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Vegetation dynamics following resource manipulations in herb-rich woodland

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Abstract Changes in species richness, turnover, composition and above-ground biomass of herb-rich woodland were documented following fertilizer application and water addition over three growing seasons. Addition of fertilizer significantly reduced species richness relative to unmanipulated control and water addition plots after 3 years. This change coincided with significant increases in biomass, which were largely due to increased growth of exotic annual grasses. The reductions in richness observed in the fertilized plots were a consequence of both lower rates of local colonization and enhanced rates of local extinction of the resident species. Species loss was not random; native species were lost after nutrient addition whereas exotic species were not. Nutrient limitation was more important for species coexistence in these communities than was water availability.

Keywords Community dynamics · Exotic species · Nutrient addition · Species richness · Species turnover

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Introduction

Resource availability is one of the important drivers of vegetation patterns at landscape and local scales and has often been manipulated to examine its role on patterns of species richness at small scales. Nutrient addition has been shown to increase above-ground biomass in a variety of ecosystems and is commonly associated with declines in local species richness (Tilman 1984, 1987; DiTommaso and Aarrsen 1989; Willems et al. 1993; Gough et al. 2000; Rajaniemi 2003). Nutrient addition has also been associated with changes in plant species composition and growth-forms (Heddle and Specht 1975; Tilman 1984, 1987; Bobbink 1991; Inouye and Tilman 1995; Willems et al. 1993; Bowman et al. 1993, 1995). Fewer studies have examined water as a limiting resource, or the interaction between different limiting resources (DiTommaso and Aarssen 1989), and clear patterns have not emerged.

The mechanism by which nutrient addition, in particular, causes a decline in species richness has been attributed to a variety of factors including an increase in total competition (Grime 1973), a shift from below-ground to above-ground competition (Wilson and Tilman 1991, 1993) and changes in dominant species or growth-forms (McMaster et al. 1982; Willems et al. 1993; Bowman et al. 1993, 1995). Most studies assume reductions in diversity are due to local extinction of species due to competitive exclusion (Grime 1973; Goldberg and Miller 1990). Importantly, Tilman (1993) found decreases in diversity in productive habitats were also due to lower rates of local colonization.

Water enrichment has been found to have a similar impact on species richness as nutrient addition by increasing productivity and competition (McIntyre and Lavorel 1994). However, increased water availability has also been shown to increase species richness (Stevens et al. 2005). Increases in biomass are often greatest when both nutrients and water are added (Kirchner 1977; Sharifi et al. 1988), although this has not consistently resulted in declines in species richness (Goldberg and Miller 1990). Anthropogenic disturbances have dramatically altered nutrient and water levels globally (McIntyre and Lavorel 1994; Vitousek et al. 1997); understanding mechanisms of community change following resource enrichment in a variety of ecosystems is therefore important for future management of biodiversity.

The current study examines the role of two resources, water and nutrients, on herb-rich woodland community dynamics such as species richness, species turnover, community composition, above-ground biomass and vegetation structure. The herb-rich woodlands studied in western Victoria are some of the most species-rich communities in temperate Australia at small spatial scales, with up to 45 species found in 1 m^2 (Lunt 1990) and are comparable to the species-rich chalk grasslands in Europe (Willems 1978). The communities are characterized by low nutrients and low productivity and it is hypothesized that this may influence local species richness. Additionally, water may be limiting in these communities on the coarse textured, well-drained sands. Water enrichment has been associated with declines in species richness in other Australian ecosystems (McIntyre and Lavorel 1994). These woodlands have been internationally recognized as botanically significant (Lunt 1990); however, mechanisms driving vegetation dynamics in these systems are unclear.

