OSU ILLIAD TN#: 83700.0

Oregon State University

ILL -- Phone: (541) 867-0249 Email: valley.ill@oregonstate.edu Fax: (541) 737-1328 Ariel: 128.193.170.35

Journal Title: Plant protection quarterly.
Volume: 6
Issue: 4
Month/Year: 1991
Pages: 99 -- 104

ILL Number: 8025229

Article Author:
Article Title: Hobbs, R.J. / Distrubance a precursor to weed invasion in native vegetation

Borrower: WOS

Borrower: WOS
Lending String: *ORE,IRU

Patron: Taylor, Steve
Maxcost: postage

Ariel: 140.211.112.16

Fax: 503-838-8645

This item will be invoiced at the end of the month

Photocopy/Loan/Invoice/Postage Charges: Summit - No Charge

OCLC Number: 12617904

Shipping Address:
WESTERN OREGON UNIVERSITY
HAMERLSY LIBRARY - ILL
345 N MONMOUTH AVE
MONMOUTH OR 97361-1396

HL
8/26

Disturbance a precursor to weed invasion in native vegetation

Richard J. Hobbs, CSIRO Division of Wildlife and Ecology, LMB 4, PO Midland, WA 6056, Australia.

Summary

This paper examines the problem of disturbance in native vegetation and its relation to invasion by weeds. Disturbance can be defined as anything that directly kills or damages individuals within a given area, or affects resource levels in that area. Weed invasion is generally enhanced by disturbance, and a survey of Australia's most serious weeds confirms that most require some form of disturbance for their dispersal or establishment. All disturbances do not lead to invasions. Increased invasion is likely only if disturbance increases the availability of a limiting resource, and if propagules are available. Natural disturbance regimes are essential to the maintenance of native vegetation, but human activities usually add new types of disturbance to the existing regime. Management of disturbance must be carried out in recognition of the requirements of the native vegetation and with adequate assessment of the relative importance of different disturbance types in promoting invasion. Human-induced disturbances generally need to be minimized.

Introduction

This paper considers the link between disturbance and invasion by weedy plant species. It begins by considering what is meant by disturbance, and then examines whether weed invasion depends on disturbance. This is done by assessing the importance of disturbance in the spread and establishment of Australia's most serious environmental weeds, as recently defined by Humphries *et al.* (1991). It then discusses whether disturbance always leads to invasions using a series of examples from native plant communities in the Western Australian wheatbelt. Finally, the management implications of the interaction between disturbance and invasions are considered.

Definition of disturbance

There has been considerable debate on the definition of disturbance, and on what constitutes a disturbance to any given community or ecosystem (e.g., Rykiel 1985, van Andel and van den Berg 1987). Definitions of disturbance vary from Grime's (1979) view of disturbance as a process removing or damaging biomass to Pickett and White's (1985) definition of 'any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment'. Petraitis *et al.* (1989) expand the definition further to include any 'process that alters the birth and death rates of individuals present in the patch', by directly killing individuals or by affecting resource levels, natural enemies, or competitors in ways that alter survival and fecundity. Temporal and spatial scale are clearly important in our recognition of the 'discreteness' of a disturbance event, as nearly any ecological or physical process might fall under the last, most inclusive definition. Pickett *et al.* (1989) define a disturbance as a change in ecosystem structure caused by factors external to the hierarchical level of the system of interest; this is necessary to distinguish disturbance from other changes in the system.

Both direct disturbances (those affecting the survivorship of individuals directly) and indirect disturbances (those affecting resource levels or other conditions that then influence individuals in the patch) are included in this review. Disturbances thus include large-scale events such as fires, storms, and floods; smaller-scale phenomena such as soil disturbance by animals; and direct human disturbance (digging, trampling, vegetation removal, road construction etc.). Less direct changes such as altered grazing regimes or nutrient inputs will be considered as disturbances where they affect resource levels and demographic processes.

Individual disturbances are generally considered in the context of the overall disturbance regime, which is characterized by the types, sizes, intensities, timing and frequencies of disturbances (Pickett and White 1985). Important in this context are the modifications in natural disturbance regimes caused by human intervention. Aboriginal settlement in Australia undoubtedly altered disturbance regimes, and European settlement had further significant impacts (Hobbs and Hopkins 1990). Following European settlement, besides the direct impacts of clearing, mining, forestry and urbanization, grazing and fire regimes were significantly modified over much of Australia. The fragmentation of natural ecosystems by agricultural development has also significantly affected disturbance regimes in the remnant vegetation left after clearing (Hobbs 1987). It is in this context of greatly altered disturbance regimes that weed invasion must be considered.

Is weed invasion dependent on disturbance?

