PREDICTING THE IDENTITY AND FATE OF PLANT INVADERS: EMERGENT AND EMERGING APPROACHES

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Abstract
Prediction of the potential for plant species to invade new ranges has long attracted the attention of ecologists motivated by both fundamental and practical considerations. Consequently, a conceptually diverse array of correlative and experimental approaches have been developed to predict the identity and fate of future invaders. The most straightforward approach has long involved simply compiling lists of species known to be aggressive either in their native range or a new range. Although these lists can be encyclopedic, they often fail to include species that have yet to become aggressive anywhere. As a result, much effort has been devoted instead to searching for commonality in the ecological traits of invading species as a predictive tool. Success in using such distillations is hampered by the emphasis on the traits of ruderals, despite the ability of non-ruderals to become naturalized, and the frequent inability to decipher which traits contributed to a species' naturalization from those that are merely coincidental with naturalization. The intuitively appealing approach of identifying a region's future invaders among species that are aggressive in regions with a similar climate ('climatic-matching') fails to account for the often quite different biotic restrictions among regions with similar climates. A fourth correlative tool, predictions of an alien species' future distribution and prominence based on its initial rate of spread, is handicapped by our lack of comprehensive knowledge on the areal patterns and temporal course that invasions may follow. In contrast to these correlative tools, prediction has also been sought by determining the constraints of the physical environment on alien species in controlled-growth facilities and glasshouses. Although such facilities certainly provide instructive results, potential interactions between and among factors, especially biotic factors, are difficult to simulate. Three other experimental approaches offer a higher rate of prediction: simultaneous field comparisons between congeners (e.g. one naturalized, one native), and following the fate of a species deliberately sown in a natural community beyond its current range, with or without environmental manipulation. Evaluation of the efficacy of these last three approaches awaits their wider application. Although the experimental approaches hold greater promise, none is a panacea. Prediction will be the highest when several approaches are combined simultaneously (e.g. manipulating the environment for congeners in the field). Copyright © 1996 Elsevier Science Limited

Keywords: invasions, naturalizations, climate-matching, weeds, alien plants.

INTRODUCTION
Plant invasions describe the proliferation and persistence of a species in a new range such that it has detrimental consequences (abiotic or biotic, or both). This persistence is not dependent on deliberate human intervention. Motivation for predicting the course, character, and location of future plant invasions stems from at least two broad-based interests or needs. Such biotic invasions provide some of our best opportunities to study an array of contemporary evolutionary, ecological, and genetic processes (e.g. competition, genetic drift, founder effects, introgressive hybridization) (Mack, 1985; Barrett & Husband, 1990; Novak et al., 1991). In addition, the need for prediction is the same as in epidemiology: early detection of an invader combined with a knowledge of its attributes and limitations allows maximization of any control effort (Eplee, 1981; Watson, 1985).

Whatever the motivation, prediction of the next plant invasion(s) for any locale has often been poor; species that were not originally deemed as potential invaders (e.g. Pueraria thunbergiana, Rosa multiflora, Lonicera japonica) continue to arrive and prosper in new ranges (Mack, 1991). Part of the problem may inadvertently stem from the anecdotal character of the literature on plant invasions; it is so vast and seemingly so disparate that syntheses of it so far explain past invasions much better than predict the next one (Foy et al., 1983; Mack, 1986). Often the information on a species is exclusively descriptive, incomplete or not germane to its performance in a new range. Despite these limitations, a variety of methodologies or approaches for predicting plant invasions has emerged: the rudiments of some were formed in the 19th century; others arose much more recently and await wide application. My purpose here is to identify and categorize these methodologies and assess their predictive ability.
The terminology for plant invasions has been often applied inconsistently. Consequently, I will define several terms at the outset. I distinguish between alien species that are merely ‘transient’ i.e. leave no persistent descendants, from species that become ‘naturalized’, i.e. their descendants apparently become permanent members of the local flora. In a strict sense, a naturalization may not develop into an invasion, i.e. an alien species which has a detrimental effect in the new range, although this distinction can obviously become murky (e.g. is the mere presence of a naturalized species detrimental?). Distinguishing transients from future naturalized species becomes a common goal of the approaches I discuss here. These definitions specify neither the specific agent of dispersal nor the events after immigration, although the vast majority of immigrants today are transported to the new range through human activity.

Regardless of the method of prediction used, it is motivated by the pursuit of one or more basic questions that reflect either a species-oriented or a habitat-oriented view. What habitats and circumstances would permit the naturalization of a species that is aggressive elsewhere? Will a species that has already arrived in a new range or has the potential to immigrate become naturalized? Which species could (and could not) become naturalized in a given habitat, region, etc.? Which species merit the maximum effort to prevent their entry and naturalization into a given habitat, region, etc.?

To varying degrees, predictions based on current methods of whether a species will become naturalized are hampered by the potential for a ‘false positive’ result (i.e. a spurious prediction of naturalization) and a ‘false negative’ result (a spurious prediction of no ability to become naturalized) results (sensu Remington & Schork, 1985). For example, a false positive result could arise with the establishment of a species from sowing trials beyond the species’ current range that coincided with clement weather or the temporary absence of a virulent pathogen. The species would nevertheless be eliminated through an infrequent (but inevitable) lethal event. A false negative result could arise by incorrectly deducing that an alien species could not persist in a particular locale because of the climatic dissimilarity between its native range and this foreign locale. Yet species sometimes display heretofore unrecognized amplitude in climatic tolerance (e.g. Eichhornia crassipes in central California, Bock, 1969; Andropogon virginicus in Hawaii, Sorenson, 1991).

Failure to consider a species’ genetic variation could readily create both false positive and false negative results from all the methodologies I describe below. This problem is worrisome in part because a misnomer has long been used in describing plant invasions—i.e. that species invade new ranges. In a strict sense, it is usually small populations drawn from only part of the species’ home range or elsewhere that give rise to naturalization and subsequent invasion (Rice & Mack, 1991; Novak & Mack, 1993). These founders often display little of the genetic variation in the species as a whole (Barrett & Richardson, 1986), and consequently their fate in a new habitat may bear little relation to the outcome for genetically-different members of the species.

By my accounting, there are at least eight methodologies or approaches that have been used to predict the fate of plant immigrants in a new range (cf. Patterson, 1990a). The order in which I consider them here follows simultaneously several axes: roughly from oldest to most recently employed, from strictly descriptive to strictly experimental, and in my opinion, from those with the most limitations to those with the most (and usually unfulfilled) promise.

