Fluctuating resources, disturbance and plant strategies: diverse mechanisms underlying plant invasions

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Abstract: This paper examines the hypothesis that non-native plant invasions are related to fluctuating resource availability as proposed by Davis et al. (2000). I measured relative functional responses of both invasive and native plants to changed resource availability due to nutrient enrichment and rainfall, and to increased disturbance. Data are presented from studies in two contrasting ecosystems. First is a series of glasshouse and field experiments on the invader *Hieracium lepidulum* and associated invasive and native species in subalpine temperate New Zealand. Second is a field study of invasive and native plant responses to altered disturbance regimes and rainfall from tropical savannas of north eastern Australia. Invaders responded differently from native species to changes in resource availability in both subalpine and tropical studies. However, invaders differed among themselves showing that different species exploit different functional niches to invade their respective habitats. These findings contribute to the contention that the fluctuating resource hypothesis does not provide a universal explanation for plant invasions. The diverse functional responses to increased resource availability among invaders in this and previous studies suggest that the cause of invasion depends on unique combinations of habitat and functional attributes of invaders and native assemblages. Such findings imply that universal predictions of what will happen under climate change scenarios across the globe will be difficult to make.

Keywords: plant invasion; plant strategies; C-S-R triangle; fluctuating resources; disturbance

The fluctuating resource hypothesis is a major unifying theory that provides a general mechanism to explain plant invasions globally (Davis et al., 2000). This hypothesis suggests that invasion occurs when invaders are able to acquire plant resources (nutrients, light, water) in excess of what native residents acquire or have access to because of changes in resource availability in time and space. Within this hypothesis, disturbance (e.g. grazing) and enrichment (e.g. nutrient addition) are seen as key factors increasing the availability of resources. However, natural fluctuations in resource availability, for instance with variation in weather conditions and drought, could also theoretically lead to increased resource availability to invaders. The formulation of the fluctuating resource theory was based on a series of experiments showing that nutrient enrichment and artificial disturbance treatments increased plant invasion within UK grasslands (Burke and Grime, 1996; Thompson et al., 2001). Many studies across multiple ecosystems provide supporting evidence that increased resources associated with disturbance and nutrient enrichment lead to increased invasion by non-native species (Milchunas and Lauenroth, 1995; Holmgren et al., 2000; Huston 2004; Thomson and Leishman, 2005; Hobbs and Atkins, 2006).

But is the fluctuating resources hypothesis a useful general theory explaining plant invasions? There have

been few tenable unifying explanations or characteristics identified among plant invaders or their recipient communities despite much research effort (e.g. Baker, 1965; Perrins et al., 1993; Rejmanek and Richardson, 1996; Radford and Cousens, 2000; Daehler, 2003; Hierro et al., 2005). The idea that invaders generally differ in ecology from native species was challenged by Huston (2004) who showed that both non-native invader and native plant species richness responded positively to increased resource availability. The results of some studies also suggest that invaders might exploit situations of resource limitation or stress, rather than elevated resources (e.g. Radford et al., 2006; Funk and Vitousek, 2007) as implied by the fluctuating resource theory (Davis et al., 2000). These lines of evidence collectively throw into doubt the generality of increased availability of resources as a mechanism underlying all plant invasions.

Plant strategy theory may provide a useful framework to analyse functional attributes of plant invaders relative to native resident species. Plant strategy theory was developed by Grime et al. (1988, 1997). Plant strategy theory conceptualises plants as functioning within an environmental space defined by factors affecting plant growth. These factors are conceptualised as three axes of a triangle (Fig. 1) with plant available resources (e.g. nutrients and light), disturbance (e.g. grazing or fire which remove competitive plant tissue) and nutrient stress (e.g. edaphic factors such as soil acidity which affect rates of resource uptake) defining these axes. Within this construct, plant strategies are the sets of plant functional attributes that enable each species to acquire resources and to reproduce. Although species strategies are highly variable, three primary strategies are associated with the primary environmental axes. The first are competitive strategies (C), which exploit conditions of high resource availability while competing with other plants. Competitors use functional attributes including high relative growth rates (RGR), high biomass, large plant stature, high shoot to root ratios and high specific leaf area to achieve success in competitive environments (Grime et al., 1997; Keddy et al., 2002; Jabot and Pottier, 2012). In contrast, ruderal strategies (R) allow plants to compensate for repeated loss of tissue associated

with disturbance. Ruderal functional attributes include high RGR, low shoot to root ratios, fast leaf turnover, low palatability, low tissue construction costs and rapid reproduction (Grime et al., 1988; Hodgson et al., 1999; Jabot and Pottier, 2012). Finally, stress tolerant strategies allow persistence in resource limited or stressed environments. Stress tolerant functional attributes include high root to shoot ratios and mycorrhizal associations to allow greater access to scarce soil resources, long-lived plant tissue and the ability to use alternative nutrients to compensate for stress (Grime et al., 1997; Garnier, 1998; Caccianiga et al., 2006; Jabot and Pottier, 2012). Assessing non-native plant invaders and their native counterparts in terms of C-S-R strategies and environmental factors may increase our understanding of processes leading to invasion. It may also provide greater insight into whether invaders generally respond in similar ways as natives to factors such as disturbance and increased resource availability (Davis et al., 2000).
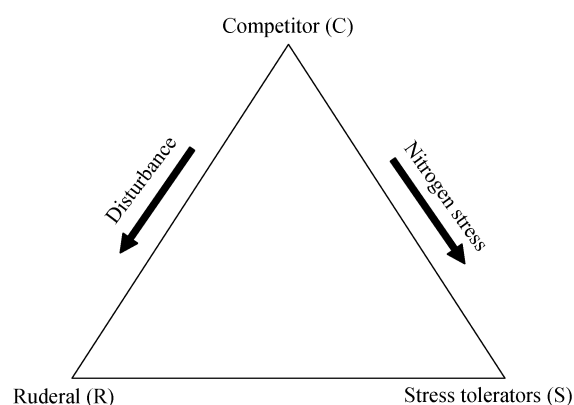

