of the village in a road ditch	49°34′49″	13°52′42″	387.9	9
R. ×*bohemica*	B4	Mařikov (distr. Semily), Jizera river shore	50°40′57″	15°27′26″	50.0	1
R. ×*bohemica*	B5	Luštěnice (distr. Kolín), abandoned garden center	50°19′25″	14°56′44″	95.0	2
R. ×*bohemica*	B6	Vlkava (distr. Mladá Boleslav), abandoned garden	50°16′29″	14°57′50″	37.7	6
R. ×*bohemica*	B7	Karlštejn (distr. Beroun), railway station	49°55′86″	14°09′98″	78.8	8
R. ×*bohemica*	B8	České Budějovice, along a road in allotment area near the Stromovka park	48°57′92″	14°27′63″	674.3	3
R. ×*bohemica*	B9	Praha-Stodůlky, rubbish dump near Hůrky underground station	50°02′56″	14°20′24″	30.0	1
R. sachalinensis	S1	Bystřice (distr. Benešov), bus stop on E55 road	49°44′50″	14°39′91″		
R. sachalinensis	S2	Loučeň (distr. Nymburk), castle park	50°17′15″	15°01′29″		
R. sachalinensis	S3	Loučeň (distr. Nymburk), castle park	50°17′15″	15°01′29″		
R. sachalinensis	S4	Konopiště (distr. Benešov), near fishpond in the castle park	49°47′14″	14°39′62″		
R. sachalinensis	S5	Konopiště (distr. Benešov), clearing in the castle park	49°47′22″	14°39′59″		
R. japonica	J	Mařikov (distr. Semily), Jizera river shore	50°40′57″	15°27′26″		

(Bímová et al., 2003) had shown that regeneration from rhizomes is the major mode of regeneration in the complex of taxa studied, other parts of the plant body were not considered in this study. Rhizomes were collected, brought to Průhonice, and kept at 4°C until 30 May when the experiment was established.

A randomized block design with 10 replicates was used. Rhizome segments were cut from rhizome branches of the same clone, 0.5–2 cm in diameter depending on taxon. Each segment contained one node with two adjacent internodes. They were placed on the soil surface in pots (approximately 13 × 13 × 15 cm in size) filled with garden substrate, watered, and slightly pressed into the soil. Bud position was random to simulate the conditions in the wild. The size of planted segments, termed ''initial rhizome mass,'' was species-specific ($F = 7.73$, df $= 1, 12$; $P < 0.05$). For this reason and because a previous study had shown that the initial rhizome size had no significant effect on the regeneration of the three taxa (Bímová et al., 2003), rhizome segment size was taken into account only when comparing the growth of genotypes within taxa. A single treatment with the rhizome segment placed on the soil surface was adopted, based on the results of a previous study in which this treatment provided good regeneration (Bímová et al., 2003). It also most reasonably simulates the real situation, when rhizome fragments are spread by water and laid on the soil surface along stream banks.

In the present study, regeneration was understood as asexual (vegetative) production of ramets from rhizome segments. Growth was monitored every 2–3 d starting on 30 May (= day 1); the germinated buds were recorded, and the bud was considered germinated if it was swollen and bright red. For each shoot, the day of emergence was recorded and the interval between day 1 and the day of emergence was termed ''emergence time.'' On day 30, regenerated shoots were counted and the percentage of regenerated rhizome segments was recorded and used as a measure of ''regeneration rate'' of each genotype. Shoots were harvested, separated to roots, stems, leaves, and rhizomes, then dried and weighed. No new rhizome growth was realized throughout the duration of the experiment. Mass at harvest was termed ''final shoot mass'' and included dry mass of roots, stems, and leaves produced during experiment.

To estimate the relatedness of hybrid genotypes within *R.* ×*bohemica* to the parental species, the genetic marker data were used to calculate the hybrid index (HI) for each genotype:

$$\mathrm{HI} = (N_s \times 1 + N_{js} \times 0.5 + N_j \times 0)\Big/\sum N,$$

where N_s is the number of alleles typical of *R. sachalinensis*, N_j is the number of alleles typical of *R. japonica*, and N_{js} is the number of nonspecies-specific alleles. The calculation of HI was based on isozyme analysis and the modified method (Reisenberg et al., 1998; Carney et al., 2000) was used for these data in combination with the knowledge of ploidy level (all hybrids were $2n = 66$). Since the chromosome number of hybrids was known, nonspecies-specific alleles were also taken into account. The values of HI obtained by this method are applicable for comparative purposes in the present paper and valid for the introduced geographical range considered here. They cannot be interpreted in terms of the overall genetic variation within the whole complex, however, because the range of the parental genetic characteristics from the native geographical range is unknown.

Field data—To assess whether the clonal growth recorded at the genotype level influences the performance of *R.* ×*bohemica* genotypes in the landscape, the following data were obtained for each genotype: (1) number of localities in the Czech Republic recorded by field sampling and subsequent isozyme analysis of material transferred to the common garden, (2) total area covered by the genotype in the field, and (3) mean clone size (total clone area divided by the number of localities). Variation in these characteristics was related to the regeneration parameters obtained in the experiment described. Note that this analysis was performed only for *R.* ×*bohemica*, because there is only a single genotype of the parent *R. japonica* in the country, and the number of genotypes available for the second parent, *R. sachalinensis*, are too few for an analysis.

