Biological Invasions: a Global Perspective
Edited by J. A. Drake *et al.*

CHAPTER 17

The Nature and Effects of Disturbance Relative to Invasions

RICHARD J. HOBBS

17.1 INTRODUCTION

Biological invasions are a fact of life today, and many natural communities have been or are being invaded by non-native species which affect natural community and ecosystem process. There is still a lot of debate on the characteristics of invasive species and invasible communities (e.g. Crawley, 1986, 1987; Newsome and Noble, 1986). For plant communities several authors have suggested that some form of disturbance is an important precursor to invasion, especially where this disturbance disrupts strong species interactions and hence reduces competition (e.g. Kruger *et al.*, 1986; Macdonald *et al.*, 1986; Crawley, 1986, 1987; Orians, 1986; Fox and Fox, 1986). Although we have a considerable amount of information on invasions, most of the available data are observational or historical and there has been little attempt to assess experimentally the effects of disturbance on the invasibility of communities.

In this chapter I therefore illustrate the potential for experimentation in the field of biological invasions, especially with respect to disturbance. I will firstly examine the nature of disturbance in natural communities and then discuss in detail a series of experiments on the effects of disturbance on the invasibility of natural plant communities, and finally discuss the relevance of these rather local experiments to the global perspective aimed at in these proceedings.

17.2 DISTURBANCE AND PATCH DYNAMICS

Although disturbance is frequently cited as a factor leading to invasions, the nature of the disturbance is not usually explored. Recent reviews have emphasized the importance of disturbances of various types in the functioning of many natural communities and ecosystems (White, 1979; Sousa, 1984; Pickett and White, 1985; Hobbs, 1987), particularly in relation to patch dynamics. White and Pickett (1985) give a broad definition of disturbance as 'any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment'. Problems of scale arise when, for instance, events causing disruption are actually part of longer-term environmental fluctuations—a flood or a drought may constitute a disturbance but still be part of the normal hydrologic or climatic cycle. These problems have been addressed elsewhere (e.g. Pickett and White, 1985) and will not be pursued here.

Disturbances are viewed as creating patches of either open ground or increased resource availability, often through the removal of the species present before disturbance. There has been increasing interest in 'patch dynamics', or the processes of patch creation and filling, and many studies have examined the formation and colonization of patches caused by different types of disturbance, e.g. by animal disturbance (Platt, 1975; Collins and Barber, 1985; Hobbs and Mooney, 1985), treefalls (Brokaw, 1985; Collins *et al.*, 1985), or wave action in intertidal and subtidal environments (Sousa, 1985; Connell and Keough, 1985). Although immigration into patches is recognized as an important process, the invasion of pre-existing or newly formed patches by non-native species has been little studied. Indeed, invasive species have often been considered outside normal community processes, but biological invasions are now simply a subset of normal community process (e.g. Diamond and Case, 1986; Chesson, 1986). Human activities have rendered many introduced species part of the 'natural' community. Fragmentation has led to the juxtaposition of natural and human-made systems, and intentional and unintentional human transport of non-native species often provides a pool of such species able to disperse into natural systems.

The invasion of natural plant communities can be characterized by a number of stages. Firstly, seed must disperse into the community and remain there long enough to germinate. Subsequent establishment and growth to seed set, followed by retention of seed in the soil until at least the following season, are then required for persistence in the community. In this chapter I take the view that the invasion process requires not only the availability of an invading species able to disperse into an area but also the formation of a patch suitable for colonization. I will explore the characteristics which make a patch susceptible to invasion and examine whether these vary in different communities. Rather than examining this question on a wide scale, I will first discuss a series of different communities occurring in the same location. I take an experimental approach to these questions to assess whether communities can be made more invasible.

17.3 DISTURBANCE, RESOURCES AND INVASIBILITY

17.3.1 Background to experiments

I carried out a series of experimental manipulations within five different plant communities occurring in close proximity to one another. The studies were carried out on Durokoppin Nature Reserve near Kellerberrin, 200 km east of Perth, Western Australia. The area has a Mediterranean-type climate with a mean annual rainfall of 340 mm, falling predominantly in winter, and a strong summer drought with only occasional cyclonic storms. The study site lies in the Western Australian wheatbelt, an area extensively cleared for agriculture containing a large number of small (mostly < 200 ha) remnants of native vegetation (Kitchener *et al.*, 1980). Durokoppin Reserve (1030 ha) is the largest remnant in the Kellerberrin area where only 2.8% of the land area can be classed as 'natural' vegetation (i.e. uncleared land not grazed by sheep).

The native vegetation of the Western Australian wheatbelt is very diverse, with high species numbers and complex vegetation mosaics, related partially to soil patterns (Beard, 1983; Hopkins and Griffin, 1984). Clearance has converted communities dominated mainly by perennials into pasture and cropland dominated by annual species. Here, as in other parts of Australia, invasion of natural vegetation by non-native annual species is recognized as a major problem in conservation (Bridgewater and Backshall, 1981; Adamson and Fox, 1982; Hopper and Muir, 1984). Invading species include species common in surrounding pasture land, particularly *Arctotheca calendula, Avena fatua*, and *Bromus* spp., and others such as *Ursinia anthemoides* and *Hypochaeris glabra* (nomenclature follows Green (1985) throughout). Soil disturbance is a common phenomenon in the native plant communities, both through the activities of the fauna and by humans. In addition, non-native pasture species are known to respond well to addition of major nutrients, particularly N and P (Rossiter, 1966; McIvor and Smith, 1971). Soil disturbance and nutrient addition were therefore the two principal foci of these experiments.

