

CHAPTER 16

Invasibility of Plant Communities

MARCEL REJMÁNEK

16.1 INTRODUCTION

One of Elton's classical arguments for a positive causal relationship between community species richness and stability was the ease with which alien species can invade species-poor oceanic islands (Elton, 1958, p. 147). This has been often interpreted as 'the more native species present the more invasion resistant the community.' Certain data from small mammal and bird communities support this relationship (Fox and Fox, 1986; Pimm, personal communication). Properly collected data from plant communities are either unavailable; or are confounded by species-area effects or by species richness changes during succession and/or by dependence on environmental gradients. Decline of invasibility (openness to invasions) during the course of successions is generally admitted (Crawley, this volume) but has never been quantified. Similarly, the maximum number of aliens in mesic and riverine environments has been indicated (Fox and Fox 1986; MacDonald *et al.*, 1986) but no generalizations over the whole moisture gradient have been made. Invasions into successional mature communities with no anthropogenic disturbances are the objects of careful statements and supported by very few persuasive examples. There seems to be no community without some degree of natural disturbance (Pickett and White, 1985; Rejmánek, 1984; Sousa, 1984). What is the role of this disturbance, competitiveness and recolonization ability of native species, and of the amount of imported propagules of aliens in an invasion process? We have only partial answers for a few simple cases but, unfortunately, the existing studies are too few to warrant generalizations.

In this chapter I will first briefly examine a plausible procedure for the collection of data which could tell us something about the species richness-invasibility relationship. Then the available data on invaders in successional series from Europe and North America will be summarized and interpreted. Plant invasions in relation to moisture gradients will be also examined. Finally, some examples of plant invasions into natural communities will be discussed and the role of disturbance will be illustrated using a simple simulation model. All examples and considerations will be limited to vascular plants and their communities.

16.2 SPECIES RICHNESS VERSUS INVASIBILITY

Available data on numbers of native and invading species are not usually comparable, because they are based on samples of different size and different homogeneity. This fact suggests that percentages of invading species, instead of their actual numbers should be used as a measure of invasion vulnerability of sampled communities or areas. A percentage is certainly a useful expression but, because it is in fact the ratio of the number of invader (A) and native (N) species ($100A/(N + A)$), it can not be used for the study of invasibility dependence on the number of native species. If such a comparison is done, and the percentage of invader species is plotted against the number of native species (Fox and Fox, 1986), a parabolic negative relationship is the inevitable outcome. The resulting relationship is negative even if correlation between absolute numbers of invaded and native species is positive!

It is a commonplace that large samples contain more species than smaller samples. Unfortunately, the rate of species increase with increasing sample area differs from community to community (Moravec, 1973; Williamson, 1988). It is, therefore, virtually impossible to define 'the best' sample size for invasibility comparisons over several communities. One way to approach this problem is (1) take a series of samples of different size from each community under interest, (2) calculate the regression coefficient for the number of invading species on the log of the sample area, b_A , and the regression coefficient for the number of native species on the log of the sample area, b_N , in each community, and (3) calculate the correlation coefficient between the resulting values of b_A and b_N over all communities and test for null hypothesis $r=0$. Unfortunately very few species-area community data sets are available for such an analysis. Species-log area regression coefficients calculated on the basis of check lists or manuals covering large heterogeneous areas (Crawley, 1987) are not helpful in community invasibility investigations. Also, it would be particularly useful to know the values of b_N before invasions started. And finally, even if we have all these data, if there is any dependence of invasibility on species richness, this dependence may in practice be masked by the influence of many other factors. I will deal briefly with three of them: succession, moisture gradient, and natural disturbance.

16.3 INVADERS IN SUCCESSIONAL SERIES

Succession of plant communities from those consisting mainly of ruderals (r -strategists) to communities of competitors and stress-tolerators (*sensu* Grime, 1979), represents a gradient of constraints placed on potential invaders. Because most non-native species are ruderals by their nature (Baker, 1965; Heywood, this volume), it is not surprising that pioneer communities exhibit a higher number and proportion of invaders than successional more advanced stands. There is a consistent exponential decline of the proportion of invaders in all series where complete lists of species are available (Figures 16.1 and 16.2). The absolute

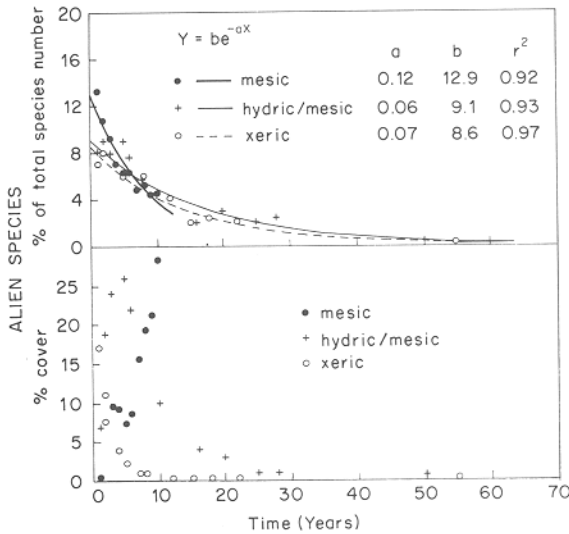


Figure 16.1. Changes in relative number and cover of invading species in three successional series from central Europe. Secondary *mesic* series: old field, Göttingen, West Germany, after Schmidt (1981). Primary *hydric/mesic* series: artificial islands in fishponds, Trebon area, Czechoslovakia, after Rejmánek and Rejmánková (unpublished data). Secondary *xeric* series: old fields in Bohemian Karst Protected Area, Czechoslovakia, after Huml (1977), Baumova (1985) and author (unpublished data)

number of invaded species differs considerably from series to series but also declines exponentially in the course of succession.

How much does this result reflect different exposure of different successional stages to the propagule import? We should expect more intensive human-mediated import of propagules at the beginning of secondary successions. Only one series seems to be free of this confounding effect. All communities along the primary successional gradient in the Atchafalaya delta and Atchafalaya Basin (Rejmánek, *et al.*, 1987) are flooded and exposed to propagule deposition every spring. Possibly, more propagules are trapped in older communities located upstream. However, the trend here is the same as in the remaining series. There are many invaders in initial stages including for example; *Cyperus difformis*, *Eichhornia crassipes*, *Sphenoclea zeylandica*, *Alternanthera phyloxeroides*, and *Colocasia esculenta*. These are replaced by only two invaders in stands older than 30 years (*Sapium sebiferum*, *Vigna unguiculata*); and the Japanese climbing fern (*Lygodium japonicum*) is the only alien species in forests older than 50 years.