Statistical analysis—The regeneration rate of a genotype within taxa is a binomial variable and was therefore generalized using linear models following

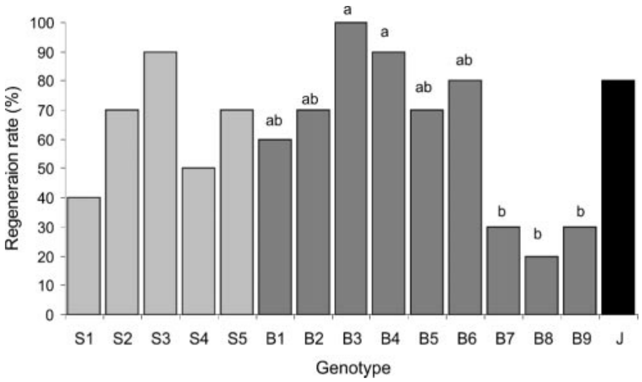

Fig. 2. Percentage of 10 rhizome fragments of each genotype of planted *Reynoutria japonica* (black bar), *R. sachalinensis* (light gray bars) and *R.* ×*bohemica* (dark gray bars) that regenerated after 30 d. For *R.* ×*bohemica*, bars bearing the same letter were not significantly different (*t* test followed by Bonferroni correction). Genotypes of *R. sachalinensis* were not significantly different from each other in their regeneration rate, and only one genotype of *R. japonica* is present in the Czech Republic. See Table 1 for genotype codes and characteristics.

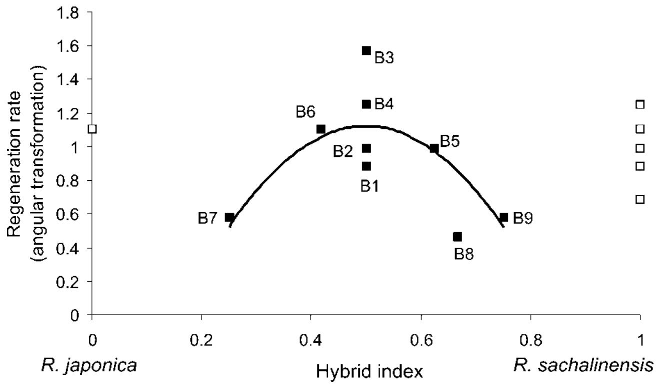

Fig. 3. Relationship between the regeneration rate of *Reynoutria* ×*bohemica* genotypes and the hybrid index showing the relatedness of particular genotypes to parental species. The relationship is described for angular-transformed regeneration rates by the symmetric quadratic equation: regeneration rate = −1.286 + 9.637 (relatedness) − 9.637 (relatedness)^2 (F = 4.156; df = 2, 6; P = 0.07; R^2 = 58.1%). Regeneration rates of parental species are indicated by empty squares.

logistic regression (Jongman et al., 1987). Genotype was used as a fixed effect, and the *t* test followed by Bonferroni correction (Rice, 1989) was used for comparison between particular genotypes within each species. The difference between regeneration rate of taxa, *R.* ×*bohemica* and *R. sachalinensis*, was tested using angular-transformed average proportions of regenerated rhizomes for individual genotypes of *R.* ×*bohemica* and *R. sachalinensis*.

To evaluate whether the final shoot mass was an intrinsic feature of a taxon or genotype, the data were analyzed by ANCOVA with the natural log of shoot mass as the response variable. Rhizomes that failed to regenerate were not included in the analysis. The difference between *R.* ×*bohemica* and *R. sachalinensis* was tested using average values for individual genotypes of *R.* ×*bohemica* and *R. sachalinensis*. Taxon was a fixed effect, and the regeneration rate for each genotype was a covariate. The differences between species-specific genotypes were tested separately for *R.* ×*bohemica* and *R. sachalinensis*, using emergence time and initial rhizome mass for each replicate of each genotype as a covariate. Because the regeneration rate was a specific trait of genotype (Fig. 2), each replicate of a given genotype possessed the same value of regeneration rate. Therefore, the regeneration rate was used as a surrogate for the genotype and treated as a fixed effect. The exceptions were two pairs of genotypes in *R.* ×*bohemica*, which had the same regeneration rate but had different genotypes. These pairs, analyzed separately, were genotypes B9 and B7 with 40% regeneration rate and B2 and B5 with 70% regeneration rate (Fig. 4). The ANCOVAs started by the maximal model, in which each covariate was regressed on a factor with a different intercept and slope. The parameters of this model were inspected, and the least significant term was removed in a deletion test. If the deletion test did not cause a significant increase in deviance, the term was removed. The deletion tests were repeated until only significant terms, creating minimal adequate models, remained (Crawley, 1993, pp. 199–204). The minimal adequate models are presented in Tables 2–4.

To evaluate the relationship between regeneration rate of *R.* ×*bohemica* genotypes and the hybrid index, showing the relatedness of particular genotypes to parental species, angular-transformed proportions of regenerating rhizomes for individual genotypes were the response variables, and the linear and quadratic term of the hybrid index were covariates. The quadratic term was used to test for parabolic shape of the hybrid index, indicating that genotypes distant from both parents have a high regeneration rate that decreases when the hybrid is close to one of the parents. To test the a priori notion that the regeneration rate decreases symmetrically to both parents, the linear and quadratic terms of the hybrid index were constrained to have a numerically the same value with a reverse sign, by specifying the absolute value of the quadratic term equal to the linear term instead of estimating the quadratic term by the maximum likelihood method. The assumption that this simplification of parameters did not result in a significant decrease in the model's explanatory power was tested by assessing whether the fit of the simplified model did not significantly increase the residual deviance of the model.

To evaluate whether the characteristics of genotype regeneration can be used to predict the distribution of *R.* ×*bohemica* in the landscape, the number of localities, total clone area, and mean clone size of each genotype (response variables) were compared with its regeneration rate, final shoot mass, and emergence time (explanatory variables). To achieve a comparable influence in absolute values, the explanatory variables were standardized to have a zero mean and variance of one and analyzed for the response variables using the analysis of deviance table for multiple regression, in which all deviances were assessed by removal from the maximal model (Crawley, 1993, pp. 192–195). Numbers of localities were square-root transformed to obtain an appropriate transformation for count data (e.g., Sokal and Rohlf, 1981, pp. 421–423).