17.3.2 Communities studied

The vegetation of Durokoppin Reserve consists of a mosaic of many different communities, falling into the main structural categories of woodland, mallee, shrubland and heath. I selected for study examples of the most common communities.

1. Casuarina shrubland dominated by *Allocasuarina campestris*, with a sparse understorey of *Hakea scoparia* and *Verticordia chrysantha* and few annuals.
2. Heathland composed of many species of Proteaceae (including *Grevillea* spp., *Hakea* spp.), Myrtaceae (*Verticordia* spp., *Baeckia* spp.) and Epacridaceae (e.g. *Andersonia lehmanniana*), with scattered annuals including *Blennospora drummondii, Helipterum demissum* and *Trachymene cyanopetala*.
3. 'Edge'; open shrubland with scattered *Hakea recurva, Verticordia crysantha* and *Grevillea paradoxa* on an area cleared approximately 50 years ago for agriculture and subsequently abandoned. Dense patches of native annuals are

present, including *Helipterum hyalospermum*, *Waitzia acuminata* and *Myriocephalus gracilis*.

4. Woodland dominated by jam, *Acacia acuminata*, and York gum, *Eucalyptus loxophleba*, with little understorey and a ground layer of scattered *Stackhousia monogyna*, *Borya nitida*, and abundant native annuals including *Helichrysum lindleyi*, *Waitzia acuminata* and *Trachymene cyanopetala*.
5. Woodland dominated by wandoo (*Eucalyptus wandoo*) with a sparse understorey of *Acacia* spp. and scattered native annuals, particularly *Podolepis lessonii*.

17.3.3 Experimental procedure

All of these communities had large areas of bare ground (i.e. > 30% cover) within them, either between shrubs or underneath tree canopies. The areas chosen for study were relatively free of non-native annual species. I set up 1 m^2 plots in bare areas and carried out the following treatments:

C: control (no manipulation).
D: disturbance of the soil by breaking the soil crust (if any) and turning the soil over with a spade to a depth of 5 cm.
F: fertilized with 50 g slow-release 'Osmocote' fertilizer (18% N as 7.5% NO_3, 10.5% NH_4; 4.8% P; 8.3% K and 3.0% S as K_2SO_4).
DF: Disturbance (as above) combined with fertilizer (as above).

A plot size of 1 m^2 was selected to fit into bare areas between shrubs or herbaceous perennials. Each treatment was replicated four times in each community. Within each set of plots, treatments were allocated randomly to plots, and individual plots were separated by at least 0.5 m. Nitrogen and phosphorus are generally considered the major limiting nutrients in the soils studied (e.g. Groves, 1981; Bettenay, 1984).

The experiment ran from May to September 1985 in the wandoo woodland and May to September 1986 in all other communities. To remove the effect of 'opportunity' (i.e. difference in invasion due to differential availability of propagules), I added seed of introduced species to the plots. I scattered into one half of each plot 100 seeds of *Avena fatua*, a non-native annual grass, and into the other half 100 seeds of *Ursinia anthemoides*, a non-native annual forb. Both are common invasive species which are widespread both around the study area and in southwest Western Australia as a whole, but were absent from the immediate vicinity of the study plots. Seed bank trials indicated that seeds of these species were present in the soil in low numbers; this was not controlled for during the experiments.

I counted numbers of established seedlings in June/July following the start of the experiment and all above-ground material was harvested in September, sorted into species, dried and weighed.

17.3.4 Results and discussion

The experimental treatments could possibly increase the invasibility of the communities in two ways, either by increasing resource availability (adding nutrients, which represents a chemical disturbance) or by producing patches of altered substrate characteristics (representing a physical disturbance). Both manipulations could act by directly enhancing the establishment and survival of non-native species or by altering competition for resources between native and non-native species. The five communities studied had quite different attributes (Table 17.1). The shrub communities (Casuarina and heath) had high densities of shrubs with few native annual species while the woodland communities had few shrubs and more native annuals. The 'edge' or old-field plot was intermediate, with scattered shrubs and relatively high densities of native annuals. Soil nutrient status was roughly similar in all communities except for the jam–York gum woodland which had significantly higher levels of N, P and K (Figure 17.1).

Despite these differences between communities, the effects of experimental manipulation were remarkably constant over all the communities (Figure 17.2). Establishment of *Avena* was greatly enhanced by disturbance, with or without fertilizer addition, while fertilizer on its own had little effect. The same was true for *Ursinia* in the wandoo woodland in 1985, but establishment in 1986 was low in all communities, and there was little treatment effect. This difference in *Ursinia* establishment between years may indicate the importance of climatic variations in determining the success of invasions. We have observed similar links between climatic fluctuations and shrub invasion of grassland in northern California (Williams *et al*., 1987). There was some establishment of *Avena* and/or *Ursinia* in the control plots in all communities, but the Casuarina and Jam–York gum controls contained the most seedlings.