In this study, we explore the relationship between resource availability and vegetation dynamics by examining changes to herb-rich woodland vegetation over a 3-year-period following nutrient and water addition. We ask the following questions:

(1) Does species richness decline with resource addition?
(2) Are changes in species richness due to increases in local extinction or decreases in local colonization?
(3) What is the effect of nutrient addition, water addition, and a combination of the two, on above-ground biomass?
(4) Are increased resources associated with changes in species composition and growth-forms?

Methods

Study site

The study was conducted in a *Eucalyptus camaldulensis* herb-rich woodland located on a flat outwash plain at Langi Ghiran State Park, western Victoria, Australia (37°17′45″ S, 143°04′50″ E). Soils are coarse sandy loams above a weathered bedrock of Devonian granite and are of low fertility and water holding capacity (Lunt 1990). The climate is temperate with cool winters (mean minimum temperature of the coldest month (July) is 3°C) and warm summers (mean maximum temperature of the warmest month (February) is 27°C) (Bureau of Meteorology, Ararat Prison recording station, unpubl. data). The average annual rainfall is 602 mm with 73% of this falling between April and December and a mean monthly maximum of 70 mm in August and minimum of 33 mm in February. Rainfall over the duration of the experiment was generally below-average (around 440 mm), except in 2001 (the first year of floristic sampling but prior to applying treatments, when annual rainfall was 661 mm). The site has been grazed in the past by sheep and is currently grazed by introduced rabbits (*Oryctolagus cuniculus*) and grey kangaroos (*Macropus giganteus*) at moderate densities (Lunt 1990). The community is primarily herbaceous with woody plants accounting for 8% of the total flora (Lunt 1990); the vegetation was mostly perennial (61%, of which 20% were geophytes) and mostly native (80%).

Experimental design

The experiment consisted of two blocks, separated by 200 m, each containing 20, 1 m^2 plots with a 0.5 m buffer between each plot. Each block had five replicates for each of four randomly applied treatments: (1) unmanipulated control; (2) fertilizer added; (3) water added; (4) fertilizer and water added. A complete fertilizer was applied at the beginning of each growing season (April) from 2002 to 2004, at the rate of 15 g m^{-2} (as slow release granules, 16% Nitrogen, 10% Potassium, 4.4% Phosphorus). This amount was selected because it is in the range found to have an effect on productivity in a number of other systems (Gough et al. 2000). Water (4 l m^{-2}) was applied at 14–17 day intervals for the entire growing season (April–December) from 2002 to 2004 (total seasonal inputs of water were 64 mm water m^{-2}). The amount of water selected was observed to saturate the plots and therefore, was estimated to be at field capacity. The aim of adding water was to reduce water stress over the growing season by increasing growing season water inputs by 18%. For each 1 m^2 plot, a central area of 0.25 m^2 was used to document vegetation change following treatment with the remaining treated area used for soil and biomass extraction.

Floristic surveys were conducted annually for 4 years in austral spring. Year 1 was prior to treatment (2001) while years 2–4 document change following treatment. In each 0.25 m^2 quadrat, the presence of all vascular plant species was recorded. Vegetation cover was determined using the point quadrat method (Kent and Coker 1993) in 2004. The quadrat frame used for floristic analysis was placed over the plots and a pin was placed at the intervals of all the grid squares (16 points/0.25 m^2). Each species, and the number of contacts each species made with the pin, were recorded. Ground cover type (litter and bare ground) was also determined using this method. Vegetation structure was assessed by mean luxuriance (overlapping cover); this was measured as the number of contacts made with the pin for all species divided by the total number of points per plot (Kent and Coker 1993). Above-ground biomass was harvested in November (2003, 2004) at the time of peak standing crop. The harvested material was sorted into growth-forms (perennial graminoid, perennial forb, annual graminoid, annual forb), dried at 80°C for 48 h and weighed.

Yearly changes in species composition following treatment were expressed by measuring species turnover. Turnover is measured as the number of species gained or lost in a plot divided by the initial species richness of that plot, giving a proportion of species formerly present that were lost or gained. Turnover indices were calculated for each treatment plot in each successive year (2001–2004), based on the method of Milberg and Hanson (1994); values range from 0 (no turnover) to 1 (complete turnover). The mean number of local immigrations and local extinctions in each plot was also measured from 2003 to 2004.

