

# Invasive plants: approaches and predictions

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**Abstract** Successful management of invasive weeds will require active attempts to prevent new introductions, vigilant detection of nascent populations and persistent efforts to eradicate the worst invaders. To achieve these objectives, invasion ecology offers five groups of complementary approaches. (i) Stochastic approaches allow probabilistic predictions about potential invaders based on initial population size, residence time and number of introduction attempts. (ii) Empirical taxon-specific approaches are based on previously documented invasions of particular taxa. (iii) Evaluations of the biological characters of non-invasive taxa and successful invaders give rise either to general or to habitat-specific screening procedures. (iv) Evaluation of environmental compatibility helps to predict whether a particular plant taxon can invade specific habitats. (v) Experimental approaches attempt to tease apart intrinsic and extrinsic factors underlying invasion success. An emerging theory of plant invasiveness based on biological characters has resulted in several rather robust predictions which are presented in this paper.

**Key words:** invader attributes, eradication, invasion ecology, invasions, weeds.

## INTRODUCTION

Since the publication of Elton's (1958) classic *The Ecology of Invasions by Animals and Plants*, invasion biology, as a new discipline, has been developing: first slowly (Salisbury 1961; Baker & Stebbins 1965) and later explosively (Williamson 1996; Vitousek *et al.* 1997; Sandlund *et al.* 1999). The scope of contemporary invasion biology is inevitably broad, ranging from essentially theoretical studies (Shigesada & Kawasaki 1997) to practical recommendations of how to deal with particular species and ecosystems (Groves *et al.* 1995; Bossard *et al.* 2000).

Invasive taxa (spreading where they are not native) represent a subset of naturalized taxa (non-native, forming sustainable populations without direct human help but not necessarily spreading). This distinction is important because not all naturalized taxa reported in local floras (e.g. Du Puy 1993; Webb *et al.* 1988; Gould *et al.* 1998) are *invasive* taxa. Not all naturalized plant taxa and even not all invaders are weeds (pests). Many weeds are colonizers (taxa appearing early in vegetation succession), either native or non-native (see Fig. 1; and Fig. 1 of di Castri 1990 and Fig. 3.1 of Williamson 1996). A majority of weedy species in Europe and Mexico are native species (Williamson 1996; Espinosa & Sarukhán 1997). In contrast, the majority of weedy species in Australia, the USA, New Zealand and South Africa are non-native species. Since introduced plant taxa differ in their invasiveness and impact, we should be able to prioritize weed surveillance and management actions. However, what guidelines should direct this prioritization? Are there some useful generalizations that contemporary invasion biology can provide?

There are three fundamental management objectives when dealing with invasive weeds and these are as follows:

- A prevention/exclusion;
- B early detection/rapid assessment; and
- C control/containment/eradication.

How to meet these objectives, in particular within political and economic limitations, is more a question of policy and technology. First, however, we need to know (a) what kind of species we should prevent from entering a country, (b) what kind of new species we should look for and where, and (c) which of the detected exotics we should preferentially control or eradicate. Needless to say, adequate taxonomic training is a prerequisite for achievement of all three objectives.

To achieve objective (b), proper field experience and relevant sampling techniques (e.g. adaptive sampling, Thompson & Seber 1996) are necessary. Early detection of the presence of an invasive organism can make the difference between being able to employ feasible offensive strategies (eradication) and the necessity of retreating to defensive strategies with their long-term financial commitments. Our analyses of available data on eradication attempts by the California Department of Food and Agriculture (Fig. 2, and unpublished data on another 14 noxious weedy species) clearly illustrate this point. Obviously, realistic management options for infestations of <1 ha, 1–100 ha and >100 ha can be very different. It is easier and less expensive to eradicate small infestations (Fig. 2; Rozenfelds *et al.* 1999; Smith *et al.* 1999).

To achieve all three objectives, but mainly (a) and (b), invasion ecology offers five, largely complementary, approaches.