For weed invasion to occur, there must be an opportunity for invasion, which requires the availability of propagules of an invasive species capable of dispersing into the area. Then there has to be a suitable micro-site for germination and establishment to occur, i.e., a suitable invasion 'window' (Johnstone 1986). Disturbances generally act to change the characteristics and availability of microsites for establishment, although they also may affect the opportunity for dispersal, e.g., where non-native herbivores or floods transport seeds into new areas.

There is general agreement in the literature that disturbances usually act to enhance the likelihood of invasion into native vegetation (Amor and Piggin 1977, Fox and Fox 1986, Crawley 1987, Rejmanek 1989) and there are many examples that illustrate the role of different

Table 1. Species identified as the most serious environmental weeds in Australia, and types of disturbance favouring spread and/or establishment (derived from Humphries *et al.* 1991).

Species	Disturbance type
Acacia nilotica (L.) Willd. ex Del.	Cattle dung, flooding
Cenchrus ciliaris L .	Floods, cattle
Chrysanthemoides monilifera ssp. *rotundata* (DC.) Norlindh	Rabbits, cattle, roading, sandmining, natural disturbances
Cryptostegia grandiflora R. Br.	Drought followed by floods, fire, grazing
Eichhornia crassipes (C. Martius) Solms	Human interference, nutrient enrichment
Mimosa pigra L.	Clearing, water level fluctuations
Myrsiphyllum asparagoides (L.) Willd.	?
Parkinsonia aculeata L.	Flooding
Pennisetum polystachion (L.) Schultes	Vehicular spread along roads, small scale disturbance by pigs, bandicoots
Prosopis spp.	Flooding
Salvinia molesta D. Mitch.	Human transport, nutrient enrichment
Tamarix aphylla (L.) Karst	Flooding, high rainfall years
Thunbergia grandiflora (Rottler) Roxb.	Edge or gap formation

types of disturbance in allowing invasions to occur (Hobbs and Huenneke, personal communication). Invading species frequently have attributes which allow them to take advantage of disturbances at the expense of native species; for instance, generalist modes of dispersal, rapid germination and growth and relatively short maturation times. However, it is not yet clear whether all invasions require disturbance.

Humphries *et al.* (1991) compiled a list of the plants considered to be Australia's most serious environmental weeds, together with a summary of information on each. Table 1 lists these species (except for a group of four aquatic grasses, about which limited information was given), and the types of disturbance influencing their spread and/or establishment. From Table 1 it can be noted that all species except *Myrsiphyllum asparagoides* (L.) Willd. (bridal creeper) had a clear link with at least one disturbance type. Many of the species are found predominantly in wet areas such as drainage channels or flood plains, and hence floods may result in propagule dispersal or promote establishment. Other disturbance agents such as cattle, rabbits, animal diggings and human activities were implicated to some extent in the spread or establishment of one or several of the species. Spread of the two aquatic species, *Eichhornia crassipes* (C. Martius) Solms (water hyacinth) and *Salvinia molesta* D. Mitch. , was related in each case to human disturbance and nutrient enrichment.

Clearly, therefore, it can be argued that some form of disturbance is implicated in the invasion of almost all the major environmental weeds of Australia. This may be natural disturbance (such as floods or bandicoot diggings), disturbances caused by introduced stock and feral animals (cattle, rabbits, pigs), and direct human disturbance (road construction, mining, clearing). *M. asparagoides* appears to be the only species on the list that has no apparent need for disturbance for spread or establishment. While it is relatively easy to link invasion by a particular species with disturbance events, it is much more difficult to prove unequivocally that invasion occurs in the absence of disturbance. Natural disturbances are an important feature of most Australian ecosystems (e.g., fire, flooding, animal digging and grazing), and human modifications of natural disturbance regimes have occurred over most of Australia. The question of whether invasions can occur in the absence of disturbance thus may be academic. We should instead be asking which disturbances are the most likely to lead to invasions.