The adequacy of the fitted models was checked by plotting standardized residuals against fitted values and by the normal probability plots of the fitted values (Crawley, 1993). Calculations were made using general linear modeling (McCullagh and Nelder, 1989) in the commercial statistical package GLIM version 4 (Francis et al., 1994).

RESULTS

Effect of genotype on regeneration—In total, pooled across taxa and genotypes, 100 of 150 rhizomes regenerated (66.6%). Six germinated buds (3.0%) later died; of these, five were *Reynoutria sachalinensis* and one was *R.* ×*bohemica*. Some of the rhizomes germinated but did not produce measurable shoot biomass before the experiment was finished; 47 shoots (of N = 90, i.e., 52.2%) of *R.* ×*bohemica*, 26 (N = 50, i.e., 52.0%) of *R. sachalinensis*, and 6 (N = 10, i.e., 60.0%) of *R. japonica* plants exhibited some shoot growth.

Within taxa, there was a significant effect of genotype on regeneration rate in *R.* ×*bohemica* (P = 0.038, df = 8, Wald statistics = 16.34), but not in *R. sachalinensis* (P = 0.220, df = 4, Wald statistics = 5.67). Between taxa, the effect of taxon on average regeneration rate was not significant (F = 0.0008; df = 1, 12; NS). However, there was greater variation in regeneration rate of the hybrid (coefficient of variation 50.3%, N = 9) than of *R. sachalinensis* (30.5%, N = 5).

Regeneration rates had a distinct pattern with respect to the genetic relatedness of genotypes to parental taxa. Genotypes

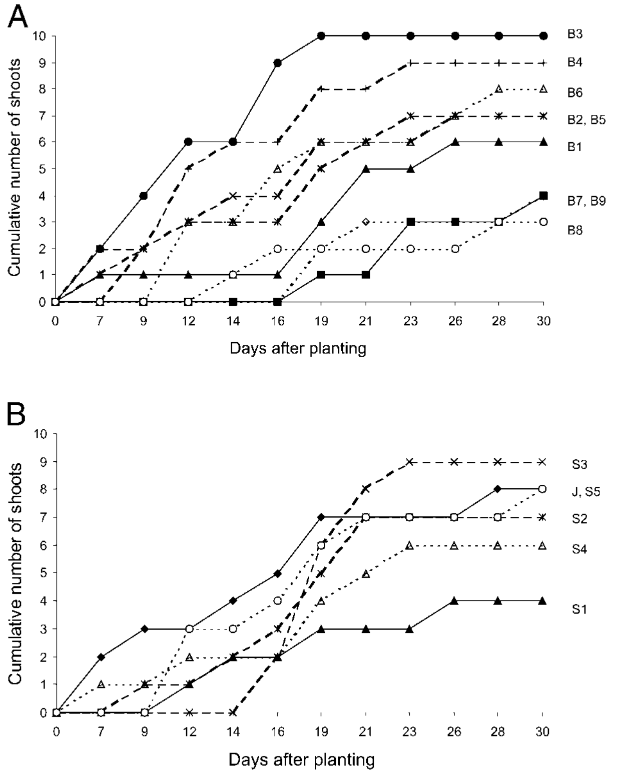

Fig. 4. Cumulative increase in the number of regenerated shoots over the course of the experiment. (A) *Reynoutria* ×*bohemica*. (B) *R. japonica* and *R. sachalinensis*. The abundance of genotypes in the landscape, ascertained during field research, is indicated by solid (common genotypes with more than 10 localities), dashed (5–10 localities), and dotted (less than five localities) lines. See Table 1 for genotype codes and characteristics.

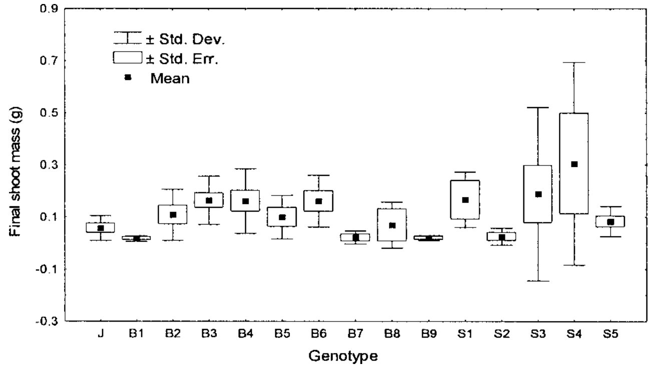

Fig. 5. Box-and-whisker plot of dry shoot mass (stem, leaves, and roots) produced after 30 d for each genotype of *Reynoutria japonica*, *R. sachalinensis*, and *R.* ×*bohemica*. Mean value is shown for each genotype. Number of regenerated shoots in particular genotypes: J, 8; S1, 4; S2, 7; S3, 9; S4, 6; S5, 8; B1, 6; B2, 7; B3, 10; B4, 9; B5, 7; B6, 8; B7, 4; B8, 3; B9, 4.

with genetic characteristics intermediate between the parents tended to have a high regeneration rate, which symmetrically decreased when the hybrid index was very low or very high, indicating closer similarity of genetic markers to one of the parents (Fig. 3).

Shoots of *R.* ×*bohemica* emerged first (day 14.5 ± 5.2, $N = 47$, CV = 35.9%) (Fig. 4A) followed by *R. japonica* (day 16.8 ± 6.0, $N = 6$, CV = 35.5%) and *R. sachalinensis* (18.7 ± 4.9, $N = 36$, CV = 26.5%) (Fig. 4B). The difference between taxa ($P = 0.013$, Wald statistics = 8.54) as well as between particular genotypes ($P = 0.009$, Wald statistics = 29.22) was statistically significant.

