

## CHAPTER 12

# *Attributes of Invaders and the Invading Process: Terrestrial and Vascular Plants*

IAN R. NOBLE

### 12.1 INTRODUCTION

In a summary paper on the consequences of biological invasions Holdgate (1986) concluded 'what is clear . . . is that many species reach potential new habitats, but that establishment depends critically on habitat features and that success may have counterintuitive attributes'. Here I examine whether, by looking at the attributes of invaders and the invasion process, we can find ways of improving our understanding so that we may better predict which species are potential invasives.

Newsome and Noble (1986) described four major types of invasions. The first dealt with new habitats associated with human settlements. Human activities have radically changed most ecosystems and the spread of new agricultural and pastoral techniques and areas of habitation has created a range of new environments in many regions. We must expect that a group of fortuitously pre-adapted species will invade and dominate these environments. Much of the world's literature on invasions deals with this commensal flora and fauna and I do not want to emphasize this material here. Instead I will concentrate on the invasion of localities where little prior alteration has occurred.

A second type of invasion is associated with the filling of vacant niches (Lawton, 1984). I have not been able to find evidence that such vacancies occur in plant communities, or even of how they should be recognized (e.g. Weiss and Noble, 1984a), and thus they appear to be of little importance.

The remaining invasions occur in habitats where native species are displaced from relatively undisturbed communities. Newsome and Noble (1986) recognized two types here. In one the invading species has distinct competitive superiority over an ecologically similar native species and thus might be expected to become a permanent feature of the flora (without necessarily leading to the extinction of native species). The other occurs where the invasive species have characteristics that allow them to survive under only some conditions and not under other conditions (such as extreme events). The continued success of these risk-taking invaders is dependent on either the prevention of the extreme events by human

actions (e.g. the prevention of fires in some native forests in Australia and the invasion by *Pinus radiata*), the existence of local refuges, or on continual re-invasion. It is these last two types of invasions that I will emphasize here.

## 12.2 THE IDEAL INVADER

There are many descriptions of the attributes of the ideal invader. Most reflect our concern with the invasion of agricultural crops and must be treated with caution if we are to retain the emphasis on natural communities that is the theme of this volume.

The best known description of invasive plants is Baker's (1965) description of the 'ideal weed'. In summary, an ideal weed is a plastic perennial which will germinate in a wide range of physical conditions, grow quickly, flower early, is self-compatible, produces many seeds which disperse widely, reproduces vegetatively and is a good competitor. However, as Baker points out, no one species is likely to possess all these characters; nor does a species need all these features to be a successful invader. Conversely, the possession of a single, or indeed several, characters from the list does not mean the species will be a successful invader.

Baker's list is over 20 years old and we might ask whether it can be revised to add more recent information about eco-physiological properties such as photosynthetic pathways. For example,  $C_4$  grasses from Africa have been successful in displacing native grasses elsewhere (Baruch *et al.*, 1985). Fourteen out of the first 18 species listed in *The World's Worst Weeds* (Holm *et al.*, 1977) are  $C_4$  species compared with only three out of 15 of the world's major crop plants (Harlan, 1975).  $C_4$  species appear 17 times more frequently than expected in some lists of weeds (Elmore and Paul, 1983). However, we should be cautious about interpreting  $C_4$  species as potentially invasive in all environments and especially in temperate regions (Percy and Ehleringer, 1984). Each characteristic must be assessed in relation to the environment subject to invasion. The prominence of  $C_4$  species in weed lists may reflect the compilers' concerns with tropical crops where weed control practices tend to be less effective or rigorous.