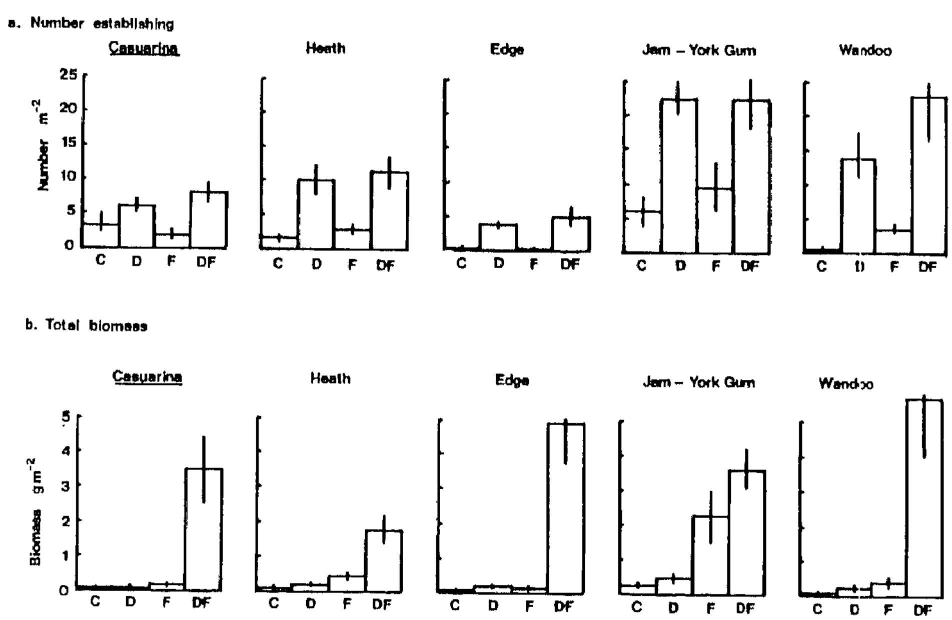

Figure 1. Responses of *Avena fatua* L. sown into experimental plots (each 1 m²) in five different vegetation communities in the Western Australian wheatbelt. Treatments are: C, control; D, disturbed; F, fertilized; DF, disturbed and fertilized. Plant communities are; Casuarina, shrubland dominated by *Allocasuarina campestris* ; heath, species rich sandplain heath; edge, regenerating community on previously-cleared sandplain heath; jam-york gum, *Eucalyptus loxophleba*/ *Acacia acuminata* woodland; wandoo, *Eucalyptus wandoo* woodland. Histograms give mean values ± 1 S.E. (n= 4), and letters above bars indicate results of SNK test; treatments with different letters are significantly different at $p < 0.05$. (a) Number of seedlings established in each plot, (b) total dry weight per plot. (Data from Hobbs and Atkins 1988, redrawn from Hobbs 1989).

Does disturbance always lead to invasions?

Because of the pervasiveness of disturbance in natural and human-modified ecosystems it is important to consider whether all disturbances are likely to result in increased invasion, or whether some types of disturbance are likely to be more important than others. Timing of disturbance (for instance in relation to seed set and dispersal) also may be important in determining the relative effect of individual disturbances. If the types of disturbance most likely to result in increased invasion can be identified, disturbance regimes could be modified to minimize the opportunities for invasion.

It has been argued elsewhere that disturbance will enhance invasions only if it increases the availability of a limiting resource (Hobbs 1989). Thus, where light is limiting, as in a dense forest or woodland, the creation of gaps or edges (through treefalls, logging or fragmentation) which increase light levels at the ground surface might be expected to enhance invasibility (Amor and Stevens 1976). Other disturbances, such as soil disturbance or nutrient addition, would have little effect on invasibility if light remained limiting, even if other resources were made more abundant. In more open communities, however, where light is not limiting, soil disturbance or nutrient addition could be expected to enhance invasion since these increase the supply of scarce resources (soil disturbance could increase available nutrients, water retention and the availability of 'safe sites' for establishment). Similarly, flooding temporarily increases the availability of water, a major limiting resource in arid and semi-arid areas.

In these cases, disturbance alters microsite conditions which in turn influence the success of establishment of invasive species. In some cases, such as flooding, the disturbance may also influence the dispersal of the invader. The dispersal and establishment phases are the critical stages in the initial invasion of an area. Subsequent survival and reproduction determine the long-term success of the invasion, and may be dependent on factors quite different from those determining dispersal and establishment. In this paper the establishment phase is examined in more detail.

A series of studies were carried out in the Western Australian wheatbelt into the factors affecting the invasion of native plant communities by non-native species. The studies concentrated on the annual grasses and forbs that invade native communities in vegetation remnants. The disturbances considered were soil disturbance, nutrient addition and fire. All of these have been considered to enhance invasions in Australia and elsewhere (Bridgewater and Backshall 1981,