Factors affecting shoot growth—Final shoot mass after 30 d of growth varied between taxa (Fig. 5). Regeneration growth, measured as final shoot mass, was faster in *R. sachalinensis* than *R.* ×*bohemica*, as indicated by a significant increase in log shoot mass between taxa (Table 2). However, the genotype affected final shoot mass only in *R.* ×*bohemica*, as indicated by a positive and significant regression slope of log shoot mass on regeneration rate (Table 2). The genotype did not affect regeneration rate in *R. sachalinensis*, for which the regression slope of log shoot mass on regeneration rate was nonsignificant ($F = 0.19$; df = 1, 11; NS). The fact that genotype significantly affected shoot growth only in *R.* ×*bohemica* is consistent with the previous finding that the regeneration rate was significantly affected by genotype in *R.* ×*bohemica* but not in *R. sachalinensis*.

A significant positive relationship between the genotype final shoot mass and its regeneration rate in *R.* ×*bohemica* was further confirmed by the analysis of individual genotypes of the hybrid. There was a significant increase in shoot growth from the genotype with a low regeneration rate (30%, genotype B8) to that with intermediate (60%, genotype B1) to those with high regeneration rates (80, 90, and 100%, genotypes B6, B4, and B3, respectively; Table 3). Late-emerging genotypes of *R.* ×*bohemica* produced lighter shoots (regression slope of log shoot mass on emergence time was negative and significant, Table 3). Genotypes with high initial rhizome mass produced heavier shoots, but this was true only for those genotypes with a low regeneration rate (regression slope of log shoot mass on initial rhizome mass was significant only for the genotype B8 with the lowest regeneration rate 30%, Table 3). The shoot mass in genotypes B9 and B7 (40% regeneration rate) and B2 and B5 (70% regeneration rate), respectively, with each pair analyzed separately, did not show significant

TABLE 2. Factors affecting the final shoot mass of *Reynoutria* ×*bohemica* vs. *R. sachalinensis*. The overall model of ANCOVA explains R^2 = 40.82% of variance.

Parameter	Estimate	SE	df	F	P
Common intercept	−4.599	0.8092			
(*R.* ×*bohemica*)[a] × (regeneration rate)[b]	0.029	0.0119	1, 12	6.043	<0.05
R. sachalinensis[a]	+2.435[c]	0.8857	1, 12	7.556	<0.05
Total			2, 11	3.793	0.056

[a] Factor.
[b] Covariate.
[c] Increase compared to *R.* ×*bohemica*.

TABLE 3. Factors affecting final shoot mass of individual genotypes of *Reynoutria* ×*bohemica*. The overall model of ANCOVA explains R^2 = 70.0% of variance. Genotype-specific regeneration rate was used as a surrogate of genotype. Two pairs of genotypes with the same regeneration rate were analyzed separately (see Material and Methods for details).

Parameter	Estimate	SE	df	*F*	*P*
Common intercept	−5.352	1.010			
Emergence time[a]	−0.066	0.026	1, 26	6.255	<0.05
Regeneration rate[b] 60% (genotype B1)	+2.395[c]	1.034	2, 27	18.91	<0.000
Regeneration rate[b] 80–100% (B6, B4, and B3)	+4.249[c]	0.956			
(Regeneration rate 30%)[b] × (initial rhizome mass)[a]	1.031	0.302	1, 26	11.61	<0.01
Total			4, 25	14.59	<0.000

[a] Covariate.

[b] Factor.

[c] Increase compared to 30% regeneration rate (genotype B8).

differences for genotype, initial rhizome mass, or emergence time.

A nonsignificant effect of genotype on final shoot mass in *R. sachalinensis*, as revealed in the between-taxa analysis (Table 2), was confirmed in the analysis of individual genotypes within this species (Table 4). As in *R.* ×*bohemica*, final shoot mass increased with initial rhizome mass (regression slope of log shoot mass on rhizome mass was positive and highly significant, Table 4) and decreased with late emergence time (regression slope of log shoot mass on emergence time was negative and significant, Table 4). However, the effect of genotype was not significant ($F = 1.237$; df = 4, 23; NS).

Effect of genotype regeneration characteristics on distribution in the landscape—Mean clone size recorded in the field for individual genotypes of *R.* ×*bohemica* was not significantly related to final shoot mass and genotype regeneration rate, but there was a marginally significant effect of emergence time (Table 5, Fig. 6). All predictors were nonsignificant ($P > 0.3$) when predicting the number of localities and total area of clones recorded in the field. Clone area and the number of localities were significantly correlated ($r = 0.96$), but the mean clone size was not correlated with either clone area ($r = 0.08$) or number of localities ($r = 0.009$).

DISCUSSION

Literature on alien plants suggests that the success of invaders in exploiting new environments is often based on the use of phenotypic plasticity rather than genetic change (Levin, 2000). Niche breadth of invaders along environmental gradients seems to be more often the result of phenotypic plasticity than correlated with genetic variation within populations (Sultan, 1987). However, genetic change in ecologically marginal populations allows the exploitation of habitats that otherwise would be off limits, thus promoting invasion (Rejmánek et al., 2003). The role of adaptive evolution following the colonization of new environment was recently highlighted for both plants and animals (Ellstrand and Schierenbeck, 2000; Daehler and Carino, 2001; Lee, 2002). The complex of polyploid *Reynoutria* taxa invading Europe provides a unique opportunity to study the effect of genetic variation on invasion success. Although ecological consequences of polyploidy are still not clear, polyploids tend to have more genetic diversity and occur across a large range of habitats with respect to stress, competition, and disturbance (Rejmánek et al., 2003). In the case of *Reynoutria*, a species genetically uniform in the introduced geographical range (Hollingsworth et al., 1998) hybridizes with its alien congener, which exhibits limited genetic variation, and genetically more variable progeny is produced (Bailey and Stace, 1992; Child, 1999). The present paper shows that this process has ecological consequences detectable at the regional level.