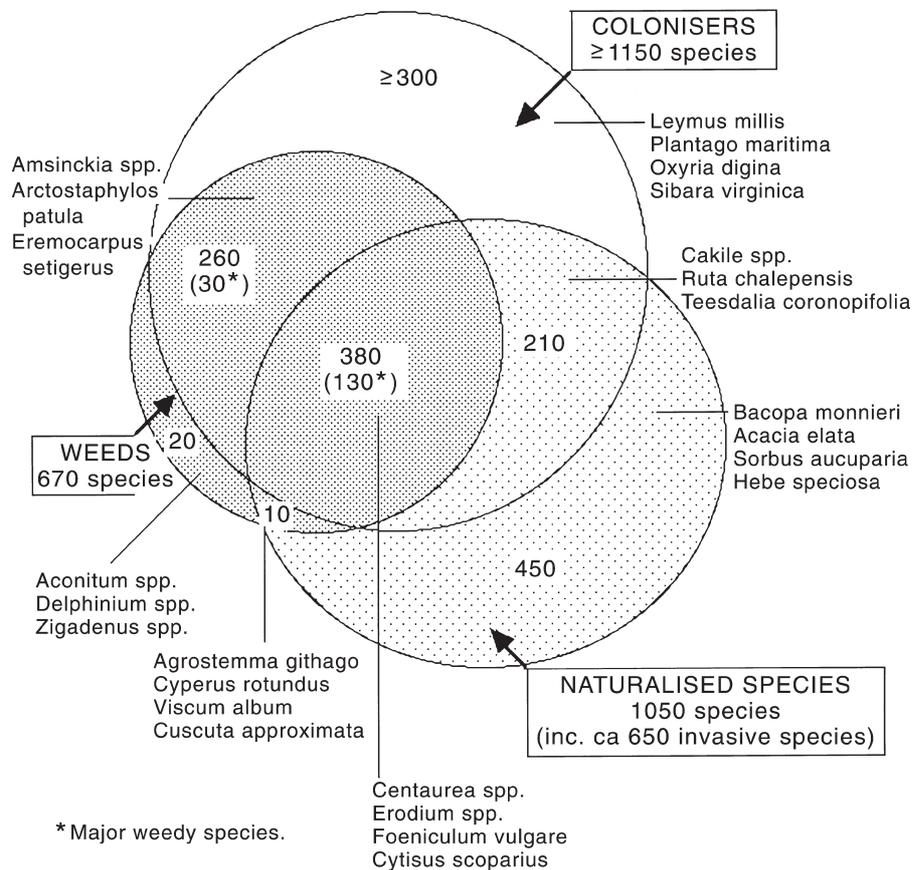
1. Stochastic (roles of inoculum sizes and residence times).
2. Empirical, taxon-specific (does a particular species invade elsewhere?).
3. Evaluation of biological characters responsible for, or associated with, invasiveness.
4. Evaluation of habitat compatibility.
5. Experiments.

**1. STOCHASTIC APPROACH**

The most robust but admittedly trivial, generalization in invasion ecology is that the probability of invasion success increases with initial population size and with the number of introduction attempts. This was documented, for example, by analyses of success rates in biological control of insects by insects in Canada (Williamson 1989) and successful introductions of exotic birds in New Zealand (Dawson 1984 in Williamson 1996) and Australia (Newsome & Noble 1986). The same ‘gambling opportunity’ (Egler 1983) seems to be true for exotic plants as well. For example, there is a highly significant ( $r = 0.44$ ,  $P < 0.001$ ) correlation between the number of records of spontaneous occurrences and the number of plantations of 57 *Eucalyptus* species introduced to Southern