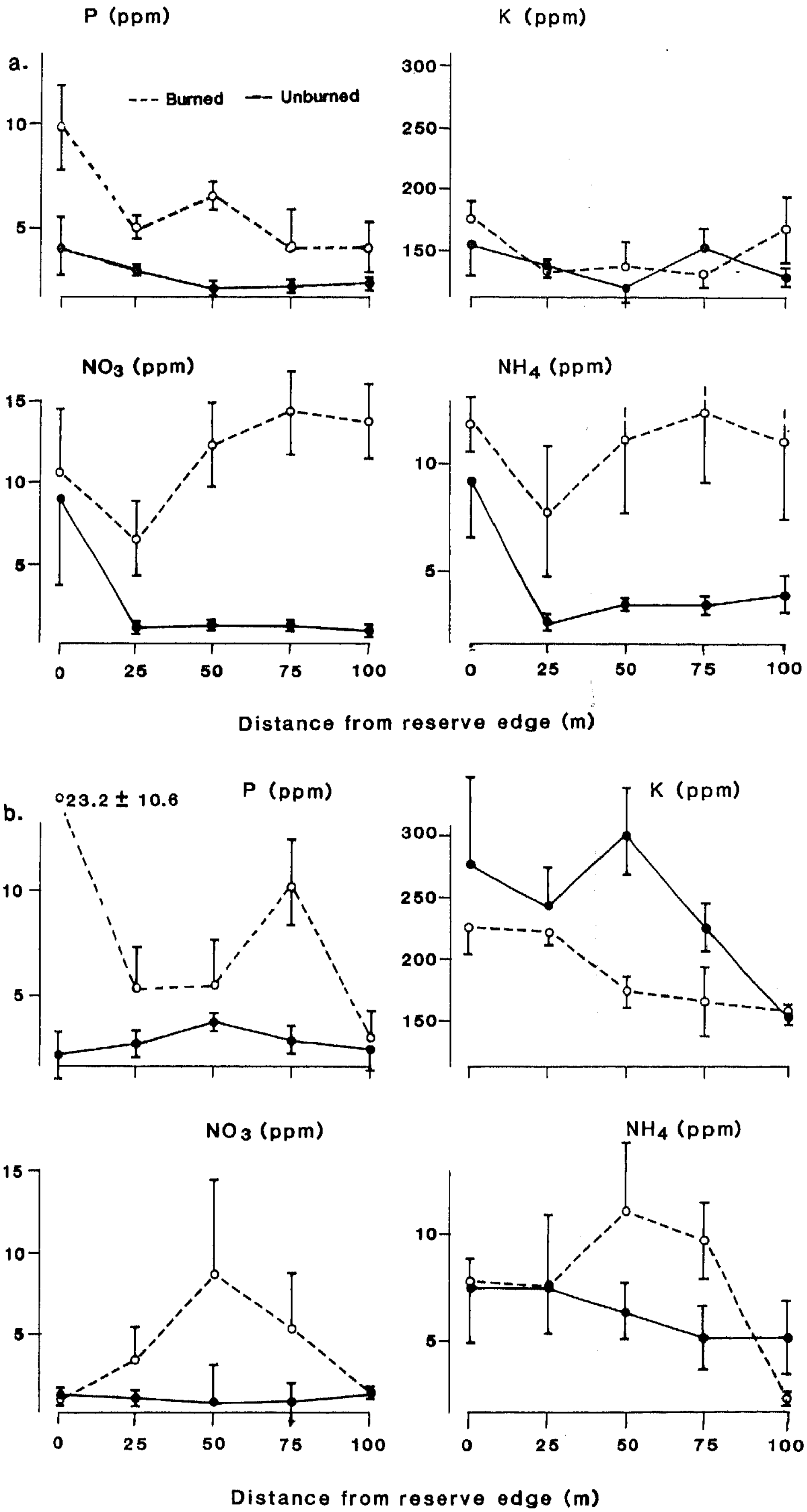

Figure 2. Available nutrients in soils along transects in burnt and unburnt vegetation at the edge of Durokoppin reserve in the Western Australian wheatbelt in September 1988, following a fire in April 1988. Mean ± 1 S.E., n=5. Burnt (–○–), unburnt (–●–), (a) shrubland dominated by *Allocasuarina campestris* (b), woodland dominated by *Eucalyptus loxophleba* and *Acacia acuminata* (redrawn from Hester and Hobbs 1992).

Christensen and Burrows 1986, Heddle and Specht 1975, Hobbs and Mooney 1985, 1991).

The studies indicate several important points:

1. Plant communities vary greatly in their susceptibility to invasion;
2. Disturbance can greatly increase the likelihood of invasion, but not all disturbances act in this way;
3. Invasion is enhanced most where a combination of disturbances is experienced.

These points can be illustrated with data from a number of different studies. Invasion into different plant communities was examined by Hobbs and Atkins (1988) and Hester and Hobbs (1992). Hobbs and Atkins (1988) conducted experiments in a number of different shrubland and woodland communities, and found that woodlands were more easily invaded than shrub-dominated communities. In general, woodland communities in the Western Australian wheatbelt occur on richer soils and the greater degree of weed invasion could be due at least in part to the higher levels of nutrients found there (Hobbs 1989). Also, most woodland areas have been grazed by stock in the past. Observations suggest that grazing can increase invasion by non-natives (Hobbs, unpublished data), possibly because of removal of native species, nutrient transfer and disturbance through trampling. Stock are less likely to graze in dense shrublands due to their impenetrability, or in more open heathlands due to the lack of palatable species. Hester and Hobbs (1992) also found that a woodland community was much more invaded than an adjacent shrubland.

