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Post-fire vegetation dynamics in nutrient-enriched and non-enriched sclerophyll woodland

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Abstract Exotic plant invasions are a significant problem in urban bushland in Sydney, Australia. In low-nutrient Hawkesbury Sandstone communities, invasive plants are often associated with urban run-off and subsequent increases in soil nutrients, particularly phosphorus. Fire is an important aspect of community dynamics in Sydney vegetation, and is sometimes used in bush regeneration projects as a tool for weed control. This study addressed the question: 'Are there differences in post-fire resprouting and germination of native and exotic species in nutrient-enriched communities, compared with communities not disturbed by nutrient enrichment?' We found that in non-enriched areas, few exotic species emerged, and those that did were unable to achieve the rapid growth that was seen in exotic plants in the nutrient-enriched areas. Therefore, fire did not promote the invasion of exotic plants into areas that were not nutrient-enriched. In nutrient-enriched areas after fire, the diversity of native species was lower than in the non-enriched areas. Some native species were able to survive and compete with the exotic species in terms of abundance, per cent cover and plant height. However, these successful species were a different suite of natives to those commonly found in the non-enriched areas. We suggest that although fire can be a useful tool for short-term removal of exotic plant biomass from nutrient-enriched areas, it does not promote establishment of native species that were not already present.

Key words: ecological restoration, Hawkesbury Sandstone soil, nutrient enrichment, phosphorus, weed invasion.

INTRODUCTION

Invasion of natural and seminatural areas by exotic plants is regarded as a serious threat to native diversity (Lodge 1993; Adair & Groves 1998) and restoration of ecosystems has become an important priority globally (Hobbs & Harris 2001). Many disturbance factors are thought to be associated with successful invasion of communities by exotic plants, including physical disturbance, changes to fire and grazing regimes and resource enrichment (D'Antonio *et al.* 1999). In this study we examine vegetation dynamics in response to the combination of two factors, nutrient enrichment and fire, in fire-adapted sclerophyll vegetation of the Sydney region.

Fire is historically an important aspect of community dynamics in Australian vegetation (Whelan 1995) and is a common source of temporal and spatial change in plant species composition. For example, in sandstone communities in Sydney, Australia, fire intensity or frequency accounts for about 10–20% of the floristic variation (Bradstock *et al.* 1997; McLoughlin 1998; Morrison 2002). Fire can alter natural ecosystems by changing the soil structure and increasing soil nutrients (including nitrogen and phosphorus), volatilizing allelochemicals, removing the litter layer and increasing the light intensity at ground level (Humphries & Craig 1981; Grove *et al.* 1986; Hobbs & Huenneke 1992; Buchanan 1994; Tyler 1996; Duggin & Gentle 1998). Additionally, fire can stimulate seed germination, remove competitors and natural enemies and alter the microbial and invertebrate communities (Buchanan 1994; Tyler 1996).

Since the arrival of Europeans, fire regimes across the continent have altered significantly (Gill 1975; Ward *et al.* 1998). Changes to fire regimes are frequently cited as important factors facilitating plant invasion (Hester & Hobbs 1992; Sher & Hyatt 1999). Fire has been found to be associated with exotic plant invasion of arid and semiarid communities (D'Antonio *et al.* 1999), oceanic islands such as Hawaii (Hughes *et al.* 1991) and South African fynbos (Richardson & Bond 1991). Many exotic species have physiological attributes that allow them to survive, regenerate and compete favourably after disturbances such as fire (Christensen & Burrows 1986). Once exotic species are established in an area, they may alter the subsequent fire regime to their advantage (Hughes *et al.* 1991; D'Antonio *et al.* 2000).

However, fire and vegetation have a long association on the Australian continent, and native plants have evolved traits that enable them to survive and reproduce in fire-prone environments (Christensen &

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Burrows 1986). As such, fire may not increase the susceptibility of Australian plant communities to invasion. Indeed, for communities with a long history of fire there is little evidence for the role of fire in facilitating invasion (D'Antonio *et al.* 1999), with the exception of pine invasion in fynbos (Richardson & Bond 1991). Rather, the reverse may be true, in that many native species in fire-adapted systems respond positively to fire while exotic species are suppressed (Hester & Hobbs 1992). Furthermore, the prevention of fire can itself be seen as a disturbance, as this can cause a decline in species diversity, a shift in composition towards more mesic species, and a consequent shift towards moister conditions, which favour exotic species (Fox & Fox 1986; Benson & Howell 1990; McLoughlin 1997).

Fire is often used in Australia as a tool in restoration of degraded vegetation communities (Buchanan 1989). The use of fire is thought to have two main advantages. First, it can very rapidly remove aboveground weedy biomass from a degraded area, allowing easy access and reducing manual labour. Second, fire is thought to promote the germination and establishment of many native species in disturbed habitats that were originally present in the vegetation before disturbance but are no longer found above-ground (McLoughlin 1997).

