THE NATURE OF EXOTIC INVASIONS IN HERBACEOUS VEGETATION OF HIGH AND LOW SPECIES RICHNESS: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

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Summary. Sixty quadrats from grassland vegetation were divided into those with above and below average richness of native species. Low richness sites were more highly disturbed and mainly dominated by exotic perennial grasses. High richness sites were typically dominated by native perennial grasses. The most abundant exotic species showed two patterns of occurrence: greater frequency in low richness sites or similar frequency over both low and high richness. The data indicate that exotic species may vary in their impact on native vegetation, and that selective control could be a useful strategy to maintain, or regain, native species richness following disturbance.

INTRODUCTION

Combinations of disturbance and invasions by exotic species are considered to be a major threat to the survival of native plants in Australia (5). In a survey of native grassland sites on the New England Tablelands, 97% of samples were found to contain exotic species, even though the sampling was stratified to include examples of the vegetation in its most natural state (McIntyre, unpublished data). For vegetation such as natural grasslands, exotic invasions are a fact of life. The challenge in conserving the native component of such herbaceous communities lies in understanding and manipulating synthetic communities of exotic and native species.

The relationship between exotic invasions, exogenous disturbances (human-induced) and loss of native species is widely recognized in Australia (1). In field situations, it can be difficult to differentiate the direct effects of disturbances on native species from the competitive effects of exotic invasions, as well as the interactions arising from these two factors. Despite this, field observations give us direct information on the nature of exotic invasions and at least correlative evidence of the relationship between invasion, disturbance and persistence of native plants.

There is disagreement regarding the impact of exotics, with some arguing that the displacement of natives by exotics is reduced by virtue of their use of unoccupied niches. However, Herbold and Moyle (4) have argued convincingly that undisturbed communities are not invaded without disturbance or without displacement of native species in undisturbed communities. In the case of herbaceous vegetation in Australia, even after disturbance, native species would eventually recolonize in the absence of exotic propagules and it would be difficult to argue that exotics have no direct impact on native communities, given the space they occupy. Nonetheless, the relative impacts of different exotics may vary. The inevitable presence of exotics in some vegetation types makes it worthwhile considering how species may differ in the the impact they can have on native communities and whether there are some that should be targetted for control under particular circumstances. With these questions in mind, this paper compares the exotic component of species poor and species rich herbaceous vegetation and asks whether particular exotic species, life-histories or life-forms are associated with low or high species richness?

METHODS

A survey of herbaceous vegetation was conducted in grassy ecosystems on the New England Tablelands of New South Wales during 1990-91. The vegetation sampled had been subjected to varying degrees of modification resulting from exogenous disturbances, mainly grazing, soil disturbance (mostly from earth-moving equipment), water enrichment (sites receiving extra runoff resulting from human-modified drainage) and (although not measured) nutrient enrichment. Details of methods and a full species list are presented in McIntyre *et al.* (6). Of the 120 quadrats originally sampled (one 6x5 m quadrat per site), a subset of 60 ungrazed sites was taken to examine the relationship between richness of native species and exotic invasions. Due to the complexity of vegetation response to stock grazing and the interactions that are likely to occur between grazing and other disturbances, the 60 sites that had physical evidence of grazing at the time of sampling, were excluded from the current analysis.

The sample was divided into two groups of 30 sites; a <u>low richness group</u>, with below-average richness and a <u>high richness group</u> with above-average richness of native species. The average richness of the sample was 19.9 native species. Two simple measurements of floristic abundance were used: <u>frequency (or counts)</u> of species or groups of related species derived from presence/absence data collected for all species in the quadrats; <u>dominance</u> was recorded for all species that had a projected canopy cover of >10%. Although this cover rating is well below what might be considered true dominance, there was an average of only 1.6 dominant species per quadrat, and the majority of species had very low percentage cover. Each taxon was classified into an additional two categories: annual or perennial <u>life-history</u> and forb or grass <u>life-form</u>. These traits were compared over the two richness groups.