Hobbs and Atkins (1988) conducted disturbance experiments in five different communities, including two woodland (*Eucalyptus wandoo* Blakeley, and *Acacia acuminata* Benth./*Eucalyptus loxophleba* Benth.) and three shrubland types (mixed sandplain heath, dense shrubland dominated by *Allocasuarina campestris* (L.) Johnson, and an area cleared for agriculture and allowed to regenerate). They carried out treatments which involved nutrient addition, physical disturbance of the surface soil and a combination of these two. They found that physical disturbance of the soil increased the rate of establishment of two non-native species whose seeds were introduced to the experimental plots. However, subsequent growth of these species was greatly increased where soil disturbance was combined with nutrient addition (Figure 1). This was true in all the communities studied, but the effect was much less evident in the heath community. Further studies into why heath should be less invasible have proved inconclusive (Hobbs and Atkins 1991). Neither fire nor removal of

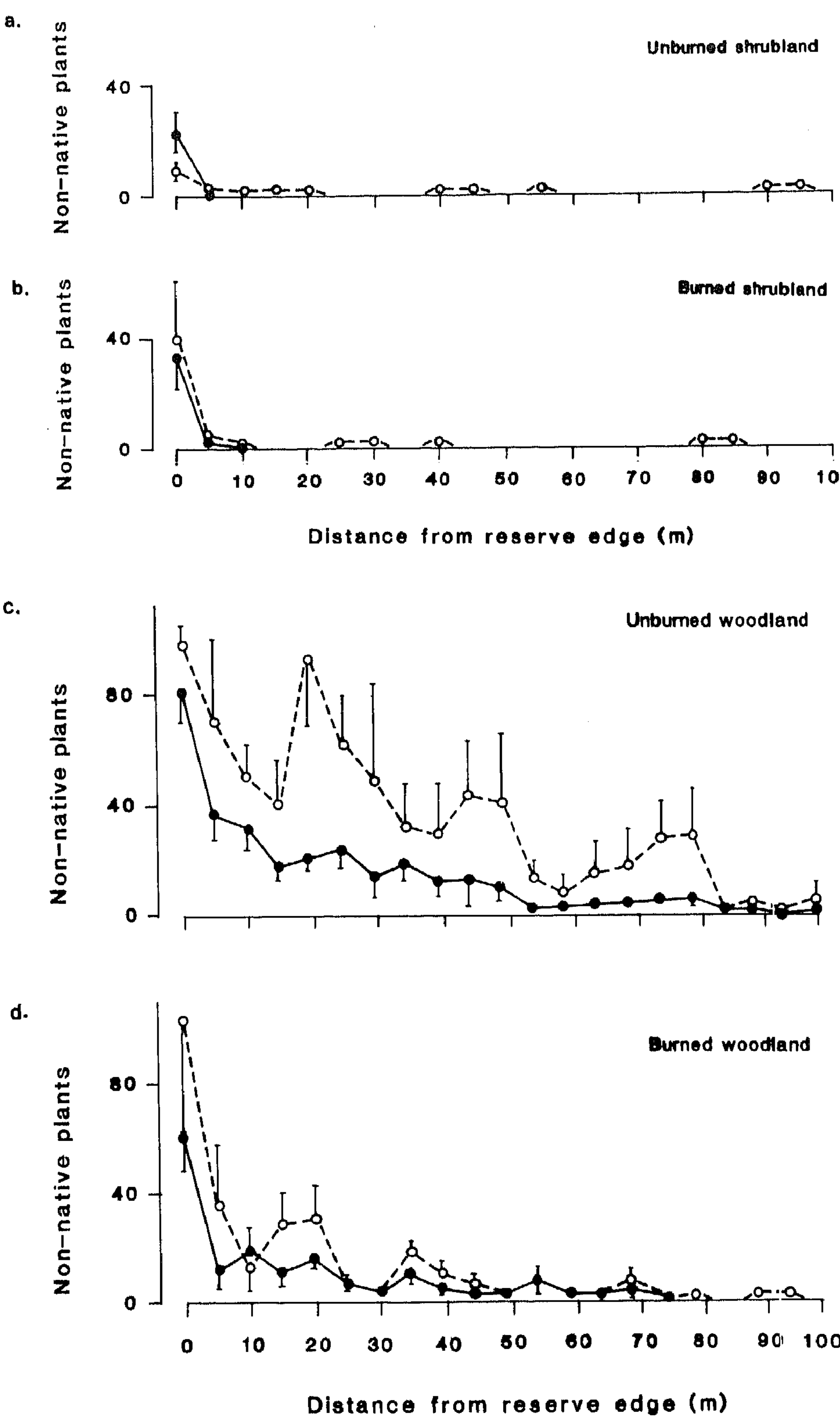

Figure 3. Abundance of non-native annuals in 50 × 50 cm quadrats along transects through burnt and unburnt shrubland and woodland in September 1988, following a fire in April 1988 (as in Figure 2). Mean ± 1 S.E., n=5. number of plants per quadrat (–o–), percentage cover (–●–). (a) unburnt shrubland, (b) burnt shrubland, (c) unburnt woodland, (d) burnt woodland.

shrubs by cutting had any effect on the abundances of non-native annuals.

Clearly, some community types are more easily invaded than others. This may be related largely to the overall degree of past and present disturbance in the community: in general, shrub-dominated communities in the Western Australian wheatbelt have been subjected to less disturbance in the past than woodlands, and this may have left them better able to resist invasions. The lower levels of nutrients in the shrub communities also could be important. It should be noted, however, that these results are valid only for the pool of non-native species available at the moment. Other non-native species might be able to invade but currently lack a local seed source.

The effects of fire on weed invasion were studied by Hobbs and Atkins (1991) and Hester and Hobbs (1992). The latter found that fire significantly increased levels of soil phosphorus, nitrate and ammonium in a shrubland community dominated by *Allocasuarina campestris*, at the edge of a vegetation remnant (Figure 2). In adjacent woodland, dominated by *Eucalyptus loxophleba* and *Acacia acuminata*, soil phosphorus and nitrate again were increased after fire. These increases in soil nutrients were not matched by an increase in weed abundance; in fact, numbers and cover of non-native species remained about the same in the shrubland and decreased following fire in the woodland (Figure 3). Hobbs and Atkins (1991) similarly found no effect of fire on abundance of weedy species in a heath community.