We found significant differences in the regeneration rate of individual genotypes of *R.* ×*bohemica*. Easily regenerating genotypes also grew faster, indicating that measures of regeneration success are closely associated. Emergence time affected the regeneration rate but only in genotypes with low regeneration rates. It also appears that poorly regenerating genotypes grow better if they regenerate from a larger rhizome fragment, a characteristic that is irrelevant in genotypes capable of high regeneration. A genotype with poor regeneration capability is therefore dependent also on other characteristics, such as early germination of rhizome buds and amount of reserves provided by the rhizome fragments, while those with superior regeneration do well regardless of these characteristics. These results suggest that major characteristics contributing to the fitness of a plant spread almost exclusively by vegetative means (i.e., early and effective regeneration and subsequent fast growth) act in concert and are an intrinsic feature of each genotype. It should be also noted that a potential ‘‘maternal’’ effect of the local environment could be involved in explaining variation observed among genotypes. However, the vast majority of genotypes were sampled from comparable nutrient rich habitats, where these species typically

TABLE 4. Factors affecting the final shoot mass of individual genotypes of *Reynoutria sachalinensis*. The overall model of ANCOVA explains $R^2 = 51.1\%$ of variance.

Parameter	Estimate	SE	df	*F*	*P*
Common intercept	−2.444	0.8504			
Emergence time[a]	−0.109	0.0408	1, 24	7.17	<0.05
Initial rhizome mass[a]	0.304	0.0722	1, 24	17.79	<0.001
Total			2, 23	12.01	<0.001

[a] Covariate.

TABLE 5. Analysis of deviance table for multiple regression with all deviances of mean clone size of *Reynoutria* ×*bohemica* from the explanatory variables assessed by removal from the maximal model.

Explanatory variable	Deviance	df	*F*	*P*
Shoot mass	127 093	1, 6	2.567	0.16
Regeneration rate	2853	1, 6	0.057	0.82
Emergence time	174 066	1, 6	3.515	0.11

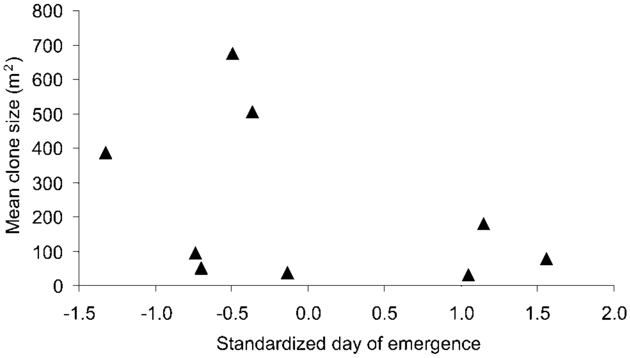

Fig. 6. The relationship between mean clone size of *Reynoutria* ×*bohemica* genotypes in the landscape and the standardized value of their day of emergence in the experiment.

grow, and there was a little variation in climatic conditions among regions. We therefore believe that the results reflect intrinsic features of the genotypes and that the bias resulting from a ''maternal'' local environment is minor.

In a previous study showing differences in regeneration between taxa, the hybrid *R.* ×*bohemica* performed better than the parents (Bímová et al., 2003). Here, we focused on the genotype level, and differences between taxa were taken only marginally into account. No significant differences in regeneration rate were found either between taxa or between genotypes within *R. sachalinensis*. It must be borne in mind, however, that the lack of significant results at the taxa level may be, to some extent, explained by the low number of *R. sachalinensis* genotypes available for statistical analysis. The present paper also elucidates rather inconsistent results of previous studies comparing particular taxa in the UK (Child, 1999) and the Czech Republic (Bímová et al., 2003). The results may vary with respect to the regeneration hierarchy of particular taxa within the complex because of the genetic distance of the hybrid from the parents. Hence, the regeneration potential may depend on which genotype of *R.* ×*bohemica* was used in the particular experiment.

Our results indicate that regeneration characteristics, and hence the genetic identity, may be related to the extent of *R.* ×*bohemica* invasion at a regional scale. The size of a clone established in the field seems to depend on its ability to emerge soon after the rhizome was deposited on the soil surface. This relationship was only marginally significant since there were only a limited number of genotypes available for statistical analysis and the success of a rhizome fragment in the wild also depends on other circumstances that were not addressed by the present study (e.g., resistence of rhizome fragments to drought, their buoyancy, and response to microsite conditions). In addition, other factors bias the observed pattern, namely, the duration of a clone in a site. There is evidence that in *Reynoutria* species, some clones have persisted for more than a century in the same site while the introduction of others might have been quite recent (Pyšek et al., 2001). The time over which clones were allowed to expand is an important determinant of their size. Another factor impossible to take into account in this study is the effect of local disturbances and occasional control measures, which also increase the variation in clone size. Knowledge of exact dates of introduction of a particular clone to the given site and of past events is beyond the reach of most such studies, reflecting the limitation in using the post-hoc character of studies on invasive plants. Nevertheless, our results justify speculation about the role regeneration plays in shaping invasion potential.

It is not surprising that, of the measures used to characterize the invasion at the landscape scale—number of localities, total area occupied, and mean clone size—the latter characteristic provided the best results because it integrates the capability for both long-distance dispersal and local spread, which are both important determinants of invasion success.