We must also be cautious of drawing conclusions about the interactions of plant populations based on a few eco-physiological characteristics. For example, the South African Shrub *Chrysanthemoides monilifera* is displacing *Acacia longifolia* from coastal dunes in Australia. Counter to expectations, pot experiments show that *C. monilifera* has a lower per unit leaf area assimilation rate and lesser drought tolerance than *A. longifolia* (Weiss and Noble, 1984b). However, when grown in competition, seedlings of *C. monilifera* out-grow those of *A. longifolia* through a more effective arrangement of their photosynthetic tissue. This study and others such as that of Patterson *et al.* (1984) gives emphasis to the comments by Mooney and Chiariello (1984) and Ehleringer *et al.* (1986) on the necessity to move eco-physiological studies away from the single leaf and

towards the whole plant in interaction with its environment. Only in this way will an integration of physiological and population biology be achieved.

Lists such as Baker's (1965) are of value as checklists of potential warning signs, but they have little predictive value about the likelihood that a particular species will be a problem in particular environment.

### 12.3 PLANT STRATEGIES

There has long been interest amongst ecologists in describing ecological strategies. King (1966) has summarized some of the schemes that have been applied to 'weeds'. One approach (e.g. Thellung, 1912, quoted in King, 1966) is based on the relationship between the weed and humans and emphasizes the method of introduction. Such schemes have little value as a predictive tool. By contrast, the classification by Korsmo (1930) is based on method of reproduction and is a precursor to some more recent classifications (e.g. Purdie and Slatyer, 1976).

The relationship between invasive properties and the  $r$ - $K$  continuum of MacArthur and Wilson (1967) has been described by many. In fact, Baker's list of properties of the ideal weed are similar to the properties of a typical  $r$  strategy species. Southwood (1976) classified 'pest' species on this continuum and concluded that both  $r$  and  $K$  pests exist. Further, knowledge of an organism's position on the continuum provided not only a convenient framework on which to discuss 'pests' but also an indication as to which control strategies might be successful. However, since both  $r$  and  $K$  pests occur, the classification has little value in predicting whether a species is a potential invader.

One of the most general, and most widely applied, descriptions of ecological strategies is an extension of the McArthur and Wilson (1967)  $r$ - $K$  continuum by Grime (1974, 1979). He argued that stress and disturbance are two dominant factors in the environment of a plant and a species' reaction to these factors can be classified along three axes representing its degree of tolerance to stress, to competition and its tendency towards ruderal behaviour. Grime suggested a methodology by which a competitive index and  $RGR_{\max}$  (maximum relative growth rate) can be used to position species on a triangular graphical representation of the strategy. The position of a species on the triangle tends to convey some information about other properties that the species might have. Similarly, particular life forms tend to cluster together; thus the life form of a species gives some indication about the strategies the species might exhibit. Grime (1979) has pointed out that many colonists are ruderals by his classification. Although this point has been confirmed by many others it provides little predictive value. Just as Southwood (1976) recognized both  $r$  and  $K$  pests, some invaders have C (competitive) or S (stress tolerant) properties.

Milton (1979) classified the invasive Australian acacia species on South West Cape of South Africa on to Grime's triangle and concluded that the acacia were

C-strategists with some tendency towards S. The classification was based on their observed fast growth rates and tall erect habit compared with the native fynbos species. The acacias were able to displace the largely S-strategy native species of the fynbos by spreading along the less stressful water-courses and gradually reducing the degree of stress by nitrogen fixation and soil modification. They, therefore, created an environment that was less suited to the fynbos species and when subsequent disturbances (usually fires) occurred, the fynbos species did poorly in competition with the acacias and other invasive species.

In this example, Grime's strategies were a useful framework on which to describe the observed invasion of the fynbos by acacias. However, I doubt that they would have given much direct insight into the potential for acacias to invade if the classification had been known before the introduction of acacias into the fynbos. It is true that this is an unfair test of the overall utility of Grime's scheme. Grime (1982) defended his scheme against over-specialized application and he (1985) asserted that many ecologists were nervously 'putting from the tee' in avoiding generalizations. But, we must also avoid the pitfall of staying with schemes which are overly generalized for the task in hand (Grubb, 1985).