1. COMPILATION OF SPECIES THAT HAVE BEEN WEEDS IN THEIR HOME RANGE OR ELSEWHERE

The weed (sensu Baker, 1974) flora of most regions is comprised mainly of alien species, and these species often recur as aliens in other regions (e.g. Avena fatua, Capsella bursa-pastoris, Gallium aparine, Poa annua, Rumex crispus). Consequently, the most straightforward approach for predicting a future invader has long been to use lists of species that are already invasive, or at least weedy, somewhere else (e.g. Holm et al., 1977; Parsons & Cuthbertson, 1992). For instance, the US Noxious Foreign Weed Act of 1974 includes alien species that have limited distribution in the US but whose aggressive or destructive performance elsewhere gives sufficient cause to prohibit their introduction or persistence (Westbrooks, 1981). A few may not even currently occur in the US (e.g. Striga senegalensis, Striga densiflora) but are presumed to have the potential for naturalization.

Similar reasoning led Reed (1977) to compile a list of approximately 1200 weedy species that he deemed capable of becoming naturalized in the US, based on the species’ performance either in their home range or a new range, or both. Reed compiled his list from foreign weed Floras and quarantine lists, plus references to species’ weedy performance outside the US. Although some of these species have been already introduced in the US, he estimated they are found only locally or in cultivation. In at least one case, his prediction of naturalization has been realized: Lepidogyne holostoides has become locally prominent in Idaho and eastern Washington since 1977 (Rable & Old, 1992). As might be expected, such a compilation from foreign literature could readily overlook species that have become pests in the US in the last few decades. For example, the cucurbit vine Bryonia alba has spread in the last 20 years along river valleys in parts of Idaho, Montana, Utah and Washington (Novak & Mack, 1995).

Perhaps the most well-known list of alien weeds was compiled by Holm et al. (1977). They assembled a list
of less than 100 weeds that they considered the world’s worst—all of which are invasive. Their list is a veritable ‘roll-call’ of species acting as pestiferous aliens: e.g. *Cyperus rotundus, Imperata cylindrica, Lantana camara, Mimosa pudica, Rottboellia exaltata* and *Sorghum halepense.* As useful as Holm et al.’s list may be in drawing attention to species that have become repeatedly (and disastrously) naturalized, it does not provide guidance on future, but as yet unidentified, naturalized species.

For whatever reasons, naturalized species in temperate biomes are not proportionately distributed among plant families: a few families, such as the Poaceae and Asteraceae, contain many species that are widely naturalized (Heywood, 1989). Yet these families are obviously so large that knowing that a potential invader is a familiar member is probably of little predictive value. Generalities are even more tenuous for species in subtropical and tropical plant families because most of these species have had so far little opportunity for immigration. Members of the Melastomataceae may constitute an exception. Fifteen melanostoms occur in Hawaii (Wagner et al., 1990); all are alien, and almost all have become naturalized. Among them are at least two aggressive species, *Clidemia hirta* and *Miconia calvscens* (Cuddihy & Stone, 1990). The distribution of naturalized species among families does however reveal that many (perhaps a simple majority of) families have few or no species that have yet become naturalized. In analyzing the data of Holm et al. (1979), Heywood (1989) found 44 angiosperm families with only one species that had become naturalized (e.g. Restionaceae, Magnoliaceae, Gesneriaceae). Members of the small, primitive family Winteraceae seem a case in point: the low opportunity for their dispersal, their common dependence on beetle pollination, and their apparently limited ecological amplitude make the likelihood of their naturalization anywhere quite low.

Prediction of future invaders has often been extended to the generic level; some genera (e.g. *Bromus, Cirsium, Poa, Centaurea*) do indeed contain many species that have become naturalized repeatedly. These species are mostly ruderals, and as such they possess many traits that Baker (1974) considers ideal for a weed. In contrast, a much longer (and yet equally intriguing) list can be compiled of genera with one or only a few species that have become naturalized (e.g. *Isatis tinctoria, Robinia pseudo-acacia, Tridax procumbens, Eichhornia crassipes*). Unfortunately, the specific differences among such congeners with regard to naturalization ability have seldom been investigated. In one exception to this record, the principal congeneric differences relating to the catastrophic naturalization of *Eichhornia crassipes* are its ability to form stolons asexually and a free-floating life form (Barrett & Richardson, 1986).

The chief limitation of any taxonomic compilation in predicting future naturalizations is its restriction to species with a record of such activity. Aside from naturalized species that have remained undetected in their new ranges, there must be many species that have yet to demonstrate their naturalization potential simply because they have lacked an opportunity to immigrate. The prominence of species native to the Mediterranean Basin in many alien floraxes may be due as much to the opportunity these species have had to emigrate in ballast, forage and other cargo from a long-time maritime region, as to their biological traits. In contrast, we lack any assessment of the invasive ability for some other floraxes. For example, some species in the Tibetan flora (e.g. *Carex moorcroftii, Erodium tibeticum, Stipa baxiplumosa*) (Wang, 1988) belong to genera in which there are invasive congeners elsewhere. Yet, the lack of any apparent opportunity, so far, for these Tibetan species to emigrate has meant that their ability to invade other ranges remains unknown.

In conclusion, compilations of species known to be weedy are not sufficiently reliable to serve as the sole predictors of a community’s vulnerability to naturalizations.

II. COMPILATION OF THE TRAITS OF INVADING SPECIES

The frequency with which some species occur in alien floraxes—often in widely-separated parts of the world—has long suggested a direct link between their traits and their recurring naturalization. But are there as many combinations of traits spelling naturalization as there are species that become naturalized, or only a few? If there is a tractable number of traits and their combinations, the rewards in prediction would be substantial: new or potential immigrants could be readily scrutinized for these traits. Investigators since Asa Gray (1879) have compiled and assessed the traits of invasive species looking for such commonality.

Baker (1974) compiled the most well-known list of such traits; it is especially useful for several reasons. Most of Baker’s characteristics for an ‘ideal weed’ are discrete, and their potential value to an invader are readily perceived, e.g. continuous seed production, high overall seed output, a lack of special requirements for germination (cf. Perrins et al., 1992). Many of the world’s most successful invaders do indeed possess many of these traits (e.g. *Capsella bursa-pastoris, Eleusine indica, Portulaca oleracea, Imperata cylindrica*); there are, of course, many exceptions. First, no one invader has (or could have) all the features proposed for ideal weeds, e.g. annuals lack vegetative propagation. In addition, many invaders have remarkably few of these features (such as invasive pines in general, e.g. *Pinus pinaster* in South Africa, Kruger, 1977), begging the question as to whether there is any minimum number of requisite traits. In contrast, many other species that have not become extensively or abundantly naturalized display many of these traits,
including the land races of wheat and barley, and the congeners of *Eichhornia crassipes* (Barrett & Richardson, 1986).

In the past 10 years, commonality among the traits of plant invaders has been examined repeatedly, and collectively these studies represent an evolution in the view of this topic. Bazzaz’s (1986) assessment comes perhaps closest to reaching conclusions similar to those of Baker. He considered that the traits and generalities of ‘colonizers’ apply to invaders, i.e. invaders are commonly species with attributes that allow them to take advantage of recently-disturbed sites (efficient dispersal, a flexibility of response to changing environmental conditions, and may have high photosynthetic and respiration rates). Newsome and Noble (1986) concentrated on identifying eco-physiological traits among invaders. They found only limited support for Baker’s list in their analysis of weeds in Victoria (Australia). In a view that was subsequently expanded by Noble (1989), they contended that species (and their traits) were better handled as suites of traits in relation to specific habitats. Perrins et al. (1992) have taken perhaps the most iconoclastic view: they conclude from several lines of evidence that weeds cannot be reliably distinguished from non-weeds based on their traits.