The high genotype variability found within *R.* ×*bohemica* taxa suggests that under favorable conditions, hybridization between *R. japonica* and *R. sachalinensis* does occur in the introduced geographical range (B. Mandák et al., Institute of Botany Průhonice, unpublished data). Until recently, it was believed that although seed was produced by *R. japonica* in the Czech Republic, hybridization was mostly due to pollination by a related species, *Fallopia aubertii*. Even when *R. japonica* is pollinated by *R. sachalinensis*, progeny does not survive as a result of low temperatures at the end of the growing period (Beerling et al., 1994). A rather low number of genotypes within *R.* ×*bohemica* suggests selection by environmental conditions against progeny originating by generative reproduction. The origin of novel genotypes has been unknown until now; in both the native and introduced geographical ranges they can originate by (1) hybridization between *R. japonica* var. *japonica* and some of the *R. sachalinensis* genotypes or (2) crossing within the range of *R.* ×*bohemica* taxa. Consequently, novel genotypes can originate in the introduced geographical range or be introduced from the native geographical range; the relative importance of both events requires further study.

Successful sexual reproduction is rare, but the evidence that it does occur in *Reynoutria* taxa has important ecological consequences. Novel genotypes resulting from this process differ in their regeneration characteristics; regeneration is a crucial stage in species spread by water, with rhizome fragments laid on the shores of streams, and this mode of spread becomes even more efficient during the floods that occur regularly in central Europe. Our results suggest that some hybrids consist of novel genotypes with higher fitness than that of their parental taxa (as measured by regeneration features) and supports the hypothesis that hybridization increases the invasion potential of *Reynoutria* taxa in their introduced geographical range. Positive effects of hybridization on invasion potential have been reported (Ellstrand and Schierenbeck, 2000; Perry et al., 2001), possibly as a result of increased genetic variation, new gene interactions or the transfer of favorable genes (Lee, 2002). Examples of adaptation through hybridization are also known, e.g., higher hybrid fitness in habitats where parental taxa do not occur (*Artemisia*, *Iris*) or adaptations to changing environment conditions (*Geospiza*; Arnold, 1997).

That successful regeneration is associated with fast growth, providing the plant with an effective means to occupy space, and that these species do not retreat from sites once occupied during succession (Pyšek et al., 2001) suggest that early regeneration might determine the success of invasive *Reynoutria* taxa not only locally but also at a regional scale. In taxa relying almost exclusively on vegetative reproduction, new hybrid combinations are fixed by clonal growth and may become widespread (Room, 1990; Lee, 2002). Compared to other mechanisms capable of fixing heterotic genotypes originating through hybridization (agamospermy, allopolyploidy, permanent translocation heterozygosity), clonal spread is the most frequent, being involved in 32% of 28 documented cases (Ellstrand and Schierenbeck, 2000). A rare hybridization event may thus represent a permanent addition of highly invasive genotypes to the genetic makeup of the complex, and, as pointed out by Ellstrand and Schierenbeck (2000), the fitness boost afforded by fixed heterozygosity may be all that is necessary to make a hybrid lineage invasive. Hybridization therefore generates new genotypes with invasion potential that can exceed that of their parents and represent an additional threat to the native vegetation.

LITERATURE CITED

ABBOTT, R. J. 1992. Plant invasions, interspecific hybridisation and the evolution of new plant taxa. *Trends in Ecology and Evolution* 7: 401–405.

ADACHI, N., I. TERASHIMA, AND M. TAKAHASHI. 1996. Central die-back of monoclonal stands of *Reynoutria japonica* in an early stage of primary succession on Mount Fuji. *Annals of Botany* 77: 477–486.

ARNOLD, M. L. 1997. Natural hybridisation and evolution. Oxford University Press, Oxford, UK.

ASHTON, P. J., AND D. S. MITCHELL. 1989. Aquatic plants: patterns and modes of invasion, attributes of invading species and assessment of control programmes. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [eds.], Biological invasions: a global perspective, 111–154. John Wiley and Sons, Chichester, UK.

BAILEY, J. P., L. E. CHILD, AND M. WADE. 1995. Assessment of the genetics variation of British populations of *Fallopia japonica* and its hybrid *Fallopia* × *bohemica*. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [eds.], Plant invasion—general aspects and special problems, 141–150. SPB Academic, Amsterdam, Netherlands.

BAILEY, J. P., AND C. A. STACE. 1992. Chromosome number, morphology, pairing, and DNA values of species and hybrids in the genus *Fallopia* (Polygonaceae). *Plant Systematics and Evolution* 180: 29–52.

BAKER, H. G. 1965. Characteristics and modes of origin of weeds. *In* H. G. Baker and C. L. Stebbins [eds.], The genetics of colonizing species, 147–169. Academic Press, New York, New York, USA.

BAKER, H. G. 1986. Patterns of plant invasions in North America. *In* H. A. Mooney and J. A. Drake [eds.], Ecology of biological invasions of North America and Hawaii, 44–57. Springer, New York, New York, USA.

BEERLING, D. J., J. P. BAILEY, AND A. P. CONOLLY. 1994. *Fallopia japonica* (Houtt.) Ronse Decraene (*Reynoutria japonica* Houtt.; *Polygonum cuspidatum* Sieb. & Zucc.). *Journal of Ecology* 82: 959–979.

BÍMOVÁ, K., B. MANDÁK, AND P. PYŠEK. 2001. Experimental control of *Reynoutria* congeners: a comparative study of a hybrid and its parents. *In* G. Brundu, J. Brock, I. Camarda, L. Child, and M. Wade [eds.], Plant invasion: species ecology and ecosystem management, 283–290. Backuys, Leiden, Netherlands.