Results from single disturbances should be treated with caution. Timing and intensity of a fire can be important in determining the recovery of the native vegetation and also may be important in determining the extent to which invasion will be enhanced. For instance, Hobbs and Atkins (1990) found that invasion by non-natives was greater in a *Banksia* woodland following an autumn fire than following a spring fire. This may be because the annual weedy species were able to take advantage of the short-term increase in nutrients following an autumn fire, but that this effect had disappeared in the spring fire area before the next winter growing season commenced. Alternatively, rapid regrowth of the native woody species following the spring fire may have prevented establishment of weeds. Again, few definite conclusions can be drawn from a small number of individual fires.

Hester and Hobbs (1992) demonstrated an increase in the abundance (cover and density) of non-native species at the edge of vegetation remnants (Figure 3). This is evident in both the shrubland and the woodland. In the shrubland, weed abundances declined dramatically just a few meters in from the edge, while in the woodland abundances declined less rapidly. Greater weed abundances at remnant edges were also found by Hobbs (1989), despite the fact that non-native seed was available at considerable distances from the edge (Hobbs and Atkins 1988). This indicates that remnant edges are of particular concern in terms of weed invasion. Clearly, conditions at the remnant edge differ significantly from those further inside the remnant in terms of microclimate (Saunders *et al.* 1991) and nutrient status (Muir 1979, Figure 2). The important question is how 'closed' the vegetation edge is. In Figure 3, it appears that the shrubland edge is a significant barrier to weed invasion, whereas the woodland edge is not. This probably relates to the cover of the upper canopy, which is dense in the shrubland but open in the woodland. The effect of the existing vegetation could be in modifying light intensities or water and/or nutrient availability.

Considerations about edge effects are particularly important in roadverge vegetation, where edge:area ratios are generally very high (Loney and Hobbs 1991). Cale and Hobbs (1991) found that the degree of weed invasion on roadverges dominated by mallee vegetation was positively correlated with the levels of soil nutrients (phosphorus and ammonium). In wide verges (50 m), there were distinct gradients in soil phosphorus and weed cover away from the paddock boundaries, indicating that spread of nutrients from the paddocks into verge vegetation was an important correlate of weed invasion. This is in contrast to the results discussed above for vegetation in larger remnants, where nutrient levels per se could not explain degree of weed invasion. However, it appears likely that road verges represent a much more disturbed system than larger remnants, due to road maintenance operations, sheep movements along roads and greater impacts from the surrounding agricultural lands. This greater background level of disturbance is therefore likely to predispose roadverge vegetation to invasion if further disturbance is superimposed. For instance, Hobbs and Atkins (1991) found that weed growth was prolific in areas of roadside heath vegetation that were burned, whereas the same fire had no effect on invasion in heath in an adjacent large remnant. Clearly, disturbance in roadverge vegetation is likely to increase weed invasion, and maintenance of an intact canopy may be the best way to prevent invasion (Cooke 1983, Breckwoldt 1986, Panetta and Hopkins 1991).