Africa (Rejmánek & Richardson, unpublished data). This corroborates our observations in California: only the two most commonly cultivated species (*Eucalyptus globulus* and *Eucalyptus camaldulensis*) are somewhat invasive. In south-eastern Australia, Mulvaney (unpublished data) found a strong correlation between the amount of planting and the probability that a woody species has become naturalized. Residence time is also important. In Venezuela, for example, there is a highly significant correlation ( $r = 0.67$ ,  $P < 0.001$ ) between the log of the total number of known localities and minimum residence time (years since the first record in the country) for 116 exotic grass species (Rejmánek, unpublished data). Table 1 also illustrates this point: the most widespread invaders in New Zealand are those which were introduced early. (This pattern is not likely to be related to differences in generation times of early and more recent invaders; P. A. Williams, unpublished data.) Rozenfelds & Mackenzie (1999) make the same point when analysing the history of plant invasions in Tasmania. Consequently, it is unlikely that there are some constant proportions of invasive species within pools of introduced species (a suggestion made recently by some ecologists).

Some generalizations based on population viability analyses, Allee effects, and metapopulation dynamics



**Fig. 1.** Weeds, colonizers and naturalized species (including invaders) are three overlapping but not identical concepts reflecting three different viewpoints: anthropocentric (weeds are plants growing where they are not desired), ecological (colonizers appear early in successional series), and biogeographical (naturalized species are species locally established or spreading in areas where they are not native). A subset of naturalized species are invaders, namely those non-native species that are spreading. Estimated species numbers and examples of species representing seven resulting categories of Californian vascular flora are given. Native colonizers (≥300 + 260 species) represent about 12% of native flora, which consists of 4840 species (Rejmánek & Randall 1994). Native weeds that are not colonizers (~20 species) are mostly poisonous plants growing in successional-ly advanced communities.

are relevant in this context (Gilpin & Hanski 1991; Groom 1998; Akcakaya *et al.* 1999). Practical management suggestions based on dispersal patterns in populations of introduced species (spread from one large focus versus several small foci) are discussed by Moody and Mack (1988) and Higgins (1998). In general, all models and empirical data suggest that even a moderate increase in resources for early detection and eradication of invasive weeds would be the most profitable investment (Fig. 2; Cook *et al.* 1996; Smith *et al.* 1999).

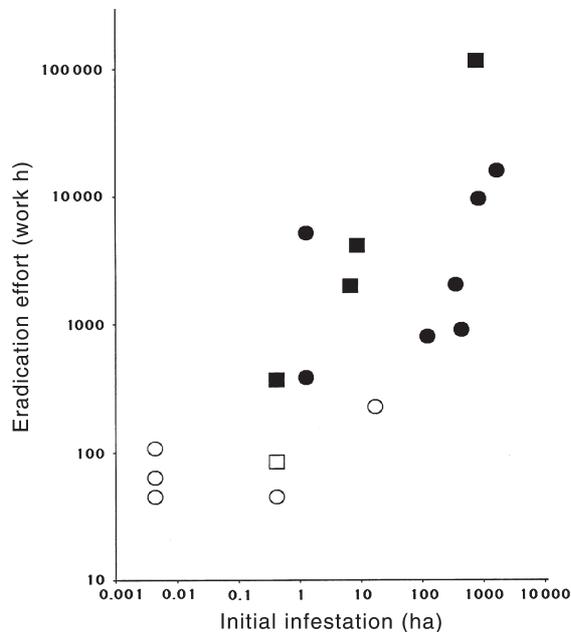
What we may expect is that stochastic invasion effects, which depend on initial inoculum size, residence time, and number of introduction attempts and their spatial distribution, will be more important as

life-history similarity between species of interest increases. It is possible that species within the genus *Eucalyptus* represent such a case. It is important to realize, however, that this stochastic approach allows us to make only some probabilistic predictions about establishment and spread. This approach tells us nothing of potential impact unless we take into account other phenomena used in approaches (2) and (3). Nevertheless, outcomes of these probabilistic predictions can serve as ‘multipliers’ for predictions made by the other approaches.