Sydney is fortunate to have substantial areas of bushland that provide valuable aesthetic, recreational and educational opportunities, as well as habitat for native flora and fauna (Benson & Howell 1990; Howell & Benson 2000). However, natural vegetation in the Sydney region has undergone a significant change as a result of human activities (Clements 1983; Rose & Fairweather 1997). Much of Sydney's remnant bushland is located on Hawkesbury Sandstone-derived soils, which are characterized as shallow, well drained and depauperate in nutrients. For these sandstone communities, increased suburb age is associated with an increased proportion of exotic species, a decreased proportion of native species, and an increase in mesic, fire-sensitive, shade-tolerant species (Clements 1983; Rose & Fairweather 1997).

Much of the change in vegetation composition of urban bushland remnants is associated with changes in the nutrient status of the soil. For example, areas receiving stormwater run-off can have total phosphorus levels up to 900 mg kg^{-1}, compared with typical background levels of 40–100 mg kg^{-1} (Clements 1983; Leishman 1990; Leishman *et al.* 2004). The addition of phosphorus and other nutrients to the soil facilitates exotic plant invasion, with the relationship between suburban development, soil phosphorus levels and plant invasion being well established for Hawkesbury Sandstone soils (Clements 1983; Lambert & Turner 1987; Riley & Banks 1996; King & Buckney 2002; Lake & Leishman 2004; Leishman *et al.* 2004).

The aim of this study was to compare the post-fire regeneration potential of native and exotic plant species in nutrient-enriched compared with non-enriched communities, for Hawkesbury Sandstone vegetation in the Sydney region.

Specifically, we addressed the following questions:

1. Are there differences in germination and establishment success of exotic and native species after fire, in both nutrient-enriched and non-enriched habitats?
2. Are there differences in growth rates between exotic and native species after fire in both nutrient-enriched and non-enriched habitats?
3. Are there differences in the ability to resprout after fire between native and exotic species?
4. Are any exotic species promoted or suppressed by fire?

METHODS

Study sites

Three sites were chosen for the study, located within the Lane Cove Valley in the northern suburbs of Sydney, Australia, on low-fertility Hawkesbury Sandstone-derived soil. The sites were located at West Pymble, Wahroonga and Pennant Hills. All sites were burnt in early January 2002 by either a wildfire (West Pymble site) or a hazard-reduction control burn (Wahroonga and Pennant Hills sites). The sites were near residential development, and contained both an area enriched by nutrients from a stormwater outlet or a stormwater-affected creek and an adjacent non-enriched area. At all sites the nutrient-enriched and non-enriched areas were within 200 m of each other.

The nutrient-enriched areas of all sites were invaded by exotic plants before the fires occurred, and were undergoing bush regeneration by local bushcare groups. The West Pymble and Wahroonga sites were both disturbed by stormwater run-off from the surrounding suburbs, and were similar in both exotic species composition and the native species composition of the undisturbed area. The most common pre-fire exotic species at West Pymble included *Rubus fruticosus*, *Solanum nigrum*, *Solanum mauritianum*, *Phytolacca octandra*, *Sida rhombifolia* and *Verbena bonariensis*. Bush regeneration in this area had been practised for over 6 years, and much of the weedy biomass had been removed before the fire (A. Ashhurst, pers. comm.; bushcare co-ordinator, February 2003). The most common pre-fire exotic species at Wahroonga included *Acetosa sagittata, Cardiospermum grandiflorum, Lantana camara, Ligustrum lucidum, Ligustrum sinense* and *R. fruticosus*. Approximately half of the weedy biomass had been cleared in pre-fire bush regeneration work done at this site (N. Lock, pers. comm.; bushcare co-ordinator, February 2003). The Pennant Hills site was located on slightly richer soil, and had a different native species composition in the undisturbed area. The nutrient-enriched area was disturbed by a creek that receives run-off from the surrounding suburb, and had additional nutrient input from an adjacent sporting ground. Exotic species including *Ochna serrulata*, *Li. sinense*, *Li. lucidum*, *Lonicera japonica*, *L. camara* and *Tradescantia fluminensis* had been mostly removed pre-fire (R. Leslie, pers. comm.; bushcare co-ordinator, February 2003).

Vegetation sampling

Within each site, we mapped out a 20 m × 20 m area near the stormwater outlet or creek, which was invaded by exotic plants before the fire (hereafter referred to as 'nutrient-enriched plot'). We also mapped an equivalent sized area within 200 m of each nutrient-enriched plot that was not affected by stormwater run-off and contained few exotic plants before the fire (hereafter referred to as 'non-enriched plot'). As far as possible, we matched the nutrient-enriched and non-enriched plots in each site for physical characteristics such as aspect and slope. Within each plot, we randomly placed five 1 m × 1 m quadrats. The vegetation in each quadrat was sampled approximately 6 weeks after the fire (West Pymble and Wahroonga only), and the survey was repeated 9, 12, 16 and 20 weeks after the fire for all sites and at 42 weeks for two sites. The West Pymble site had been treated with glyphosate by the local bushcare group and could not be resampled.

To verify that there was a difference in soil fertility between our nutrient-enriched and non-enriched plots, a soil core sample to a depth of 10 cm was taken from just outside each quadrat at 9 weeks after fire. Samples were bulked for each plot, air-dried and sieved to 2 mm, and analysed for total phosphorus using the hydrochloric acid digestion method (Murphy & Riley 1962).