The generally low predictive value of using commonly-held traits for identifying future invaders arises from at least two sources. First, Baker (1974) compiled a list of traits for weeds [species for which its ‘... populations grow entirely or predominately in situations markedly disturbed by man (without, of course, being deliberately cultivated plants),’ especially those ruderals that occupy such frequently-disturbed sites with abundant light. A list that emphasizes the traits of such species is appropriate where the vast majority of invaders immigrate and spread accidentally with agriculture, such as seed contaminants of crop seeds, forage, or animal feces. But plants obviously become naturalized in habitats other than arable fields. Traits that would lead to their naturalization in forests, e.g. a low light compensation point, animal (especially bird) dispersal, a viney habit, a protracted immature stage, may bear little relationship to the traits of ruderals. As both accidental and deliberate introductions increase from heretofore isolated parts of the world, we can expect to see more species with such traits becoming naturalized, e.g. *Miconia calvescens*, a native of the Neotropics, which is now invading forests in both Tahiti and Hawaii, Cuddihy and Stone (1990).

More importantly, current lists of traits pay insufficient attention to the well-known advantages that many aliens experience in a new range devoid of their native parasites, pathogens and competitors (Elton, 1958; Strong et al., 1984). Thus, an immigrant population may gain no advantage from discontinuous germination in a new range in which no native predators include its seedlings within their diet any more than brittleness or rapid seedling growth may be important for an invader in an environment that lacks large grazers or intense competition. Lack of such biotic barriers may have contributed to the naturalization of some seemingly unlikely candidates, such as citrus in Paraguay (Gade, 1976).

The immigration barriers for many more species will fall as international commerce accelerates. As a result, species with combinations of traits heretofore unrecognized as conducive to naturalization will likely occupy new ranges. In turn, lists of traits—certainly lists consisting of only a few characteristics—may become increasingly restricted in their predictive power.

### III. ASSESSMENT OF INVASIVE POTENTIAL BASED ON SIMILAR CLIMATES

Identifying a connection between the distribution of organisms and the climate(s) in which they occur has long been a major topic of investigation in ecology. Although some species are seemingly cosmopolitan (e.g. *Echinocloa crus-galli*, *Pteridium aquilinum*, *Ricinus communis*), many regions now support alien floras drawn largely from similar native ranges (Baker, 1974). Such general examples have given rise to expressions, such as the ‘Africanization’ of Neotropical grasslands (Parsons, 1970). As a result, the climates in the home ranges of potential invaders have been used as guides to new, potential regions of infestation; in effect, the attempt here is to ‘match’ the climate of the home range of an aggressive species with similar climates elsewhere. Incentive for such prediction is strong: efforts at quarantine and control can be marshalled in anticipation of the direction of future spread, rather than dissipated across areas where naturalization cannot occur.

Johnston’s (1924) prediction on the spread of prickly pear cactus (including *Opuntia stricta*) in Australia represents an early success with this approach. By 1920, *O. stricta* had occupied an estimated 235,000 km² with no evidence that its advance was slowing (Dodd, 1940). Johnston estimated the direction of future advances for several alien cacti based on the climates in their home ranges. For example, the home range of *O. stricta* is a large, climatically-diverse region on the Gulf Coast of North America. In his estimation it was characterized by annual temperatures between 10 and 21°C, annual precipitation < 800 mm, and less than 5 months with pronounced drought. He correctly predicted that the threat of naturalization in southern and western New South Wales, Victoria and South Australia would be low, while major spread would occur into those parts of Queensland that most closely matched climate in the home range. Despite his success in predicting this future spread (*O. stricta* eventually covered somewhat more area before being controlled), he was unable to account for parts of the eventual range of other cacti in Australia, such as *O. maidenii*.

Recent attempts at predicting plant invasions based on climatic similarities have also been concentrated in
Australia, based largely on the Bioclimatic Prediction System (BIOCLIM) (Busby, 1986), BIOCLIM seeks to identify 'homoclines', i.e. areas with similar climates (sensu Russell & Moore, 1970) from mathematical surfaces based on commonly-measured meteorological parameters, such as annual mean precipitation, precipitation of the wettest and driest months, and minimum and maximum temperatures of the coldest and warmest months, respectively (Panetta & Mitchell, 1991). Climates of sites that support a species (either in its native range or a new range) are then compared to climates in areas where it is not yet found. The predictive power of this approach has varied (Wilson et al., 1992), dependent in part on the number of meteorological parameters included and the parsimony of the criteria for matching climates (Panetta & Mitchell, 1991; Sindel & Michael, 1992). In some cases, e.g. Homeria flaccida and Chondrilla juncea in New Zealand (Panetta & Mitchell, 1991), there is close correspondence between climates of the putative source and the introduced range. In contrast, Wilson et al. (1988) found little correspondence between the climates of regions occupied by an alien assemblage in New Zealand and the climate where these same species occurred as natives in Britain.

Climate-matching is not restricted to comparisons between native and new ranges: comparisons also commonly involve the climate in a new range with areas the alien might yet invade. Such investigations are highly correlative. For instance, Chicoine et al. (1985) assessed the future spread of Centaurea maculosa in Montana based on annual precipitation, length of the frost-free period, potential evapotranspiration, and mean maximum July temperature for 116 infested sites. They concluded that C. maculosa has a broad ecological amplitude and a potentially large, new range in Montana: nearly 15 million ha could yet support this knapweed.

Despite the intuitive appeal of this approach, it has serious limitations that can produce both false negative and false positive results. First, the new (or even native) range of a species may not exhibit the entire amplitude of climatic features that it can tolerate (Michael, 1981), thereby producing false negative results—what Panetta and Mitchell (1991) term 'cryptic climatic adaptation'. Eichornia crassipes, the water hyacinth, provides a spectacular example of the inability of climate-matching to predict an alien's future range. The history of this aggressive South American hydrophyte's invasion in the US is well-known. It was deliberately introduced into North America in the late 19th century and quickly spread through rivers in Florida, a subtropical area (Mack, 1991). Despite its tropical origin, it now persists through vegetative propagation as far north as the Central Valley in northern California (37° 45' N latitude) (Bock, 1969). Clearly, climate-matching would have failed to predict the full extent of this plant's new range. Other species for which the match is poor between climates in their home and new ranges include Sorghum halepense in Canada and Andropogon scoparius in Hawaii (Warwick et al., 1984; Sorenson, 1991).