RESULTS AND DISCUSSION

The low richness group occurred in habitats with a greater frequency of soil disturbance and water enrichment (Table 1). Significant losses of native species and increases of exotics with these disturbances have been confirmed statistically for the entire data set (7). Low richness was also associated with either thick litter or >5% bare ground while high richness sites tended to have thin litter cover (Table 1). These proportions varied significantly ($\chi 2= 8.3$, d.f.= 3, $p<0.05$). The dominance of chalk grassland vegetation by perennial grasses, and their ability to suppress smaller statured, interstitial species through litter accumulation has been described by Grubb (3). A similar situation appears to occur in New England where *Poa* spp. and *Themeda australis* are the most common dominants (6). The bare ground at low richness sites was most commonly due to disturbances whereas it appeared more frequently to be due to constrained production at the high richness sites.

The two groups had similar numbers of dominants overall, although low richness sites had a greater proportion of exotic dominants and high richness sites had more native dominants. The same trends were evident in the number of non-dominant exotics (Table 2).

Perennial grasses were the most common dominants overall, although amongst exotics, annual grasses and perennial forbs were also well represented (Table 3). At high richness sites, all the dominant perennial grasses were native, while at low richness sites there were similar numbers of records of native and exotic dominant perennial grasses. Thus perennial native grasses may also be capable of reducing richness of interstitial plants in some cases. There were only four low richness sites that were dominated only by natives. Of these, none appeared to be soil disturbed, two had water enrichment and three had litter >5 cm deep. In contrast, the presence of dominant exotic plants was never associated with high native richness, except in the case of annual grasses.

Table 1. Comparison of sites with above- and below-average species richness (30 m^{-2}). Numbers of sites in each of three soil disturbances classes and two water enrichment classes are given.

Richness of native species	Soil disturbance			Water enrichment		Average number of non-dominant exotic species			
	Low	Mod.	High	No	Yes	>5% bare	<1	1-5	>5
Low (mean = 12)	5	4	21	17	13	13	1	3	13
High mean = 28)	22	7	1	28	2	9	2	12	7

Table 2. Average number of exotic and native dominant (cover >10%) taxa and exotic non-dominant taxa recorded in 30 m^{-2} plots at sites of low and high native species richness.

	Average number of dominants			Average number of non-dominant exotic species
	Exotic	Native	Total	
Low richness (n=30 sites)	0.97	0.70	1.67	8.0
High richness (n=30 sites)	0.13	1.37	1.50	4.3

Table 3. Distribution of species records across life-history categories

Life history	Native dominants		Exotic dominants		Non-dominant exotics	
	Richness		Richness		Richness	
	Low	High	Low	High	Low	High
Perennial grass	16	32	12	0	36	13
Annual grass	0	0	8	4	47	18
Perennial forb	5	7	7	0	99	61
Annual forb	0	0	2	0	56	35
Other	0	2	0	0	2	1
Total	21	41	29	4	240	128

Records of non-dominant exotics were much more frequently associated with high native richness (Table 3), with 35% of all records being at high richness sites compared with 12% of dominants. Species from all life-history categories were found to occur both as dominants and non-dominants in the plots.

Table 4 lists the ten most frequently occurring exotic taxa. They represent a range of life-histories, but all show one of two patterns of occurrence: 1) Tolerant species - these had similar frequencies at sites of low and high richness and tended to be non-dominant, perennial or annual forbs (although *Hypochoeris* spp. and *Trifolium arvense* each dominated at one low richness site); 2) Disturbance specialists - these had a higher frequency at sites of low richness (disturbed) sites and could achieve dominance at sites of low richness (with the exception of *Vulpia* spp. which also dominated at two high richness sites). Dominance was distributed over a number of taxa. Apart from the native grasses *Poa* spp. and *Themeda australis*, with 25 and 12 dominance records respectively, only *Plantago lanceolata* was dominant at more than 4 of the 60 sites.