Fig. 1 Schematic representation of Grime et al. (1988, 1997) plant strategy triangle

The plant strategy conceptual framework then gives us the ability to test the basic premise of the fluctuating resource theory of plant invasion. In this paper I present data from two case studies, one from temperate grassland/shrublands in New Zealand (Radford et al., 2007, 2010) and the other from tropical savanna in northern Australia (Radford et al., 2008). In both cases, I compare invader and native plant functional response to environmental variables. This approach is used to address the questions: (1) Do elevated resources and disturbance lead to positive responses

among invaders? (2) Do all invaders respond in the same way to resources/disturbance? (3) Will plant invaders become more dominant as global change progresses?

1 Materials and methods

1.1 Case study 1–New Zealand subalpine

1.1.1 Study area and species

The first case study was conducted in temperate New Zealand. The invasive asteraceae *Hieracium lepidulum* occurs in a range of subalpine habitats (ca. 500–800 m altitude) on the south island of New Zealand including tall and short native tussock grasslands, shrublands and forests in medium to high rainfall areas (750–4,000 mm). The species occurs in both pastoral and conservation land where in some instances it replaces dominant native tussock grass, shrub or invasive grass species, even species much larger and apparently more competitive than itself (Keddy et al., 2002). *H. lepidulum* co-occurs and sometimes dominates in habitats with a range of plant groups which otherwise dominate vegetation. These groups include invasive, mostly European, grasses (e.g. *Agrostis capillaris*, *A. stolonifera*, *Anthoxanthum odoratum*, and *Holcus lanatus*), native tussock grasses (e.g. *Chionocloa* spp., *Festuca novae-zealandiae*, and *Poa colensoi*) and native shrubs and sub-shrubs (e.g. *Coprosma rugosa*, *Gonocarpus aggregatus*, and *Leucopogon fraseri*). Also represented in the vegetation are subordinate herbaceous components including introduced forbs/legumes (*Rumex acetocella*, *Trifolium repens*, *Taraxacum* spp.), Cyperaceae (e.g. *Uncinia viridis*), Juncaceae (e.g. *Luzula rhizomatous*) and various ferns (*Blechnum penna-marina*), mosses and lichens (e.g. *Cladia aggregata*). I assumed that these species, particularly the dominant species, are interacting and competing with the invader.

1.1.2 Studies

In this study, I and my colleagues addressed the question do invasive species including *H. lepidulum* differ from one another and from native groups in their functional responses to increases in resource availability and disturbance? We used two approaches to address this question. First we undertook a glasshouse

based functional comparison of non-native invaders and native subalpine species to artificial nutrient resource gradients (Radford et al., 2007). We then undertook a field-based experiment where disturbance and resource availability were manipulated, and ecological responses of invasive and non-invasive plant groups compared (Radford et al., 2010).

1.1.3 Functional comparisons in glasshouse experiments

The functional glasshouse study is described in more detail elsewhere (Radford et al., 2007); however, I provide a brief description here. Plants were grown in 15-L pots on mineral sand and were provided with 300 ml per week of nutrient solutions modified from Rorison's solution. Nitrogen was diluted at 1.0, 0.7, 0.4 and 0.1 from the standard nutrient solution to provide an artificial nutrient resource gradient. Following observations that macro-nutrient dilutions other than N (e.g. P, K, Ca, Mg, and S) caused little response among target species (Radford et al., 2006, 2007), only responses to nitrogen gradients are presented here. Plants were grown from seedlings for 4 to 8 months in two time periods. Plant growth attributes including relative yield, relative growth rate, root:shoot ratio responses were measured. All growth responses were presented as a proportion to those grown at the lowest N nutrient solution (0.1 N).

An additional glasshouse microcosm experiment was conducted to test for the relative effects of disturbance and competition on the invasive forb *H. lepidulum*, the invasive grasses *A. stolonifera* and *A. odoratum* and the native tussock grass *P. colensoi* (Radford et al., 2007). Thirty seeds of each species were sown, and plants were grown together on mineral sand in 15 L pots as for the growth comparison experiments described above. A minimum of 50% seed germination was observed for all species. Three nitrogen concentrations (1.0, 0.4, 0.1 of standard, as above) were provided to plants as a resource availability gradient. Clipping disturbance was applied uniformly 1 cm above sand surface every week of the experiment. This mixed species microcosm experiment was run for 8 months over the growing season. All above ground plant tissue was carefully removed using fine scissors and separated into species for analysis. As for the

other growth study, plant tissue was dried and weighed to a constant weight (5 days at 60°C).

1.1.4 Field functional comparisons

Two additional field studies were undertaken to test hypotheses generated about mechanisms underlying *H. lepidulum* establishment relative to resident and other introduced species in the same environments (Radford et al., 2010). Manipulation of resources (Nitrogen addition/control) and disturbance regimes (clipping, ambient grazing and grazing exclosure using wire cages) were undertaken at 2 field sites. The first study was conducted in habitat with low *H. lepidulum* density locally, but which had dense populations nearby (<500 m). This site was dominated by the native tussock grass *P. colensoi*. We addressed the question: what processes facilitate invasion by *H. lepidulum* into intact native tussock grassland? The second study was undertaken in herbaceous vegetation already invaded and dominated by *H. lepidulum*, although co-occurring with a range of other species. In this study we asked, what processes help maintain *H. lepidulum* dominance? Both experiments were run for two growing seasons, and then all above ground plant tissue was harvested, with major species or groups separated for analysis.