Climatic comparisons are unlikely to be so fine-grained as to account for local environmental heterogeneity. Thus, an invader could persist in a region drier than its home range by its restriction to local wet sites. For instance, Sindel and Michael (1992) account for part of the distribution of Senecio madagascariensis in New South Wales through such site restriction. Similar local persistence along stream courses in an otherwise inhospitable physical environment also likely accounts for the naturalization of Bryonia alba, native to much of eastern and central Europe, in the arid Intermountain West of the US (Novak & Mack, 1995). The naturalized range of Pinus radiata has been repeatedly cited as a climatic mis-match. Although this pine's native range consists of small coastal sites in California, it has become naturalized in New Zealand, Australia and South Africa (Richardson & Bond, 1991 and references therein), including areas with climates unlike those of coastal California.

Sources of false positive results are varied (Wilson et al., 1992) and constitute the chief limitation. Climate is obviously only one part of the environmental complex to which organisms respond: other forces (e.g. competition, pathogens, predation) shape the realized niche and preclude a species from occupying an otherwise suitable habitat. For example, were it not for diligent husbandry, cocoa could not occur in West Africa because of its susceptibility to cocoa swollen shoot disease (Baker, 1970). An unsuitable soil can also thwart an invasion into a climatically-suitable region. Old (1981) correctly predicted that Chondrilla juncea would remain restricted to sites with either shallow or sandy/gravelly soils in eastern Washington (USA) and would thereby not invade the adjacent silt or clay loam soils. Genetic variation across a species' home range further hampers these comparisons. Without direct comparison between the specific region from which immigrants were drawn and a possible new range, both false positive or negative results could emerge from the mis-match between a specific array of genotypes and a possible new range (Howden, 1985). Prediction based on comparisons between a naturalized range as the source for immigration to another new range require that the species has reached its climatic boundaries in the source area (Panetta & Mitchell, 1991). False negative results could clearly arise if a species has not yet displayed its full environmental amplitude in the source area.

IV. MATHEMATICAL MODELS TO PREDICT THE COURSE OF PLANT INVASIONS

Many plant invasions begin with the arrival of a few immigrants in a new range. Small founder populations place obvious initial constraints on the growth of the alien population. Thus, alien populations often remain small and inconspicuous for generations, even if the
environment is suitable for proliferation (Moody & Mack, 1988). At least three general fates however await these immigrants and their descendants: (1) the founders or their descendants are extirpated (they are 'transients'); (2) the population becomes naturalized but not prolific or widespread (e.g. alien species referred to as 'casual' or 'infrequent' in regional Floras) (Salisbury, 1961); (3) the naturalized population persists in low numbers for widely varying lengths of time but then increases rapidly (and potentially spatially) (Salisbury, 1961; Mack, 1985). Scenario (3), in which the numbers of individuals in the population or the new range occupied grow in a logistic manner, has long been recognized (Salisbury, 1961). This scenario characterizes invasions.

Ability to distinguish among these scenarios early in the course of the invasion holds much benefit since accurate prediction would allow control efforts to be maximized against those alien species following scenario (3) before they become uncontrollable (McWhorter & Chandler, 1982). Geographic spread of populations under scenarios (2) and (3) may however be seemingly indistinguishable for prolonged periods. This initial period of population growth for an alien population may reflect a time in which the population is undergoing selection that results in the emergence of a new array of highly-adapted genotypes in the range (Baker, 1974), the accumulation of sufficient nascent foci to affect spread (Moody & Mack, 1988), the simple increase in the population's ability to produce sufficient propagules for local immigration (Salisbury, 1961) or some combination of these explanations.

Forcella (1985) predicted the future spread of alien populations by examining the relationship between the final geographic distribution of 40 alien species in their new range (the northwestern tier of states in the US) and the rate at which they had occupied that range. His data consisted of the number of counties per decade in which the species had been reported for the first time from 1890 to 1980. When plotted these data consistently formed the sigmoidal curves that have been reported repeatedly for plant invasions (Mack, 1985). He was particularly interested with what he termed the migration rate, 'the initial rate of spread of the plant (i.e. alien plant species) up to the approximate midpoint of its calculated final distribution'. He contended that species with high migration rates were among the worst alien weeds in a region. In contrast, none of the species with low migration rates, i.e. with much lower geographic spread since 1890, have become pests in this region.

Limitations with predicting the outcome of an invasion through a model of the initial spatial spread (or numerical growth) are both readily identifiable and challenging. First, exceptions to the sigmoidal spatial spread of an invasion do occur. Based on herbarium records, Forcella and Harvey (1982) contend that Filago arvensis invaded counties in Montana at an exponential rate, i.e. there was no prolonged initial period of slow growth. Other, unquantified accounts of non-sigmoidal spread for an alien that eventually became widespread are reported by Salisbury (1961). These examples do not in themselves, however, call into question the general view of sigmoidal spread for widespread (and usually abundant) aliens. Instead, the problems lie with the detail of the data required to test models of final distribution based on initial spread. Herbarium records provide irrefutable evidence of the date and general location of an alien, but these records are rarely collected at the density and frequency required to predict direction and rates of spread. It is also unlikely that aliens are detected (and collected) the first year they appear in a county. Furthermore, a simple 'present' or 'absent' basis for recording data from an area as large as counties can easily provide a misleading picture of the rate and character of spread. Until the detection and sustained censusing of alien plants rivals that provided in human disease epidemiology, prediction of the fate of a newly-discovered alien species based on mathematical models will remain low.

V. EXPERIMENTAL MANIPULATION OF THE ENVIRONMENT (CONTROLLED-GROWTH CHAMBERS AND GLASSHOUSES)

Much of our knowledge of the ecological amplitude of plants has been assembled from monitoring the response of plants in controlled-growth facilities, such as glasshouses and controlled-growth chambers. I will largely limit my remarks to studies in controlled-growth chambers, since glasshouses display similar attributes and limitations for predicting the fate of plants in new ranges. Controlled-growth chambers have long been employed in agriculture and allow rapid assessment of the environment in which crops will (and equally important, will not) grow. For instance, a species that lacks frost resistance would be readily detected in this manner (Wilcut et al., 1988). Similarly, a wild alien species can be assessed under a wide range of conditions under which it is not currently found, in order to gauge the scope of any new range. Furthermore, these facilities allow assessment of the ecological range for species deemed too hazardous to release in experimental sowings beyond their current range (Patterson, 1983), e.g. aquatic vascular plants, such as Hydrilla verticillata or Salvinia molesta.

Often this approach stems from concern about the potential range expansion of an invader in relation to a single environmental parameter. As a result, there is much similarity in the experimental design among many of these studies in which temperature followed by photoperiod is the most commonly investigated parameter. For instance, Patterson et al. (1979) investigated the potential spread of itchgrass Rottboellia exaltata, an aggressive tropical Asian weed, from Louisiana and Florida to the rest of North America. They reasoned
that it would most likely be limited by low temperature in its spread. Using 36 regimens of day and night temperature, they found that plant growth was not substantially reduced until either the night temperatures fell below 20°C or the day temperatures fell below 26°C. They concluded that the entire southern US along with sites further north in the Middle Atlantic states and the Sacramento Valley of California was within the potential range of the itchgrass population they had examined. Similar studies have outlined the wide potential geographical limits for *Crepis vulgaris* in the US, a noxious alien currently restricted to three counties in Idaho (Patterson & Mortensen, 1985).