**2. EMPIRICAL, TAXON-SPECIFIC APPROACH**

To know whether a particular species is invasive elsewhere can certainly help to make practical decisions. This approach has been called ‘tautological’ (Crawley, personal communication). However, pragmatically, extrapolations based on previously documented invasions are extremely important. With the development of relevant data-bases, this approach should lead to immediate rejection of imports of many invasive species (prevention) and prioritized control of those that are already established. This knowledge is very powerful and its importance has been recognized by the US Department of Agriculture for more than two decades (Reed 1977). Using data from previously invaded countries, we can learn much not only about individual species’ invasiveness but also about ecological and economic impacts of the species. There even may be some valuable management experience that can be drawn upon. Many local data-bases (e.g. Swarbrick & Skarratt 1994; Rice 1998; Ridgway *et al.* 1999), floras (e.g. Sharma & Pandey 1984; Webb *et al.* 1988), biological floras (Poschlod *et al.* 1996) and weed manuals are helpful, even if incomplete.

Extrapolations of this kind have been used either on their own, or in combination with approach (3) in several regional screening procedures (Panetta 1993; Scott & Panetta 1993; Williams 1996; Owen 1997; Reichard & Hamilton 1997; Walton & Ellis 1997). An assessment of predictive abilities of some of these procedures was recently made by Daehler (1998a) using a set of known invaders and non-invaders in



**Fig. 2.** The dependence of eradication effort (work hours) on the size of initial infestations of two invasive weeds, *Hydrilla verticillata* (eradicated, □; ongoing, ■) and *Onopordum acanthium* (eradicated, ○; ongoing, ●), in California. To estimate the actual cost of the eradication effort (including transportation, herbicides, etc.) in US\$, work hours should be multiplied by 98. Based on data from the California Department of Food and Agriculture (Pitcairn & Rejmánek, unpublished data), with permission.

**Table 1.** Ecological weeds on conservation land in New Zealand (data in Owen 1997)

	Established with an isolated distribution	Established with a limited distribution, but spreading	Widely distributed and extending their ranges	Widespread, having reached almost all suitable habitats
Mean minimum residence time (years)	26.4a	65.0a	83.3b	117.9c
n	8	52	88	11

One factor ANOVA:  $n = 158, F = 12.3, P = 0.0001$ . Means with different letters are significantly different from each other (Scheffé test,  $P < 0.05$ ).

Hawaii. Again, the knowledge of whether a species is invasive elsewhere turned out to be the key information for correct predictions.

Regrettably, the major obstacle to efficient implementation of this approach is the lack of long-term commitment of any international agency to create and update a truly universal data-base of invasive plant species. After many discussions with interested colleagues and after considering several organizations such as Food and Agriculture Organisation, International Union for Conservation of Nature, World Wildlife Fund, International Association for Ecology, and CAB International, my opinion is that this task should be a responsibility of the United Nations.

Recently, some attention has been paid to taxonomic patterns of invasive angiosperm plants (Daehler 1998b; Pysek 1998). In terms of relative numbers of invasive species, some families seem to be consistently over-represented: Amaranthaceae, Brassicaceae, Chenopodiaceae, Fabaceae, Gramineae, Hydrocharitaceae, Papaveraceae and Polygonaceae. Among large families, there is only one that is conclusively under-represented: Orchideaceae. There are also other currently under-represented families: e.g. Acanthaceae and Rubiaceae. Recent invasion of *Cinchona pubescens*, Rubiaceae, in highlands of Santa Cruz Island, Galapagos (one of the worst invasions I have ever seen), however, reminds us of the danger of making any conclusions based solely on taxonomic affiliation.