Plant nomenclature follows Ross and Walsh (2003).

Data analysis

Statistical analyses were conducted using Systat version 10. We used two-factor repeated measures ANOVA to compare differences between treatments through time for the total species richness and above-ground biomass data (Quinn and Keough 2002). Compound symmetry was satisfied. For all other response variables (exotic and native species richness, turnover, species colonization and local extinction), we used two-factor ANOVA with fertilizer and water as factors. These were used rather than repeated measures ANOVA because significant changes were not detected until the final sampling period. We tested for block effects for all response variables and there were no significant interactions between blocks and treatments. We found occasional differences in effect size between the blocks; however, the blocks always responded the same way to the treatments so all blocking values have been combined in the charts and tables. ANOVA assumptions of normality and homogeneity of variances were satisfied.

Results

Effect of resource addition on species richness and turnover

Pre-treatment mean species richness did not differ significantly between treatments (fertilizer $F = 0.0$, $P = 1.0$; water $F = 1.1$, $P = 0.3$; Fig. 1). In 2002 and 2003, 1 and 2 years after treatment, fertilized plots significantly increased in mean species richness (2002; $F = 6.1$, $P = 0.02$; 2003: $F = 23.9$, $P < 0.01$). By 2004, 3 years after treatment, fertilized plots declined significantly ($F = 9.2$, $P < 0.01$) in mean species richness. The pattern of change in species richness across time for the fertilized treatments differed significantly (i.e. the time–treatment interaction was significant for all tests, $F = 19.5$, $P < 0.01$). There were no significant water and fertilizer interaction effects in any years.

There was a significant reduction in native species richness in fertilized plots ($F = 7.21$, $P = 0.01$) with a mean of 13±1 in fertilized plots compared to 16±1 in control plots after 3 years of treatment. There was no effect of water addition on native species richness ($F = 2.3$, $P = 0.14$). There was no significant difference in exotic species richness between fertilized ($F = 1.5$, $P = 0.23$) and water ($F = 0.06$, $P = 0.81$) treatments compared to control plots. There was no significant interaction between water and fertilizer treatments for exotic ($F = 0.04$, $P < 0.85$) or native species richness ($F = 0.08$, $P = 0.93$) after 3 years of treatment.

Species turnover did not differ significantly between treatments with annual turnover rates ranging from relatively high (ranging from 0.56 to 0.68 in 2001–2002) to moderate (0.38–0.42 in 2002–2003 and 0.42–0.44 in 2003–2004) (van der Maarel and Sykes 1993). However, a clear pattern emerged where significantly fewer new species were gained ($F = 20.8$, $P < 0.01$) and a greater number of existing species ($F = 24.78$, $P < 0.01$) were lost in fertilized plots than in unfertilized plots (Fig. 2). There was no significant interaction effect between the fertilizer and water treatments on immigrations ($F = 0.18$, $P = 0.67$) or extinctions ($F = 0.42$, $P = 0.52$).

Effect of resource addition on productivity and ground cover conditions

Total percent vegetation cover after 3 years of treatment was significantly higher in fertilized plots in comparison to unfertilized plots ($F = 75.7$, $P < 0.01$, Table 1). There was no significant effect of water addition on total vegetation cover ($F = 0.28$, $P = 0.6$). There was also no significant interaction effect of the water and fertilizer treatments ($F = 0.69$, $P = 0.4$). Mean luxuriance (overlapping cover) was also significantly higher in fertilized plots ($F = 88.8$, $P < 0.01$), indicating a structural change in the