Thus, I have rejected two approaches to finding a general description of invasive organisms—namely the checklist of properties which are likely to contribute to the invasive success of an organism and the use of a framework based on broadly defined plant strategies. Is there a better classification of terrestrial plants which may help us recognize potentially invasive species?

## 12.4 FUNCTIONAL GROUPS

In the past few years there has been increasing interest in the concept of 'functional groups' in plant ecology. The idea has sometimes been expressed indirectly (MacArthur, 1972, quoted in May 1986; Mooney *et al.*, 1977; Noble and Slatyer, 1980; Jain, 1983; Grime, 1985) or in different terminology such as the functional types of Huston and Smith (1987). The goal of a classification based on functional groups is to describe a set of physiological, reproductive and life history characteristics where variation in each characteristic has specific, ecologically predictive (rather than descriptive) value. It is argued that related groups of plants can be recognized because there are a limited number of sets of physiological, morphological and life history options that are feasible in dealing with the trade offs necessary to cope with the multiple requirements of survival and reproduction.

Botkin (1975) was apparently the first to use the term (although without a precise definition) when he defined the purpose of a functional grouping of organisms to be 'to reduce the analysis of ecosystems to tractable problems from the mathematical point of view, while still allowing consideration of the important population interactions'. If the functional groups concept is to be useful, the groups should be defined by the minimal set of characters necessary to distinguish

between groups, otherwise the classification will become unwieldy. However, the set of characters should not be reduced to the point where the classification is over-generalized for the task in hand. Thus if we are to have functional group classification appropriate to dealing with invasive organisms, we need to establish the important combinations of population processes that determine the likelihood of successful invasion, i.e. an 'invasive syndrome'. Only with these insights will we be able to choose the set of characteristics which will define the functional groups.

Here I use a simple model of the process of invasion which gives some insights into the important population processes. Initially, I omit the process of dispersal and assume that some individuals of the invading species have reached the site. There are several reasons for this omission. Most species with a potential for true long distance dispersal (i.e. unaided by humans) have already spread around the globe. Humans are now the dominant vector of plant dispersal and any attempt to classify the properties of a plant that increased its susceptibility to long distance dispersal is more likely to be based on the psychology of higher primates than the biology of plants. Short distance dispersal is an important property in determining the rate (e.g. Nip-van der Voort *et al.*, 1979) and likelihood of spread (Forcella, 1985; Davis and Mooney, 1985) and I will discuss this below.

I also assume that the species is invading an area where the physical environment is similar to its native habitat. This assumption is supported both by general reviews of invasive organisms (e.g. Groves, 1986) and by specific case studies (e.g. Forcella and Wood, 1984; Milton, 1979). Kruger *et al.* (1986) use South African examples to show that pre-adaptation to the new habitat increases the chances of successful establishment, but does not guarantee it.

Thus, if we assume that the species is present, but rare, on a recently invaded site, the subsequent population dynamics can be described by the stage grouped Leslie matrix equation in Table 12.1 (cf. Sarukhan and Gadgil, 1974). Here,  $S$  is the number of seeds successfully incorporated in the seed pool or in potential establishment sites (i.e. where dispersal is complete),  $J$  is the number of successfully established but not yet reproductively mature individuals and  $A$  is the number of reproductively mature individuals. In the matrix,  $s$  is the rate of seed survival over a year (or growing season) and  $e$  the rate of establishment;  $j$  is the rate of juvenile survival,  $m$  is the rate of maturation of juveniles and  $a$  is the

Table 12.1. Stage grouped Leslie matrix of the simplified invasion process. The symbols are defined in the text

		Current state					
		seed	juvenile	adult	$t$	$t + 1$	
Next	Seed	$\begin{bmatrix} s & 0 & r \\ e & j & 0 \\ 0 & m & a \end{bmatrix}$				$\begin{bmatrix} S \\ J \\ A \end{bmatrix}$	$= \begin{bmatrix} S \\ J \\ A \end{bmatrix}$
	Juvenile						
	Adult						

survival rate (inverse of longevity) of the adults. The reproductive output of the adults, measured as seeds incorporated in the seed pool is  $r$  and it can be considered to be made up of two terms,  $f$ , the flowering (or fruiting) effort and,  $v$ , which is a measure of all reproductive losses between flowering and the seed pool.