### 3. EVALUATION OF BIOLOGICAL CHARACTERS

However useful taxon-specific transregional extrapolations may be in many situations, our lack of a mechanistic understanding makes them intellectually unsatisfying. Understanding how and why certain biological characters promote invasiveness in species will be an important predictive tool, as even an ideal whole-Earth database might not cover all (or even most) potentially invasive species. In New Zealand, for example, Williams *et al.* (1999) reported that 20% of exotic weedy species collected for the first time in the second half of this century have never been reported as invasive outside New Zealand. Rapoport (1991, 1992) estimated that at least 10% of 260 000 vascular plant species are potential invaders; some 85% of them still have not been recognized. These are the reasons why several attempts have been made to find differences in biological characteristics of invasive and non-invasive species or, at least, to find differences between invasive non-native and native species in particular floras (Baker 1974; van Wilgen & Siegfried 1986; Richardson *et al.* 1990; Reichard 1994; Trepl 1994; Pysek *et al.* 1995; Thompson *et al.* 1995; Tucker & Richardson 1995; Baruch 1996; Binggeli 1996; Crawley *et al.* 1996; Rejmánek & Richardson 1996;

Rejmánek 1996a, 1999; Thebaud *et al.* 1996; Williamson & Fitter 1996; Pysek 1997).

Baker made his predictions of the biology of 'an ideal weed' a priori, using characters he believed should be beneficial for invasive species. Predictions of others are constructed a posteriori, based on comparisons of characters of 'invasive' and 'non-invasive' species. In a sense, these are again extrapolations but character-specific and, to a large extent, taxon-free extrapolations. Among these, Rejmánek and Richardson (1996) derived the first region-independent rigorous screening procedure for woody species based exclusively on species biology and some interactions with the environment. An inherent problem with this approach is finding truly 'non-invasive' species. Reichard (1994) and Reichard and Hamilton (1997), for example, used for their analyses of woody invaders in North America as 'non-invasive' not only species that are invasive elsewhere (e.g. *Acacia decurrens*, *Cotoneaster microphyllus*, *Cryptomeria japonica*, *Pinus banksiana*, *Duranta erecta*) but also species that are invasive in North America (*Acer pseudoplatanus*, *Berberis darwinii*, *Gleditsia triacanthos*, *Hibiscus rosa-sinensis*). Even in a much more carefully screened data set (Rejmánek & Richardson 1996), one 'non-invasive' species (*Pinus caribaea*) turned out to be somewhat invasive in some countries.

Discriminant analysis, multiple logistic regression, path analysis and classification and regression trees (CART) are the most promising statistical tools in the assessment of biological characters responsible for invasiveness (Breiman *et al.* 1984; Verbyla 1987; Retherford & Choe 1993; Huberty 1994; Christensen 1997). Investigating the relationships of present-day species traits to phylogeny certainly can bring benefits and is to be encouraged (Crawley *et al.* 1996; Kotanen *et al.* 1998; Westoby *et al.* 1998).

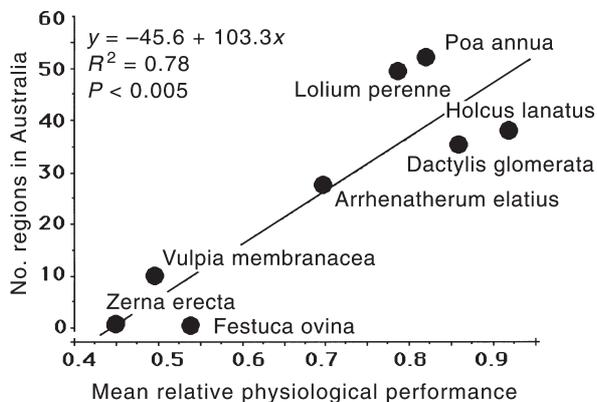
The most reliable predictions based on biological characters are limited to invasiveness (likelihood of species establishment and spread). Predictions of potential impact are necessarily less reliable than such predictions produced by approaches (2) and (5). For example, one such impact predictor can be 'index of weed size' (Bogaard *et al.* 1998). Other obvious impact indicators may be biological characters of plants which are known to have ecosystem consequences (e.g. high transpiration rates or nitrogen fixation). It is important to realize, however, that invasiveness and impact do not have to be positively correlated. Some fast spreading species, such as *Aira caryophylla* or *Cakile edentula*, probably do not exhibit any measurable environmental or economic impact. On the other hand, some relatively slowly spreading species, such as *Ammophila arenaria* or *Robinia pseudoacacia* may have far reaching environmental effects (stabilization of coastal dunes in the first case and nitrogen soil enrichment in the second).