In all communities, biomass of individual *Avena* and *Ursinia* plants showed little response to disturbance alone (Figure 17.2b). In the Casuarina, edge and wandoo communities there was a small increase in biomass in the fertilized plots and a much larger increase where disturbance was combined with fertilizer addition. In the heath and jam–York gum plots, individual plant biomass in the disturbance + fertilizer plots was not significantly different from that in the fertilized treatment. Although seed output was not measured directly, there was a

Table 17.1. Main biotic characteristics of the communities studied; density and diversity of the shrub layer and of native annuals

	Shrub layer	Native annuals
Casuarina shrubland	High density/diversity	Low
Health	High	Low
Edge	Low	High
Jam–York gum woodland	Very Low	High
Wandoo woodland	Very low	Medium

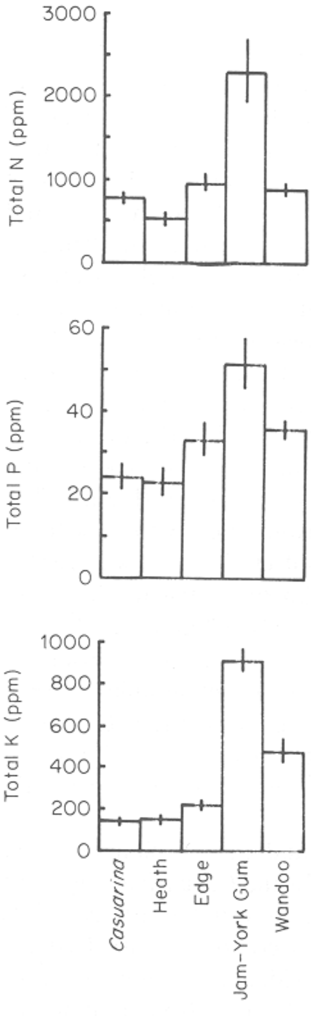

Figure 17.1. Soil nutrient status in the five communities studied. Values for total N (honda digest) and total P and K (nitric acid/sulphuric acid digest), expressed as ppm (mean of 5 samples + 1 SE)

strong correlation between plant biomass and numbers of seed produced for both species. Plant biomass can therefore be equated with reproductive output.

Total biomass of the species added showed the same patterns, with little effect of disturbance or fertilizer alone but a very large effect when they were combined (Figure 17.2c). Only in the jam–York gum community was biomass of *Avena* in the disturbance + fertilizer plots not significantly different from that in the fertilized only plots.

Despite the qualitatively similar treatment responses in different communities, there were some quantitative differences, both in numbers establishing and in biomass. Highest numbers establishing for both species occurred in the woodland sites. The heath site had significantly lower biomass of both species than the other sites.

From these results I conclude that disturbance enhanced the successful establishment of the two added non-native species in all the communities studied, but that these species grow considerably better where disturbance is coupled with