1.2 Case study 2–Australian tropical savannas

1.2.1 Study area and species

The study was conducted in grazed savanna woodlands of north eastern Australia in three sub-catchments of the Burdekin River. The dominant woody species were the trees *Eucalyptus crebra* and *Corymbia erythrophloia*, the invasive woody shrub/vine *Cryptostegia grandiflora* and a number of non-eucalypt riparian species (e.g. *Melaleuca leucodendra*, *Casuarina cunninghamiana*, and *Corymbia tessellaris*) and mid canopy trees/shrubs (e.g. *Acacia* spp., *Atalaya hemiglauca*, *Maytenus cunninghamii*, *Eremophila mitchellii*, *Erythroxylum australe*, *Petalostigma pubescens*, *Pleiogynium timorense*, and *Santalum lanceolatum*). The herbaceous layer was made up of a complex of invasive and resident native species and groups. These included introduced invasive grasses (e.g. *Bothriochloa pertusa*, *Melinis reprens,* and *Chloris barbata*), native perennial tussock grasses

(e.g. *Heteropogon contortus*, *Bothriochloa ewartiana*, *Aristida* spp., *Chrysopogon fallax*, and *Themeda triandra*), invasive (*Stylosanthes scabra*, *S. hamata*) and native legumes (*Indigofera linnifolia*, *I. colutea*, *Glycine tomentella*, and *Crotalaria* spp.), invasive (e.g. *Sida cordifolia*) and native forbs (e.g. *Waltheria indica*) and a range of annual grasses and sedges. The study was conducted on commercial pastoral properties that ran domestic cattle (*Bos indicus*) and were typical of much of the surrounding savanna woodland and riparian forest in the Dalrymple region.

1.2.2 Fluctuating plant resource and enhanced disturbance treatments

In this study, we asked do plant invaders and native residents respond in the same way to fluctuating plant resource availability and to enhanced disturbance regimes in tropical savannas? We conducted a 4-year experiment at these sites from 1999 to 2002 (Radford et al., 2008). Resource availability was not manipulated directly in this study, but varied naturally between years due to marked differences in annual wet season rainfall. Wet season rainfall equates to annual net primary productivity in seasonal tropical environments. Rainfall varied from 1,116 mm in the 1999/2000 wet season down to 511 mm in the 2001/2002 wet season (mean rainfall ca. 660 mm) leading to major differences in savanna productivity and herbaceous biomass. The enhanced disturbance treatment was a combination of fire treatments followed by increased grazing as cattle are attracted to recently burnt grasses (Ash et al., 1982; Winter, 1987). Four burning disturbance treatments were implemented to landscape scale blocks (>25 hm^2): a control treatment (unburnt and grazed), two low intensity wet season burning treatments (once and twice burnt) and a dry season burning treatment. Treatments represented different fire intensity with wet season fires of relatively low intensity, and dry season fires of moderate intensity (Radford et al., 2008) based on standard fire intensity indices (Williams et al., 1998).

1.2.3 Plant measurements

Woody plants were measured at the beginning and at the end of the experiment in 1999 and 2002 (Radford et al., 2008). Density of all major tree and shrub species in predetermined size classes was estimated at

fixed points along 5 transects in each treatment plot representing upland woodland, levee and creek bank habitats. Density was estimated for each species within a 10-m radius of each fixed point. Herbaceous savanna vegetation was assessed annually along each transect within experimental plots, with a minimum of 150 random 1-m² quadrats used for this assessment per plot. All herbaceous species were identified and classified to functional groups within each 1-m² quadrat. We visually estimated and ranked the percentage of the total herbaceous biomass for each herbaceous species/functional group. Total herbaceous biomass was estimated using a standard scale (from 0 to 10). Biomass scale estimates were converted to actual biomass by harvesting a set of 15 standard quadrats in the range of the predetermined scale each day that herbaceous measurements were conducted. Harvested herbaceous material was dried to constant weight to give a measurement of herbaceous biomass relative to standard biomass estimations made in the field.

1.3 Statistical analyses

Full analyses of experiments are found in Radford et al. (2007, 2008 and 2010). In this paper, only the primary resource and disturbance responses are presented from these experiments, along with a qualitative assessment of comparative invasive and native plant strategies. New Zealand glasshouse studies (Radford et al., 2007) addressed individual responses of invasive and native species to nutrient resource addition (nitrogen and combined macronutrients (P, K, Mg, Ca)) and used fully factorial ANOVA to test for differences among species, nitrogen concentration levels, combined macro-nutrient concentration levels and all orthogonal combinations of these factors (Radford et al., 2007). In this paper F and P values for nitrogen concentration (N) alone are presented, and the magnitude of the responses presented as a percentage increase or decrease with respect to the lowest N levels that plants were grown at (Table 1). The other glasshouse study presented is a microcosm experiment in which three nitrogen resource concentrations and two disturbance treatments (clipped and unclipped) were provided to a group of four species grown together in single pots (Radford et al., 2007). A fully factorial ANOVA was undertaken to test for differences in response among

disturbance treatments, invader treatments (with and without *H. lepidulum*), nitrogen concentrations and all orthogonal interactions of these factors (Radford et al., 2007). Only F and P values for species with Nitrogen and disturbance treatments are presented (Table 1). Where significant responses were found, percentage increases or decreases in biomass from the low N or no disturbance treatments are presented.