Controlled-growth facilities are particularly well-suited for investigation of plants that invade ponds and lakes; the still water conditions can be easily duplicated in containers, while simultaneously modifying light, temperature and especially nutrient levels (Mitchell & Tur, 1975). *Salvinia molesta*, which displayed rapid spread in lakes in east and southern Africa in the 1960s, was found to grow exponentially with increasing temperature from 22 to 30°C; its growth declines rapidly at 35°C. Since this plant spreads only through vegetative propagation (Thomas & Room, 1986), the factor(s) that control formation of lateral buds are particularly important. Mitchell (1970) (as cited in Mitchell & Tur, 1975) found that bud formation in laboratory-grown plants was much dependent on dissolved nitrate nitrogen (4.2 mg/litre). Thus, growth of the plant could be expected to diminish only where trace amounts of N occur.

Photosynthetic properties have also been examined under controlled-growth conditions as predictors of future geographic spread, e.g. *Parthenium hysterophorus*, a native of the New World tropics, that has become established in Asia and Oceania. This annual composite is insensitive to widely varying light levels; light saturation occurred at approximately 50% noon sunlight. Furthermore, its photosynthetic rate is not excessively sensitive to drought in Queensland, even though it displays little stomatal control of gas exchange. If no other factors restricted its distribution, it could become prominent throughout much of the warm humid/subhumid regions of Australia (Doley, 1977). But clearly other factors would eventually control its spread, potentially even those related to its light responses. One recurring gap in our knowledge of the restrictions on aliens is their response to shade (but see Patterson, 1975, 1982). An inadvertent consequence of the imperfect, yet widely-practiced, synonymy between 'weeds' and 'invaders' has been neglect of the growing list of species that become naturalized under forest canopies (e.g. *Allaria petiolata*, *Atlantus altissima*, *Miconia calvescens*) because ruderals are commonly intolerant of low light. For shade-tolerant aliens, the response to diminished light takes on special importance in predicting the habitats they will invade.

The limitations of this approach are varied. So far, it has been much easier to manipulate the abiotic compared to the biotic environment in controlled-growth facilities, i.e. an irrigation regime more likely duplicates an annual moisture cycle than clipping duplicates herbivory. Even duplicating the physical environment can have severe constraints, such as duplicating fluctuations in weather. In addition, studies in controlled-growth facilities usually assess only a few physical parameters (Patterson et al., 1982; Wilcut et al., 1988). With most other factors at an optimum, the results from varying one other factor may not be seen in nature; e.g. Mitchell and Tur (1975) found much higher rates of growth for *Salvinia molesta* in the laboratory than in the field.

Conclusions from many studies in controlled-environmental facilities are further limited by restricting the investigation to a few life stages. For instance, transferring newly-emergent seedlings from a common temperature regime to a treatment environment (Patterson et al., 1979; Patterson, 1990b) precludes the ability to gauge the effect of any treatment on emergence itself, an especially vulnerable stage for many terrestrial plants (Harper, 1977). If experiments are terminated by harvesting the juvenile plants, subsequent survival and the extent of flowering and seed set obviously cannot be examined (Patterson et al., 1979; Patterson, 1990b). Finally, exclusive reliance on comparisons of biomass (or leaf area, tiller number, plant height) among treatments rather than comparisons based on fitness (Patterson et al., 1979, 1980; Patterson, 1990b) make problematic any predictions about the spread of a sexually-reproducing alien species into a new range. Ideally, all stages and modes of persistence (whether by seeds, bulbils, rhizomes, etc.) need to be examined.

Once again, this approach is also subject to the limitations intrinsic in basing conclusions on the response of a population that may encompass little of the genetic variation displayed by the species across its ranges. Patterson et al. (1980) found that differences in performance among populations of *Imperata cylindrica* in the US stem from the species having arrived in at least two separate introductions. In addition, postimmigration selection may extend the range of an invader, e.g. the recent spread of *Sorghum halepense* into sites in southern Canada once thought beyond its range (Warwick et al., 1984). Thus, repeated assessment may be necessary for rapidly-spreading aliens at the current limits of their range.

VI. DETAILED COMPARISONS AMONG CONGENERS

The great variation in range and abundance often displayed among congeners provides the basis for a potentially powerful tool for predicting the fate of alien species. The many traits shared by closely-related congeners provide a template for reliably identifying
and examining traits they do not share; one or more of these different traits likely accounts for the interspecific differences in performance often seen among congeners in a new range (Mack, 1985; Barrett & Richardson, 1986). Although comparisons among species’ traits are the basis for Approach II, I am concerned here with experimental assessment of the consequences of differences among traits. Furthermore, these assessments are strongest when performed with congeners growing simultaneously under field conditions.

Two variants of this approach have been used. (1) Simultaneous comparisons can be made among species that are all alien in a new range. Here the attempt has been to explain their different levels of success in naturalization. (2) Comparisons between a native and a congeneric alien in the same range can be even more informative. Greater abundance of the alien suggests it has circumvented hazards that restrict the native; repeated failure in naturalization suggests the alien lacks traits found in the native that are essential for survival in this range. The ability exists in both variants to discriminate between traits essential for naturalization compared to those merely coincident with it.

Hubert’s (1955) examination of annual alien bromes in the arid Intermountain West (USA) provides an early and exceptionally-detailed investigation of reasons for the different fates among alien congeners in a new range. In the steppe between the Rockies and the Sierra Nevada/Cascade Ranges, the Eurasian annual grass Bromus tectorum has achieved dominance (Mack, 1986). Although other annual bromes from Eurasia have also been introduced, these species have remained only locally prominent, infrequent or rare. Employing both controlled-growth facilities and common gardens in the region, Hubert simultaneously compared B. tectorum with nine other alien bromes in phenology (e.g. germination, initiation of flowering, anthesis, rate of root growth), and their response to diverse factors, including depth of seed burial, seed longevity, N fertilizer, clipping, frost, and smut infestation. Using elegantly simple experiments, he showed that each of the other bromes lack one or more traits found in B. tectorum that are relevant to its proliferation and abundance: e.g. autumn germination, rapid root growth, tolerance of repeated clipping and frost. Many more alien congeners deserve this attention, e.g. Centaurea in the US, Carduus in Australia.

The extensive tree plantation trials conducted worldwide for over a century represent a much more extensive, but as yet unutilized, resource of comparisons among alien congeners. Merchantable species, particularly in the genera Abies, Picea, Pinus, Eucalyptus, and more recently Swietenia and Populus, have been grown sympatrically in long-term experiments (e.g. Booth & Saunders, 1984; Zobel et al., 1987). These trials await re-evaluation to detect species that could invade new ranges.

