# Functional group identity does not predict invader impacts: differential effects of nitrogen-fixing exotic plants on ecosystem function

Stephanie G. Yelenik<sup>1,2,\*</sup>, William D. Stock<sup>3,4</sup> & David M. Richardson<sup>1,5</sup>

<sup>1</sup>Institute for Plant Conservation, University of Cape Town, Rondebosch, 7701, South Africa; <sup>2</sup>Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, 93106, USA; <sup>3</sup>Botany Department, University of Cape Town, Rondebosch, 7701, South Africa; <sup>4</sup>Centre for Ecosystem Management, Edith Cowen University, Joondalup, 6027, WA, Australia; <sup>5</sup>Centre for Invasion Biology, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa; \*Author for correspondence (e-mail: yelenik@ lifesci.ucsb.edu)

Received 18 October 2005; accepted in revised form 20 January 2006

Key words: Acacia saligna, available soil nitrogen, exotic plants, fynbos, litter decomposition, Lupinus luteus, organic soil nitrogen, South Africa

## Abstract

The introduction of exotic plants can have large impacts on ecosystem functions such as soil nutrient cycling. Since these impacts result from differences in traits between the exotic and resident species, novel physiological traits such as N cycling may cause large alterations in ecosystem function. It is unclear, however, whether all members of a given functional group will have the same ecosystem effects. Here we look at a within functional group comparison to test whether an annual (Lupinus luteus) and a perennial (Acacia saligna) N-fixing exotic species cause the same effects on soil N cycling in the fynbos vegetation of South Africa. We measured litterfall quantity and quality, and soil total nitrogen and organic matter for each vegetation type as well. Available nitrogen was quantified using ion exchange resin bags monthly for 1 year. We used microcosms to evaluate litter decomposition. Although both exotic species increased the available nitrogen in the soil, only Acacia increased the total soil N and organic matter. This could be explained by the slow decomposition of Acacia litter in the microcosm study, despite the fact that Acacia and Lupinus litter contained equivalent N concentrations. Presumably, low carbon quality of Acacia litter slows its decomposition in soil, resulting in retention of organic nitrogen in Acacia stands after clearing for restoration purposes. The differences in long term impacts of these annual and perennial species highlight the fact that not all N-fixing exotic species exert equivalent impacts. Ecologists should consider multiple traits rather than broadly defined functional groups alone when predicting invader impacts.

## Introduction

Given that exotic species can have severe impacts on the ecosystems they invade (Vitousek et al. 1997), but that only a small fraction actually exert these large impacts (Williamson and Fitter 1996), ecologists would benefit from a better understanding of which invaders exert significant effects and of the mechanisms by which they do so. A popular approach to understanding plant impacts on ecosystems is to group species into discrete functional groups (Chapin 1993). Yet this approach is not without criticism (Eviner 2004). Our goal here is to see if the ecosystem impacts of plant species from within the same functional group are better understood from a multiple trait standpoint. 118

Among the best studied invader impacts are those involving ecosystem processes. Invasions by exotic plants can alter nitrogen cycling (Vitousek and Walker 1989; Stock et al. 1995; Maron and Jefferies 1999; Yelenik et al. 2004), carbon cycling (Vinton and Burke 1995; Gill and Burke 1999), hydrology (van Wilgen et al. 1998), and fire regimes (D'Antonio and Vitousek 1992). These changes in ecosystem function are of particular concern because of the potential of these shifts in ecosystem function to further increase the abundance of the invader (i.e. a positive feedback; Vinton and Burke 1995; Callaway et al. 2004), or to facilitate invasion by other exotic species (Maron and Connors 1996).

Since impacts on ecosystem function result from differences in traits between the exotic and resident species, the functional group concept has been thought to be useful to predicting those species most likely to affect ecosystem function (Chapin et al. 1994). Theoretically, grouping together species with similar physiological or life history traits in functional groups can allow us to generalize how exotic plants affect ecosystem functioning in their new environment (Eviner 2004).

A recent review found that the only discrete invader trait that consistently changes nutrient cycling is the ability to fix nitrogen (Ehrenfeld 2003). Examples of nitrogen-fixers altering N cycling include Myrica faya in Hawaii (Vitousek and Walker 1989), Lupinus arboreus in California (Maron and Conners 1996; Pickart et al. 1998; Maron and Jefferies 1999), Cytisus scoparius in California (Haubensak and Parker 2004) and Acacia species in South Africa (Stock et al. 1995; Yelenik et al. 2004). Although it is tempting to assume that the effects of all nitrogen fixing invaders will be equivalent, nitrogen fixing species vary widely in other life history traits (e.g. annual vs. perennial, woody vs. herbaceous, early season vs. late season, etc.) that may have very different long-term effects on soil nitrogen cycling (Corbin and D'Antonio 2004).