Spatial isolation of young successional communities from sources of alien propagules may change the absolute numbers substantially. In the first 3 years of

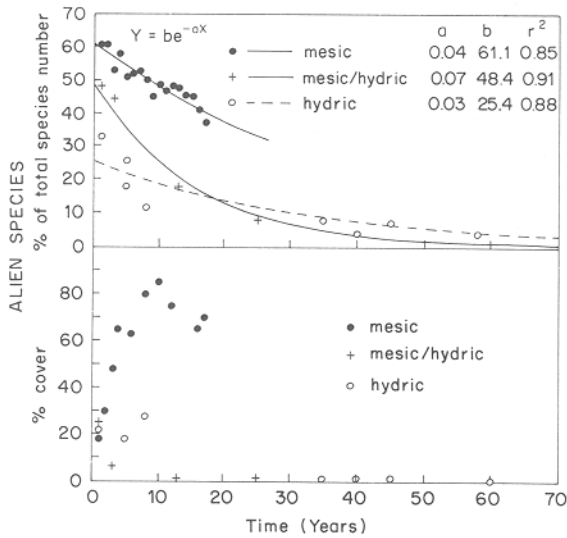


Figure 16.2. Changes in relative number and cover of alien species in three successional series in the USA. Secondary *mesic* series: old field, New Jersey, after Pickett (1982, 1983). Secondary *mesic/hydric* series: old fields in Louisiana, after Bonck and Penfound (1945) and author (unpublished data). Primary *hydric* series, the Atchafalaya Basin and Atchafalaya delta, Louisiana, after Rejmánek and Sasser (unpublished data)

postlogging succession in Oregon only four invading species can be found (less than 3%) (Dyrness, 1973).

The total cover of invading species very often does not have its maximum at the beginning but increases in the first 5 to 10 years and declines later. This trend seems to be characteristic especially for secondary mesic series (Figures 16.1 to 16.3 and Table 16.1, p. 374).

The proportion and absolute number of alien species are higher in American mesic series than in European ones. This is in agreement with general trends in exchange of alien species between North America and Europe (Di Castri, this volume).

It is difficult to find data from other continents for comparison. Nowhere else do studies on succession have such a long tradition as in Europe and the USA. Unfortunately, full species lists are published rather infrequently. Lists of dominant species from different stages of secondary succession in South Africa (Davidson, 1964) indicate the same decline of invaders as in successional series from Europe and North America.

It seems that this successional 'repairing' function of native vegetation is rather universal in continental situations. Of course, the proximity of diaspore sources

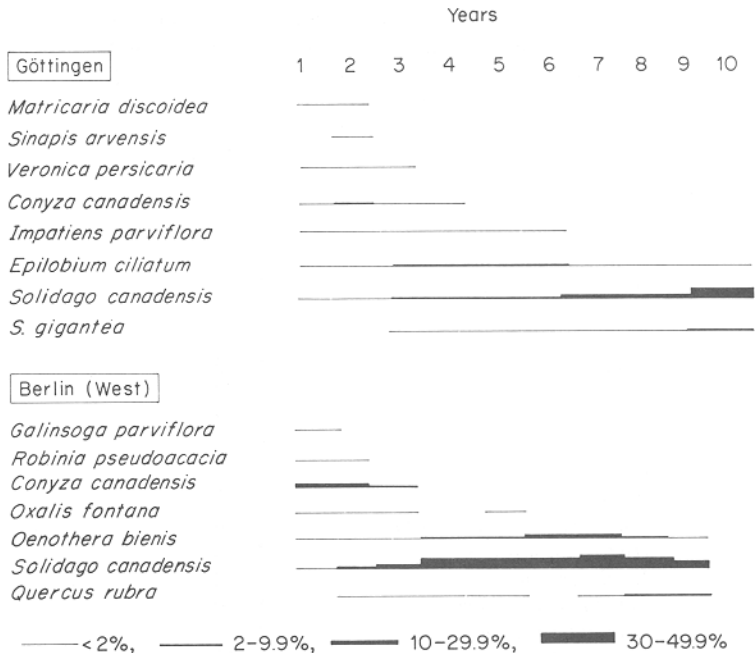


Figure 16.3. Invading species cover in two secondary mesic successional series in Germany (Bornkamm and Hennig, 1982; Schmidt, 1981)

of native plants plays a crucial role in the rate of recovery. Compared with continents, natural recovery of native flora on islands seems to be much slower or incomplete. The reasons for this difference are complex and still not fully understood (Mueller-Dombois, 1981; Loope and Scowcroft, 1985; Loope and Mueller-Dombois, this volume).

16.4 INVADERS ALONG MOISTURE GRADIENTS

In the successional series discussed above, both the maximum cover and the maximum proportion of alien species was found in mesic series, or at least, in initial stages of mesic succession (Figures 16.1 and 16.2). The absolute numbers of species are not directly comparable, because of different sample sizes. But, taking sample sizes into account, it is not only the proportion but also the number of invaded species which is highest in the first years of mesic succession. Invaders seem to be rather rare also in other xeric and hydric series described in literature (Symonides, 1985; Burbank and Philips, 1983; Carpenter, 1983; Vasek, 1980; Eicke-Jene, 1960). The number of invading species in initial stages of succession is apparently the greatest in mesic environments and decreases at both ends of the

Table 16.1. Dominant species and year of peak cover during 20 years of vegetation succession at Hutcheson Memorial Forest, NJ. Alien species are indicated by asterisks. After Pickett (1982)

Species	Year
<i>Ambrosia artemisiifolia</i>	1
<i>Mullugo verticillata</i>	* 1
<i>Digitaria sanguinalis</i>	1
<i>Barbarea vulgaris</i>	* 2
<i>Frigeron canadensis</i>	2
<i>E. annuus</i>	3
<i>Plantago lanceolata</i>	* 3
<i>P. rugellii</i>	2-3
<i>Oxalis stricta</i>	3
<i>Rumex acetosella</i>	* 5
<i>Daucus carota</i>	* 5
<i>Aster</i> spp.	7
<i>Chrysanthemum leucanthemum</i>	* 8
<i>Hieracium pratense</i>	* 10
<i>H. florentinum</i>	* 12
<i>Lepidium campestris</i>	* 10
<i>Trofolium pratense</i>	* 11
<i>Convolvulus sepium</i>	* 13
<i>Poa pratensis</i>	15
<i>Agrostis alba</i>	*? 12
<i>Rhus glabra</i>	19-20
<i>Lonicera japonica</i>	* 17
<i>Juniperus virginiana</i>	19
<i>Acer rubrum</i>	20
<i>Poa compressa</i>	* 17
<i>Acer negundo</i>	18
<i>Solidago graminifolia</i>	19
<i>Rhus radicans</i>	20
<i>Rosa multiflora</i>	* 20
<i>Solidago juncea</i>	19

moisture gradient. This is in agreement with changes of the total species number in young communities along a moisture gradient (Auclair and Goff, 1971; Peet, 1978).

The only complete list of all invading species in plant communities along the moisture gradient in a rather undisturbed landscape is, as far as I know, the one published by Falinski (1968) from Bialowieza Primeval Forest, Poland. A simplified version of his analysis is summarized in Table 16.2.