Each plant within the quadrat was identified to at least family level, and in most cases, to genus or species. If a species could not be identified, it was given a morpho-species name so that the abundance and growth of the species through time could still be recorded. For each species, we counted the number of individuals within the quadrat, and measured the height (to nearest cm) of the tallest individual from base to meristem (dicots) or leaf tip (monocots). For plants that were resprouting at ground level, we recorded the number of stems in the quadrat, as it was impossible to count the number of individuals. We recorded a visual estimate of the per cent cover of the quadrat for each species. We also recorded the regeneration mode of the species (seed, vegetative resprout, or both) and whether the species was native to the Sydney region or exotic. At week 42, we only recorded presence and absence of species and the total per cent cover of each quadrat.

Data analysis

Before analysis, all variables were examined for homogeneity of variance and normality, and were log transformed to meet assumptions when necessary. The richness, density, average maximum height and average per cent cover of native and exotic plants were analysed using a repeated measures ANOVA. The repeated factor was the week of measurement, and each quadrat was considered a subject. The fixed factors included the plot (nutrient-enriched or non-enriched), site, week of measurement, and all three-way interactions. Analyses were performed using SPSS Version 11.0 (SPSS Inc., November 2001, Chicago, IL, USA).

RESULTS

The total phosphorus concentrations in the soil were consistently higher in the nutrient-enriched areas than in the non-enriched areas (Table 1).

There was a significant interaction between soil nutrient × site × week for native species richness ($P < 0.001$, Table 2). The three nutrient-enriched sites had consistently lower native species richness than the non-enriched sites following fire, however, there was variation among sites within soil nutrient status. Native species richness on the nutrient-enriched plots at the Pennant Hills site was higher than on the nutrient-enriched plots at the other sites and was comparable with the non-enriched plots at all sites (Fig. 1a). In the non-enriched and the Pennant Hills enriched plots, native species richness increased until week 20 but declined slightly at week 42.

There was also a significant interaction between soil nutrient × site × week for exotic species richness ($P < 0.001$, Table 2). Exotic species richness of the three non-enriched sites and the Pennant Hills enriched plots was much lower than for the enriched plots at the other two sites (Fig. 1b). Indeed, these

Table 1. Total phosphorus levels (mg kg^{-1}) for the nutrient-enriched areas and the non-enriched areas at each of the three sites

	Undisturbed area	Nutrient-enriched area
Pennant Hills	85	110
Wahroonga	67	370
West Pymble	53	270

Table 2. Results of repeated measures ANOVA for native species richness and exotic species richness. The factors were soil nutrient (enriched or non-enriched), site (West Pymble, Wahroonga and Pennant Hills) and week

	Factor	d.f.	*F*	*P*
Native species richness	Soil nutrient	1,23	51.1	<0.001
	Site	2,23	7.5	0.003
	Week	5,25	13.3	<0.001
	Soil nutrient × site	2,23	2.5	0.106
	Soil nutrient × week	5,25	12.2	<0.001
	Week × site	8,28	5.7	<0.001
	Soil nutrient × site × week	8,28	5.6	<0.001
Exotic species richness	Soil nutrient	1,25	146.6	<0.001
	Site	2,25	28.8	<0.001
	Week	5,30	28.7	<0.001
	Soil nutrient × site	2,25	39.6	<0.001
	Soil nutrient × week	5,30	15.4	<0.001
	Week × site	8,30	6.5	<0.001
	Soil nutrient × site × week	8,30	11.1	<0.001

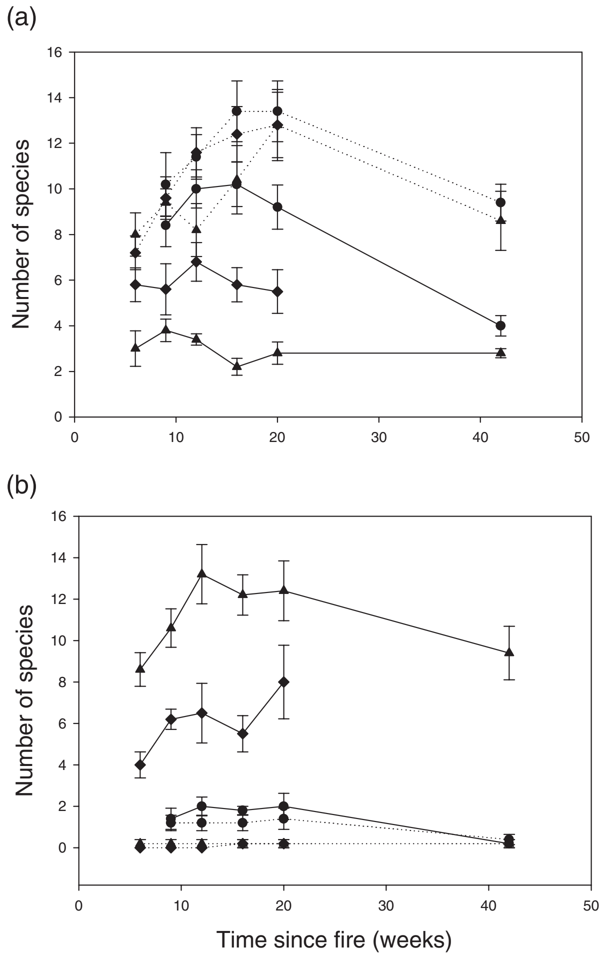

Fig. 1. Mean species richness per quadrat of (a) native plants and (b) exotic plants. Solid lines represent nutrient-enriched areas and dotted lines represent non-enriched areas. The symbols indicate the three sites: Pennant Hills; Wahroonga; West Pymble. Error bars represent standard error.