Species identity within functional groups may be a more important determinant of ecosystem level impacts than functional groups themselves (Hooper and Vitousek 1998; Wardle et al. 2003). Indeed, some within functional group comparisons have corroborated this idea. For example, Wedin and Tilman (1990) found that different perennial grass species differentially altered nitrogen mineralization rates. Wardle et al. (1998) found that within various functional groups, shorter-lived, smaller species tended to concentrate more nitrogen in their tissue and decompose faster, potentially altering nitrogen cycles. Therefore, it may be necessary to incorporate multiple plant traits to predict the potential effects of exotic species on ecosystems (Craine et al. 2002; Eviner and Chapin 2003).

Here, we quantify the extent to which two N-fixing exotic plants alter N cycling regimes in South African fynbos. In this system, many woody invaders alter nitrogen (Stock et al. 1995; Yelenik et al. 2004), phosphorus (Witkowski and Mitchell 1987), and water cycles (Le Maitre et al. 1996). We have previously shown that one of our study species, Acacia saligna (Labill.) Wendl., an Australian woody perennial shrub, increases total and available nitrogen in the soil through increased inputs of N rich litter (Yelenik et al. 2004). Acceleration of the nitrogen cycle poses a particularly large threat to fynbos vegetation due to the adaptations of fynbos shrubs to low N, and the nitrophilous nature of many of its invaders (Witkowski 1991; Yelenik et al. 2004). We compared the effect of the long-lived woody acacia to another nitrogen fixing exotic, Lupinus luteus L., a Mediterranean herbaceous annual. Since the lupine is smaller, shorter lived, and possesses a higher relative growth rate, we hypothesized that it produces more decomposable litter than acacia (Wardle et al. 1998), and might therefore alter nitrogen cycling differently. To examine this, we quantified how lupine and acacia alter available inorganic soil nitrogen, total soil nitrogen pools, and how these species differ in litter quality, quantity, and decomposability. We also review the effects of alien N-fixing plants on soil properties to show that the impacts of woody N-fixing invaders result both from their nitrogen-fixing status and their longevity.

## Materials and methods

We conducted fieldwork at Riverlands Nature Reserve, 63 km north of Cape Town, South Africa. The native vegetation is broadly classified as acid sandplain lowland fynbos (Moll et al. 1984) that consists of sparse evergreen shrubs and Restionaceae. Riverlands has a Mediterranean climate, with hot dry summers, cool wet winters, and an annual average precipitation of 260.1 mm/y. The reserve is comprised of a patchwork landscape including uninvaded fynbos communities, fallow fields, and vegetation dominated by invasive alien species, especially Acacia saligna. (for a more detailed description see Yelenik et al. 2004). Using aerial photographs, we determined that Acacia saligna (acacia hereafter), which in 1995 covered 300 ha, dispersed into undisturbed fynbos from a neighboring plantation before 1968. Fields that are currently fallow were cultivated between 1968 and 1985. These contained stands of Lupinus luteus (lupine hereafter) interspersed with stands of exotic annual (Avena fatua, Lolium perenne) and native perennial grasses (mainly Cynodon dactylon) and annual forbs.

To compare the effects of two different Nfixing alien invasive species to appropriate reference areas, we sampled within four vegetation types: lupine in old fields, grass in old fields, acacia thicket on untilled land, and uninvaded fynbos. Although the lupine fields were once fynbos vegetation, we were concerned that differences in nitrogen cycling under acacia versus lupine would be to some degree a result of past tillage. Thus, while we assess the N-fixing impacts of acacia by comparing N cycling under it to that in native fynbos vegetation, we assess the impact of lupine by comparing it to grass areas within the same fields. We then can determine the differences between the two N-fixing plants on soils by comparing the size of effects on non N-fixing vegetation.

Within each vegetation type we established three different plots with 4 sub-plots each. Subplots were  $3 \times 3$  m and, except for the fynbos vegetation type, randomly located in areas that were nearly (about 90%) monotypic for the vegetation type in question. We centered each fynbos sub-plot around individuals of the dominant proteoid shrub species [*Protea scolymocephela* L. or *Leucospermum parile* (Salisb. ex Knight)], offering the closest native life history comparison to acacia (Yelenik et al. 2004).