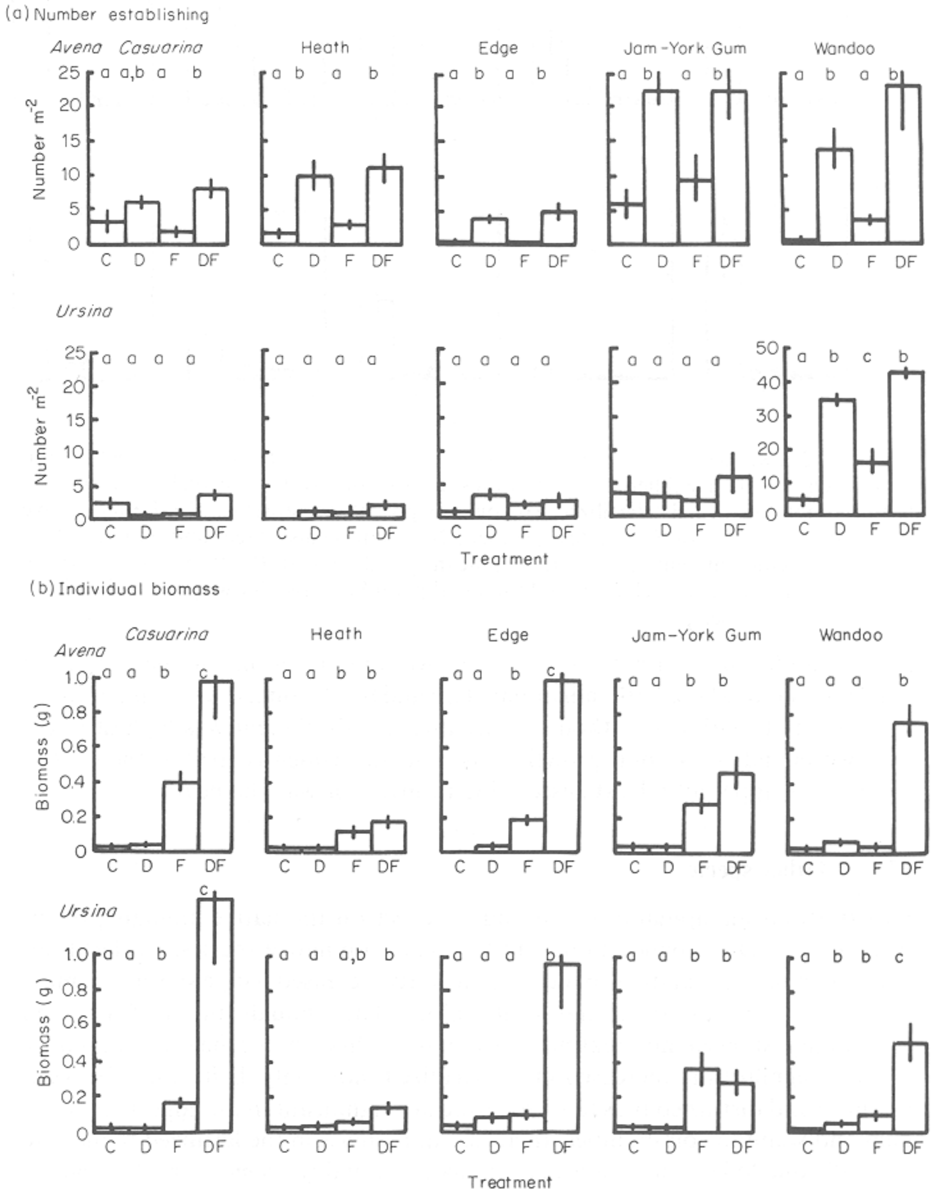

Figure 17.2. (*Caption and continuation overleaf*)

(c) Total biomass

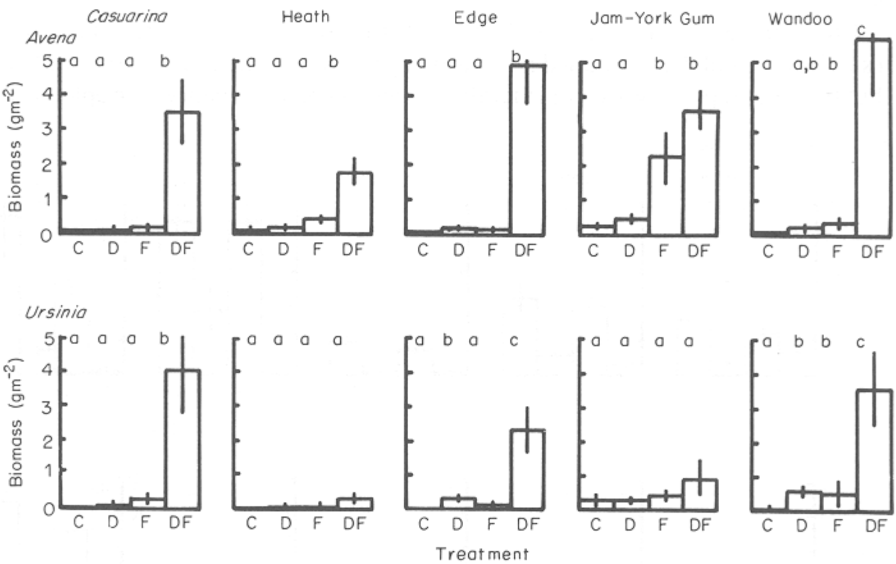

Figure 17.2. Responses of *Avena fatua* and *Ursinia anthemoides* sown in experimental plots (each 1 m^2) in five different communities. Treatments are: C, control; D, disturbed; F, fertilized; DF, disturbed + fertilized. Histograms give mean values + 1 SE. Letters above bars indicate results of S-N-K test (Student-Newman-Keuls) (Steel and Torrie, 1982): treatments with different letters are significantly different at $P < 0.05$. (a) Number of seedlings established in each plot. (b) Individual plant biomass (dry weight). (c) Total dry weight of species per plot

nutrient addition. Nutrient addition alone was important only in the jam–York gum woodland, where both individual plant and total biomass were similar in the fertilized plots with and without disturbance. Establishment was highest in the two woodland sites, but growth was not subsequently better there. The community apparently least susceptible to invasion was the heath.

17.3.5 Other species

Experimental manipulations also had an effect on the native annuals present (Figure 17.3). Disturbance alone had little effect on native species, but fertilizer, either with or without disturbance, significantly increased native species biomass in all but the Casuarina and heath plots. The annuals in the Casuarina community showed no treatment responses, while in the heath community biomass significantly increased in the fertilized plots only. Differences between fertilized and disturbed plus fertilized were not significant in the edge, jam–York gum and wandoo communities. Increases in biomass in the fertilized plots were generally due to large increases in a few species, notably *Blennospora drummondii*

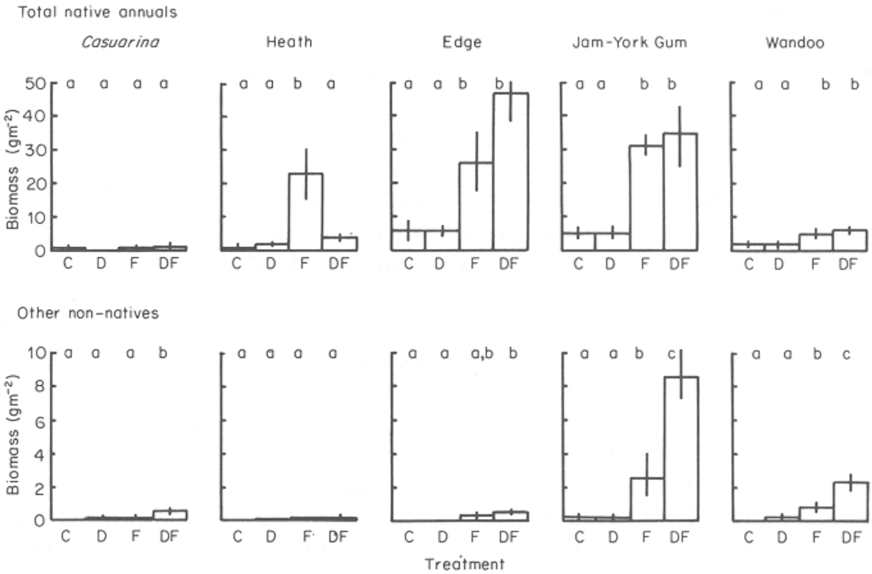

Figure 17.3. Responses of native annuals and non-native species other than *Avena* and *Ursinia* in experimental plots. Treatments and statistical notation as for Figure 17.2.

in the heath, and *Actinobole uliginosum* and *Helipterum hyalospermum* in the edge community. These results are discussed more fully by Hobbs and Atkins (1988).