plots supported only a very low number of exotic species. Exotic species richness increased following fire until week 20 and then declined at week 42 for all plots (but note no data were available for week 42 at the West Pymble site). The overall reduction in species richness between 20 and 42 weeks following the fire may have been a result of the extremely dry conditions in Sydney at this time.

There was a significant interaction between soil nutrient × site × week for native plant density ($P = 0.001$, Table 3). As for species richness, this was mainly resulting from the differences between the Pennant Hills site and the other two sites. Non-enriched plots at all three sites showed increasing native plant density with time after fire (Fig. 2a). Nutrient-enriched plots at the Pennant Hills site had the highest native plant density, which increased with time after fire, while nutrient-enriched plots at the other two sites had the lowest native plant density, which stayed stable or declined slightly with time after fire.

For exotic plant density, there was a significant interaction between soil nutrient × site ($P < 0.001$, Table 3). Exotic plant density was very low for non-enriched plots at all three sites (Fig. 2b). There were however, differences among the three sites in native plant density of the nutrient-enriched plots, with the Pennant Hills site having much lower exotic plant density than the other two sites.

There were significant interactions between week × site ($P = 0.011$, Table 4) and week × soil nutrient ($P = 0.026$, Table 4) for per cent native cover. Per cent native cover on the nutrient-enriched plots at the West Pymble site was quite variable with time since fire (Fig. 3a) while the other sites generally showed a gradual increase in per cent cover with time. Non-enriched plots had a much higher per cent cover of native species than enriched plots at the Wahroonga

Table 3. Results of repeated measures ANOVA for native plant density and exotic plant density. The factors were soil nutrient (enriched or non-enriched), site (West Pymble, Wahroonga and Pennant Hills) and week

	Factor	d.f.	*F*	*P*
Native plant density	Soil nutrient	1,114	1.9	0.168
	Site	2,83	4.9	0.010
	Week	4,58	5.5	0.001
	Soil nutrient × site	2,83	1.4	0.253
	Soil nutrient × week	4,58	11.0	<0.001
	Week × site	7,58	3.0	0.009
	Soil nutrient × site × week	7,58	4.1	0.001
Exotic plant density	Soil nutrient	1,242	90.2	<0.001
	Site	2,141	3.1	0.046
	Week	4,71	1.4	0.242
	Soil nutrient × site	2,141	13.3	<0.001
	Soil nutrient × week	4,71	0.8	0.554
	Week × site	7,71	0.8	0.642
	Soil nutrient × site × week	7,71	1.3	0.251

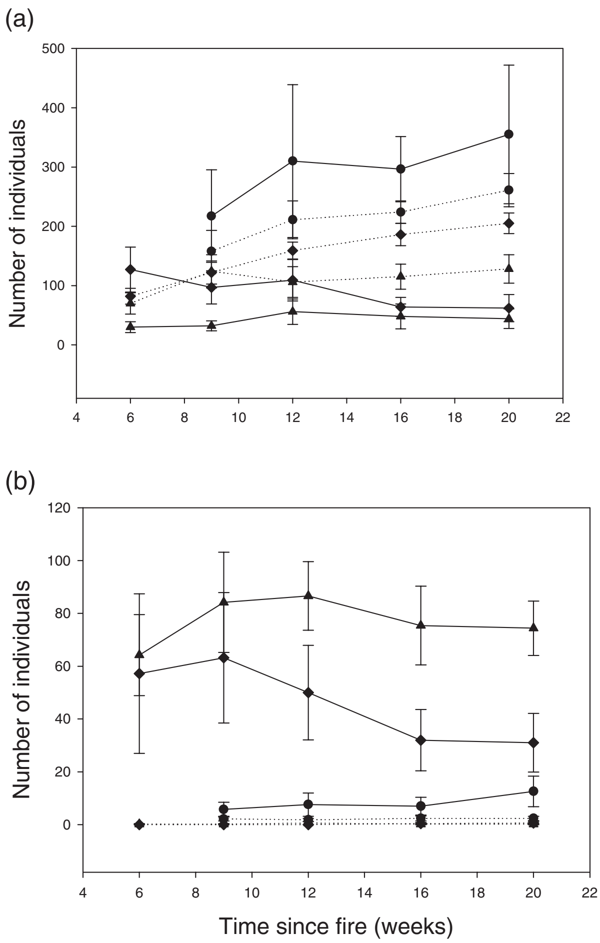

Fig. 2. Mean species density per quadrat of (a) native plants and (b) exotic plants. Solid lines represent nutrient-enriched areas and dotted lines represent non-enriched areas. The symbols indicate the three sites: Pennant Hills; Wahroonga; West Pymble. Error bars represent standard error.