Experimental assessments between a sympatric native and alien congeners have received more attention (Pammenter et al., 1986; Schierenbeek et al., 1994), although some of these investigations have been restricted to glasshouses or controlled-growth facilities (Collins & Wein, 1993). The most thorough example illustrating this approach was compiled by Caldwell and his colleagues for Agropyron spicatum and Agropyron desertorum in the arid steppe of Utah (USA). Although these investigations concern a widespread naturalization that has already taken place, the experiments nevertheless indicate the potential of predicting the fate of an alien species introduced into the home range of a congener.

Agropyron spicatum is the most characteristic native grass throughout the Intermountain West in North America (Mack, 1986). Its dominance in the Intermountain steppe has however declined substantially, a consequence of agriculture beginning in the mid-19th century. The apparent inability of A. spicatum to tolerate frequent livestock grazing prompted the deliberate introduction of Agropyron desertorum, a native of arid Eurasia, as substitute forage (Mack & Thompson, 1982). This alien grass has now become naturalized in the native range of A. spicatum. Through a series of innovative field and glasshouse experiments, Caldwell and his colleagues investigated the basis for the comparative success of the Eurasian congener.

By examining both congeners simultaneously in the field, they first identified shared traits that play no role unique to the naturalization of A. desertorum. Both grasses are caespitose and share similar shoot phenology, water-use efficiency and even seasonal patterns of photosynthesis (Caldwell et al., 1981, 1983; Nowak & Caldwell, 1986). These congeners do however differ strikingly in other features that relate directly to their relative performance. Agropyron desertorum tolerates grazing much better than A. spicatum through its ability to replace lost tillers rapidly. Most of the lost photosynthetic tissue in A. desertorum is replaced through new, quickly-growing tillers, rather than regrowth among existing tillers (Caldwell et al., 1981). Part of this rapid replacement can be attributed to the comparatively lower investment A. desertorum makes in each leaf: less nitrogen and biomass per unit of photosynthetic tissue is contributed. As a result, its leaves are thinner than those of A. spicatum (Caldwell et al., 1981).

Results obtained in a comparison of the dynamics of the grasses’ root growth reveal the re-marshalling of resources that allows A. desertorum rapidly to replace lost tillers. After defoliation, root growth in A. desertorum is half that of controls; root growth of similarly-defoliated A. spicatum is unchanged (Richards, 1984). Clearly, defoliated A. desertorum have the ability to respond internally to tissue loss by redirecting photosynthetic to the formation of new tillers, while the allocation pattern for A. spicatum is much less flexible (Richards, 1984). As a result, almost all the photosynthate allocated after defoliation in A. desertorum comes from current photosynthesis, rather than reserves stored in the roots (Richards & Caldwell, 1985).
This detailed investigation of differences in the ecology of *A. spicatum* and *A. desertorum* is notable for several reasons. The investigators were able to distinguish among attributes in the congeners that were not different and those that were different but played no apparent role in the species' performances from those traits that relate directly to the proliferation of *A. desertorum*. Many of their experiments were manipulative. And finally, almost all their conclusions were derived from field studies. Collectively, these studies serve as a valuable illustration of the power of congeneric comparisions when coupled in the field with a variety of experimental techniques.

A chief limitation of this potentially valuable approach is apparent: not all species that enter a new range have closely-related congeners, especially appropriate congeners native to the new range. Thus, other approaches would need to be employed to predict the fate of species such as *Cannabis sativa*, *Lepidodiscus holostoeides*, and *Pueraria thunbergiana* in many areas to which they may yet immigrate.

### VII. ASSESSMENT OF SPECIES DELIBERATELY SOWN BEYOND THE CURRENT RANGE (NO MANIPULATION OF THE ENVIRONMENT)

Deliberate attempts to sow or otherwise establish plant species beyond their current ranges represent a potentially huge reservoir of knowledge for predicting the outcome of plant immigrations. These attempts fall roughly into two categories: those studies with no manipulation of the environment (i.e. beyond the introduction of the immigrants themselves) and those that apply cultivation to enhance plant survival (see Section VIII below). The deliberate introduction of forage crops, woody species for fiber and fuel and species used in land reclamation, often involves little if any further manipulation of the environment (Van Cleve, 1977; Zobel et al., 1987). In addition, the taxa used are often the products of minimal (if any) deliberate breeding. Consequently, their performance and persistence can be a gauge of the ability of these species to invade a new range.

Despite the agricultural tradition of experimentally sowing or planting a species beyond its current range, this straightforward approach has been used much less frequently for predicting the outcome of immigrations by wild plants (Cavers & Harper, 1967; Prince & Carter, 1985). Levin and Clay (1984) investigated the putative range restriction of *Phlox drummondii* in Texas (USA). By using both sown seeds and transplanted young plants, they discriminated among those factors that caused the death of seeds and seedlings from those that affected adult plants and reproduction. Although this species is common on loose sand, they found that it survived when introduced as either sown seeds or transplants on non-sandy soil. They concluded that *P. drummondii* was restricted from otherwise habitable sites by a seed rain that was insufficient to offset the demographic stochasticity on non-sandy sites.

In Britain, *Lactuca serriola*, a widely naturalized annual, is restricted to the southeastern part of the country. Prince and Carter (1985) investigated reasons for this restriction by sowing seeds and planting seedlings for two consecutive years in southwest and northern UK. Their results were equivocal in that plants in all the sown populations survived and grew well, even those sown 150 km beyond the species' current boundary. They concluded that no single factor could alone account for the species' apparent range limitation. These results illustrate a recurring limitation of this approach: the factor(s) that apparently restrict the range may operate infrequently.

Beyond examples in agriculture, studies simultaneously investigating the fate of multiple alien species in a potential new range are unfortunately rare. In the course of investigating the ability of species to persist on serpentinite soils, Kruckeberg (1986) introduced 20 alien species and 20 species native to the Pacific Northwest (USA) as cuttings, seedlings grown from seed in a greenhouse or seeds onto sites in the Cascade Range of Washington. Almost all of these introductions failed, often within the first year after introduction, including the European species *Lychins alpina*, *Melandrium firmum*, *Saponaria ocyroides*, *Silene nutans*, and *Vicia vulgaris* (A. Kruckeberg, pers. comm.). Transplants of *Silene paradoxa* from southern Europe not only persisted, but its population also increased 25-fold within 15 years (Kruckeberg, 1986). The population was still present in 1990 (A. Kruckeberg, pers. comm.). This study is unusual not only for the quantified records of introductions but also for the much more unusual attention paid to recording failures in naturalization. If comprehensively applied, such an approach could address successfully issues as diverse as the reasons for failures in biological control, identification of community resistance to naturalization, and explanations of the intrinsic boundaries among biomes (Elton, 1958; Harper, 1982; Simberloff, 1986).