Table 16.2. Alien plant species in plant communities of the Bialowieza Primeval Forest in 1968 year (after Falinski, 1968)
(+, sporadic; *, common; #, very common)

Species	Moisture																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Elodea canadensis</i>	+	+	+	#	+	#	#	#	*	+	+	+	+	+	+	+	+	+	+	+
<i>Acorus calamus</i>									*						*	#	+	#		
<i>Carex brizoides</i>																				
<i>Cytisus scoparius</i>																		*		*
<i>Lupinus polyphyllus</i>																			+	
<i>Sambucus racemosa</i>																			+	
<i>Pulmonaria mollissima</i>																			+	
<i>Rosa</i> sp. div.																			+	
<i>Deschampsia flexuosa</i>																				+
<i>Luzula luzuloides</i>																				+
<i>Juncus macer</i>																				+
<i>Elsholtzia patini</i>																				+
<i>Rudbeckia laciniata</i>																				+
<i>Solidago serotina</i>													+							+
<i>Erigeron ramosus</i>													+							+
<i>Viola odorata</i>																				+
<i>Myosotis sylvatica</i>																				+
<i>Poa chaixii</i>																				+
<i>Sambucus nigra</i>																				+
<i>Quercus rubra</i>																				+
<i>Acer negundo</i>																				+
<i>Reynoutria japonica</i>																				+
<i>R. sachalinensis</i>																				+

1, Lemnetum gibbae; 2, Lemnetum minoris-trisulcae; 3, Potamion; 4, Hottonietum palustris; 5, Hydrocharo-Stratiotetum; 6, Myriophyllo-Nupharetum; 7, Sparganio-Sagittarietum; 8, Acoratum calami; 9, Phragmition; 10, Magnocaricion; 11, Salicetum pentandro-cinereae; 12, Carici elongatae-Alnetum; 13, Salicetum triandfro-viminalis; 14, Salicetum albo-fragilis; 15, Alno-Padiion; 16, Tilio-Carpinetum; 17, Potentillo albae-Quercetum; 18, Pino-Quercetum; 19, Quercio-Pinetum; 20, Peucedano-Pinetum.

Several species from Falinski's list occur only in disturbed stands, such as forest clearings. It is also unclear whether all species included in the list are true aliens (*Carex brizoides*, *Deschampsia flexuosa*). Nevertheless, the maximum number of alien species is found in mesic communities located in the central part of the moisture gradient (*Alno-Padion*, *Tilio-Carpinetum*). Accordingly, Loope and Mueller-Dombois (this volume) found lack of competitive superiority of alien species in extreme habitats like montane bogs and new lava flows.

At this point we may ask a similar question to the one we asked in connection with successional stages. How much does this result reflect a difference in exposure of mesic and extreme habitats to propagule import? And another question: does this result reflect preadaptation of introduced species (coming from mesic environments) rather than higher vulnerability of mesic communities to invasions? Neither of these possibilities can be completely ruled out. Apparently the number of alien species declines faster from mesic environments towards extreme ends of the moisture gradient than does the number of native species in the same directions. In other words, there seems to be a lower percentage of alien species in extreme environments, at least in young successional stages (Figures 16.1 and 16.2). The above indicates the relevance of both questions. Properly designed experiments in this area are badly needed.

The only experiment in which plants were sown into different communities along a moisture gradient was done by Juhász-Nagy (1964). Unfortunately, he never published the full list of non-native species used, or the examined communities (nine different vegetation types). The most resistant community to the establishment of 11 sown species was, in agreement with our findings, the extremely dry one (*Festucetum pseudodalmaticae*).

Apparently xeric environments are not favorable for germination or the establishment of many non-native species and, on the other hand, wet productive habitats support strong resident competitors (Grime, 1979; del Moral, 1983) which do not leave much space for potential invaders. Both these unfavorable factors for invasion, stress preventing ecesis and competition preventing survival to reproduction stage, seem to be weaker in mesic environments.

In many areas, river banks and floodplains in general often host the highest percentage of alien species (Kopecky, 1967; Crawley, 1987; Nilsson *et al.*, 1988). These habitats represent a transition between mesic and hydric environments. Besides a high frequency of natural disturbance which promotes invasions (see later), riverine habitats have traditionally been disturbed and exposed to propagules of alien plants due to human activities (communications and settlement).

16.5 INVADERS IN 'UNDISTURBED' COMMUNITIES

So far, the list of plant species invading undisturbed (= naturally disturbed) and successional advanced communities is very short and many questions remain concerning possible direct or indirect effects of human disturbance. The fact that

this preliminary list (Table 16.3) is so short is not surprising if we recall what tremendous mortality native and established species have in mature communities. The probability of survival from seed to a reproducing plant is usually in the range 10^{-4} to 10^{-6} for trees (Hett, 1971; Guittet and Laberche, 1974; Van Valen, 1975; Vacek, unpublished data). There is no reason to expect a lower mortality rate for introduced non-native trees in temperate regions. This means that about 100 000 seeds of a non-native tree species would be required to examine invasibility of a relatively undisturbed forest. Nobody has tried to do it, as far as I know.

Table 16.3. Invaders in natural communities

Species (Family) Country of origin	Adventive distribution	Reference
<i>Acacia saligna</i> (Fabaceae) Australia	South African fynbos shrublands	Wilgen and Richardson (1985)
<i>Acaena anserinifolia</i> (Rosaceae) New Zealand	Great Britain, sand dunes	Ratcliffe (1984)
<i>Acer pseudoplatanus</i> (Aceraceae) Continental Europe	British Isles, woodlands	Crawley (1987)
<i>Acorus calamus</i> (Araceae) Himalayas	Europe, reedswamps	Kornas (1988) Wein (1942)
<i>Ailanthus altissima</i> (Simarubiaceae) Asia	California, 'invades areas of native vegetation	McClintock (unpublished)
<i>Alnus viridis</i> (Betulaceae) Alps, eastern Carpathian Mountains	Sudeten Mts., tall herb sub- alpine communities	Rejmánek <i>et al.</i> (1971)
<i>Amaranthus spinosus</i> (Amaranthaceae) North America	Phan Rang, Vietnam, <i>Barringtonia</i> floodplain forests	Rejmánek (unpublished)
<i>Ammophila arenaria</i> (Poaceae) Western Europe	California, coastal dunes	Mooney <i>et al.</i> , (1986)
<i>Ardisia crenata</i> (Myrsinaceae) East Asia	Mauritius, evergreen wet forest	Lorence and Sussman (1986)
<i>Arundo donax</i> (Poaceae) Southern Europe	South Africa, reedswamps	Wells <i>et al.</i> (1980)
<i>Butomus umbellatus</i> (Butomaceae) Europe	Michigan, Ohio, Ontario, marshes along rivers and lakes	Stuckey (1968)
<i>Cakile edentula</i> and <i>C.</i> <i>maritima</i> (Cruciferae) Europe	Coastal dunes in western USA and Australia	Barbour and Rodman (1970) Boyd (1986) Rodman (1986)
<i>Centranthus ruber</i> (Valerianaceae) Mediterranean region	England, Wales, Southern Ireland, cliffs, dry banks	Crawley (1987)

(Contd.)