Management considerations

The picture presented above is rather confusing from a management perspective. What can the manager do about disturbance in relation to weed invasion? It seems clear that disturbance is likely to increase the likelihood of weed invasion, but a more detailed analysis indicates that not all disturbances act in this way. Should we then advocate that managers try to eliminate disturbance from natural vegetation? The simple answer to this is that this is neither possible nor desirable. It is not desirable because disturbance is a natural part of most of the natural ecosystems of Australia, and most plant communities depend on either small-scale or large-scale disturbances for regeneration and maintenance of species richness (Hobbs and Huenneke, personal communication). To exclude all disturbances would in itself constitute a major disturbance which would severely disrupt the natural processes within native vegetation. It is also unrealistic to think that we could exclude all disturbance since it is impossible to do so from a practical viewpoint.

We can, however, try to assess the types of disturbance prevalent in any particular area and assess their importance in terms of their effects on invasion. We can consider the acute disturbances such as fire, as compared with the more chronic disturbances such as stock grazing and nutrient input. We also can compare natural large-scale natural disturbances such as floods, about which we can do little, with smaller-scale disturbances such as road construction and maintenance, about which we can do a great deal. In this way we can determine which disturbances are most important in enhancing invasions, and which can be treated in a sensible and cost-effective way. If the most important disturbances can be treated easily, then the problem of weed invasion can be minimized, preventatively. If, however, the major disturbances prove to be intractable problems, we then have to move away from prevention of invasions and more towards direct control measures.

The examples from the Western Australian wheatbelt have highlighted some problems involved in managing disturbance. Contrary to current predictions, fire per se did not increase the degree of weed invasion in native vegetation, providing other types of disturbance were absent. Thus, in this situation, fire may be a good management tool to regenerate native plant communities. However, this is not so on roadverges, where other forms of disturbance are experienced. Nutrient levels also appear to be important in determining weed invasion; this will become increasingly important if nutrient inputs into remnant vegetation from surrounding farmland continue. Simple control of the weeds present in an area with elevated nutrients will not solve the problem. This corresponds to treating the symptoms, not the cause of the problem. In the long-term, nutrient levels will need to be reduced. Similarly, in light-limited forests, weed control will not succeed unless it is accompanied by re-establishment of native vegetation cover.

Generally managers need to consider all aspects of the disturbance regime within native vegetation. Those aspects of the natural regime that are essential for regeneration and community dynamics need to be maintained. Other disturbances, especially those arising from external human activities, such as adjacent agriculture, stock grazing or road building should be kept to a minimum. The pervasive problem of invasion makes the management of disturbance difficult, but not impossible. Disturbance regimes cannot be left to themselves, however; active decisions are required on which disturbances, and hence which species, are to be encouraged.

The major principles for management of disturbance can be summarized as follows:

1. The natural disturbance regime should be maintained as far as possible.
2. Prevention should be used to manage weeds rather than direct control, except where disturbances are intractable.
3. Any disturbance due to human activities should be minimized.
4. Causes rather than symptoms of problems should be treated.
5. Synergism often operates between different types of disturbance, and the approach to introducing any human disturbance should thus be conservative.

Acknowledgements

I thank S. Humphries and D. Panetta for comments on the manuscript.

References

Amor, R.L. and Piggin, C.M. (1977). Factors influencing the establishment and success of exotic plants in Australia. *Proceedings of the Ecological Society of Australia* 10, 15-26.

Amor, R.L. and Stevens, P.L. (1976). Spread of weeds from a roadside into sclerophyll forests at Dartmouth, Australia. *Weed Research* 16, 111-8.

Andel, J. van and Berg J. P. van den (1987). Disturbance and grasslands . *In* 'Disturbance in grasslands: causes, effects and processes', eds J. van Andel, J.P. Bakker and R.W . Snaydon, pp. 3-13 (Junk, Dordrecht).

Breckwoldt, R. (1986). 'The last stand - managing Australian forest and woodland'. 62 pp. (Australian Government Publishing Service, Canberra).

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.

Cale, P. and Hobbs, R.J. (1991). Condition of roadside vegetation in relation to nutrient status. *In* 'Nature conservation 2: The role of corridors' eds D.A. Saunders and R.J. Hobbs, pp. 353-62 (Surrey Beatty and Sons, Chipping Norton).