New Zealand field experiments addressed invader and native responses to elevated resources (N) and disturbance (grazing and clipping) in native tussock grassland and in grassland invaded by *H. lepidulum*. Full analyses of this study are presented in Radford et al. (2010). For site 1 (native grassland), we tested for differences in species (ANOVA) and assemblages (MANOVA) due to disturbance (grazing exclusion, open grazing and clipping and grazing), resources (with and without nitrogen addition), invader seed limitation (*H. lepidulum* seeds added and not added) and orthogonal combinations of these treatments. Only individual invader and native species responses to disturbance and nitrogen are presented (Table 2). Where significant differences were found, percentage increase or decrease in plant biomass from no N addition or no disturbance (exclosure) treatment to N addition or clipping disturbance treatments is presented as an indication of the magnitude of treatment effects. For site 2 (*H. lepidulum* dominated grassland), changes in species group (ANOVA) and assemblages (MANOVA) due to disturbance (grazing exclosure and grazing treatments), resources (control and nitrogen addition), native propagule limitation (control and native seed addition), *H. lepidulum* dominance (control and dicot specific herbicide), and all orthogonal interactions of these factors were tested (Radford et al., 2010). ANOVA F and P values for species specific responses to N addition and grazing disturbance only are presented here (Table 3). The magnitude of species responses are presented as percentage change in biomass from the no nutrient addition and the grazing exclusion (exclosure) treatments.

The north eastern Australian field experiment addressed invader and native responses to elevated resources (associated with fluctuation in annual rainfall) and disturbance (fire combined with grazing) in

Table 1 Growth benefit for invasive and native species from a New Zealand subalpine ecosystem with resource enrichment treatments (grown alone and grown in mixed species microcosm) and with disturbance (in microcosm only) during glasshouse experiments

Plant species	D.F.	Grown alone	Grown in mixed species microcosm	
		Response to nitrogen (resources)	Response to nitrogen (resources)	Response to clipping (disturbance)
Invaders				
Hieracium lepidulum	3, 32	+457 (28.80***)	(2.52ns)	+109 (4.39~)
Agrostis stolonifera	3, 32	+317 (48.90***)	+390 (70.32***)	−66 (111.83***)
Anthoxanthum odoratum	5, 12	+197 (10.39***)	+1,067 (434.18***)	−99 (2,132.90***)
Native grasses				
Festuca novae-zelandiae	5, 12	+248 (5.66**)		
Poa cita		+161 (33.26***)		
Poa colensoi	5, 12	(0.38ns)	+9 (8.31**)	−96 (76.50***)
Chionochloa flavescens	3, 32	+59 (4.76**)		
Native shrubs and trees				
Kunzea ericoides	5, 12	(2.82ns)		
Coprosma rugosa	3, 32	+64 (5.35**)		
Podocarpus hallii	5, 12	(1.33ns)		

Note: *F* value and statistical significance from ANOVA results are shown in parentheses. For species that had significant changes in growth with increased N or with clipping, the percentage change from lowest to largest N and from unclipped to clipped are shown in bold font. Degrees of freedom (D.F.) for the glasshouse experiment where plants were grown alone varied among species and are shown. For mixed species microcosm experiments, D.F. were (2, 12) and (1, 12) for responses to nitrogen and to clipping, respectively, for all species. ***, statistically highly significant ($P<0.001$); **, statistically significant ($P<0.01$); ~, marginally significant ($P<0.06$); ns, not significant; +, positive response to treatment; −, negative response to treatment.

Table 2 Summary of species and group functional responses to increased resource (nitrogen addition and control) and disturbance treatments (grazing exclosure, open grazing and clipping) in a New Zealand subalpine *Poa colensoi* tussock grassland

Plant species	Response to nitrogen (resources)	Response to grazing and clipping (disturbance)
Invasive		
Hieracium lepidulum	(0.42ns)	+317 (6.85**)
Grasses (*Agrostis, Anthoxanthum, Holcus*)	(2.24ns)	+523 (21.85***)
Forbs (e.g. *Rumex acetocella*)	(1.28ns)	+72 (5.00*)
Native		
Poa colensoi	(0.52ns)	−90 (10.64***)
Uncinia/Luzula spp.	(1.59ns)	(0.60ns)
Rytidosperma gracile	+587 (5.87*)	(1.18ns)
Mosses, lichens, ferns, etc.	−71 (7.56*)	(0.18ns)

Note: *F* value and statistical significance from ANOVA results are shown in parentheses. For species that had significant changes in growth with increased N or with disturbance, the percentage changes with increased N and from undisturbed to disturbed are shown in bold font. Degrees of freedom were (1, 34) and (2, 34) for responses to nitrogen and to disturbances, respectively. ***, statistically significant ($P<0.001$); **, statistically significant ($P<0.01$); *, statistically significant ($P<0.05$); ns, not significant; +, positive response to increased resources of disturbance; −, negative response to treatment.

Table 3 Summary of species and group functional responses to resource treatments (nitrogen addition and control) and disturbance treatments (grazing exclosure and open grazing) in *H. lepidulum* dominated herbaceous vegetation located in the New Zealand subalpine

Plant species or group	Response to nitrogen (resources)	Response to grazing (disturbance)
Invasive		
Hieracium lepidulum	−13 (20.39***)	(0.02ns)
Grasses (*Agrostis, Anthoxanthum, Holcus*)	+452 (22.89***)	(0.34ns)
Native		
Monocots (*Poa colensoi* and *Uncinia/Luzula*)	(1.18ns)	(0.02ns)
Mixed		
Subdominants (e.g. exotic forbs and legumes, native sub-shrubs)	−54 (15.84***)	(2.34ns)

Note: *F* value and statistical significance from ANOVA results are shown in parentheses. For species that had significant changes in growth with increased N or with grazing, the percentage change with increased N and from ungrazed to grazed are shown in bold font. Degrees of freedom were (1, 46) and (1, 46) for responses to nitrogen and to grazing, respectively. ***, statistically significant ($P<0.001$); ns, not significant; +, positive response to treatment; −, negative response to treatment.