Table 16.3. (Contd.)

Species (Family) Country of origin	Adventive distribution	Reference
<i>Chrysanthemoides molinifera</i> (Asteraceae) South Africa	Coastal dunes in Australia	Weiss and Noble (1984)
<i>Cytisus scoparius</i> and <i>C. monspesulanus</i> (Fabaceae) Europe	Western USA, 'invades areas of native vegetation'	McClintock (unpublished)
<i>Elaeagnus angustifolia</i> (Elaeagnaceae) Eurasia	Southwestern USA, arid riparian communities	Knopf and Olson (1984)
<i>Epilobium brunnescens</i> (Onagraceae) New Zealand	British Isles, rocky beds and banks of streams	Crawley (1987)
<i>Epipactis heleborine</i> (Orchideaceae) Europe	Northeastern USA, British Columbia, deciduous and Douglas fir forests	Luer (1975) Antos (unpublished)
<i>Eucalyptus globulus</i> (Myrtaceae) Australia	California, 'spreading from previous plantings, crowding out the native vegetation'	McClintock (unpublished)
<i>Geranium robertianum</i> (Geraniaceae) Europe	British Columbia, along streams in hemlock forests	Antos (unpublished)
<i>Hedera helix</i> (Araliaceae) Europe	California, British Columbia, 'displacing native ground cover plants', Douglas fir forests	McClintock (unpublished) Antosh (unpublished)
<i>Hakea sericea</i> (Proteaceae) Australia	South Africa, fynbos	Macdonald and Richardson (1986)
<i>Hypericum androsaemum</i> (Guttiferae) Southern Europe	New Zealand, native forests	Johnson (1982)
<i>Impatiens glandulifera</i> (Balsaminaceae) Himalaya	Central Europe, England, stream banks	Kopecky (1967) Crawley (1987)
<i>I. parviflora</i> Asia	Central and western Europe, in many types of <i>Carpinus</i> , <i>Fagus</i> , and <i>Alnus</i> forests	Coombe (1959) Trepl (1984) Csontos (1984)
<i>Iris pseudacorus</i> (Iridaceae) Europe	North America, swamps, ponds, stream banks	Raven and Thomas (1970)
<i>Lantana camara</i> (Verbenaceae) Southern America	Southern Africa, riparian vegetation	Macdonald (unpublished)
<i>Ligustrum robustum</i> (Oleaceae) Ceylon	Mauritius, evergreen wet forest	Lorence and Sussman (1986)
<i>Linum austriacum</i> (Linaceae) Southern Europe	Island of Gotland, alvar grasslands	Nilsson (1981)
<i>Litsea glutinosa</i> (Lauraceae) Southeast Asia	Mauritius, evergreen wet forest	Lorence and Sussman (1986)

Table 16.3. (Contd.)

Species (Family) Country of origin	Adventive distribution	Reference
<i>Lonicera japonica</i> (Caprifoliaceae) Japan	Eastern USA, deciduous forests	Slezak (1976)
<i>Lygodium japonicum</i> (Schizaceae) Japan	Bottomland hardwood forests from Florida to Eastern Texas	Thieret (1980) Rejmánek (unpublished)
<i>Melaleuca quinquenervia</i> (Myrtaceae)	Southern Florida, dwarf cypress forest	Myers (1983) Ewel (1986)
<i>Melia azedarach</i> (Meliaceae) West Asia	Southern Africa, riparian vegetation along major rivers	Macdonald (unpublished)
<i>Mesembrianthemum</i> spp. (Aizoaceae) South Africa	California, coastal dunes, cliffs, and grasslands	Vivrette and Muller (1977)
<i>Mimulus guttatus</i> (Scrophulariaceae)	Europe, stream banks	Rothmaler (1976)
Western North America		Crawley (1987)
<i>Mycelis muralis</i> (Asteraceae) Europe	New Zealand, native forests	Johnson (1982)
<i>Myrica faya</i> (Myricaceae) Canary Island	Hawaii, young volcanic areas	Vitousek (1986)
<i>Ossaea marginata</i> (Melastomataceae) Brazil	Mauritius, evergreen wet forest	Lorence and Sussman (1986)
<i>Pinus lutchuensis</i> (Pinaceae) Ryukyu Islands	Bonin Islands, native vegetation lacking tree conifers	Shimuzu and Tabata (1985)
<i>P. pinaster</i> Southern Europe	Southern Africa, Cape fynbos	Kruger (1977)
<i>P. radiata</i> California	Australia, native eucalypt forests, South Africa, fynbos	Burdon and Chilvers (1977)
<i>Pittosporum undulatum</i> (Pittosporaceae) Eastern Australia	Central Victoria, Australia, sclerophyll forests	Gleadow and Ashton (1981)
<i>Psidium cattleianum</i> (Myrsinaceae) Brazil	Mauritius, evergreen wet forest	Lorence and Sussman (1986)
<i>Pterolepis glomerata</i> (Melastomataceae) Tropical America	Oahu, tropical rain forests	Gerrish and Mueller-Dombois 1980
<i>Rhododendron ponticum</i> (Ericaceae) Turkey	Ireland, semi-natural oakwoods (<i>Quercus petraea</i>)	Cross (1981)
<i>Robinia pseudoacacia</i> (Fabaceae) Eastern USA	Central and southern Europe, xerotherm grasslands	Holzner (1982)
<i>Rubus moluccanus</i> (Rosaceae) Southeast Asia	Mauritius, evergreen wet forest	Lorence and Sussman (1986)
<i>Senecio mikanoides</i> (Asteraceae) Southern Africa	California, 'native' plant areas in canyons and gullies'	McClintock (unpublished)

(Contd.)

Table 16.3. (Contd.)

Species (Family) Country of origin	Adventive distribution	Reference
<i>Smyrniium olusatrum</i> (Umbelliferae) Continental Europe	British Isles, sea-cliffs	Crawley (1987)
<i>Spartina alterniflora</i> (Poaceae) North America	Widely distributed <i>S. anglica</i> resulted from hybridization of <i>S. alterniflora</i> with <i>S. maritima</i>	Ranwell (1972)
<i>S. patens</i> From Newfoundland to Texas	Cox Island, Oregon, low marsh communities	Frenkel and Boss (1982)
<i>Spathoglottis plicata</i> (Orchideaceae) Asia	Oahu, tropical rain forests	Gerrish and Mueller- Dombois (1980)
<i>Tamarix</i> spp. (Tamaricaceae) Eurasia	Southwestern USA, arid riparian communities	Ohmart and Anderson (1982)
<i>Ulex europaeus</i> (Fabaceae) Europe	California, 'invades areas of native vegetation'	McClintock (unpublished)
<i>Viscum album</i> (Loranthaceae) Europe	Sonoma County, California, on 9 native host tree or shrub species	Hawkswort and Scharpf (1986)

The diversity of species invading natural or seminatural communities (about 60 species from 40 families representing all major growth-forms in our table) suggests extreme difficulty or even impossibility of quantifying invasibility of plant communities. It is simply technically impossible to expose an experimental set of some, for example, temperate plant communities to all 50 000 species which could be potential candidates for invasion.