Seeding transplants alone are usually employed in silviculture to investigate possible range extension. Such experiments beg the question however as to whether an immigrant population of seeds—the most likely means by which a species would accidentally enter a new range—would lead to a naturalization. Pierson and Mack (1990) introduced seeds alone to investigate the potential of *B. tectorum* to become naturalized in forest habitats in Washington and Idaho (USA) where it is uncommon or rare. By repeatedly mapping individual plants throughout their lives, it was possible to characterize the morbidity among the populations on the environmentally-different sites. Although the grass readily germinated in most of these forests, it did not persist. Repeated censuses revealed that immigrant plants died not through a catastrophe each year but because of a diverse and changing array of lethal events.
Experimental introductions beyond a current range have several attractive features, not the least of which is the comparative simplicity of the experiments. The fate of seeds drawn from the same founder population can be simultaneously compared among a diverse range of habitats (Pierson & Mack, 1990). Furthermore, the approach readily lends itself to the investigation of questions on the minimum size of the immigrant population necessary for establishment (Simberloff, 1989). Nevertheless, spurious results can be obtained. As mentioned in connection with the work of Prince and Carter (1985), a lethal factor in the potential new range may operate so infrequently as not to appear during the experiment. Hurricanes and epidemics are obvious catastrophes (sensu Harper, 1977), forces that operate infrequently, yet still restrict naturalization. Detecting such forces might require trials in the same sites over many years—a practice not likely to be routinely employed except in agriculture. Alternatively, the persistence of a species sown experimentally beyond its current range may mean that the species’ range is still expanding (Davis, 1983) and that naturalization has been limited by chance dispersal alone. Holland (1980) reached this conclusion based on planting bulbs of the native *Erythronium americanum* beyond its current range in Quebec. This explanation could account as well for the persistence of alien species.

**VIII. EXPERIMENTAL SOWINGS BEYOND THE SPECIES’ CURRENT RANGE (WITH MANIPULATIONS OF FIELD CONDITIONS)**

The most obvious interpretation gleaned from the persistence of a species derived from experimental sowings is that its naturalization could occur. Yet, as outlined above, this interpretation could stem from a ‘false positive’ result, i.e. establishment may have occurred in a year(s) in which a reliably lethal factor did not operate. The timing and circumstances of the immigration can greatly influence the outcome (Crawley, 1989). Coupling experimental sowings with simultaneous environmental manipulation in the new range minimizes this limitation. Such manipulations allow the creation and assessment of rare environmental conditions. Even for unchanging components of the environment (e.g. daylength, soil texture, chronic soil nutrient status), this approach has the potential to demonstrate the character and magnitude of the vulnerability (or resistance) of the community to plant invasion.

There are abundant precedents for this approach, although once again these occur mainly in agriculture. As a result of cultivation (e.g. tillage, irrigation, pesticide application), the current geographic ranges of most crops are far larger and more diverse than the native ranges of their progenitors. Viewed in this manner, cultivation becomes a powerful tool for identifying the reasons for a failure in naturalization. Furthermore, this human-intervention is multi-faceted and can be readily partitioned to assess subtle environmental differences as they relate to naturalization: e.g. amount and character of litter, soil structure, even size of the peds (Harper, 1977 and references therein). The widespread use of smoke pots, bird-netting, irrigation and pesticides are all testimony to the manipulative experimentation (even if by trial-and-error) that has preceded cultivation of a crop in regions that would otherwise be outside its range.

Surprisingly this field manipulation has been rarely implemented for the explicit assessment of the potential of alien species to persist in a new range, although many exclusion studies have coincidently dealt with aliens. A striking exception was provided by Wardle (1971), who in 1961 began a series of manipulative experiments to investigate the causes of upper timberline in New Zealand. He introduced both seeds and seedlings of nine alien woody species, including three congers each of *Pinus* and *Eucalyptus*, in common gardens that straddled the natural timberline (1300 m) in the Craigieburn Range. Knowing that the species differed in their responses to radiation, Wardle employed lath structures so that plants were subjected to 27, 54, 80 and 100% of full sunlight. Other treatments included covering the laths with netting to retard foraging grasshoppers and surrounding the seedlings with gravel to reduce frost heaving. All seedlings were planted in a fertilized potting mix and were watered when drought seemed imminent.

Status of plants in these experiments was last reported in 1985 and displays the variety of responses among the aliens (Wardle, 1985). The North American conifers germinated from 900 to 1780 m but differed widely in their survival and growth rate due to shade, extent of their apparent infection with ectotrophic mycorrhizae, or attack by Collembola. *Pinus contorta* consistently displayed the most vigorous growth and was most vigorous under 80% sunlight. *Picea engelmannii*, which was initially susceptible to Collembola attack and inconsistent mycorrhizal infection, persists at the highest garden (1600 m) but only under 27% sunlight. *Pinus hartseli* initially survived at 1600 m but died by 1985. Very few *Pinus flexis* seeds ever germinated, regardless of elevation or other treatment. Seedlings, both transplants and those that germinated in situ, of the *Eucalyptus* congeners experienced high mortality, except at elevations well below the natural timberline. These results were largely duplicated in later transplant trials; survival and growth were generally highest at elevations near the natural timberline. Two tropical timberline species, *Dacrycarpus punctatus* from New Guinea and *Sophora chrysophylla* from Hawaii, both failed to survive even at the lowest elevation, 900 m (Wardle, 1971). In addition to illustrating the strength of a manipulative approach to predicting plant invasions, Wardle’s work also illustrates some of the practical limitations. Simultaneously employing even a few treatment levels of a single factor (shade) to nine species
(both seeds and transplanted seedlings) at five elevations presents formidable statistical and logistical problems. Most sobering however is the realization that the factors chosen for manipulation may not include those contributing most to the naturalization (or extirpation) of an alien species.

Recent assessment of the potential for transgenic plants to enter habitats beyond the range of the 'conventional' crop has sparked new interest in invasion biology in this manipulative approach. In the most comprehensive example so far, Crawley et al. (1993) compared transgenic oilseed rape *Brassica napus* subsp. *oleifera* with the traditionally produced oilseed rape. The experimental protocol created all combinations of treatments that eliminated vertebrate herbivores (mainly rabbits) with fenced exclosures and native competitors by hand cultivation, plus the application of pesticides in a factorial design that eliminated fungal parasites and insect and molluscan grazers. By this partitioning of the potential barriers to naturalization, they were able to discriminate those factors that significantly affected fitness (competition and vertebrate grazing) from those that did not (insect grazers and fungal parasites).

Crawley et al.'s (1993) experiment deserves imitation and amplification with many other alien species. As implied above, the novelty of this experiment is not that it represents a new means of examining the ecological amplitude of plants but rather in its application to a potentially invasive species. This approach could be readily extended to assess many potential physical and biotic barriers for which the methods have already been developed in agronomy. For two environmental factors, I illustrate below established agronomic procedures that could be more widely adopted in ecology.