savanna woodland and riparian forest vegetation (Radford et al., 2008). Species specific and assemblage responses to the three experimental sites (blocks), treatment plots (within sites), sites×treatment plots, time (before and after for woody vegetation), sites×time and treatment plots×time were tested for significance using a split plot design ANOVA (Radford et al., 2008). The full analysis for woody species is presented elsewhere (Radford et al., 2008). Full analysis of herbaceous vegetation is in an unpublished manuscript, and this analysis includes an additional factor, habitat (woodland, riparian levee and riparian bank and creek bed habitat) nested within treatment plots, in the split-plot ANOVA. In the present paper, only resource responses (to annual increases in rainfall by year–herbaceous plants only) and response to burning treatment (treatment plot×time) are presented in Tables 4 (herbaceous species) and 5 (woody species). Where significant differences to resource change were detected, the magnitude of treatment effects is presented as percent change in biomass between the low (511 mm in 2002) and high rainfall years (1,116 mm in 2000). Where disturbance (fire) responses were detected, percentage differences between unburnt and burnt treatment plots in the year where fire responses were measured are presented (Tables 4 and 5). Woody responses were measured in terms of plant density, and herbaceous responses were measured in terms of composition (percentage of total quadrat vegetation for that species) and frequency (percentage of quadrats with the species present).

Plant strategy interpretations according to a C-S-R triangle are qualitatively based on observed relative responses of invader and native species within experiments reported here. Where available, additional published data were used to inform plant strategy interpretations. Positioning of species was based on relative functional species responses along the disturbance and nutrient stress C-S-R axes. These interpretations are speculative and may be seen as hypothesis generating only. More formal C-S-R interpretations using morphological plant attributes was not attempted in this study, although methods for this are currently being developed (see Hodgson et al., 1999; Pierce et al., 2007 for earlier versions).

2 Results and discussion

2.1 Case study 1

2.1.1 Functional differentiation among New Zealand invaders and native residents

From the glasshouse screening studies where plants were grown in isolation, invaders had stronger positive resource responses (197%–457% increases) than native species (2%–248%) (Table 1; Radford et al., 2007). Yield (plant biomass), above and below ground yield, relative growth rate (end yield–start yield/months of study), root: shoot ratio and fecundity differed among species, resource levels (N, combined P/K/Mg/S) and for species by resource interactions indicating differences in species specific responses to resource levels (full analyses in Radford et al., 2007; Table 2, Fig. 1). Large positive growth responses to increased resources relative to that at low resource levels among the invaders (*H. lepidulum*, *A. stolonifera* and *A. odoratum*) and two of the native tussock species (*F. novae-zelandia* and *P. cita*) (Table 1) indicate intolerance to resource depletion (resource stress) and suggests that these species are disturbance or competitor strategists (Grime et al., 1997). A number of native species had no significant response to increased N (Table 1), indicating stress tolerant strategies (Grime et al., 1997).

In glasshouse mixed species microcosms, invaders had divergent responses to elevated N (resources) and clipping (disturbance) (Table 1). Invasive grasses *Agrostis stolonifera* and *A. odoratum* both had strong positive responses (>350%) to elevated resources and negative responses (–66% – –99%) to clipping disturbance (full analysis Radford et al., 2007; Tables 1, 4, 5, and Fig. 4). Conversely, the invasive asteraceae *H. lepidulum* had no response to elevated N in the microcosm and had a positive response (+109%) to clipping disturbance (Table 1). Like the invasive grasses, the native grass *P. colensoi* had a positive (although muted) response to elevated N (+9%) and a negative response (–96%) to clipping (Table 1).

Invasive and native species at field sites responded differently to added nitrogen (nutrient resources) and grazing and clipping disturbance depending on the context (Tables 2 and 3; Radford et al., 2010). At the

first site within native tussock grassland, added N resulted in a dramatic increase (+587%) in the subdominant native grass *Rytidosperma gracile*, and reduced biomass (–71%) among lower plants including mosses, ferns and lichens (full analysis Radford et al., 2010; Table 2; Fig. 1). Clipping reduced biomass of the dominant native tussock grass, *Poa colensoi*, by 90% (Table 2). Presumably as a response to reduced competition by the dominant native grass species, invasive groups increased with clipping (disturbance). Invasive groups increased by as much as 523% for introduced grasses and by 72% for introduced forbs (e.g. *Rumex acetocella*) (Table 2). At the second field site in *H. lepidulum* dominated vegetation, invaders had opposing responses to added N (resources) but did not respond to grazing disturbance at this site (full analysis Radford et al., 2010; Table 3, Fig. 3). Added N resulted in a 452% increase in invasive grass biomass, whereas biomass of the dominant *H. lepidulum* decreased by 13% (Table 3). Similar to *H. lepidulum*, minor components of the vegetation, including invasive forbs/legumes (*Rumex acetocella* and *Trifolium repens*) and native dwarf-shrubs (e.g. *Galium perpusillum*) declined by 54% under increased N (Table 3). Declines of *H. lepudulum* and other invasive forbs/legumes are presumably due to increased competition with large increases in biomass among invasive grasses.