The list in Table 16.3 represents a bizarre collection of extremely diverse adaptations which have been necessary for invasions into a variety of more or less natural communities in different environments. While it seems to be possible to make some generalizations about successful invaders in disturbed and successional young communities (Baker, 1965; Heywood, this volume), there is apparently nothing unifying for invaders in 'undisturbed' natural communities. Some of them form a new stratum in communities where the tree or tall shrub strata were missing but the environment can support them (*Pinus radiata* and *Hakea sericea* in South African fynbos, see Campbell *et al.*, 1979; *Robinia pseudoacacia* in xerotherm grasslands in central Europe). Some apparently did find an 'open niche' like the climbing fern, *Lygodium japonicum*, in bottomland hardwoods from Louisiana to Florida. No climbing ferns were present in these communities originally. Some are apparently dependent on natural disturbance (*Cakile* spp. and *Chrysanthemoides molinifera* in coastal dunes). Some had been only in disturbed habitats for some time and invaded undisturbed communities only recently (*Impatiens parviflora*, Figure 16.4). What happened with such species?

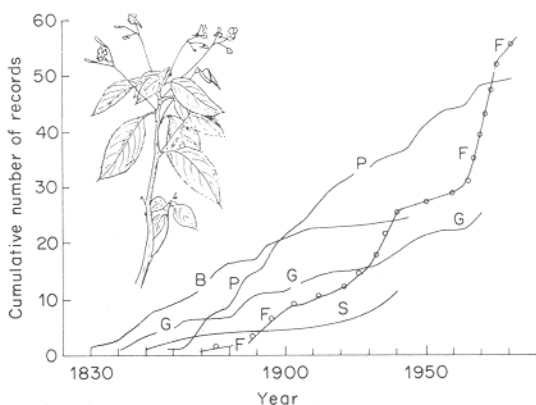


Figure 16.4. Number of *Impatiens parviflora* records from different habitats in central Europe from 1830 to 1971. After Trepl (1984). B, Botanical gardens; G, gardens; P, parks and cemeteries; S, International sowing; F, forests

According to some authors, genetic changes can make some introduced populations better adapted for spread (Baker, 1965). There is no evidence for this in listed species. But very often, it could be simply a matter of the amount of propagules available in disturbed areas and transported into 'undisturbed' ones.

16.6 THE ROLE OF DISTURBANCE

There is overwhelming evidence that several types of disturbance promote biological invasions (e.g. Eglar, 1983; Forcella and Harvey, 1983; Pickard, 1984; Ewel, 1986; Hobbs, this volume; Mack, this volume). Basically, the probability of successful invasions seems to be crucially dependent on the extent and type of disturbance, on the number of non-native species propagules deposited in the community per year, and how long the community is exposed to import of propagules. The amount of biomass or cover may be the most efficient indices of community resistance to invasions in some situations.

Peart and Foin (1985) found that invasion success of *Anthoxanthum odoratum* into coastal grasslands in California is a negative exponential function of resident vegetation biomass, rather than dependent on its species composition or species number. Open space, therefore, created by biomass destruction might be the only really general factor responsible for plant invasions.

Some disturbance occurs in all natural communities because of herbivory, rodent digging activity, tree-falls, soil frost disturbance, fires, etc. Senescence in almost all plant species is also responsible for stochastic space openings in plant communities. In spite of the fact that the majority of invasion situations are nonequilibrium ones, almost all mathematical models of invasibility assume an

equilibrium (e.g. Robinson and Valentine, 1979; Post and Pimm, 1983; Shigesada *et al.*, 1984).

A simple model may be used to simulate the invasion of a new species (say species D) into a community consisting of three species (A, B, C). Assume that the community is experiencing disturbances that are both temporally and spatially stochastic. Some disturbances could create not only an open space but changes in the amount of available nutrients (Tilman, 1982; Hobbs, this volume). To simplify the problem, I will limit disturbance using Grime's (1979) definition: partial or total destruction of biomass. Technically, the model consists of a system of four Lotka–Volterra competition equations with one dimensional diffusion (see Williamson, this volume) and a spatially and temporally discrete stochastic harvest (Rejmánek, 1984). Even if D is a weaker competitor than any of the three resident species and, in the absence of disturbance, D would be extinct, some realistic regimes of disturbance allow its invasion. Moreover, the invasion might be successful even if an external source of propagules exists only temporarily and D does not disperse faster than B and C (Figures 16.5 and 16.7). The invading species in presented simulations spreads rather slowly like, for example, *Impatiens parviflora* dispersing ballistically only about 2 m per year (Coombe, 1959). Even if in a very crude way, the model shows how a low level of natural disturbance and/or vegetation senescence can allow the spread of a competitively inferior non-native species. On the other hand, from a similar simulation model (Dostalkova *et al.*, 1984) it follows that in the absence of any disturbance, selfinhibition or senescence, even invaders which are stronger

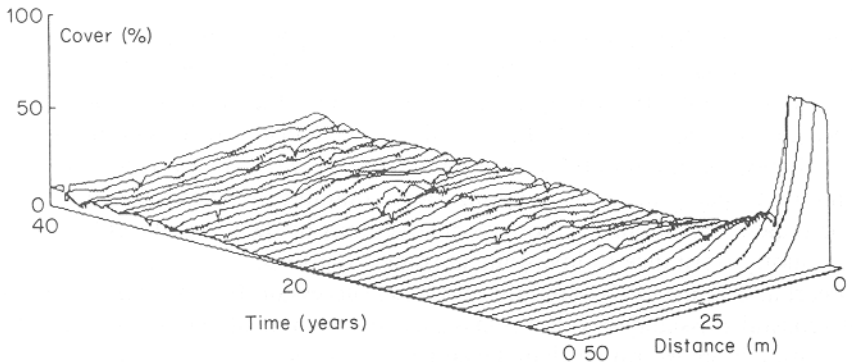


Figure 16.5. A simulation of the invasion of a hypothetical species (D) into a community consisting of three stronger competitors (A, B, C). Propagule diffusion from one end of transect (forest boundary) took place between year 1 and 4. Invading species has a lowest position in a competitive hierarchy ($A > B > C > D$) and cannot survive in the community without stochastic disturbance. The disturbance in this simulation was realized by a complete harvest of all species in randomly selected 30 (in average) out of 200 intervals forming 50 m long transect every year. Such disturbance corresponds to a complete destruction or death of vegetation in about 15% of an area every year