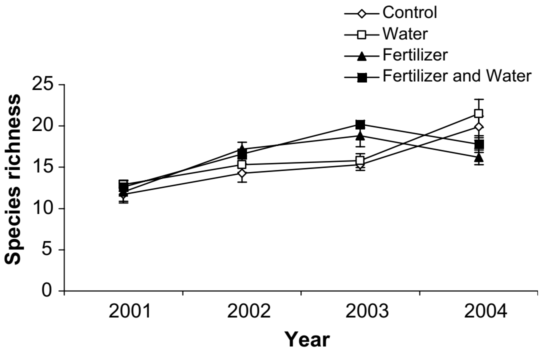

Fig. 1 Mean (±1 SE) species richness per 0.25 m^2 in each of the treatments over 4 years. 2001 data was collected before treatments were first applied in autumn 2002. Significant differences were found between treatments in 2002, 2003 and 2004 ($P < 0.05$)

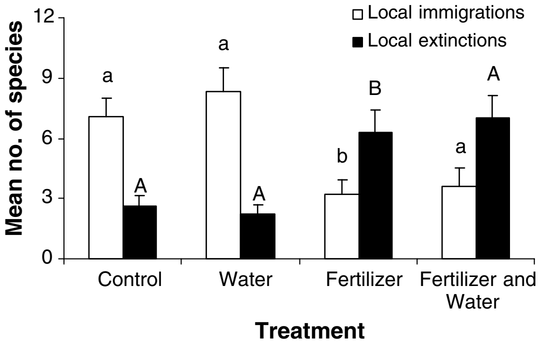

Fig. 2 Mean (±1 SE) number of local immigrations and local extinctions in permanent plots from 2003 to 2004 in each of the four treatments. Treatments not significantly different from the control have the same letter

Table 1 Mean values (±1 SE) for the point quadrat data within each treatment in 2004

	Control	Water	Fertilizer	Fertilizer and water
Total % cover	53±6	47±5	**86±6**	87±4
Mean luxuriance	1.5±0.1	1.5±0.1	**4.3±0.4**	3.5±0.4
Percent frequency				
**Aira* spp.	22±5	18±3	**78±6**	76±7
Austrodanthonia setacea	2±1	1.2±1	6±4	6±2
Ground cover				
Litter	23±9	9±4	**70±14**	67±11
Bare ground	44±8	59±12	**4±3**	12±6

Treatments significantly different from the control are in bold. Percent frequency has been presented for the dominant exotic annual grass (*Aira* spp.) and the dominant native grass (*Austrodanthonia setacea*)

vegetation, with an increase in leaf density per volume of canopy in fertilized plots.

There was a significant difference in above-ground biomass of fertilized plots after 2 years (in 2003; $F = 8.2$, $P = 0.01$, Fig. 3). By 3 years of treatment (2004), there was a highly significant increase in above-ground biomass in fertilized plots ($F = 30.1$, $P < 0.01$, Fig. 3). Yield on the fertilized plots exceeded that of the control and water addition plots by a factor of three. The pattern of change in biomass across time differed significantly in fertilized plots (i.e. the time × fertilizer interaction was significant, $F = 13.8$, $P < 0.01$). Ground cover conditions were significantly different between treatments with an increase in litter cover ($F = 33.7$, $P < 0.01$) and a decrease in bare ground ($F = 37.4$, $P < 0.01$) in fertilized plots.

Effect of resource addition on species composition

The distribution of biomass across growth-form categories differed between treatments with significantly increased biomass of annual graminoids in fertilized plots ($F = 11.2$, $P < 0.01$, Fig. 4). This change in dominance was mostly due to an increase in the cover of the exotic annual grass, *Aira* spp. (Table 1). In control plots, no one species dominated, with *Austrodanthonia setacea* a common native species with comparatively little cover (Table 1).