Non-native species other than those sown (notably *Arctotheca calendula*, *Hypochaeris glabra* and *Vulpia myuros*) established in control plots only in the Jam–York gum woodland. There and in the edge and wandoo woodland there was a marked increase in other non-natives in the fertilized and disturbed plus fertilized plots. In the Casuarina, wandoo and Jam–York gum communities, biomass of these species was significantly higher in the disturbance plus fertilizer treatment than in the fertilized only plots. Few other non-native species established in the heath plots, again indicating that this community is the least susceptible to invasion.

The result in Figures 17.2 and 17.3 indicate a difference in response between native and non-native annual species, with natives responding to higher nutrients, with or without disturbance, but non-natives responding most to the combination of disturbance and fertilizer addition. Care must be taken, however, when comparing the response of native species already present as seed in the soil with that of the added non-native species, since disturbance would affect placement of the seeds already present.

17.3.6 Interpretation

Successful invasion of a natural community requires dispersal, establishment and subsequent persistence. In most reserves in the Western Australian wheatbelt, dispersal is not the process limiting invasion since most areas receive propagules, as evidenced by the presence of other non-native species in the treatment plots. These experiments thus considered mainly germination, establishment and growth. Increased germination and establishment in the disturbed areas is probably due to reduced seed loss through secondary dispersal by wind and water or predation by ants, combined with increased germination following the disruption of the soil crust. Seeds in disturbed plots were probably partially buried during rainfall events and thus would experience a markedly different microenvironment from those on the undisturbed surface. Disturbance thus provides a more heterogeneous environment and more safe sites (Harper, 1977; Grubb, 1977, Silvertown 1981; Fox, 1985) for the non-native species. I have not yet investigated the effect of soil disturbance alone on nutrient availability, but there is likely to be at least a small and temporary increase following disturbance although this will not be of the same magnitude as the results of fertilizer addition. The large increase in growth in the disturbed plus fertilized plots suggests that the non-native species are usually extremely nutrient limited in the unaltered soil. Disturbance combined with nutrient addition thus not only provides a safe site but increases resource availability to the established plants. Native annual species respond less dramatically to the combination of disturbance and nutrient addition, and observations suggest that they do not germinate preferentially in disturbed areas.

It is usually assumed that disturbance temporarily increases resource availability (Tilman, 1982; Pickett and White, 1985) or causes a resource shift (Fox and Fox, 1986). However, I suggest that certain types of disturbance need not significantly increase resource availability, expecially in community where light is not limiting. In the present case, soil disturbance may alter resource availabilities sufficiently to affect the germination response of the non-native species but does not significantly increase the resources available to the established plant. Such a disturbance will not therefore lead to increased invasion success, whereas a disturbance which increases resource levels is more likely to.

In Western Australian wheatbelt plant communities, many natural small-scale soil disturbances occur through the activities of ants, echidnas (*Tachyglossus aculeatus* Shaw) and other soil fauna. These probably do not lead to large increases in nutrient availability at the same time, although some ant species produce middens composed of discarded seed and other material which probably increases nutrient levels in the immediate vicinity. Rabbit disturbance is also usually accompanied by the deposition of faces, which leads to increased nutrient levels. These areas then provide foci for invasion by non-native annuals. The same result can be produced by fertilizing echidna scrapes. Fires also produce a

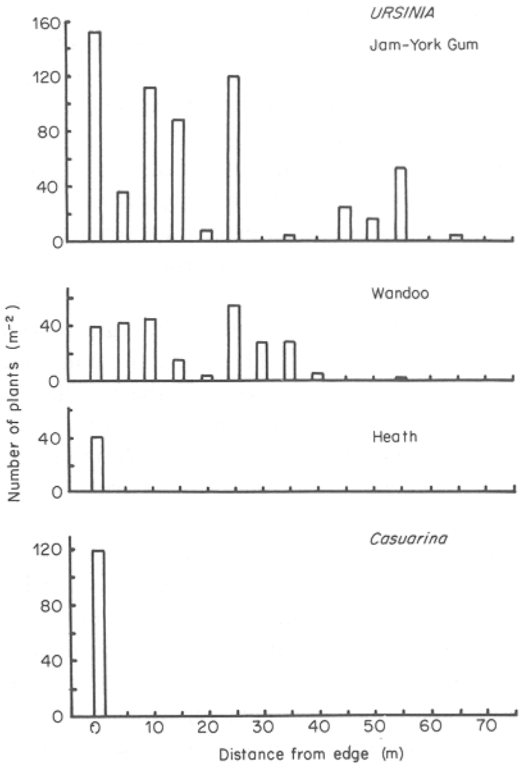

Figure 17.4. Degree of invasion into vegetation remnants from the remnant edge in different communities. Results from transects situated at the edges of Durokoppin Reserve with adjacent road and pasture. 50 × 50 cm quadrats recorded every 5 m in from the edge

temporary increase in nutrient availability and may also lead to increased invasion. Windblown fertilizer, sand or stubble from adjacent farmland into small remnant areas provides another potentially large source of nutrient input. The combination of natural soil disturbance and increased overall nutrient levels is likely to lead to increased invasion by non-native annual species unless transfer of nutrients between farmland and natural vegetation can be minimized.