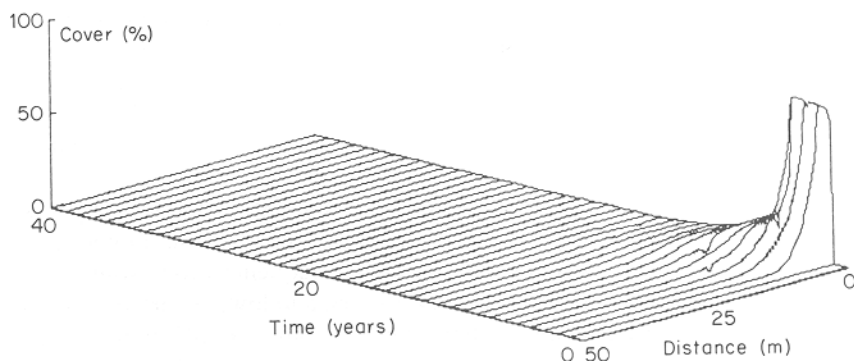


Figure 16.6. The same simulation parameters as in Figure 16.5 but the frequency of disturbance is reduced to two-thirds. The invader (D) is unable to establish itself

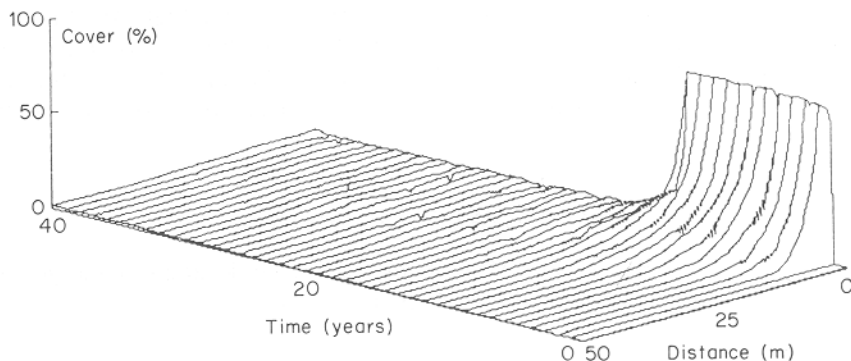


Figure 16.7. The same simulation parameters as in Figure 16.6 but with the propagule diffusion from external source between year 1 and 12. The invader (D) is spreading and survives in the community

competitors than native species can scarcely invade their community. Paleobotanical evidence for communities resistant to invasion of species superior to established ones from the Pleistocene–Holocene period comes from Cole (1985); (see also Levin, 1985; Markgraf, 1986; and Cole, 1986).

16.7 CONCLUSIONS

All analysis of community invasibility based just on field observations (*a posteriori*) are unsatisfying. Usually, it is impossible to separate the resistance of a biotic community from resistance determined by an abiotic environment. Also, in most of the cases we do not know anything about the quality and quantity of imported propagules. Nevertheless, available evidence indicates that only very

few alien species invade successional advanced plant communities. Plant communities in mesic environments seem to be more invadable than communities in extreme environments. Apparently xeric environments are not favorable for germination and seedling survival of many introduced species and wet habitats do not provide open space for invaders because of fast growth and high competitiveness of resident species.

It is not easy to make generalizations from simulation models of invasion processes. Still, one rather qualitative conclusion can be made. Longer lasting and faster spread from external sources; a higher frequency (up to some level) of disturbance; a higher competitiveness of invaders; and lower overlap in resource requirements with native plants;—all these factors can, to some extent, substitute for one another and can, especially in combination, promote the success of invasions in plant communities. This generalization is in agreement or, at least, not in contradiction with existing field data.

While we have identified several factors that are important determinants of plant community invasibility, we still lack experimental data that would permit us to quantify and sort out the combined effects of these traits. Far more experimental studies are needed to add to those few that already exist (Juhász-Nagy, 1964; Sagar and Harper 1960; Cavers and Harper 1967; Stebbins, 1985; Hobbs, this volume).

ACKNOWLEDGEMENTS

I thank C. Stoddart, R. J. Hobbs, M. Williamson, J. A. Drake and F. J. Kruger for comments on earlier versions of this chapter.

REFERENCES

- Auclair, A. N., and Goff, F. G. (1971). Diversity relations of upland forests in the western Great Lakes area. *Amer. Nat.*, **105**, 499–528.
- Baker, H. G. (1965). Characteristics and modes of origin of weeds. In: Baker, H. G., and Stebbins, G. L. (Eds), *The Genetics of Colonizing Species*, pp. 147–169. Academic Press, New York.
- Barbour, M. G., and Rodman, J. E. (1970). Saga of the west coast sea-rockets: *Cakile edentula* ssp. *Californica* and *C. maritima*. *Rhodora*, **72**, 370–86.
- Baumova, H. (1985). Influence of disturbance by mowing on the vegetation of old-fields in the Bohemian Karst. *Folia Geobot. Phytotax.*, **20**, 245–65.
- Bonck, J., and Penfound, W. T. (1945). Plant succession on abandoned farm land in the vicinity of New Orleans, Louisiana. *Amer. Mid. Natur.*, **33**, 520–9.
- Bornkamm, R., and Henning, U. (1982). Experimentell-ökologische Untersuchungen zur Sukzession von ruderalen Pflanzengesellschaften auf unterschiedlichen Böden. *Flora*, **172**, 267–316.
- Boyd, R. S. (1986). Comparative ecology of two west coast *Cakile* species at Point Reyes, California. Ph.D. Thesis, Dept. of Botany, UC Davis. 128 pp.
- Burbanck, M. P., and Phillips, D. L. (1983). Evidence of plant succession on granite outcrops of the Georgia Piedmont. *Amer. Midl. Nat.*, **109**, 94–104.