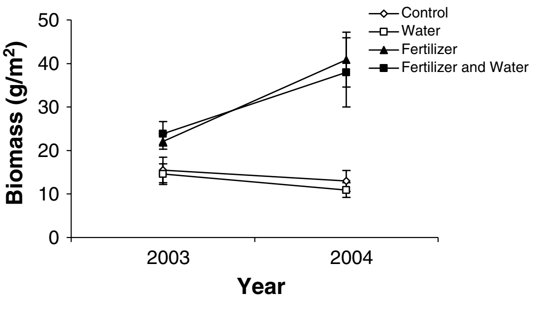

Fig. 3 Mean (±1 SE) above-ground biomass in each of the treatments in 2003 and 2004

Discussion

Key findings

Addition of fertilizer significantly reduced species richness in herb-rich woodland vegetation after three growing seasons, consistent with numerous studies on the effects of fertilizer on grassland vegetation (Tilman 1984, 1987; DiTommaso and Aarrsen 1989; Willems et al. 1993; Gough et al. 2000). After 3 years of treatment, the reduction in species richness coincided with a significant

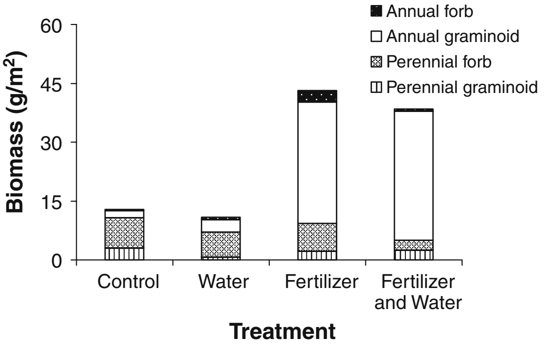

Fig. 4 Mean (±1 SE) above-ground biomass (g m^{-2}) in each of the growth-form categories for the four treatments for 2004

increase in above-ground biomass in fertilized plots. A shift in dominance to exotic annual grasses was also observed. Reductions in species richness were due to decreases in local colonization as well as increases in local extinction. Vegetation dynamics were slow to respond to experimental manipulations with no significant changes detected until 2–3 years after treatment.

The effect of fertilizer addition on species richness and turnover

The dynamics of the community were defined by moderate to high rates of species turnover in all treatments which may contribute to local species coexistence (Lunt 1990). There are many explanations for turnover (e.g. gap formation and short life-spans). However, given that annual variation in these systems includes large changes in rainfall, climate variability is likely to have influenced turnover in the current study. Communities were characterized by high inter-annual variability in species richness patterns and, although fertilized plots did diverge from unfertilized plots, it is unknown if the observed changes will continue with further resource manipulation.

Initially, we observed an increase in richness in fertilized plots. After 3 years of nutrient application significant declines in richness occurred, corresponding to the period of significant increases in biomass. Tilman (1993) found increases in richness after fertilization were transient and seemed to have resulted from nitrogen-dependent germination of seed banking species. Grime's (2001) 'humped back' model suggests that at very low levels of biomass, richness is limited by the number of species capable of surviving the severity of the stress or disturbance, found in these habitats. At moderate or high levels of biomass species richness is limited by competitive exclusion by dominants which may have occurred following fertilization in the current study.

The slow change is also likely to be a response to the feedback effects of fertilizer application after numerous growing seasons. Litter accumulation is expected to have important feedback effects, with increased litter deposition adding to nutrient availability in fertilized plots as well as affecting soil moisture (Weaver and Roland 1952; Chapin et al. 1979; Orndorff and Lang 1981; Shure and Gottschalk 1985; Fowler 1986). In fact, Milchunas and Lauenroth (1995) found that long-term changes in nitrogen and water addition plots years after treatments were applied were likely due to feedback effects of litter.