If the population is assumed to be in approximate equilibrium in its native habitat (i.e. its intrinsic rate of increase is approximately 1.0 and a stable age structure exists), some simple matrix algebra shows that the following relationship holds:

$$fve/[m(1-s)(1-j)(1-a)] = 1$$

Of these parameters,  $s$ ,  $a$  and  $f$  are largely genetically determined, physiological properties of the species and are unlikely to change dramatically if the species invades a site with a similar physical environment. The survival of the juveniles is also largely genetically fixed, unless they have a prolonged juvenile stage such as the lignotuberous seedling stage of the eucalypts. The remaining parameters,  $v$ ,  $e$ , and  $m$ , obviously have some genetic component, but are much more affected by the biotic and abiotic environment. The probability of survival from flowering to seed pool ( $v$ ) is largely determined by seed predation, while the probability of establishing ( $e$ ) and of reaching maturity ( $m$ ) are determined to a great degree by competition for limiting resources, i.e. site dependent factors. Thus, if on dispersing to a new site of similar abiotic conditions, any one of  $v$ ,  $e$  or  $m$  changes,  $f$  is unlikely to be appropriate to maintain approximately equilibrium populations. In particular, if any one of  $v$ ,  $e$  or  $m$  increases then an  $f$  which was appropriate for the native conditions will now be excessive and population growth rapid. If this is coupled with even limited powers of local dispersal, the species may be a successful invader.

This simple model, therefore, gives us some insight into the properties of the species which may contribute to making it a successful invader. The first clue is a large flowering or fruiting effort ( $f$ ) since this implies that in the native habitat there must be heavy losses between this point and the establishment of a replacement adult. This would probably have been a more direct warning device than Grime's strategies to the early settlers of South Africa when they introduced the prolifically flowering and fruiting Australian acacias. It should also have been a warning to the soil conservation services along the east coast of Australia when they duplicated the mistake by introducing *Chrysanthemoides monilifera* from South Africa as dune stabilizers. Table 12.2 summarizes the results of Weiss and Milton (1984) which show a dramatic increase in  $v$  for both species in their introduced habitats leading to the establishment of extraordinarily large seed pools. In terms of direct competition (i.e.  $e$  or  $m$ ) there is evidence (described above) that *C. monilifera* can out-compete *A. longifolia*, but this effect is apparently minor in comparison with the changes in  $v$  and the resultant increase in the size of the seed pools.

A change in  $e$ , or  $m$ , is an important factor in the expansion of both the range

Table 12.2. Reproductive performance of *Chrysanthemoides monilifera* (native to South Africa) and *Acacia longifolia* (native to Australia). All units are number per m<sup>2</sup>. (Adapted from Weiss and Milton, 1984.)

	<i>Chrysanthemoides monilifera</i>	<i>Acacia longifolia</i>
<i>South Africa</i>		
Fruits	3800	?
Ripe seeds	2200	2900
Soil seeds	2300	7600
Viable soil seeds	50	7400
<i>Australia</i>		
Fruits	6700	600
Ripe seeds	4500	400
Soil seeds	2500	10
Viable soil seeds	2000	10