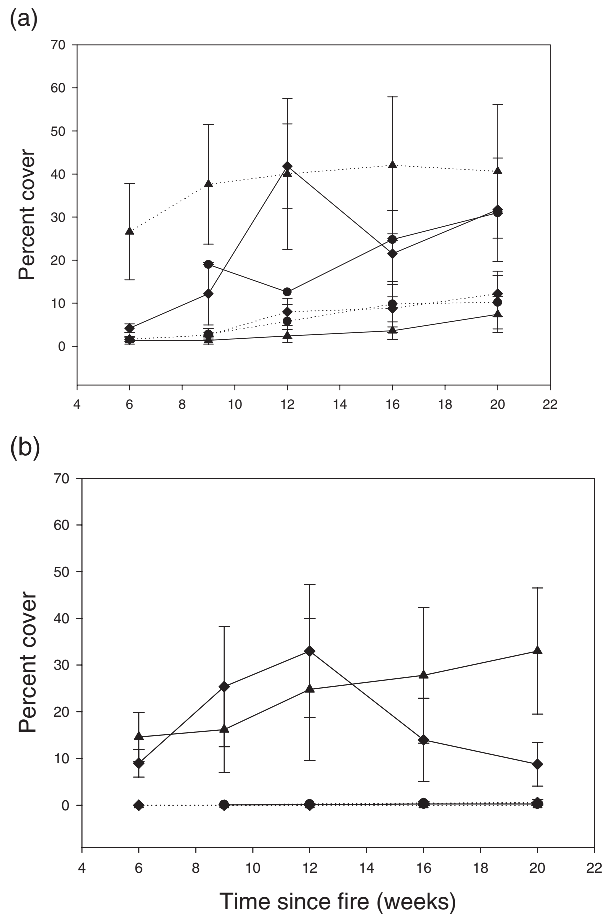

Fig. 3. Mean per cent cover per quadrat of (a) native plants and (b) exotic plants. Solid lines represent nutrient-enriched areas and dotted lines represent non-enriched areas. The symbols indicate the three sites: Pennant Hills; Wahroonga; West Pymble. Error bars represent standard error.

Table 4. Results of repeated measures ANOVA for native per cent cover and exotic per cent cover. The factors were soil nutrient (enriched or non-enriched), site (West Pymble, Wahroonga and Pennant Hills) and week

	Factor	d.f.	*F*	*P*
Native per cent cover	Soil nutrient	1,122	20.6	<0.001
	Site	2,82	5.2	0.007
	Week	4,76	2.1	0.096
	Soil nutrient × site	2,82	5.5	0.006
	Soil nutrient × week	4,76	2.9	0.026
	Week × site	7,76	2.8	0.011
	Soil nutrient × site × week	7,76	1.7	0.114
Exotic per cent cover	Soil nutrient	1,24	5.0	0.034
	Site	2,24	4.2	0.027
	Week	5,20	21.3	<0.001
	Soil nutrient × site	2,24	2.5	0.104
	Soil nutrient × week	5,20	1.4	0.254
	Week × site	8,26	4.3	0.002
	Soil nutrient × site × week	8,26	3.3	0.011

and Pymble sites, but the nutrient-enriched plots had higher per cent native cover than non-enriched plots at the Pennant Hills site (Fig. 3a).

For exotic plant cover there was a significant interaction between soil nutrient × site × week ($P = 0.011$, Table 4). Exotic plant cover was negligible and steady at non-enriched plots at all sites and at the enriched plots at the Pennant Hills site (Fig. 3b). Per cent exotic cover increased with time since fire on nutrient-enriched plots at the Wahroonga site and increased then decreased with time on the nutrient-enriched plots at the Pymble site.

There was significant interaction between soil nutrient × site × week ($P = 0.005$) for maximum height of native plants (Table 5). Native plant height generally increased with time after fire (Fig. 4a) but the rate of increase varied between sites. Native plant height was generally taller at the nutrient-enriched sites compared with the non-enriched sites. In contrast, maximum exotic height varied significantly with week ($P = 0.002$) and soil nutrient ($P < 0.001$) (Table 5). Maximum height of exotics increased with time since fire but was significantly less on the non-enriched sites compared with the nutrient-enriched sites (Fig. 4b).

Although it is clear that some native species were able to survive and grow after fire on the nutrient-enriched plots, the suite of species was very different to that of the non-enriched plots. Of the eight most common native species in non-enriched plots (Table 6), the only species that was also common in nutrient-enriched plots was *Entolasia stricta*, a native grass that is widespread on sandstone soils. The other common natives in the nutrient-enriched plots (Table 6) were species that are usually found on higher nutrient soils.