The major predictions made by an emerging theory of plant invasiveness based on biological characters can be summarized by the following 10 points.

1. The ability of an individual or population to maintain relatively constant fitness over a range of environments can be called 'fitness homeostasis' (Hoffman & Parsons 1991). Individual fitness homeostasis (supported by phenotypic plasticity) seems to be equivalent with Baker's (1974, 1995) 'general purpose genotype.' Population fitness homeostasis can, as a result of both individual fitness homeostasis and population genetic polymorphism, contribute to species invasiveness (Rejmánek 1999). Unfortunately, the population fitness homeostasis is not a readily quantifiable variable. Quantities such as mean 'relative physiological performance' or mean 'relative ecological performance' across environmental gradients (Austin 1982; Austin *et al.* 1985) can be used as surrogates for population fitness homeostasis (Fig. 3).

2. Small genome size seems to be a result of selection for short minimum generation time and, as it is also associated with small seed size, high leaf area ratio and high relative growth rate of seedlings in congeners, may be an ultimate determinant of plant invasiveness in disturbed landscapes (Rejmánek 1996a, 1999; Bennett *et al.* 1998; Grotkopp *et al.* 1998).

3. Invasiveness of woody species in disturbed landscapes is associated with small seed mass (<50 mg), short juvenile period (<10 years) and short intervals between large seed crops (1–4 years) (Rejmánek & Richardson 1996). These three attributes are directly or indirectly contributing to higher values of three parameters that are critical for population expansion: net reproduction rate ( $R_0$ ), reciprocal of mean age of reproduction ( $1/\mu$ ), and variance of the marginal dispersal density ( $\sigma^2$ ) (see Van den Bosch *et al.* 1992). Long fruiting periods seem also to be associated with invasiveness (Reichard 1994). Invasions of woody species with very small seeds (<3 mg), however, are



**Fig. 3.** Relationship between the number of regions infested by eight European grasses in Australia (after Hnatiuk 1990) and their mean relative physiological performance over 15 nutrient concentrations (calculated from results of Austin's (1982) experiments which were conducted in Bangor, UK).

limited to wet and preferably mineral substrates (Rejmánek & Richardson 1996). Based on invasibility experiments with herbaceous species, it seems that somewhat larger seeds (3–10 mg) extend species habitat compatibility (Burke & Grime 1996).

4. Vertebrate dispersal is responsible for the success of many woody invaders in disturbed as well as 'undisturbed' habitats (Binggeli 1996; Rejmánek & Richardson 1996; Rejmánek 1996b).

5. The size of primary (native) geographical ranges of herbaceous species is a promising predictor of their invasiveness (Forcella & Wood 1984; Rejmánek 1995; 1996a, 1999; Goodin *et al.* 1998). Both population fitness homeostasis and dispersal abilities seem to be behind this generalization. Exceptions are discussed by Rejmánek (1999) and Williamson (1996).

6. Vegetative reproduction is responsible for an increase of habitat compatibility and, therefore, for successful establishment and spread of many species in terrestrial environments and even more so for dispersal in aquatic habitats (Auld *et al.* 1983; Pieterse & Murphy 1990; Henderson 1991; Aptekar & Rejmánek 1999). The importance of vegetative reproduction for successful invasions increases with latitude (Pysek 1997).