BÍMOVÁ, K., B. MANDÁK, AND P. PYŠEK. 2003. Experimental study of vegetative regeneration in four invasive *Reynoutria* taxa (Polygonaceae). *Plant Ecology* 166: 1–16.

BRABEC, J., AND P. PYŠEK. 2000. Establishment and survival of three invasive taxa of the genus *Reynoutria* (Polygonaceae) in mesic mown meadows: a field experimental study. *Folia Geobotanica* 35: 27–42.

BROCK, J. H. 1995. Standing crop of *Reynoutria japonica* in the autumn of 1991 in the United Kingdom. *Preslia* 66: 337–343.

BROCK, J. H., L. E. CHILD, L. C. DE WAAL, AND M. WADE. 1995. The invasive nature of *Fallopia japonica* is enhanced by vegetative regeneration from stem tissues. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [eds.], Plant invasion—general aspects and special problems, 131–139. SPB Academic, Amsterdam, Netherlands.

BROCK, J. H., AND M. WADE. 1992. Regeneration of Japanese knotweed (*Fallopia japonica*) from rhizome and stems: observation from greenhouse trials. *In* Proceedings IXth International Symposium on the Biology of Weeds, 85–94. European Weed Research Society, Dijon, France.

CARNEY, S. E., K. A. GARDNER, AND L. H. REISENBERG. 2000. Evolutionary changes over the fifty-year history of a hybrid population of sunflowers (*Helianthus*). *Evolution* 54: 462–474.

CHILD, L. E. 1999. Vegetative regeneration and distribution of *Fallopia japonica* and *Fallopia bohemica*: implications for control and management. Ph.D. thesis, Loughbrough University, Loughborough, UK.

CONOLLY, A. P. 1977. The distribution and history on the British Isles of some alien species of *Polygonum* and *Reynoutria*. *Watsonia* 11: 291–311.

CRAWLEY, M. J. 1993. GLIM for ecologists. Blackwell Scientific, Oxford, UK.

CRAWLEY, M. J. 1997. Plant ecology, 2nd ed. Blackwell Scientific, Oxford, UK.

CRAWLEY, M. J., P. H. HARVEY, AND A. PURVIS. 1996. Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London, B* 351: 1251–1259.

CRONK, Q. C. B., AND J. L. FULLER. 1995. Plant invaders: the threat to natural ecosystems. Chapman and Hall, London, UK.

DAEHLER, C., AND D. A. CARINO. 2001. Hybridization between native and alien plants and its consequences. *In* J. L. Lockwood and M. L. McKinney [eds.], Biotic homogenization, 81–102. Kluwer Academic/Plenum, New York, New York, USA.

DAEHLER, C. C., AND D. R. STRONG. 1994. Variable reproductive output among clones of *Spartina alterniflora* (Poaceae) including San Francisco Bay, California: the influence of herbivory, pollination and establishment rate. *American Journal of Botany* 81: 307–313.

DAEHLER, C. C., AND D. R. STRONG. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. *Biological Conservation* 78: 51–58.

ELLSTRAND, N. C., AND K. SCHIERENBECK. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Science* 97: 7043–7050.

FRANCIS, B., M. GREEN, AND C. PAYNE. 1994. The GLIM system. Release 4 manual. Clarendon, Oxford, UK.

GROTKOPP, E., M. REJMÁNEK, AND T. L. ROST. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159: 396–419.

HIGGINS, S. I., D. M. RICHARDSON, R. M. COWLING, AND T. H. TRINDER-SMITH. 1999. Predicting the landscape distribution of invasive alien plants and their threat to native plant diversity. *Conservation Biology* 13: 303–313.

HOLLINGSWORTH, M. L., AND J. P. BAILEY. 2000. Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese Knotweed). *Botanical Journal of the Linnean Society* 133: 463–472.

HOLLINGSWORTH, M. L., P. M. HOLLINGSWORTH, G. I. JENKINS, AND J. P. BAILEY. 1998. The use of molecular markers to study patterns of genotypic diversity in some invasive alien *Fallopia* ssp. (Polygonaceae). *Molecular Ecology* 7: 1681–1691.

JONGMAN, R. H., C. J. F. TER BRAAK, AND O. F. R. VAN TONGEREN. 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen, Netherlands.

KLIMEŠ, L., J. KLIMEŠOVÁ, R. HENDRIKS, AND J. VAN GROENENDAEL. 1997. Clonal plant architecture: a comparative analysis of form and function. *In* H. de Kroon and J. van Groenendael [eds.], The ecology and evolution of clonal plants, 1–30. Backhuys, Leiden, Netherlands.

LEE, C. E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* 17: 386–391.

LEVIN, D. A. 2000. The origin, expansion and demise of plant species. Oxford University Press, Oxford, UK.

LONSDALE, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. Chapman and Hall, London, UK.

MCNEELY, J. A., H. A. MOONEY, L. E. NEVILLE, P. SCHEI, AND J. K. WAAGE [EDS.]. 2001. Global strategy on invasive alien species. IUCN (International Union for Conservation of Nature and Natural Resources) on behalf of the Global Invasive Species Programme, Gland, Switzerland and Cambridge, UK.

MITCHELL, D. S., AND B. GOPAL. 1991. Invasion of tropical freshwaters by alien aquatic plants. *In* P. S. Ramakrishnan [ed.], Ecology of biological invasion in the tropics, 139–155. International Scientific Publications, New Delhi, India.

NOBLE, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [eds.], Biological invasions: a global perspective, 301–313. John Wiley and Sons, Chichester, UK.

PERRY, W. L., J. L. FEDER, G. DWYER, AND D. M. LODGE. 2001. Hybrid zone dynamics and species replacement between *Orconectes* crayfishes in a northern Wisconsin lake. *Evolution* 55: 1153–1166.