To measure litterfall in fynbos and acacia thickets, we placed four mesh-bottom litter traps  $(20 \times 16 \text{ cm})$  in each of the sub-plots in February 1999. Litter was allowed to collect in the traps for three months before it was harvested, dried for 48 h at 80 °C, weighed, and coarse ground through a 1 mm mesh. We collected litter samples four times to complete one annual cycle, after which the ground samples were bulked. Samples of standing biomass were taken in lupine and grass plots in December 1998 (the beginning of summer, after plant senescence), dried, weighed, and coarse ground as above. Lupine seeds were excluded from measures of litterfall and litter N. Subsamples of litter were ground to a fine powder using a mixer mill (Retsch Inc., Haan, Germany) and analyzed for total N using a Kjeldahl digest with 0.1 g plant material and subsequent colorimetric determination of ammonium (Stock and Lewis 1986).

We assessed an integrated measure of inorganic N availability throughout one full year for each of the four vegetation types using ion exchange resin (IER) bags following the protocols described by Yelenik et al. (2004). Soil samples for total N, pH, and organic matter were taken with a 7 cm deep, 5 cm diameter soil core within each sub-plot, air dried and sieved to 2 mm before analysis. Total N was analyzed as above with 1 g soil. Soil pH was measured using a WTW pH meter (Hoskin Scientific, Vancouver, Canada) in slurries created by shaking 20 g of soil material in 50 ml 0.01 M CaCl<sub>2</sub>·2H<sub>2</sub>O for 30 minutes. We quantified percent organic matter as percent mass lost after combustion of soils at 420 °C in a muffle furnace. Soil samples were sent to Matrolab (Brakenfell, South Africa) for analysis of  $Na^+$ ,  $K^+$ ,  $Mg^{2+}$ , and  $Ca^{2+}$  using flame photometry and atomic absorption.

We compared potential rates of litter decomposition among vegetation types using laboratory microcosms in July 2000. Soil microbe respiration, measured as  $CO_2$  release over 1 month, was used as the quantitative measure of decomposition for each of the following five treatments: acacia, lupine, grass, and fynbos litter, and a control with soil only. Microcosms consisted of six replicates of coarse ground litter layered over 50 g of field soil. Although not equivalent, our laboratory microcosm decomposition rates correlate with actual field decomposition rates, allowing us to compare different treatments. The length of the experiment (1 month) precludes the data from being representative of full litter decomposition, but rather measures the flush of soluble organic matter during the initial phase of decomposition.

The soils for all microcosms were taken from within fynbos plots such that soil type would not confound litter decomposition results. Soil cores were taken to a depth of 7 cm, air dried, and homogenized. In order to measure water holding capacity (WHC) of the soil mixture we placed 50 g oven dried soil into a glass funnel lined with glass wool under a Whatman #1 filter. Soil was thoroughly wetted, capped to prevent evaporation, left for 72 h, and reweighed. The resultant WHC, 19.23% (±0.001), was then approximately halved to 10% to be used in the microcosms. Glass jars (100 ml) with screw caps were filled with 50 g oven dried soil and 5 ml of distilled water to achieve 50% WHC. Jars were left with caps over, but unscrewed, for 48 h in order to retain moisture but release the initial  $CO_2$ flush caused by stimulation of soil microbes. After 48 h we added a 1 cm layer of coarse ground litter, with each microcosm receiving litter from a different replicate sub-plot (as described above). A 10 ml glass vial with 8 ml of 0.6 M NaOH was placed inside each microcosm before it was sealed and placed in a 25 °C incubation chamber. Vials of NaOH were switched daily for 1 week and then on days 9, 11, 15, 19, 25, and 31 of the experiment. After being taken from the microcosm, vials were capped until they were titrated with a phenolphthalein indicator and HCl (Rowell 1994).

Prior to analysis, data from the four sub-plots were averaged to give three plot observations in each treatment (fynbos, grass, lupine, and acacia). We used natural log transformations of the data to correct for homoscedasticity. Percentage data (organic matter) were arcsine transformed. Variables were analyzed using one-way analysis of variance (ANOVA) and post-hoc Tukey tests. Data from the decomposition experiment were analyzed with a repeated measures ANOVA and post-hoc Tukey tests.

### Results

In order to compare the effects of the different N-fixers on nitrogen cycling it was first necessary to compare each N-fixer to its reference non Nfixing community. Therefore, for each quantitive measure of ecosystem function, we will first compare acacia to fynbos, then lupine to grass, and then compare the relative changes caused by acacia and lupine. Both acacia and lupine increased inorganic available nitrogen relative to the relevant non N-fixing community that was invaded (fynbos and grass, respectively). When monthly measures of resin available nitrogen were summed over the study year, acacia plots had twice as much nitrate and 2.5 times as much ammonium as fynbos plots (Figure 1a, b). Similarly, lupine plots contained nitrate levels that were three times higher and ammonium levels that were 1.3 times higher than grass plots (Figure 1a, b).