Although differences between communities were apparent, all those studied were shown to be invasible. Only the heath community showed a significantly greater resistance to invasion. The reasons for this are not immediately obvious. The heath is very species rich, and it could be suggested that the degree of species packing and internal organization influences the susceptibility of the community to invasion. This explanation is not really satisfactory because it is difficult to see how woody shrub diversity affects growth of herbaceous species in the inter-shrub gaps. The results cannot be explained by looking only at the 'guild' of annual species. Competition with native annual species will be most intense in the edge and jam–York gum communities, but there is no real evidence that these 'keep the invaders out'. There are many possible factors which may explain the low invasibility of the heath, including microclimatic factors or differential ant predation. All plots were also open to herbivory; further experiments controlling for this are planned. The next step will be further experimentation in the heath, including the creation of larger patches by removal of shrubs or fire.

If we look at the present degree of invasion of the communities studied (Figure 17.4) we can see that the experimental results give a good indication of the actual invasibility of the communities. The woodland communities already have large numbers of non-natives present, whereas the heath community does not. The Casuarina community also has few non-natives present, despite the experimental result that non-natives can do well within it. Here, perhaps, is a case where dispersal into the dense shrub community is restricted; this again requires further investigation.

It is of some comfort to find that the community which contains the largest proportion of the botanical diversity in the region is the least susceptible to invasion. On the other hand, the woodland communities, which are the least well represented in nature reserves through preferential clearing, are susceptible to invasion. Invasion of these communities by non-native herbaceous species may strongly affect community and ecosystem properties by preventing regeneration of the tree species or altering fuel configurations and hence fire regimes (e.g. Wycherley, 1984).

17.4 COMPARISON WITH OTHER SYSTEMS

I have presented results of an experiment on a series of diverse communities in one geographical location. What relevance do these results have to the broader perspective aimed at in these proceedings? This question is difficult to answer since few data are available which specifically address the problem. Other chapters in this symposium have discussed the importance of disturbance in allowing plant invasion (e.g. Kruger *et al.*, this volume; Rejmanek, this volume). Fox and Fox (1986) concluded that, 'There is no invasion of natural communities without disturbance', while Mack (1985) stated that 'Sufficient examples can now be assembled to indicate that invasion can proceed without continuing disturbance.' Thus, for instance, pines in Australia and South Africa are apparently able to invade native plant communities in the absence of disturbance (Burdon and Chilvers, 1977; Kruger, 1977). This does not preclude the necessity for an initial disturbance to create a focus for establishment, however. There are other examples from Australia which suggest that fertilizer application in the absence of soil disturbance will allow non-native species to invade native communities (e.g. Rossiter, 1964; Armor and Piggin, 1977; Heddle and Specht, 1975). Clearly soil characteristics will be important, and in the Western Australian case reported here, the integrity of the soil surface crust may be an important feature preventing invasion even following nutrient addition. It is clear that a particular disturbance type does not have a 'generic' effect in all situations.

Different responses to disturbance may also arise where the invasive species are predominantly perennial rather than annual. For instance L. Cameron (personal communication) found little interaction between nutrient addition and disturbance when perennials such as *Hypochoaris radicata* and *Lolium perenne* were sown in three different communities in northern New South Wales.

Recent experiments on serpentine grasslands in northern California have shown that it is possible to change the grassland dominated by native forbs into one dominated by non-native grasses by adding nutrients (Hobbs *et al.*, 1988; L. Huenneke and coworkers, personal communication). Hobbs *et al.*, (1988) have shown that physical disturbance of the soil by gophers may reverse the invasion process. After spot applications of fertilizer, they found that non-native grasses, mainly *Bromus mollis* and *B. trinii*, increased greatly in abundance. The mulch formed by the dead grasses led to enhanced germination of *Bromus* in the following year, coupled with reduced survival of the native species. Fertilised plots that were subsequently disturbed by gophers had this mulch removed and native species were able to recolonize. Thus it appears likely that continual soil disturbance by gophers at some sites plays an important part in preventing non-native species from becoming dominant, and in retaining serpentine grasslands as natural 'islands' surrounded by seas of grasslands dominated by non-native Mediterranean grasses. In this case, therefore, although gopher disturbance is important to the internal dynamics of the serpentine grassland (Hobbs and Mooney, 1985), nutrient addition is a much more disruptive 'disturbance' in terms of invasion by non-natives.

17.5 SUMMARY AND CONCLUSIONS

I have outlined a simple experimental approach to the question of what determines the invasibility of natural plant communities. Using the example of a number of different communities in southwest Australia, I investigated the effect of soil disturbance and nutrient addition on invasion by introduced annual species. Soil disturbance enhanced establishment of introduced species, but their subsequent growth was greatly increased when soil disturbance was combined with nutrient addition. Other studies have found similar effects of nutrient adddition alone, and I conclude that the attributes of the system in question determine the influence of disturbances on invasibility. The experiments carried out so far are somewhat exploratory and leave many questions unanswered, but point the way to possible generalizations.