Table 4. Ten most frequently recorded exotic taxa, distribution of their records over sites of high and low species richness and occurrence as dominant (>10% cover) or non-dominant components of the vegetation. Where more than one species is listed, the first-named is the most frequently occurring, although not all records could be separated. a = annual, p = perennial , g= grass, f = forb

Species/ species group	Low richness		High richness		Total records	Life history
	Dominant	Non-dominant	Dominant	Non-dominant		
Hypochoeris radicata/H. glabra	1	20	0	24	45	pf/af
Plantago lanceolata	5	20	0	7	32	pf
Vulpia bromoides/V. myuros/ V. muralis	2	11	2	5	20	ag
Trifolium arvense	1	9	0	8	18	af
Centaurium erythraea/C. tenuiflorum	0	7	0	11	18	af
Bromus racemosus/B. hordeaceus/ B. molliformis	2	12	0	3	17	ag
Trifolium repens	0	7	0	9	16	pf
Petrorhagia velutina	0	9	0	6	15	af
Paspalum dilatatum	1	10	0	3	14	pg
Conyza albida	0	7	0	6	13	pf

Without finer records of abundance, it is not possible to know the extent to which tolerant species might increase their cover at sites of low richness and thus contribute to reductions in total native richness. Previous analyses of the entire survey data set (7) showed a significant negative correlation both between numbers of native species and disturbances as well as between numbers of native species and numbers of exotic species (once the effects of disturbances were removed). Thus even non-dominant exotics may displace natives through their direct presence. Nonetheless, the data and observational evidence suggest that disturbance specialists may contribute even more to the reduction in rare species by increasing their cover in response to disturbance. Perennial exotic grasses are of particular significance in this regard; the six sites of lowest richness (native species <8) were all dominated by exotic perennial grasses, had high levels of soil disturbance and all had a litter layer >5 cm deep. Thus under conditions of disturbance, exotic perennial grasses may be capable of permanently displacing native species, while smaller-statured exotic forbs such a *Centaurium* spp. and *Petrorhagia velutina* may have only a minor competitive effect.

The following events and mechanisms are likely to operate in the process leading to loss of native species richness in herbaceous vegetation and are consistent with our observations:

a) some exotic species are able to invade natural vegetation without gross levels of exogenous disturbance;
b) physical disturbances destroy populations of native and exotic plants; disturbances encourage establishment and dominance by exotics, both newly-introduced and occurring at the site;
c) pre-emptive occupation of sites by exotics, reduces post-disturbance recolonization by natives which are often slower (lower seed production, slower growth rates);
d) site enrichment (nutrients, water) can lead to competitive exclusion of less responsive species (often native) by more responsive species (often exotic);
e) in the absence of further disturbance, perennial grasses may accumulate litter and suppress smaller statured interstitial species; this may occur in native communities dominated by perennial grasses in the absence of fire or intermittent grazing or mowing.

The effects of soil disturbance, enrichment, invasion by exotic perennial grasses followed by a period of low disturbance may lead to the greatest reduction in native species richness and be effectively permanent. It is suggested that in cases of unavoidable disturbance, selective control of exotic perennial grasses may be a useful strategy where limited resources are available for conservation management. Although more detailed observations are needed to fully describe the impacts of exotics on native richness, differential effects that relate to plant morphology are indicated by the data and by theory (2,3).

ACKNOWLEDGEMENTS

This work was funded by the Australian Research Council (large grant and Fellowship) at the University of New England, Armidale NSW, Australia.

REFERENCES

1. Fox, M.D. and Fox, B.J. 1986. In: Ecology of Biological Invasions. (Eds. R.H. Groves and J.J. Burdon) (Australian Academy of Science: Canberra). pp 57-66.
2. Grime, J.P. 1979. Plant Strategies and Vegetation Processes. (Wiley: Chichester).
3. Grubb, P.J. 1986. In: Community Ecology. (Eds. J.M. Diamond and T.J. Case) (Harper and Row: New York). pp 207-225.
4. Herbold, B. and Moyle, P.B. 1986. Am. Nat. 128, 761-764.
5. Leigh, J., Boden, R. and Briggs, J. 1984. Extinct and endangered Plants in Australia. (Macmillan: Melbourne).
6. McIntyre, S., Huang, Z. and Smith, A.P. 1993. Aust. J. Bot. 41(1), in press.
7. McIntyre, S. and Lavorel, S. Predicting richness of native, rare and exotic plants in response to habitat variables across a variegated landscape (mscr).