2.1.2 Plant strategy interpretation for New Zealand invader and native species

Interpreting these results in terms of the plant strategy theory (Grime et al., 1997), invader species apparently adopted different functional strategies when faced with altered resource (nutrient) and disturbance conditions (Fig. 2). *H. lepidulum* responded positively to increased disturbance in tussock grassland (Table 2) and glasshouse microcosms (Table 1), and negatively (Tables 1 and 3) or not at all (Table 2) to nutrient addition when in competition with native or invasive grasses. These findings, plus its relative tolerance/adaptation to nutrient stress associated with acidic soils (Downs and Radford, 2005; Radford et al., 2006; Roberts et al., 2009), suggests that *H. lepidulum* is a ruderal strategist in disturbed and relatively nutrient stressed environments (R-S in Fig. 2). In contrast,

invasive grasses (*A. stolonifera*, *A. capillaris*, *A. odoratum*, *H. lanatus*) responded positively to both nutrient addition and disturbance (Tables 1–3). Subdominance of invasive grasses to *H. lepidulum* until nutrient stress was alleviated (Radford et al., 2010) suggests that these grass species are poor performers in stressed environments, making them ruderal-competitor strategists (Fig. 2). Invasive forbs responded positively to disturbance (Table 2) and negatively to nutrient addition (Table 3) and were poor performers under nutrient stress at site 2 (Table 3), suggesting they are primarily ruderal species (Fig. 2). Among native species, the grass *Rytidosperma gracile* responded positively to nutrient addition but not to disturbance (Table 2), suggesting a competitive strategy (Fig. 2). The native tussock *Poa colensoi* did not respond positively to nutrient resources (Tables 1–3) but remained dominant in enriched vegetation (Radford et al., 2010), whereas it responded negatively to disturbance (Table 2). These responses suggest a stress tolerant-competitor strategy (Fig. 2). Lower plants including mosses, lichens and ferns, and minor species like *Uncinia*/*Luzula* spp. and dwarf shrubs (e.g. *Galium perpusillum*) responded negatively to nutrient addition and disturbance (Tables 2 and 3), suggesting stress tolerant strategies (Fig. 2).

2.2 Case study 2

2.2.1 Functional differentiation among savanna invaders and natives

Full analysis of herbaceous responses to rainfall and burning treatments will be published elsewhere. However, responses of invasive and native species to annual rainfall changes (resource availability) and disturbance associated with burning treatment (treatment plot×time interaction) are presented in Table 4. Dominant invasive perennial grasses increased their composition (percentage contribution to vegetation biomass) by 45% in high rainfall (1,116 mm) compared to low rainfall (511 mm) years. In contrast, high rainfall resulted in 42% reduced composition among invasive forbs. Native herbaceous groups also diverged in their response to increased rainfall and plant available resources, with native perennial grasses decreasing in composition by 43% whereas native legumes increased by 36% and native forbs increased by
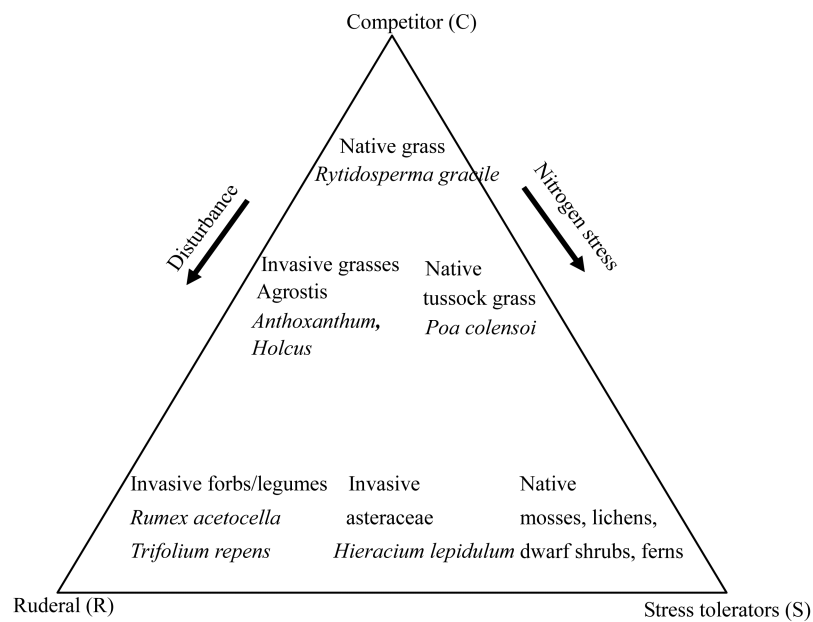
Fig. 2 Hypothesised plant strategies among invasive and native resident species in New Zealand subalpine habitats based on resource addition and disturbance responses at field and glasshouse experiments

203%. Invader groups showed no evidence of changes in biomass or composition with fire (Table 4). However, native legumes significantly increased (+264%) their contribution to herbaceous biomass after applica-tion of the wet season burning treatment in 2000 (high rainfall year), and in 2001 (intermediate rainfall year) native legumes showed a 50% reduction in percentage composition relative to unburnt controls. Na-

Table 4 Invasive and native species responses to resource increase and to disturbance in an Australian tropical savanna

Herbaceous plant species	Species composition		Species frequency
	Response to resource (annual rainfall)	Response to disturbance (burn treatment)	Response to disturbance (burn treatment)
Invasive			
Perennial grasses	**+45** (17.25^{***})	(1.15^{ns})	
Bothriochloa pertusa			**−19** $(1.55^{*})^{\#}$
Legumes	(1.64^{ns})	(0.95^{ns})	
Stylosanthes hamata			**+90** (1.55^{*})
Forbs	**−42** (9.71^{***})	(1.08^{ns})	
Richardia brasiliensis			**+290** $(1.53^{*})^{\#}$
Annual grasses	(0.61^{ns})	(0.95^{ns})	
Native			
Perennial tussock grasses	**−43** (21.43^{***})	(1.33^{ns})	
Legumes	**+36** (7.93^{***})	**+264, −50** (1.52^{*})	
Forbs	**+203** (4.43^{**})	(1.12^{ns})	
Annual grasses	(1.41^{ns})	**−70** (2.19^{**})	