7. Alien species belonging to exotic genera (and therefore possessing traits different from those of resident species) are more likely to be invasive than are alien species with native congeners (Darwin 1859; Rejmánek 1999). The success of species belonging to non-native genera or higher taxa may be partly due to the limited number of resident herbivores and pathogens able to switch to species phylogenetically distant from their native hosts.

8. Plant species depending on non-specific mutualisms (root symbionts, pollinators, and seed dispersers) are more likely to overcome many abiotic and biotic barriers in new environments (Baker 1974; Richardson *et al.* 2000).

9. Undisturbed (natural and seminatural) plant communities in mesic environments are more likely to be invaded by tall plant species (Egler 1983; Gaudet & Keddy 1988; Pysek *et al.* 1995; Crawley *et al.* 1996; Williamson & Fitter 1996). This seems to be more often the case for herbaceous communities. Forests and shrublands are often invaded also by short species (e.g. *Hieracium lepidulum*; Wiser *et al.* 1998). Undisturbed plant communities in semiarid habitats seem to be invisable especially by environmentally compatible species that rapidly develop deep root systems (Hulbert 1955; Roché *et al.* 1994).

10. The spread of many alien species is heavily dependent on human activity (Panetta & Scanlan 1995). Currently, larger and larger volumes of soil are moved around (topsoil, mud on cars, horticultural stock). Species with numerous, relatively small, seed-bank-forming seeds are preadapted for this type of

dispersal (UCPE 1996; Hodkinson & Thompson 1997).

Causal and correlative relationships among many of these factors are summarized and further discussed in Rejmánek (1999). Not surprisingly, some causal chains in this area cross several levels of biological organization. For example, the sequence, genome size + → nucleus volume + → parenchyma cell volume – → specific leaf area + → leaf area ratio + → relative growth rate + → invasiveness in disturbed environments, seems to be one of the reasons why we usually find a negative relationship between genome size and invasiveness among congeners (Grotkopp, unpublished data; Rejmánek & Rost, unpublished data).

#### 4. EVALUATION OF HABITAT COMPATIBILITY

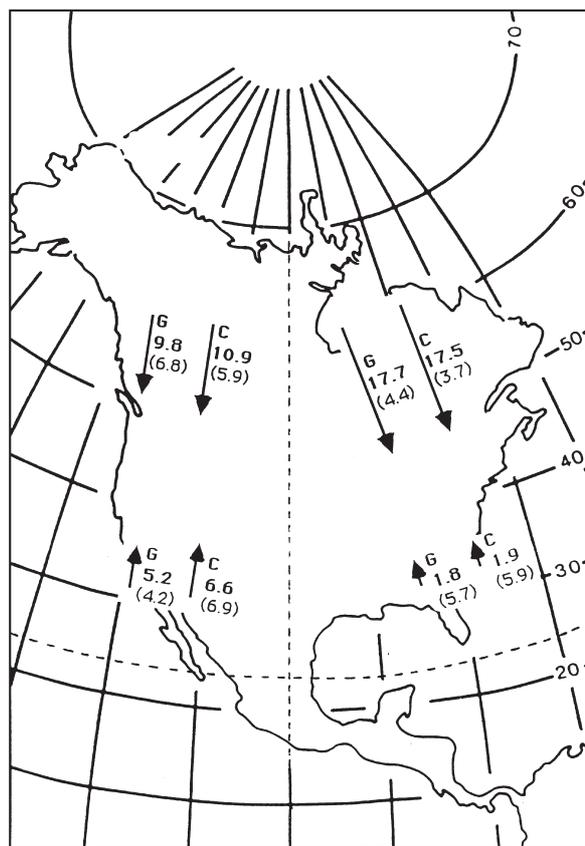
It has long been recognized that climate differences prevent the wholesale spread of naturalized plant species (Lindsay 1953). Recipient habitat compatibility is usually treated as a necessary condition for all invasions (Sanders 1976; Chicoine *et al.* 1985; Panetta & Dodd 1987; Beerling *et al.* 1995). The match of primary and secondary environments is not always perfect (Michael 1981; Wilson *et al.* 1992) but usually reasonably close (Hickman 1993; Hultén & Fries 1986; Hügin 1995). In North America, for example, latitudinal ranges of naturalized European plant species in families Gramineae and Compositae are 15–20° narrower than their native ranges in Eurasia and North Africa (Fig. 4). These differences essentially reflect the differences in the position of corresponding isotherms and major biomes in Eurasia and North America (Rumney 1968; Walter 1968).