More native species were able to resprout after fire than exotic species. There was a significant interaction

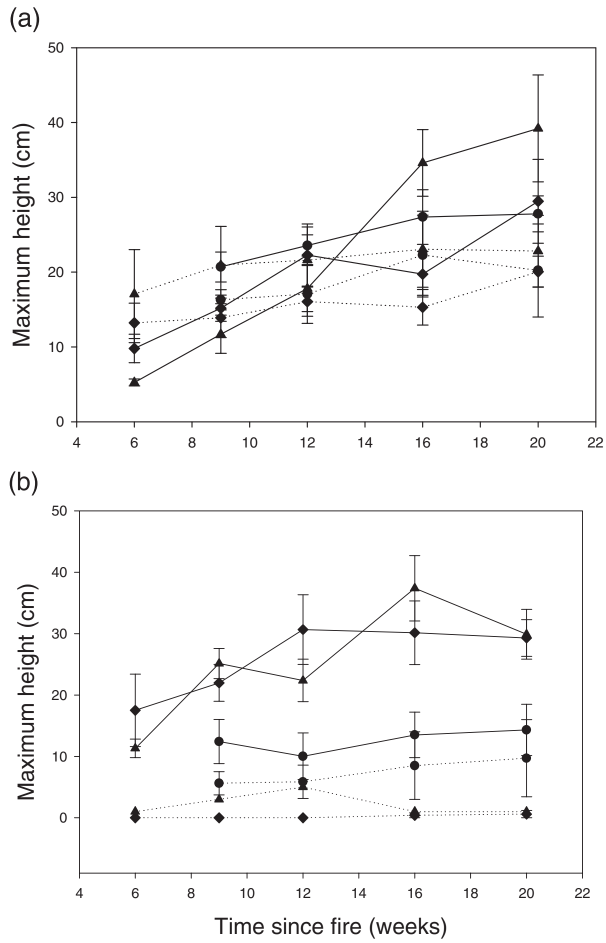

Fig. 4. Mean maximum plant height per quadrat of (a) native plants and (b) exotic plants. Solid lines represent nutrient-enriched areas and dotted lines represent non-enriched areas. The symbols indicate the three sites: Pennant Hills; Wahroonga; West Pymble. Error bars represent standard error.

Table 5. Results of repeated measures ANOVA for native maximum height and exotic maximum height. The factors were soil nutrient (enriched or non-enriched), site (West Pymble, Wahroonga and Pennant Hills) and week

	Factor	d.f.	*F*	*P*
Native maximum height	Soil nutrient	1,52	0.6	0.457
	Site	2,33	0.5	0.622
	Week	4,74	27.9	<0.001
	Soil nutrient × site	2,33	0.1	0.934
	Soil nutrient × week	4,74	9.8	<0.001
	Week × site	7,74	3.2	0.005
	Soil nutrient × site × week	7,74	3.2	0.005
Exotic maximum height	Soil nutrient	1,52	15.5	<0.001
	Site	2,38	1.0	0.364
	Week	4,36	5.3	0.002
	Soil nutrient × site	2,38	3.2	0.052
	Soil nutrient × week	4,37	2.4	0.070
	Week × site	7,36	1.4	0.232
	Soil nutrient × site × week	4,37	0.4	0.818

Table 6. The eight most common native species in both non-enriched and nutrient-enriched areas (all sites combined)

Rank	Undisturbed plots (%)	Nutrient-enriched plots (%)
1	*Entolasia stricta* (86)	*Oplismenus aemulus* (60)
2	*Acacia linifolia* (73)	*Geranium homeanum* (47)
3	*Hibbertia bracteata* (47)	*Entolasia stricta* (47)
4	*Casuarina* spp. (47)	*Dodonaea triquetra* (47)
5	*Lomandra gracilis* (40)	*Microlaena stipoides* (33)
6	*Hardenbergia violacea* (40)	*Omalanthus populifolius* (33)
7	*Lomandra obliqua* (33)	*Pratia purpurescens* (33)
8	*Lobelia dentata* (33)	*Lomandra longifolia* (33)

The percentages in brackets are the per cent of quadrats (non-enriched or nutrient-enriched) in which the species was found.

Table 7. Results of repeated measures ANOVA for per cent of resprouters that were native. The factors were soil nutrient (enriched or non-enriched), site (West Pymble, Wahroonga and Pennant Hills) and week

Factor	d.f.	*F*	*P*
Soil nutrient	1,74	1.3	0.265
Site	2,48	2.5	0.094
Week	4,56	4.9	0.002
Soil nutrient × site	2,48	1.2	0.324
Soil nutrient × week	4,56	4.9	0.002
Week × site	7,56	1.2	0.296
Soil nutrient × site × week	7,56	1.4	0.210

between soil nutrient × week ($P = 0.002$, Table 7) for the percentage of resprouters that were native. On the non-enriched plots almost all resprouters were native (Fig. 5). On the nutrient-enriched plots the percentage of resprouters that were native increased with time following fire, and was higher at the Pennant Hills and Pymble site compared with the Wahroonga site. Resprouting species were relatively uncommon among exotics, and most exotics appeared to regenerate from seed (Table 8), with the notable exception of *R. fruticosus* (blackberry).