Note: *F* value and statistical significance from ANOVA results are shown in parentheses. For species that had significant changes in composition (i.e. fraction of total biomass for an individual species) with increased rainfall, mean values for composition in the highest and lowest rainfall years were used to calculate percentage change (bold text). For species that had significant changes in composition or frequency (i.e. fraction of quadrats that contained an individual species) with disturbance (burning) treatment, only the year where responses were observed are shown (bold text). Degrees of freedom were (3, 134) and (36, 134) for responses to rainfall and to burning, respectively. ***, statistically significant ($P<0.001$), **, statistically significant ($P<0.01$); *, statistically significant ($P<0.05$); ns, not significant; +, positive response to treatment; −, negative response to treatment; #, inconsistent trend with statistical response observed in one set of treatment plots only.

tive annual grasses showed a 70% reduction in composition across burnt compared to unburnt plots during the lowest rainfall year (511 mm in 2002). Three invasive species showed significant changes in frequency (percentage of quadrats with the species) in response to fire treatments. One set of 3 treatment plots, but not the other, had a 19% reduction in *Bothriochloa pertusa* frequency after a wet season fire in the high rainfall year (2000). The invasive legume *Stylosanthes hamata* showed a 90% increase in frequency relative to unburnt areas after a single wet season fire in 2002. The invasive forb *Richardia brasiliensis* also showed an inconsistent (in one set of burnt plots) increase in frequency of 290% after dry season fires in 2001 (Table 4).

Full analysis of responses of woody savanna species to fire are found in Radford et al. (2008). Here, I report on fire (disturbance) responses only (treatment plot×time responses); analysis of response to resource variation was not possible because woody species were only measured before (1999) and after (2002) the burning treatments (Table 5). Of the four invasive shrubs, only *Cryptostegia grandiflora* responded negatively to burning disturbance with 41% reduced density in burnt compared to unburnt treatments. Only three native *Acacia* species responded to fire. *Acacia aulacocarpa* density was reduced by 71% post-fire, presumably due to mortality of adult trees. Two other species, *A. holosericea* and *A. salicina* increased by 514% and 959%, respectively, after fires resulting in major emergence and seedling recruitment. Only high intensity dry season fire treatments applied in 2001 resulted in seedling emergence and increases in density of *Acacia salicina*, whereas wet season fires in 2000 and 2002 resulted in no change in density (Radford et al., 2008).

2.2.2 Strategy interpretation for savanna invader and native species

Interpreting results from the savanna study is more difficult and therefore speculative than in the New Zealand subalpine case study due to the absence of functional screening experiments, which allows an understanding of direct growth responses. Another limitation to interpretation is that a major source of disturbance at study sites, ubiquitous grazing by cattle,

Table 5 Responses of woody plant density to burning treatments

Woody plant species	Response to burning (disturbance)
Invasive shrubs	
Cryptostegia grandiflora	-41 ($3.65^{\sim}$)
Ziziphus mauritiana	(2.19^{ns})
Lantana camara	(1.06^{ns})
Solanaum torvum	(0.25^{ns})
Native trees and shrubs	
Legumes	(0.54^{ns})
Acacia aulacocarpa	-71 ($3.58^{\sim}$)
Acacia holosericea	$+514$ (4.06^{*})
Acacia salicina	$+959$ (5.12^{*})$^{\#}$
Eucalypt trees	(0.97^{ns})
Subdominant non-eucalypts	(1.16^{ns})
Shrubs	(0.78^{ns})
Riparian trees	(0.95^{ns})
Riparian subdominants	(1.05^{ns})

Note: *F* value and statistical significance from ANOVA results are shown in parentheses. For species that had significant changes in density in response to burning treatment, mean values before and after fire application were used to calculate a percentage response relative to the unburnt control (bold text).

was not controlled directly within this experimental design (although previous studies indicate that fire temporarily increases impacts by cattle on herbaceous vegetation; (Ash et al., 1982; Winter 1987; Fuhlendorf et al., 2006). Nevertheless, interpretations based on resource and disturbance responses suggest that invader species adopted differing functional strategies (Fig. 3). Invasive grasses, including the dominant savanna grass species *Bothriochloa pertusa*, responded positively to resource addition and weakly negatively or not at all to increased disturbance (fire) (Table 4), indicating a C-strategy. However, this species is known to respond positively and strongly to high cattle grazing disturbance from a number of studies (Ash et al., 1997; Ash and McIvor, 1998; McIvor, 2006), and *B. pertusa* may rely on this disturbance to invade and persist in north Australian savanna vegetation. These additional data suggest that invasive grasses may be competitor-ruderal strategists rather than strong competitor species as suggested by the results of this study in isolation (Table 4, Fig. 3). The invasive shrub *Cryptostegia grandiflora* responded negatively to increased disturbance (Table 5), and although
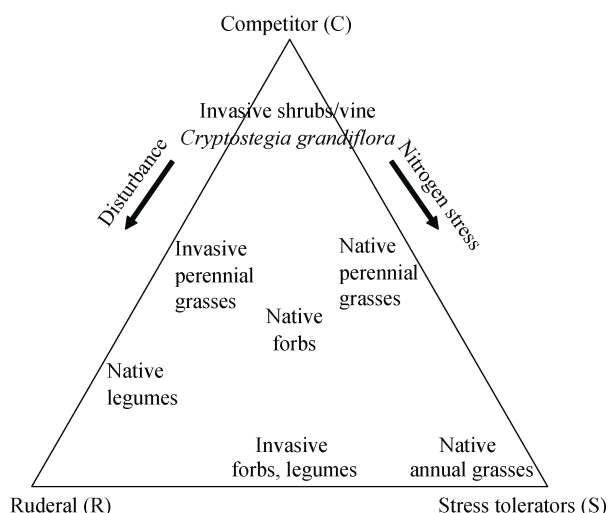
Fig. 3 Hypothesised plant strategies among invasive and native resident species in Australian savanna woodland herbaceous assemblages based on a field experiment