Recently, in order to predict the potential distribution of exotic species, several computer-based systems have been developed based on the climate analyses of primary (native) species distributions (e.g. Sutherst *et al.* 1999). These systems are useful but should be used with caution. The primary distributions may be limited by factors other than climate. Major discrepancies between primary and secondary ranges have been found for aquatic plants where secondary distributions are often much less restricted than their primary distributions (Cook 1985). Vegetative reproduction of many aquatic species seems to be the most important factor. For example, the native latitudinal range of an aquatic fern, *Salvinia molesta*, is just 8° (24°S–32°S; south-eastern Brazil; Forno 1983). However, its secondary distribution ranges from 35° to the south and 30° to the north of the equator. In most places it occupies a greater diversity of environments than in its native range (Room & Julien 1995). This is a sterile species, completely dependent on vegetative reproduction. Obviously, secondary ranges, if already

known from other invaded continents, should be employed in any predictions on habitat compatibility.

#### 5. EXPERIMENTS

Predictions made on the basis of the first four approaches to some extent can be tested in quarantine field trials. This can be time-consuming and expensive but fruitful when dealing with limited numbers of herbaceous species (Austin *et al.* 1985; Lonsdale 1994). Deliberate introductions beyond a species' current range coupled with simultaneous manipulation of the environment may be the most powerful approach (Mack 1996). However, mostly unexplained time-lags in invasions of some species (Kowarik 1995; Pysek & Prach 1995) make experimental testing less appealing as a universal tool. Very likely, extensive experimental testing will be conducted more often when introduction



**Fig. 4.** Resistances of the North American continent to European plant invasions quantified as mean differences (expressed as lengths of arrows) between latitudinal limits of Gramineae (G) and Compositae (C) species in Eurasia and in eastern and western North America. Bold numbers represent mean differences in degrees, numbers in parentheses are standard deviations. G:  $n(\text{east}) = 62$ ,  $n(\text{west}) = 55$ . C:  $n(\text{east}) = 70$ ,  $n(\text{west}) = 59$ . Data sources described in Rejmánek (1995).

of a taxon under question is highly desirable. Kareiva *et al.* (1996) provided an insightful analysis of the limitations of short-term invasion experiments.

Experiments on invasibility of different types of herbaceous communities have been gaining momentum in recent years (Burke & Grime 1997; Knops *et al.* 1997; Tilman 1997; Naeem *et al.* 1998; Crawley *et al.* 1999; Lavorel *et al.* 1999). It is hoped that these studies will result in robust non-trivial generalizations in the foreseeable future. Many new insights will also emerge from experimental studies addressing potential effects of global climate change on plant invasions (Dukes & Mooney 1999). Unfortunately, it seems that many invasive species will profit from many of the expected global trends (atmospheric N fertilization, CO<sub>2</sub> rise, climate extremes).

## CODA

Clearly, the most powerful predictions can be made by simultaneous use of several approaches. The combination of resulting predictions can be affirmative, additive or multiplicative, depending on their nature. However, the arithmetic here is not so simple. All-inclusive indices (scores for screening) might be helpful, but really relevant information may be suppressed. Undoubtedly, we should pay more attention to habitat-specific predictions. Their usefulness, however, will be rather limited in landscapes consisting of mosaics of different habitats. In such situations, the worst possible scenario (predictions for the most vulnerable habitat) should be always taken most seriously.

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