- Burdon, J. J., and Chilvers, G. A. (1977). Preliminary studies on a native Australian eucalypt forest invaded by exotic pines. *Oecologia*, **31**, 1–12.
- Campbell, B. M., McKenzie, B., and Moll, E. J. (1979). Should there be more tree vegetation in the Mediterranean climatic region of South Africa. *J. South Afr. Bot.*, **45**, 453–7.
- Carpenter, D. E. (1983). Old-field succession in Mojave desert scrub. MS Thesis, Dept. of Geography, UC Davis. 112 pp.
- Cavers, P. B., and Harper, J. L. (1967). Studies in the dynamics of plant populations. 1. The fate of seen and transplants introduced into various habitats. *J. Ecol.*, **55**, 59–71.
- Cole, K. (1985). Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. *Amer. Nat.*, **125**, 289–303.
- Cole, K. L. (1986). In defense of inertia. *Amer. Nat.*, **127**, 727–8.
- Coombe, D. E. (1959). Biological flora of British Isles: *Impatiens parviflora* DC. *J. Ecol.*, **44**, 701–13.
- Crawley, M. J. (1987). What makes community invisable? In: Crawley, M. J., Edwards, P. J., and Gray, A. J. (Eds), *Colonization, Succession and Stability*, pp. 429–53. Blackwell, Oxford.
- Cross, J. R. (1981). The establishment of *Rhododendron ponticum* in the Killarney Oakwoods, S. W. Ireland: *J. Ecol.*, **69**, 807–24.
- Csontos, P. (1984). Ecological and phytosociological studies in a stand of *Impatiens parviflora* DC, at the Vadallo Rocks, Pilis Mts., Hungary, *Abstracta Botanica*, **8**, 15–34.
- Davidson, R. L. (1964). An experimental study of succession in the Transvaal Highveld. In: Davis, D. H. S. (Ed.), *Ecological Studies in Southern Africa*, pp. 113–25. Junk, The Hague.
- del Moral, R. (1983). Competition as a control mechanism in subalpine meadows. *Amer. J. Bot.*, **70**, 232–45.
- Dostálková, I., Kindlmann, P., and Rejmánek, M. (1984). Simulation of species replacement on environmental gradient in the course of ecological succession. *Ecol. Model.*, **26**, 45–50.
- Dyrness, C. T. (1973). Early stages of plant succession following logging and burning in the Western Cascades of Oregon. *Ecology*, **54**, 57–69.
- Egler, F. E. (1983). *The Nature of Naturalization II. The Introduced Flora of Aton Forest, Connecticut*. Claude E. Phillips Herbarium Publication No. 6. Delaware State College, Dover. 145 pp.
- Eicke-Jene, J. (1960). Sukzessionsstudien in der Vegetation des Ammersees in Oberbayern. *Bot. Jb.*, **79**, 447–520.
- Elton, C. S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London. 181 pp.
- Ewel, J. J. (1986). Invasibility: lessons from south Florida. In: Mooney, H. A., and Drake, J. A. (Eds), *Ecology of Biological Invasions of North America and Hawaii*. Springer, New York.
- Fallinski, J. B. (1968). Stan i prognoza neofityzmu w szacie roślinnej Puszczy Białowieskiej. *Materialy Zakładu Fitosocjologii Stosowanej U.W.*, **25**, 175–216.
- Forcella, F., and Harvey, S. J. (1983). Eurasian weed infestation in western Montana in relation to vegetation and disturbance. *Madrono*, **30**, 102–9.
- Fox, M. D., and Fox, B. J. (1986). The susceptibility of natural communities to invasion. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: An Australian Perspective*, pp. 57–66. Australian Academy of Science, Canberra.
- Frenkel, R. E., and Boss, T. R. (1982). Introduction and establishment of *Spartina patens* in Siuslaw Estuary, Oregon. Paper presented at the Pacific Estuarine Research Society 10th Semiannual Meeting.

- Gerrish, G., and Mueller-Dombois, D. (1980). Behavior of native and non-native plants in two tropical rain forests on Oahu, Hawaiian Islands. *Phytocenologia*, **8**, 237–95.
- Gleadow, R. M., and Ashton, D. H. (1981). Invasion by *Pittosporum undulatum* of the forests of central Victoria. I Invasion patterns and plant morphology. *Aust. J. Bot.*, **29**, 705–20.
- Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, New York.
- Guittet, J., and Laberche, J. C. (1974). L'implantation naturelle du pin sylvestre sur pelouse xérophile en forêt de Fontainebleau: II. Démographie des graines et des plantules au voisinage des vieux arbres. *Oecol. Plant.*, **9**, 111–30.
- Hawksworth, F. G., and Scharpf, R. F. (1986). Spread of European mistletoe (*Viscum album*) in California, U.S.A. *Eur. J. Forest Pat.*, **16**, 1–5.
- Hett, J. M. (1971). A dynamic analysis of age in sugar maple seedlings. *Ecology*, **52**, 1071–4.
- Holzner, W. (1982). Concepts, categories and characteristics of weeds. In: Holzner, W., and Numata, N. (Eds), *Biology and Ecology of Weeds*, pp. 3–20. Junk, The Hague.
- Huml, O. (1977). Konkurenční vztahy dominant a jejich význam v iniciálních sukcesních fázích. MS Thesis, Dept of Botany, Charles University, Prague.
- Johnson, P. N. (1982). Naturalised plants in south-west South Island, New Zealand. *New Zealand J. Bot.*, **20**, 131–42.
- Juhász-Nagy, P. (1964). Investigations concerning ecological homeostasis. In: *Tenth International Botanical Congress*, p. 240. Abstracts of Papers. Edinburgh.
- Kloot, P. M. (1984). The introduced elements of the flora of southern Australia. *J. Biogeogr.*, **11**, 63–78.
- Knopf, F. L., and Olson, T. E. (1984). Naturalization of Russian-olive: implications to Rocky Mountain wildlife. *Wildlife Soc. Bull.*, **12**, 289–98.
- Kopecky, K. (1967). Die flussbegleitende Neophyten-gesellschaft Impatiens-Solidaginietum in Mittelmähren. *Presila*, **39**, 151–66.
- Kornas, J. (1988). Plant invasions in Central Europe: historical and ecological aspects. In: di Castri, F. (Ed.), *History and Patterns of Biological Invasions in Europe and the Mediterranean Basin* (in press).
- Kruger, F. J. (1977). Invasive woody plants in Cape fynbos with special reference to the biology and control of *Pinus pinaster*. *Proceedings of the Second National Weed Conference of South Africa, Stellenbosch*, pp. 57–74.
- Levin, R. (1985). Plant communities resist climatic change. *Science*, **228**, 165–6.
- Loope, L. L., and Scowcroft, P. G. (1985). Vegetation response within exclosures in Hawaii: a review. In: Stone, C. P., and Scott, J. M. (Eds), *Hawaii's Terrestrial Ecosystems: Preservation and Management*, pp. 377–402. University of Hawaii, Honolulu.
- Lorence, D. H., and Sussman, R. W. (1986). Exotic species invasion into Mauritius wet forest remnants. *J. Trop. Ecol.*, **2**, 147–62.
- Luer, C. A. (1975). *The Native Orchids of the United States and Canada*. The New York Botanical Garden, New York.
- Macdonald, I. A. W., Powrie, F. J., and Siegfried, W. R. (1986). The differential invasion of southern Africa's biomes and ecosystems by alien plants and animals. In: Macdonald, I. A. W., Kruger, F. J., and Ferrar, A. A. (Eds), *The Ecology and Management of Biological Invasions in Southern Africa*, pp. 209–25. Oxford University Press, Cape Town.
- Macdonald, I. A. W., and Richardson, D. M. (1986). Alien species in terrestrial ecosystems of the fynbos biome. In: Macdonald, I. A. W., Kruger, F. J., and Ferrar, A. A. (Eds), *The Ecology and Management of Biological Invasions in South Africa*, pp. 77–91. Oxford University Press, Cape Town.
- Markgraf, V. (1986). Plant inertia reassessed. *Amer. Nat.*, **127**, 725–6.