PYŠEK, P. 1997. Clonality and plant invasions. *In* H. de Kroon and J. van Groenendael [eds.], The ecology and evolution of clonal plants, 405–427. Backhuys, Leiden, Netherlands.

PYŠEK, P., B. MANDÁK, T. FRANCÍRKOVÁ, AND K. PRACH. 2001. Persistence of stout clonal herbs as invaders in the landscape: a field test of historical records. *In* G. Brundu, J. Brock, I. Camarda, L. Child, and M. Wade [eds.], Plant invasions: species ecology and ecosystem management, 235–244. Backhuys, Leiden, Netherlands.

PYŠEK, P., AND K. PRACH. 1993. Plant invasions and the role of riparian habitats—a comparison of four species alien to central Europe. *Journal of Biogeography* 20: 413–420.

PYŠEK, P., AND A. PYŠEK. 1995. Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. *Journal of Vegetation Science* 6: 711–718.

PYŠEK, P., J. SÁDLO, AND B. MANDÁK. 2002. Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186.

REISENBERG, L. H., S. J. H. BAIRD, AND A. M. DESROCHERS. 1998. Patterns of mating in wild sunflower hybrid zones. *Evolution* 52: 713–726.

REJMÁNEK, M. 1995. What makes a species invasible? *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [eds.], Plant invasions: general aspects and special problems, 3–13. SPB Academic, Amsterdam, Netherlands.

REJMÁNEK, M. 1996. A theory of seed plant invasiveness: the first sketch. *Biological Conservation* 78: 171–181.

REJMÁNEK, M. 2000. Invasive plants: approaches and predictions. *Australian Journal of Ecology* 25: 497–506.

REJMÁNEK, M., AND S. REICHARD. 2001. Predicting invaders. *Trends in Ecology and Evolution* 16: 545–546.

REJMÁNEK, M., D. M. RICHARDSON, S. L. HIGGINS, M. J. PITCAIRN, AND E. GROTKOPP. 2003. Ecology of invasive plants: state of the art. *In* H. A. Mooney, J. A. McNeelly, L. Neville, P. J. Schei, and J. Waage [eds.], Invasive alien species: searching for solutions. Island Press, Washington, D.C., USA.

RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.

RICHARDSON, D. M., AND R. M. COWLING. 1992. Why is mountain fynbos invasible, and which species invade? *In* B. W. Van Wilgen, D. M. Richardson, F. J. Kruger, and B. J. van Hensbergen [eds.], Swartboskloof—fire in South African mountain fynbos, 161–179. University of Cape Town, Cape Town, Republic of South Africa.

RICHARDSON, D. M., P. PYŠEK, M. REJMÁNEK, M. G. BARBOUR, F. D. PANETTA, AND C. J. WEST. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107.

ROOM, P. M. 1990. Ecology of a simple plant-herbivore system: biological control of *Salvinia*. *Trends in Ecology and Evolution* 5: 74–79.

ROY, J. 1990. In search of the characteristics of plant invaders. *In* F. di Castri, A. J. Hansen, and M. Debussche [eds.], Biological invasions in Europe and the Mediterranean basin, 335–352. Kluwer Academic, Dordrecht, Netherlands.

SAXENA, K. G. 1991. Biological invasions in the Indian subcontinent: review of invasion by plants. *In* P. S. Ramakrishnan [ed.], Ecology of biological invasion in the tropics, 53–73. International Scientific Publications, New Delhi, India.

SOKAL, R., AND F. J. ROHLF. 1981. Biometry. Freeman, San Francisco, California, USA.

SUKOPP, H., AND U. STARFINGER. 1995. *Reynoutria sachalinensis* in Europe and in the Far East: a comparison of the species ecology in its native and adventive distribution range. *In* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade [eds.], Plant invasions—general aspects and special problems, 151–159. SPB Academic, Amsterdam, Netherlands.

SUKOPP, H., AND U. SUKOPP. 1988. *Reynoutria japonica* Houtt. in Japan und in Europa. *Veröffentlichungen Geobotanischer Institut ETH, Stiftung Rübel Zürich* 98: 354–372.

SULTAN, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* 21: 127–178.

VAN GROENENDAEL, J., AND H. DE KROON. 1990. Regulation and function of clonal growth in plants: an evaluation. *In* J. van Groenendael and H. de Kroon [eds.], Clonal growth in plants: regulation and function, 177–186. SPB Academic, The Hague, Netherlands.

VILA, M., E. WEBER, AND C. M. D'ANTONIO. 2000. Conservation implications of invasion by plant hybridization. *Biological Invasions* 2: 207–217.

WEBER, E. F. 1997. The alien flora of Europe: a taxonomic and biogeographic overview. *Journal of Vegetation Science* 8: 565–572.

WELLS, M. J., R. J. POYNTON, A. A. BALSINHAS, C. F. MUSIL, H. JOFFE, E. VAN HOEPEN, AND S. K. ABBOTT. 1986. The history of introduction of invasive alien plants to southern Africa. *In* I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar [eds.], The ecology and management of biological invasions in Southern Africa, 21–35. Oxford University Press, Cape Town, Republic of South Africa.

WILLIAMSON, M. 1996. Biological invasions. Chapman and Hall, London, UK.

WILLIAMSON, M. 2001. Can the impacts of invasive species be predicted? *In* R. H. Groves, F. D. Panetta, and J. G. Virtue [eds.], Weed risk assessment, 20–33. CSIRO, Collingwood, Victoria, Australia.

WILLIAMSON, M., AND A. FITTER. 1996. The varying success of invaders. *Ecology* 77: 1661–1666.