Christensen P.E. and Burrows, N.D. (1986). Fire: an old tool with a new use. *In* 'Ecology of biological invasions: an Australian perspective', eds R.H. Groves and J.J. Burdon, pp. 97-105 (Australian Academy of Science, Canberra).

Cooke, B . D . (1983). Rabbit control and the conservation of native vegetation on roadsides. *In* 'Trees in the rural environment: towards a green-print for South Australia', ed. F.J. Van der Sommen, pp. 4.6-4.7 (Faculty of Natural Resources, Roseworthy Agricultural College, Roseworthy).

Crawley, M.J. (1987). What makes a community invasible? *In* 'Colonization, succession and stability', eds M.J. Crawley, P.J. Edwards and A.J. Gray, pp. 429-54 (Blackwell, Oxford).

Fox, M.D. and Fox, B.J. (1986). The susceptibility of natural communities to invasion. *In* 'Ecology of biological invasions: an Australian perspective', eds R.H. Groves and J.J. Burdon, pp. 57-66 (Australian Academy of Science, Canberra).

Grime, J.P. (1979). 'Plant strategies and vegetation processes'. 222 pp. (Wiley, New York).

Heddle, E.M. and Specht R.L. (1975). Dark Island Heath (Ninety-Mile Plain), South Australia. VIII. The effects of fertilizers on composition and growth. *Australian Journal of Botany* 23, 151-64.

Hester, A.J. and Hobbs, R.J. (1992). Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science*, In press.

Hobbs, R.J. (1987). Disturbance regimes in remnants of natural vegetation. *In* 'Nature conservation: the role of remnants of native vegetation', eds D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins, pp. 233-40 (Surrey Beatty, Chipping Norton).

Hobbs, R.J. (1989). The nature and effects of disturbance relative to invasions. *In* 'Biological invasions. A global perspective', eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek and M. Williamson, pp. 389-405 (Wiley, Chichester).

Hobbs, R.J. and Atkins, L. (1988). The effect of disturbance and nutrient addition on native and introduced annuals in the Western Australian wheatbelt. *Australian Journal of Ecology* 13, 171-9.

Hobbs, R.J. and Atkins, L. (1990). Fire-related dynamics of a *Banksia* woodland in south-west Western Australia. *Australian Journal of Botany* 38, 97-110.

Hobbs, R.J. and Atkins, L. (1991). Interactions between annual and woody perennial vegetation components within a Western Australian wheatbelt reserve. *Journal of Vegetation Science*, In press.

Hobbs, R.J. and Hopkins, A.J.M. (1990). From frontier to fragments: European impact on Australia's vegetation. *Proceedings Ecological Society of Australia* 16, 93-114.

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. and Mooney, H.A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics in N. California. *Ecology* 72, 59-68.

Humphries, S.E., Groves, R.H. and Mitchell, D.S. (1991). 'Plant invasions and Australian ecosystems. A status review and management directions'. 166 pp. (Australian National Parks and Wildlife Service, Canberra).

Johnstone, I.M. (1986). Plant invasion windows: a time-based classification of invasion potential. *Biological Reviews* 61, 369-94.

Loney, B. and Hobbs, R.J. (1991). Management of vegetation corridors: maintenance, rehabilitation and establishment. *In* 'Nature conservation 2: The role of corridors' eds D.A. Saunders and R.J. Hobbs, pp. 299-311 (Surrey Beatty and Sons, Chipping Norton).

Muir, B.G. (1979). Observations on windblown superphosphate in native vegetation. *Western Australian Naturalist* 14, 128-30.

Panetta, F.D. and Hopkins, A.J.M. (1991) . Weeds in corridors: invasion and management. *In* 'Nature conservation 2: The role of corridors' eds D.A. Saunders and R.J. Hobbs, pp. 341-51 (Surrey Beatty and Sons, Chipping Norton).

Petraitis, P.S., Latham, R.E. and Niesenbaum R.A. (1989). The maintenance of species diversity by disturbance. *Quarterly Review of Biology* 64, 393-418.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. and Collins, S.L. (1989) . The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54, 129-36.

Pickett, S.T.A. and White, P.S. (eds) (1985). 'The ecology of natural disturbance and patch dynamics'. 472 pp. (Academic Press, Orlando).

Rejmanek, M. (1989). Invasibility of plant communities. *In* 'Biological invasions: a global perspective', eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, pp. 369-88. (Wiley, Chichester).

Rykiel, E.J. (1985). Towards a definition of ecological disturbance. *Australian Journal of Ecology* 10, 361-5.

Saunders, D.A., Hobbs, R.J. and Margules, C. (1991). Biological consequences of ecosystem fragmentation. *Conservation Biology* 5, 18-32.