Reductions in richness were partly due to inhibition of germination and establishment by new species. The results suggest an important structural change with increased leaf density in fertilized plots which is likely to reduce light penetration and may reduce germination and establishment (Wilson and Tilman 1991, 1993). Reductions in local colonization in fertilized plots may also be due to increased litter accumulation (Tilman 1993; Foster and Gross 1998). The increased biomass in fertilized plots in this study was observed to trap litter, altering the microsite dynamics of this system in which litter plays an important role in germination and establishment (Price and Morgan unpubl. data). Increased litter may have been as important as increased biomass in reducing species richness in fertilized plots due to reduced light penetration and mechanical impediment to germination (Grime 2001; Sydes and Grime 1981; Carson and Peterson 1990; Facelli and Pickett 1991; Tilman 1993; Facelli 1994; Foster and Gross 1998; Wilsey and Polley 2003).

Increased local extinctions in fertilized plots may result from competitive exclusion of existing species due to the observed changes in dominance and vegetation cover (Grime 1973; Aerts et al. 1991; Wilson and Tilman 1991, 1993). Species loss, however, does not appear to be random; native species were those most frequently lost after fertilization. The effects of competition were not examined directly in this study and it is unclear whether native species were out-competed or simply did not tolerate increases in resource availability. The increase in productivity in fertilized plots was largely due to increased growth of exotic annual grasses such as *Aira* spp. Hence, there has been a shift in dominance in fertilized plots to annual grasses which may have resulted in competitive exclusion of native forbs (Bobbink 1991). Species that are adapted to low nutrient environments lack the capacity to increase growth with increased resources (Chapin et al. 1986) and this may play a role in the current study.

Composition changes following resource addition

Changes in species composition were observed in fertilized plots 3 years after treatment with shift in dominance to exotic annual grasses. Numerous studies have reported changes in species composition following fertilizer application (Heddle and Specht 1975; Shaver and Chapin 1980) due to differential species responses to resource additions which in turn, affect competitive relationships and lead to shifts in abundance and species diversity. Nutrient addition in this study was not associated with exotic invasions, as has been found elsewhere (Carson and Barrett 1988; Huenneke et al. 1990; Hobbs and Huenneke 1992; Ostertag and Verville 2002). Rather, increased resources were associated with increased biomass and cover of exotics that already occur in the flora. Exotic invasion is likely to be influenced by other factors such as the species pool, propagule availability and dispersal. The study plots were surrounded by high quality vegetation (Lunt 1990) and this is also likely to have slowed the rate of non-native invasion.

The effect of water addition on species richness, composition and productivity

Water addition had no significant effect on species richness and composition or biomass production. Rainfall data for the duration of the experiment indicates annual rainfall was below-average and hence, the water applied may have been too little to increase biomass production, as additions did not increase water inputs above the range which the community normally receives. However, given that water inputs were increased by 18% and no differences were detected, it is possible that water is not limiting in these communities. Water addition has been found to increase productivity but not decrease species richness due to the timing of resource limitation, i.e. water is likely to be limiting later in the growing season and therefore, does not lead to early canopy closure as in nutrient addition (Goldberg and Miller 1990). This may be important in the current study in which rainfall is seasonal and hence, water may not be limiting in these communities over the growing season. The community consists of many species which are summer drought adapted and survive the unfavourable season by dying back to underground tubers as well as many annual and short lived species (Lunt 1990). Water addition treatments may also have had no effect due to the regularity of the treatment. Rainfall manipulation experiments suggest that it is the interval between rainfall events, rather than the quantity of water, that drives grassland ecosystems (Fay et al. 2000, 2003). Increased water inputs in the current study may therefore have had no effect on productivity because the inter-rainfall period may not have been reduced.

Summary

The declines in species richness following 3 years of fertilizer addition resulted from decreases in local colonization and increased rates of local extinction. These changes may be due to the increase in biomass of exotic annual grasses and increased litter accumulation. Nutrient limitation is an important mechanism for species coexistence in these communities as increased resources result in reductions in species richness. This has implications for the management of this significant community as factors leading to changes in resource availability are likely to affect community dynamics, composition and richness.

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