What resources are limiting and the natural disturbance regime will determine which disturbances are likely to have the largest effect. One can predict, for instance, that the creation of gaps might be more important than nutrient increase in light-limited systems. A general statement might be that disturbance will enhance invasibility only if it increases the availability of a limiting resource. This is essentially a truism, since the resource must be limiting to the invading species, but it is nevertheless useful to consider which resources are being significantly altered by disturbance. It is quite possible to have a disturbance which does not significantly increase the availability of a resource which is limiting to an invader, and it is important to be able predict the effects of disturbances on this basis.

While comparisons across systems are important, detailed studies within individual systems are also needed. The long-term conservation of many natural systems now depends on our ability to understand the invasion process and find ways to arrest or prevent it. While we must still rely heavily on historical and observational data on invasions, we must also make use of other tools including modelling and experimentation to help explain some of the questions arising from observational studies. Experimentation has been used relatively little to date and, clearly, some natural systems are more suitable for experimentation than others. There is nevertheless a wealth of information to be obtained from relatively simple and inexpensive experimental techniques.

ACKNOWLEDGEMENTS

I thank L. Atkins, M. Adams and G. Towers for technical support and V. J. Hobbs, G. W. Arnold, P. Vitousek, R. Mack, M. Rejmanek and P. Ramakrishnan for comments on and improvements to the manuscript. I am indebted to Hal Mooney for providing me with the opportunity to attend the symposium and to SCOPE and the National Academy of Sciences for financial support.

REFERENCES

Adamson, D. A., and Fox, M. D. (1982). Change in Australasian vegetation since European settlement. In: Smith, J. M. B. (Ed.), *A History of Australasian Vegetation*, pp. 109–46. McGraw-Hill, Sydney.

Armor, R. L., and Piggin, C. M. (1977). Factors influencing the establishment and success of exotic plants in Australia. In: Anderson, D. (Eds), *Exotic Species in Australia—Their Establishment and Success*. Proc. Ecol. Soc. Aust. 10, pp. 15–26.

Beard, J. S. (1983). Ecological control of the vegetation of Southwestern Australia: moisture versus nutrients. In: Kruger, F. J., Mitchell, D. T., and Jarvis, J. U. M. (Eds), *Mediterranean-type Ecosystems. The Role of Nutrients*, pp. 66–73. Springer, Berlin.

Bettenay, E. (1984). Origin and nature of the sandplains. In: Pate, J. S., and Beard, J. S. (Eds), *Kwongan. Plant Life of the Sandplain*, pp. 51–68. University of Western Australia Press, Nedlands.

Bridgewater, P. B., and Backshall, D. J. (1981). Dynamics of some Western Australian ligneous formations with special reference to the invasion of exotic species. *Vegetatio*, **46**, 141–8.

Brokaw, N. V. L. (1985). Treefalls, regrowth, and community structure in tropical forests.

In: Pickett, S. T. A., and White, P. S. (Eds), *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 53–69. Academic Press, New York.

Burdon, J. J., and Chilvers, G. A. (1977). Preliminary studies on a native Australian eucalypt forest invaded by exotic pines. *Oecologia (Berlin)*, **31**, 1–12.

Chesson, P. L. (1986). Environmental variation and the coexistence of species. In: Diamond, J., and Case, T. J. (Eds), *Community Ecology*, pp. 240–56. Harper and Row, New York.

Collins, B. S., Dunne, K. P., and Pickett, S. T. A. (1985). Responses of forest herbs to canopy gaps. In: Pickett, S. T. A., and White, P. S. (Eds), *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 218–34. Academic Press, New York.

Collins, S. L., and Barber, S. C. (1985). Effects of disturbance on diversity in mixed grass prairie. *Vegetatio*, **64**, 87–94.

Connell, J. H., and Keough, M. J. (1985). Disturbance and patch dynamics of subtidal marine animals on hard substrate. In: Pickett, S. T. A., and White, P. S. (Eds), *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 125–51. Academic Press, New York.

Crawley, M. J. (1986). The population biology of invaders. *Phil. Trans. R. Soc. Lond.* **314**, 711–31.

Crawley, M. J. (1987). What makes a community invasible? In: Crawley, M. J., Edwards, P. J., and Gray, A. J. (Eds), *Colonization, Succession and Stability*. Blackwell, Oxford, pp. 629–54.

Diamond, D., and Case, T. J. (1986). Overview: introductions, extinctions exterminations and invasions. In: Diamond, J., and Case, T. J. (Eds), *Community Ecology*, pp. 65–79. Harper and Row, New York.

Fox, J. F. (1985). Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. *Arctic Alpine Research*, **17**, 199–204.

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.

Green, J. W. (1985). *Census of the Vascular Plants of Western Australia.* Western Australian Herbarium, Department of Agriculture, Perth.

Groves, R. H. (1981). Heathland soils and their fertility status. In: Specht, R. L. (Ed.), *Heathlands and Related Shrublands: Analytical Studies*, pp. 143–50. Elsevier, Amsterdam.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, **52**, 107–45.

Harper, J. L. (1977) *Population Biology of Plants.* Academic Press, London.