- Mooney, H. A., Hamburg, S. P., and Drake, J. A. (1986). The invasions of plants and animals into California. In: Mooney, H. A., and Drake, J. A. (Eds), *The Ecology of Biological Invasions of North America and Hawaii*, pp. 250–72. Springer-Verlag, New York.
- Moravec, J. (1973). The determination of minimal area of phytocenoses. *Folia Geobot. Phytotax.*, **8**, 23–47.
- Mueller-Dombois, D. (1981). Vegetation dynamics in coastal grassland of Hawaii. *Vegetatio*, **46**, 131–40.
- Myers, R. L. (1983). Site susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. *J. Appl. Ecol.*, **20**, 645–58.
- Nilsson, C., Grellson, G., Johansson, M., and Sperens, U. (1988). Patterns of species richness along river banks. *Ecology* (in press).
- Nilsson, Ö. (1981). Gräsfröinkomlingar och andra kulturspridda växter från Gotland. *Svensk Bot. Tidskr.*, **75**, 65–9.
- Ohmart, R. D., and Anderson, B. W. (1982). North American desert riparian ecosystems. In: Bender, G. L. (Ed.), *Reference Handbook on the Deserts of North America*, pp. 433–79. Greenwood Press, Westport.
- Peart, D. R., and Foin, T. C. (1985). Analysis and prediction of population and community change: a grassland case study. In: White, J. (Ed.), *The Population Structure of Vegetation*, pp. 313–39. W. Junk, The Hague.
- Peet, R. K. (1978). Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio*, **37**, 65–78.
- Pickard, J. (1984). Exotic plants on Lord Howe Island: distribution in space and time, 1853–1981. *J. Biogeogr.*, **11**, 181–208.
- Pickett, S. T. A. (1982). Population patterns through twenty years of oldfield succession. *Vegetatio*, **49**, 45–59.
- Pickett, S. T. A. (1983). The absence of an *Andropogon* stage in old-field succession at the Hutcheson Memorial Forest. *Bull. Torey Bot. Club*, **110**, 533–5.
- Pickett, S. T. A., and White P. S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.
- Post, W. M., and Pimm, S. L. (1983). Community assembly and food web stability. *Math. Biosci.*, **64**, 169–92.
- Ranwell, D. S. (1972). *Ecology of Salt Marshes and Sand Dunes*. Chapman and Hall, London.
- Ratcliffe, D. A. (1984). Post-Medieval and recent changes in British vegetation: the culmination of human influence. *New Phytol.*, **98**, 73–100.
- Raven, P. H., and Thomas, J. H. (1970). *Iris pseudacorus* in western North America. *Madrono*, **20**, 390–1.
- Rejmánek, M. (1984). Perturbation-dependent coexistence and species diversity in ecosystems. In: Schuster, P. (Ed.), *Stochastic Phenomena and Chaotic Behaviour in Complex Systems*, pp. 220–30. Springer, Berlin.
- Rejmánek, M., Sasser, C. E., and Gosselink, J. G. (1987). Modelling of vegetation dynamics in the Mississippi River deltaic plain. *Vegetatio*, **69**, 133–40.
- Rejmánek, M., Sykora, T., and Stursa, J. (1971). Fytcenologicke poznámky k vegetaci Hrubeho Jeseníku. *Campanula*, **2**, 31–9.
- Robinson, J. V., and Valentine, W. D. (1979). The concepts of elasticity, invulnerability and invadability. *J. Theor. Biol.*, **81**, 91–104.
- Robinson, T. W. (1965). *Introduction, Spread, and Real Extent of Saltcedar (Tamarix) in the Western States*. Geol. Surv. Prof. Paper 491-A, US Dept of Interior. 12 pp.
- Rodman, J. E. (1986). Introduction, establishment, and replacement of sea-rockets (*Cakile*, Cruciferae) in Australia. *J. Biogeog.*, **13**, 159–71.

- Rothmaler, W. (1976). *Excursionsflora für die Gebiete der DDR und der BRD*. Volk und Wissen Volkseigener Verlag, Berlin.
- Sagar, G. R., and Harper, J. L. (1960). Factors affecting germination and early establishment of Plantains (*Plantago lanceolata*, *P. media* and *P. major*). In: Harper, J. L. (Ed.), *The Biology of Weeds*, pp. 236–45. Blackwell, Oxford.
- Schmidt, W. (1981). Ungestörte und gelenkte Sukzession auf Brachäckern. *Scripta Geobotanica*, **15**, 1–199.
- Shigesada, N., Kawasaki, K., and Teramoto, E. (1984). The effects of interference competition on stability, structure and invasion of multi-species system. *J. Math. Biol.*, **21**, 97–113.
- Shimizu, Y., and Tabata, H. (1985). Invasion of *Pinus lutchuensis* and its influence on the native forest on Pacific island. *J. Biogeogr.*, **12**, 195–207.
- Slezak, W. F. (1976). *Lonicera japonica* Thunb. an aggressive introduced species in a mature forest ecosystem. MS Thesis, Rutgers University, New Brunswick, NJ.
- Sousa, P. (1984). The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.*, **15**, 353–91.
- Stebbins, G. L. (1985). Polyploidy, hybridization, and the invasion of new habitats. *Ann. Missouri Bot. Gard.*, **72**, 824–32.
- Stuckey, R. L. (1968). Distributional history of *Butomus umbellatus* (flowering-rush) in the western Lake Erie and Lake St. Clair region. *Michigan Bot.*, **7**, 134–42.
- Sukopp, H. (1962). Neophyten in natürlichen Pflanzengesellschaften Mitteleuropas. *Ber. Deutsch. Bot. Ges.*, **75**, 193–205.
- Symonides, E. (1985). Floristic richness, diversity, dominance and species evenness in old-field successional ecosystems. *Ekol. Polska*, **33**, 61–79.
- Thieret, J. W. (1980). *Louisiana Ferns and Fern Allies*. Lafayette Nat. Hist. Mus., Lafayette.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Trepl, L. (1984). Über *Impatiens parviflora* DC. als Agriophyt in Mitteleuropa. *Disserationes Botanicae*, **73**, 1–399.
- Valen Van, L. (1975). Life, death, and energy of a tree. *Biotropica*, **7**, 260–9.
- Vasek, F. C. (1980). Early successional stages in Mojave desert scrub vegetation. *Israel J. Bot.*, **28**, 133–48.
- Vitousek, P. M. (1986). Biological invasions and ecosystem properties: can species make a difference? In: Mooney, H. A., and Drake, J. A. (Eds), *Ecology of Biological Invasions of North America and Hawaii*, pp. 163–78. Springer, New York.
- Vivrette, N. J., and Muller, C. H. (1977). Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecol. Monogr.*, **47**, 301–18.
- Wein, K. (1942). Die älteste Einführungs und Ausbreitungsgeschichte von *Acorus calamus*. 3. *Hercinia*, **3**, 241–91.
- Weiss, P. W., and Noble, I. R. (1984). Status of coastal dune communities invaded by *Chrysanthemoides monilifera*. *Aust. J. Ecol.*, **9**, 93–8.
- Wells, M. J., Duggan, K., and Hendersen, L. (1980). Woody plant invaders of the central Transvaal. *Proceedings of the third National Weeds Conference of South Africa, Cape Town*, pp. 11–78.
- Wilgen van, B. W., and Richardson, D. M. (1985). The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: a simulation study. *J. Appl. Ecol.*, **22**, 955–66.
- Williamson, M. (1988). The relationship of species number to area, distance and other variables. In: Giller, P. S. (Ed.), *Biogeographic Analysis: Methods, Patterns and Processes* (in press).