and density of some native species. An example is the increase in density and apparent expansion in range of native, woody weed species under grazing by domestic herbivores. For example, *E. mitchellii* is a 3 to 9 m tall shrub found in eastern Australia which has dramatically increased in density in what was previously an open grassy woodland (Hodgkinson and Beeston, 1982). It is a long-lived species with a life span of 50 to 100 years and once established is resistant to grazing and resprouts quickly after fire. It establishes only rarely (about three times this century in most regions) after a sequence of rainfall events which stimulate flowering, seed set and germination. The seedlings are slow growing and poor competitors with grasses. *E. mitchellii* appears to have gained a double advantage under current land management practices. First, in areas where grazing has reduced grass densities, higher than normal establishment rates ( $e$ ) occur. Secondly, pastoral management has suppressed the fires that would normally have followed such a run of good seasons with the result that many more of the fire-sensitive juvenile plants reach maturity (i.e. increased  $m$ ).

Pulsed flowering on establishment, as shown by *E. mitchellii*, is another warning sign of a potential invader. This strategy effectively increase the value of  $f$  at any one recruitment event and usually implies that quite specific conditions are required to produce the mortality of fruit, seed and plants that leads to stable populations. A change in the biotic or abiotic environment may either increase the frequency with which the pulses occur or reduce the effectiveness of the mortality filters.

The term  $f$  is relatively insensitive to seed and adult longevities ( $s$  and  $a$ ) amongst perennials and even a change from an annual to a biennial life history can change  $f$  by a factor of only about 2. Competitive effects from other species which either increase or decrease the longevity of an established plant will usually

result in a relatively small change in the term  $(1 - a)$  especially in perennial plants. Thus the perenniality of the plant is little evidence of its invasive potential in stable environments. This last qualification is extremely important since the ability of the species to persist through adverse environmental conditions is as much a function of its ability to disperse in time as its ability to disperse in space (Comins and Noble, 1985). Also, long-lived seed pools (i.e. high  $s$ ) will often lead to problems of species eradication, but this is a separate issue from the problem of invasion itself.

Dispersal can be incorporated in the model. Net dispersal to or from the site will enter as an additive term in  $r$  but in most cases will be small with respect to local seed production and hence unimportant. Dispersal powers are important where new sites are being invaded or where site variability is such that the probability of local extinction is significant (Platt, 1975; Gleadow, 1982; Hobbs and Mooney, 1985; Marks and Mohler, 1985; McClanahan, 1986). Thus, good, short-distance dispersal abilities increase the possibility that a species will be a successful invader and species which are not reliant on special vectors (e.g. specific animals) have a greater chance of retaining those powers in the new environment. However, the problem of trade offs must be considered or else we will start to redefine the 'ideal weed'. For example, Morse and Schmitt (1985) have shown that in the wind-dispersed seeds of *Asclepias syriaca*, heavy seeds disperse shorter distances but have greater germination success and faster initial seedling growth. Similarly Stanton (1985) has shown that increases in seed size in wild radish (*Raphanus raphanistrum*) give disproportionate increases in total reproductive output from the plants arising from the seeds. Therefore, the trade offs between seed numbers, sizes and dispersal powers must always be considered.

I have discussed invasion using a simple model of population dynamics. The model has several omissions. It deals with only a limited number of life stages, although the addition of extra stages makes little difference since the effect is to split the individual terms in this model into several. It deals with only the initial stages of invasion (i.e. before the invader starts to affect the environment itself), but this is justified since this is the critical stage if we are trying to prevent an invasion. The model also assumes stable population age structures, but simulations show that these will develop quickly even when the population establishes from a single propagule. More importantly, it is deterministic and therefore under-estimates the importance of the  $s$  and  $a$  terms as described above.

In summary, the model directs our attention to several factors in determining the likely invasive potential of a terrestrial plant. First, high population numbers at any life stage in the native environment followed by high mortalities should be seen as a warning. These high numbers do not have to be produced every year, but can occur as pulses. Secondly, adult or seed longevity are not reliable indicators of invasive potential except in so far as they will allow the species to persist in variable environments over periods which are unsuitable for establishment. Thirdly, the model emphasizes that it is the invaded environment, as much



as the properties of the invading species itself, that determine invasive success.