Heddle, E. M., and Specht, R. L. (1975). Dark Island Heath (Ninety Mile Plain, South Australia) VIII. The effects of fertilisers on composition and growth. *Aust. J. Bot.*, **23**, 151–64.

Hobbs, R. J. (1987). Disturbance regimes in remnants of natural vegetation. In: Saunders, D. A., Arnold, G. W., Hopkins, A. J. M. and Burbidge, A. A. (Eds), *Nature Conservation: the Role of Remnants of Native Vegetation*, pp. 233–40 Surrey-Beattie, Sydney.

Hobbs, R. J., and Atkins, L. (1988). Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Aust. J. Ecol.*, **13**, 43–57.

Hobbs, R. J., and Mooney, H. A. (1985). Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia* (*Berlin*), **67**, 342–51.

Hobbs, R. J., Gulmon, S. L., Hobbs, V. J., and Mooney, H. A. (1988). Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia* (*Berlin*), **75**, 291–95.

Hopkins, A. J. M., and Griffin, E. A. (1984). Floristic patterns. In: Pate, J. S., and Beard, J. S. (Eds), *Kwongan. Plant Life of the Sandplain*, pp. 69–83. University of Western Australia Press, Nedlands.

Hopper, S. D., and Muir, B. G. (1984). Conservation of the kwongan. In: Pate, J. S., and Beard, J. S. (Eds), *Konwgan. Plant Life of the Sandplain*, pp. 253–66. University of Western Australia Press, Nedlands.

Kitchener, D. J., Chapman, A., Dell, J., Muir, B. G., and Palmer, M. (1980). Lizard assemblage and reserve size in the Western Australian wheatbelt—some implications for conservation. *Biol. Conserv.*, **17**, 25–62.

Kruger, F. J. (1977). Invasive woody plants in the Cape fynbos with special reference to the biology and control of *Pinus pinaster*. *Proceedings of the 2nd National Weeds Conference of South Africa.* A. A. Balkema, Cape Town.

Kruger, F. J., Richardson, D. M., and van Wilgen, B. W. (1986). Processes of invasion by plants. In: Macdonald, I. A. W., Kruger, F. J., and Ferrar, A. A. (Eds), *The Ecology and Management of Biological Invasions in South Africa*, pp. 145–55. Oxford University Press, Cape Town.

Macdonald, I. A. W., Powrie, F. J., and Siegfried, W. R. (1986). The differential invasion of South 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 South Africa*, pp. 209–25. Oxford University Press, Cape Town.

McIvor, J. G., and Smith, D. F. (1971). The effect of fertiliser application and time of seasonal break on the growth and dominance of capeweed (*Arctotheca calendula*). *Aust. J. Exp. Ag. Anim. Husbandry*, **14**, 553–6.

Mack, R. N. (1985). Invading plants: their potential contribution to population biology. In: White, J. (Ed.), *Studies in Plant Demography: A Festschrift for John L. Harper*, pp. 127–41. Academic Press, London.

Newsome, A. E., and Noble, I. R. (1986). Ecological and physiological characteristics of invading species. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: an Australian Perspective*, pp. 1–20. Australian Academy of Science, Canberra.

Orians, G. H. (1986). Site characteristics promoting invasions and systems impact of invaders. In: Mooney, H. A., and Drake, J. A. (Eds), *Ecology of Biological Invasions of North America and Hawaii.* Springer, pp. 133–48. New York.

Pickett, S. T. A., and White, P. S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, New York.

Platt, W. J. (1975). The colonisation and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. *Ecol. Monogr.*, *45*: 285–305.

Rossiter, R. C. (1964). The effect of phosphate supply on the growth and botanical composition of annual-type pasture. *Aust. J. Agric. Res.*, **15**, 61–76.

Rossiter, R. C. (1966). Ecology of the Mediterranean annual-type pasture. *Adv. Agron.*, **18**, 1–56.

Silvertown, J. (1981). Microspatial heterogeneity and seedling demography in species-rich grassland. *New Phytol.*, **88**, 117–28.

Sousa, W. P. (1984). The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.*, **15**, 353–91.

Sousa, W. P. (1985). Disturbance and patch dynamics on rocky intertidnal shores. In: Pickett, S. T. A., and White, P. S. (Eds), *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 101–24. Academic Press, New York.

Steel, R. G. D., and Torrie, J. H. (1982). *Principles and Procedures of Statistics. A Biometrical Approach.* McGraw Hill, London.

Tilman, D. (1982). *Resource Competition and Community Structure.* Princeton University Press, Princeton, New Jersey.

White, P. S. (1979). Pattern, process and natural disturbance in vegetation. *Bot. Rev.*, **45**, 229–99.

White, P. S., and Pickett, S. T. A. (1985). Natural disturbance and patch dynamics: an introduction. In: Pickett, S. T. A., and White, P. S. (Eds), *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 3–13. Academic Press, New York.

Williams, K., Hobbs, R. J., and Hamburg, S. (1987). Invasion of an annual grassland in Northern California by *Baccharis pilularis* ssp. *consanguinea. Oecologia* (*Berlin*), **72**, 461–65.

Wycherley, P. (1984). People, fire and weeds: can the vicious spiral be broken? In: Moore, S. A. (Ed.), *The Management of Small Bush Areas in the Perth Metropolitan Region.* Department of Fisheries and Wildlife, Perth.