no direct evidence on resource response is presented here, higher density in more fertile riparian parts of the landscape (Grice, 1996; Radford et al., 2008) suggests a positive response to elevated resources. These data suggest a competitor strategy (Fig. 3). Invasive forb species including *Sida cordifolia* and *Richardia brasiliensis* showed a negative response to increased plant available resources and a sometimes positive response to burning disturbance in low resource years (Table 4). These responses suggest a ruderal-stress tolerant strategy for invasive forbs (Fig. 3). Only one invasive legume showed evidence of a positive response to disturbance after below average rainfall (Table 4), suggesting a ruderal-stress tolerant strategy (Fig. 3). Native plant groups differed in functional responses from invaders and from each other. Native tussock grasses responded negatively to resource increases in high rainfall years and not to increased disturbance (Table 4). Previous work suggests that native tussock grasses in northeastern Australian tropical savannas generally respond negatively to grazing disturbance (Ash et al., 1997; Ash and McIvor, 1998; McIvor, 2006), which was not controlled in this study area. Dominance by these native grasses in non-disturbed (ungrazed) environments (e.g. McIvor, 2006) suggests these species may adopt a stress tolerant-competitor strategy (Fig. 3), although it is unclear how competitive native grasses are in the absence of

significant grazing disturbance. Native legumes responded positively to resources and to disturbance in high resource years (Table 4), but remained subordinate to invasive grasses, suggesting a mainly ruderal and partially competitive strategy (Fig. 3). Native forbs responded positively to resources and not to disturbance (Table 4), but remained competitively subordinate (Radford et al., 2008), suggesting an intermediate C-S-R strategy (Fig. 3). Native annual grasses showed a negative response to disturbance but only in the low resource year (Table 4), suggesting these may be stress tolerant species (Fig. 3).

It is difficult to assign woody native species to strategies due to a lack of data on resource responses in this study. I have therefore not included most of these species in the plant strategy analysis. However, most native woody species clearly were tolerant of burning disturbance, whereas a number of *Acacia* spp. both benefited from fire in terms of recruitment and had negative responses due to tree mortality with some burning treatments (Radford et al., 2008).

3 Functional divergence among invaders and with native species

Both case studies indicated that invaders differed from one another in terms of their functional responses to increases in resources and disturbance. The invasive asteraceae *H. lepidulum* showed a negative response to resource enrichment that contrasted with the response of invasive grasses (Radford et al., 2010). *H. lepidulum* showed little evidence of a disturbance response, which also contrasted with invasive grasses and forbs (Radford et al., 2010). Glasshouse studies supported this differentiation between invasive species (Radford et al., 2006, 2007, 2009). In a related study, growth and competition responses under nutrient gradients differed between the invasive forb *H. lepidulum* and the invasive grass *A. stolonifera* in the presence and absence of soil mycorrhiza (Roberts et al., 2009). Similarly for savanna functional groups, invasive grasses showed a positive response to elevated resources whereas invasive forbs showed a negative response. The invasive woody vine *C. grandiflora* showed a strongly negative response to enhanced

fire/grazing disturbance (see also Grice, 1996, 1997), the invasive grass *B. pertusa* showed a weakly negative response, and other invasive groups (e.g. forbs and legumes) showed no response. These findings provide evidence that invasive species do not necessarily respond positively to disturbance as assumed in the fluctuating resource hypothesis (Davis et al., 2000).

Rather than the fluctuating resource hypothesis these data provide support for the novel niche hypothesis for plant invasions (Hierro et al., 2005). In both temperate (Radford et al., 2006, 2007, 2009; Roberts et al., 2009; Radford et al., 2010) and tropical case studies (Radford et al., 2008), native species had different plant strategies than invasive species. This observation suggests that natives and invaders occupy different resource acquisition and disturbance niche space within the temperate and tropical savanna ecosystems studied here. These results also suggest that invaders and natives often differ in how they respond to increases in resources, in contrast with the findings of Huston (2004).

3.1 No support for generality of the fluctuating resource hypothesis

Research presented here does not provide support for the fluctuating resource hypothesis (Davis et al., 2000) as a unifying theory in plant invasion ecology. This study instead supports the finding of increasing numbers of studies that different functional responses among plant species can lead to invasion (Daehler, 2003; Vila and Weiner, 2004; Vila et al., 2004; Hierro et al., 2005; Radford et al., 2006, 2010; Funk and Vitousek, 2007; Lambdon et al., 2008; Quiroz et al., 2011; Perkins et al., 2011; Hulme and Barrett, 2012; Moles et al., 2012; Richardson and Pysek, 2012). These studies suggest that invasion syndromes differ widely depending on species and functional plant type, and also on the environmental context within which the invasion occurs. In order to make progress in understanding the causal factors behind plant invasion in differing contexts, future research should aim to elucidate invasion functional pathways within those environments (Radford and Cousens, 2000; Radford et al., 2010; Perkins et al., 2012).

4 Conclusions

Invasive species respond differently to resource availability and disturbance (Lambdon et al., 2008; Radford et al., 2010, Perkins et al., 2011; Moles et al., 2012), therefore making it difficult to predict how they will respond to the effects of climate change. At this stage, our understanding of what allows invasion in different habitats and biomes, for instance savannas with low- and temperate grasslands with high invasibility (Lonsdale, 1999), is insufficient to allow predictions of how changed processes affecting resource availability or disturbance regimes will influence overall invasion patterns. As with invaders at the present time, different resource or disturbance scenarios associated with global change will result in different invasive community outcomes, depending on the context. Greatest progress towards prediction is likely where a high level of functional understanding of processes leading to invasions is available through experimentation. It also will be necessary for climate models associated with these regions to have high degrees of confidence if prediction of invasion response is to be tenable.

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