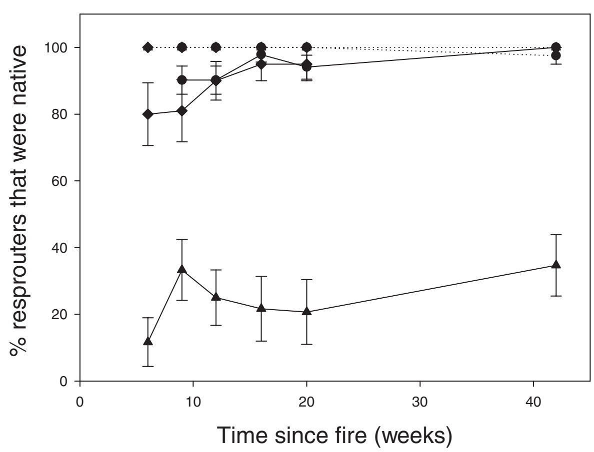

Fig. 5. Mean percentage of resprouting species per quadrat that were native. Solid lines represent nutrient-enriched areas and dotted lines represent non-enriched areas. The symbols indicate the three sites: Pennant Hills; Wahroonga; West Pymble. Error bars represent standard error.

DISCUSSION

Fire did not promote the success of exotic plants in non-enriched areas, as very few exotic plants even

Table 8. The most common native and exotic species with resprouting individuals and individuals growing from seed (all sites combined)

Rank	Resprouting species (%)	Species growing from seed (%)
Exotics		
1	*Rubus fruticosus* (17)	*Solanum nigrum* (30)
2	*Eragrostis curvula* (10)	*Phytolacca octandra* (30)
3	*Acetosa sagittata* (3)	*Solanum mauritianum* (27)
4	*Ehrharta erecta* (3)	*Cyperus conjestus* (23)
5	*Setaria glauca* (3)	*Oxalis* spp. (23)
6	*Digitaria sanguinalis* (3)	*Anagalis arvensis* (20)
7	*Ligustrum sinense* (3)	*Verbena bonariensis* (17)
8	*Ochna serrulata* (3)	*Cardiospermum grandiflorum* (17)
Natives		
1	*Entolasia stricta* (67)	*Eucalyptus* spp. (77)
2	*Oplismenus aemulus* (53)	*Dodonaea triquetra* (47)
3	*Microlaena stipoides* (47)	*Acacia linifolia* (43)
4	*Dianella* spp. (33)	*Casuarina* spp. (33)
5	*Lomandra gracilis* (27)	*Lomandra* spp. (33)
6	*Lomandra longifolia* (20)	*Geranium homeanum* (33)
7	*Lomandra obliqua* (20)	*Omalanthus populifolius* (30)
8	*Lobelia dentata* (20)	*Glycine* spp. (30)

The percentages in brackets are the per cent of all quadrats in which individuals (resprouting or from seed) of that species was found.

emerged. The exotic plants that did emerge and survive had very limited growth compared to those in the nutrient-enriched areas. The proximity of the undisturbed areas to heavily weed-infested areas (within 200 m at all sites) rules out lack of exotic seed supply as the factor limiting invasion in these areas. Studies of seed banks of urban bushland soils have also shown that exotic species are not seed-limited in undisturbed areas (Warner 1998; King & Buckney 2001). Seeds of exotic species are available in the non-enriched soil, but may be unable to germinate because of low soil moisture. Undisturbed sandstone-derived soils are typically well-drained sandy loams in contrast to soils receiving stormwater run-off, which are moisture-retaining clay loams (Leishman *et al.* 2004). Alternatively, exotic seeds may germinate, but do not emerge from the soil and are unable to survive because of low soil nutrients. Although this seems likely, exotic seedlings are able to persist in sandstone-derived soil for at least 3 months once the seeds have germinated, although their growth is limited (Leishman & Thomson 2005).

In the nutrient-enriched areas, exotic plants were able to grow in abundance, showing that fire alone is not an adequate tool for exotic plant control in these areas. In addition, the diversity of native species in nutrient-enriched areas following fire was lower than in non-enriched areas, and declined with time since fire. Some native species were able to survive and compete effectively against the exotic species (as demonstrated by their abundance and growth), however, these were not species that are commonly found in non-enriched areas on sandstone-derived soils (examples include *Geranium homeanum*, *Omalanthus populifolius*, *Oplismenus aemulus*, *E. stricta*; Table 6). Other native species, more typical of sandstone soils, germinated after fire in the disturbed areas, but were unable to persist over time and most seedlings died within 3 months of the fire. These species included many that were common in the non-enriched areas, such as *Eucalyptus* species, *Acacia linifolia*, *Acacia terminalis*, *Casuarina* species and *Hardenbergia violacea*. Their low persistence in nutrient-enriched areas suggests that they were either out-competed by faster growing exotics or natives, or that they were unable to survive under high nutrient conditions, as shown by Thomson and Leishman (2004).