I started this section by asking whether we might distinguish functional groups of plants that give insight into whether a species is a potential invader. There appear to be particular population parameters which may form a basis for defining groups but a direct test of this approach has not been tried. Some estimate of the feasibility of deriving such groups can be gained by looking at the invasive flora of a particular environment to see if groups of species with correlated sets of properties can be recognized and if the sets of properties appear to be consistent with particular strategies of invasion and survival. Newsome and Noble (1986) found that such groups could be recognized in the noxious weed species listed by Parsons (1973) for Victoria, Australia.

The evidence in this paper and several other reviews (e.g. Crawley, 1986; Lawton, 1986) emphasize the importance of the invaded environment in determining the success of an invader. Even if we assume that the abiotic properties of the invaded environment are similar to the originating environment, biotic differences will still occur. Thus the groups may have to be formulated with respect to particular environments (see Jain, 1983) and it is unlikely that we will be able to make *a priori* predictions of whether a particular species will be a successful invader. Further development of the functional groups approach may help us identify those species which present the greatest risk, however, we need additional insight into the factors determining community composition structure.

Models of community structure and composition exist (see the review by Williamson, this volume, and May, 1986). The emphasis of these models is on broad questions of how many species we might expect in a community and questions of size distributions and trophic interactions. Even if answers were available they would be of limited help in determining whether a particular species might successfully invade a community. Many of the models of community structure are based on assumptions of equilibrium conditions, but an invader need be successful for only a limited time to become 'pest' or 'weed'. The models also deal with whether species with particular broadly defined properties may be successfully inserted in a community, but we have few guidelines on whether the properties of a species will change in a new biotic environment.

Clearly we need better understanding of the way in which important characteristics of a species will change in a new environment. Crawley (1986) was pessimistic about the possibility of doing this and concluded that we would be unlikely to achieve genuine prediction until we develop models of species interactions in which competition coefficients are context specific. Austin and his colleagues (Austin and Austin, 1980; Austin 1982; Austin *et al.*, 1985) have pursued the question of predicting the performance of plant species in multi-species mixtures along environmental gradients based on their performance in isolation. Their results indicate that the performance of a species in a mixture can be predicted from a measure of its performance in isolation in comparison with

similar measures of performance in isolation of the other species in the mixture. This is promising, but the predictions are dependent on the position on the gradient, i.e. they are sensitive to the environmental context; thus the performance of a potential invader can be assessed only by trials carried out in the target environment.

The above conclusions are not encouraging and we have yet to take into account the other factors affecting the success of a new introduction to a community, including the effect of chance in community assembly (Lawton, 1986), of herbivores (Crawley, 1983) and of interactions with other non-plant species (mutualisms). Nevertheless, our best approach appears to be to look for 'syndromes' of invasiveness. Lists of ideal properties and broadly based plant strategies do not seem to be sufficient. The functional groups approach does appear to hold some promise in assisting in recognizing species with the syndrome.

## 12.5 SUMMARY AND CONCLUSIONS

I conclude with the following points.

1. Highly generalized classifications or lists of preferred characteristics are of little help in recognizing potentially invasive organisms.
2. Groups of species with correlated sets of ecological and physiological characteristics (functional groups) do seem to occur. These groups probably represent particular trade offs in the allocation of plant resources.
3. The absence of an inherent long distance (e.g. trans-oceanic) dispersal mechanism is not a hindrance to invasion as humans are now the main vector.
4. Short distance dispersal mechanisms will increase both the probability and rate of invasion.
5. Species with high reproductive output (even if massively unsuccessful) in their native habitat have a high invasive potential.
6. The properties of the invaded habitat are a critical determinant of the likely success of any invader.
7. Thus, any system to assist in the recognition of potentially invasive species will require both studies of the species in its native habitat to assess its ecological characteristics and studies in the target habitat to assess the changes likely to arise in those characteristics.

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