Precipitation: Supplemental irrigation can resolve whether water is limiting for a species in a new range and, if so, at which stages in the life cycle. For example, many woody species can indefinitely tolerate grassland habitats as adults but rarely, if ever, become established in these sites because their seedlings are drought-intolerant (Daubenmire, 1968). Establishing the influence of the annual distribution (and form) of precipitation is equally important, i.e. precipitation out of sequence with a species' phenology could preclude naturalization (Nilsen & Muller, 1980). Resolution of this issue under field conditions requires the ability to control the timing of precipitation, including the ability to prevent plants from receiving precipitation. Rain-out shelters, in effect, sheds or horizontal shields that automatically cover plants with the onset of precipitation, allow such control (Foale et al., 1986). These large structures are mounted astride the plot on parallel tracks. With a sensor's first detection of precipitation, the shelter rolls over the plots while suspended well above the plants. Once the rain, sleet, etc. ends, it automatically returns to its rest position. An experimental precipitation schedule is provided with irrigation.

Rain-out shelters are larger and more complicated mechanical/electrical devices than are usually employed in terrestrial ecology, yet their usefulness is directly dependent on their reliability. Furthermore, experimental design issues dealing with their size, shape, and the creation of independent replicate plots under them can be formidable (Legg et al., 1978; Foale et al., 1986). Despite these limitations, the potential of rain-out shelters is impressive for allowing assessment of the role of precipitation (and drought) in restricting alien plants. Their routine use would allow investigation of an extraordinary range of important questions about the role of water in the persistence or extinction of alien species on a site. So far, their closest application to invasion biology has dealt with the tolerance of alien forage grasses to varying moisture regimes (e.g. Asay & Johnson, 1990). These structures however deserve much wider application.

Length and duration of the frost-free season: Many frost-sensitive crops are maintained in frost-prone areas by cultivation inside row covers (cloches, low tunnels), variously shaped tents of plastic film stretched over the crop rows (Wells & Loy, 1985). These structures are effectively small glasshouses that prevent loss of re-emitted radiation and decrease the convective transfer of radiation. They routinely create nighttime temperature increases of 2–3°C over ambient, although higher daytime temperatures can be inadvertently achieved with detrimental effects for some crops (Wolfe et al., 1989). In temperate climates these covers are useful both in evaluating the role of intermittent frost on spring germination as well as on fruit maturation in autumn. The same issues arise with the naturalization of wild species, e.g. a species' failure to become naturalized a direct function of intermittent frosts that routinely occur in late summer/early autumn (Patterson et al., 1979)?

Despite their value in evaluating the potential range of alien species, row covers present complications in assessing temperature alteration alone; light, humidity, air movement and even the frequency of insect visitors are altered. Alteration of light is probably minimal; about 90% of the PPFD is transmitted. Substantial alteration of air movement (as well as an excessive increase in daytime air temperature) can be minimized (Wells & Loy, 1985). Alteration of availability of the plants to insects—usually deemed an asset in horticulture—remains a confounding influence for investigating the performance of wild alien species.

Approach VIII is potentially superior to the others, especially if it involves a comparison among congeners. It comes closest to satisfying the need to provide experimental demonstration of the potential for naturalization. Its limitation deals with the practical constraints on manipulating multiple factors in the field; the number of mandatory replicates for more than a handful of factors soon carries the design beyond feasible limits. More seriously, there is no assurance that the factors
limiting or allowing naturalization will be among those included in the design. Similar to the scenario cited with other approaches, field manipulations could fail to reveal any explanation for the failure of an alien to become naturalized because the causative agent operates infrequently and not within the course of the experiment, i.e. a ‘false positive’ result.

CONCLUSIONS

Although each approach outlined above has value, none is a panacea. Each has limitations, if only in the practicality of their implementation. Nevertheless, I believe the approaches can be ranked in their level of efficacy.

1) The use of groupings or lists of species that have become naturalized elsewhere is a time-honored manner of prediction. Strength of the approach is the undeniable observation that some species have become routinely naturalized in widely-separated locales. The chief limitation is that if used in isolation, the approach gives a myopic view of future naturalizations, i.e. species that have no history of naturalization are usually overlooked.

2) Perhaps the most limited approach relies on the traits of weeds, and especially ruderal species. This approach is most useful in frequently-disturbed terrestrial habitats. As the opportunity for species to immigrate increases world-wide, we can expect however to see many more species becoming naturalized with few, if any, of these characteristics.

3) Predicting a region’s future invaders based on the climate in their home range can be effective, although it is subject to many exceptions. The native ranges of many potential invaders are diverse; predictions based on one part of a species’ range may hold little meaning for predicting the response of populations drawn from another.

4) Whatever the efficacy of predictions based on the rate of spread in a new range, the requisite information to evaluate this approach is still too fragmentary. The initial period in which an ultimately naturalized species spreads little in a new range is too similar to the trajectory for alien species that are eventually extinguished. Perhaps no terrestrial plant invasion has yet been mapped with sufficient detail to evaluate these models.

5) Controlled-growth facilities and glasshouses play an effective role in predicting plant invasions, if only for those species considered too noxious for field trials. The difficulty in simulating the environmental stochasticity in a new range (especially the biotic aspects) will remain a chief obstacle in this approach.

6) Comparisons of the performance of congeners, especially through field trials in the new range, hold much potential value. Assessment can concentrate on those features that the alien and its native (or less abundant alien) congeners do not share as the likely source of differences in their performance. This approach is obviously limited to those cases in which a closely-related native congener occurs in the potential new range or to groups of alien congeners introduced simultaneously.

7) Deliberately sowing an alien beyond its current range is a straightforward and powerful tool for prediction. A chief limitation is the likelihood that the factor(s) that would inevitably cause extirpation will not be displayed during the experiment.

8) Deliberate introductions beyond a species’ current range coupled with simultaneous manipulation of the environment is the single most powerful (although also most demanding) approach. Although many environmental factors can be manipulated in a field trial, there is no assurance that among the factors chosen are those that directly explain the reasons for naturalization or repeated extirpation of an alien in a new range.

If no one approach is a universal solution, then combinations seem called for. Investigations seem prudent that employ one or more descriptive approaches as first approximations, which are then capitalized upon with experimental approaches. Depending on the question or issue, such combinations would at least distinguish the ‘plausible’ from the ‘implausible’ candidates for naturalization. Best of all are those investigations that employ several, largely experimental approaches, such as simultaneously sowing congeners beyond their current range in a manipulative field experiment. Few such studies have been performed—enough however both to serve as models and demonstrate the benefits (e.g. Cavers & Harper, 1967; Wardle, 1971, 1985; Caldwell et al., 1981; Schierenbeck et al., 1994).

ACKNOWLEDGEMENTS

I thank the organizers of the Invasion Biology Workshop at the University of California (Davis) that led to the production of this special issue on biotic invasions. I thank R. Alan Black and Michal Jasineski for helpful comments on the manuscript.

REFERENCES


Predicting the identity and fate of plant invaders