There were consistent between site differences, with the Pennant Hills site having a higher native and lower exotic species richness, density and per cent cover in the nutrient-enriched area compared with the other sites. In the non-enriched plots at Pennant Hills, exotic species richness was also slightly higher than at the non-enriched plots at the other sites. The soil in the non-enriched area was naturally more fertile at Pennant Hills, and may have also had some nutrient addition from a nearby sporting ground, resulting in a higher level of total phosphorus in the soil. Also, the soil in the nutrient-enriched area was lower in total phosphorus than at the other two sites, probably because the source of the nutrient enrichment was a creek rather than a stormwater outlet. These differences in soil nutrients may have allowed both the presence of more exotic species in the undisturbed area, and more native individuals in the nutrient-enriched area. Further, a long history of bushcare at the nutrient-enriched area of this site may have contributed to the higher native and lower exotic species richness, density and cover. At the Pymble site, bushcare over several years appears to have been much less successful than at Pennant Hills, so that the exotic seed bank is unlikely to have declined significantly. At the Wahroonga site, a large exotic seed bank would be expected as bushcare had begun only within the previous year.

The results of this study suggest that, while fire does not facilitate invasion in non-enriched areas on these low-fertility sandstone-derived soils, it does not suppress weedy regrowth in nutrient-enriched areas. Fire alone does not appear to be an important factor in determining exotic plant invasion in this environment, and other anthropogenic disturbances, such as nutrient enrichment of the soil are far more important. Similarly, Hester and Hobbs (1992) found that exotic plant invasion in both shrubland and woodland in Western Australia was not affected by fire, although overall exotic plant density decreased following fire in the woodland. They concluded that fire alone is not sufficient to allow invasion in these communities. Ross *et al.* (2002) found that fire history did not affect the degree of exotic plant invasion in bushland remnants where the numbers of exotic plants were naturally very low. In contrast, Hobbs and Atkins (1990) found that cover of exotic annual plants increased after an autumn fire, but not after a spring fire, in an undisturbed *Banksia* woodland. They attributed the success of exotics to a short-term fertilizing effect of fire, and the lack of competition from native plants in autumn. Gilfedder and Kirkpatrick (1998) also found that frequent fire, used as a management tool, significantly increased the exotic species richness in bushland remnants in Tasmania. However, frequent fire also increased the number of native species.

Hobbs (1991) and Hobbs and Huenneke (1992) argued that the interaction of more than one disturbance frequently has the largest effect. Hobbs and Atkins (1991) found that fire had no effect on exotic annual abundance in an undisturbed reserve, but promoted a large increase in exotic species in an adjacent road verge. Also in roadside remnants, Milberg and Lamont (1995) found that fire increased the number of exotic species, their frequency and cover, and that the effect was greater near the road edge than further into the remnant. In this study, we found that the effects of long-term nutrient enrichment of soils by stormwater far outweighed the temporary effect of an open canopy and increased nutrient availability after fire in facilitating invasion by exotic plants on these low-fertility sandstone-derived soils.

There were clear differences in the resprouting ability of natives and exotics. Native species were more likely to resprout following fire than exotic species and most exotic species regenerated from seed (with a few notable exceptions such as *R. fruticosus*). Typically, the initial regrowth in a plant community following fire is dominated by the adult plants that have survived the fire and are resprouting. Species whose adult plants do not survive must regenerate from the seed bank, and tend to contribute to the community later (Morrison *et al.* 1995; Morrison 2002). Several studies in Sydney's sandstone vegetation communities have shown that high fire frequency results in a relative increase in species that regenerate vegetatively and a decrease in obligate-seeders (Nieuwenhuis 1987; Bradstock *et al.* 1997). This could have important consequences in nutrient-enriched areas that retain some overstorey of native plants, as removal of the obligate-seeding exotics may allow the natives to dominate. However continual removal of exotic seedlings would be required until their seed bank is exhausted. Furthermore, there are a number of exotics that do resprout after fire (Table 8) that would require management. Finally, native overstorey species would not be replaced from the seed bank, suggesting that they will not survive in the community in the long term.

The main exotic species that appeared to be promoted by fire were annual weeds that were regenerating from seed, such as *S. nigrum*, *S. mauritianum*, *Si. rhombifolia* and *P. octandra*. These species were not present before the fire and appear to be able to take advantage of the post-fire conditions. It is likely that these will gradually be replaced by a suite of perennial exotic species that invade after fire such as *Li. lucidum*, *O. serrulata*, *Protoasparagus aethiopicus* and *T. fluminensis*, as well as by exotics that occurred pre-fire and can maintain their presence through either vegetatively resprouting or germinating from hard seeds, such as *Hedychium gardnerianum*, *A. sagittata*, *R. fruticosus* spp. and *Ricinus communis*.

The results of this study suggest that fire can be a useful tool for short-term removal of exotic plant biomass from nutrient-enriched areas. However, additional post-fire removal of exotic plants is necessary for effective weed control. Further, fire alone does not promote germination and establishment of native species that are typical of Hawkesbury Sandstone communities in nutrient-enriched sites. Instead, we must accept that soil conditions have changed so dramatically that such species will no longer survive there, and instead promote establishment of native species that are better adapted to high soil nutrient conditions.

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