Total soil nitrogen pools were only increased underneath acacia vegetation, which contained 10 times the amount of total N as fynbos soils (Figure 2). Soils underneath grass and lupine plots contained equivalent amounts of total N (Figure 2). Similarly, soil organic matter was greater in acacia than fynbos vegetation, but there was no difference between lupine and grass (Table 1). Soil pH, K<sup>+</sup>, and Na<sup>+</sup> did not differ significantly between vegetation types. Acacia soils exhibited significantly higher levels of Mg<sup>2+</sup> and Ca<sup>2+</sup> than fynbos vegetation, while lupine and grass soils did not differ (Table 1).

Litterfall was higher in acacia  $(404.16 \pm 35.1 \text{ g m}^{-2} \text{ y}^{-1})$  than fynbos vegetation  $(102.26 \pm 16.8 \text{ g m}^{-2} \text{ y}^{-1})$ , and the nitrogen concentration of acacia litter was 2.5 times higher than fynbos litter (Figure 3). Litterfall was greater in lupine plots  $(529.17 \pm 9.2 \text{ g m}^{-2} \text{ y}^{-1})$  than grass plots  $(268.30 \pm 19.8 \text{ g m}^{-2} \text{ y}^{-1})$ , and lupine vegetation contained more nitrogen (Figure 3).

The litter decomposition microcosms showed significant differences in  $CO_2$  release from the different litter types. Although lupine and acacia litter did not differ in their N content (Figure 3), lupine litter had rates of potential decomposition that were at least twice as fast as any of the other vegetation types (Figure 4). Acacia, grass,



*Figure 1.* (a) Nitrate and (b) ammonium availability as measured by resin extractable inorganic nitrogen in the fynbos, acacia, lupine, and grass vegetation types. Values are cumulative of monthly measurements taken over 1 year. Letters represent significant differences among vegetation types for one-way ANOVA with post-hoc Tukey tests (nitrate: F=7.28,  $P \le 0.01$ ; ammonium: F=7.17,  $P \le 0.01$ ).



*Figure 2.* Total soil nitrogen for fynbos, acacia, lupine, and grass vegetation types. Letters represent significant differences among vegetation types for one-way ANOVA with post-hoc Tukey tests (F = 10.54,  $P \le 0.01$ ).

and fynbos litter did not differ in their decomposition rates, although decomposition rates of all three species did differ significantly from soil alone (Figure 4).

#### Discussion

Although both species of N-fixing alien plant altered N cycling regimes, they did so in different ways; this could have large implications for restoration of previously invaded areas. It is also indicative of the functional group approach being inadequate to predict invader impacts on ecosystems. Both acacia and lupine increased N inputs to the soil through litterfall, which increases inorganic N availability in the soil and potentially impacts plant community dynamics. Only acacia, however, increased the total soil N pool, suggesting that species differentially alter soil N dynamics. The long term effects of these species on nitrogen cycling and community dynamics could therefore be very different. Specifically, the increased N cycling regime under perennial acacia stands may remain problematic following its removal for a longer period than the changes caused by the annual lupine.

This and other work demonstrate that the invasion of *Acacia saligna* into the South African fynbos is accompanied by shifts in nutrient cycling, most notably nitrogen (Yelenik et al. 2004). Acacia produces larger quantities of litter with a higher N content than fynbos vegetation, increasing N return to the soil (Figure 3, Table 1). Soil underneath acacia has more organic matter and higher levels of total N, and rates of inorganic N availability are elevated (Figures 1 and 2, Table 1). Acacia also concentrates levels of soil  $Ca^{2+}$  and  $Mg^{2+}$  (Table 1) probably through redistribution from deeper soil layers.

Lupinus luteus also alters soil N cycling within fynbos old-fields. Most notably, resin bags suggest that available soil nitrate is higher under lupine than grass vegetation (Figure 1a). Lupine has more standing biomass than the grass vegetation type and its litter contains twice as much nitrogen as grass (Figure 3), leading to higher rates of return of nitrogen from litter to the soil (Table 1). It is surprising, therefore, that levels of soil organic matter and total nitrogen are similar under lupine and grass vegetation. This is probably due to the faster rate at which lupine litter decomposes relative to grass litter (Figure 4) because of its higher nitrogen concentration (Figure 3). Numerous studies have shown that C:N of leaf litter correlates with decomposition rates

	Fynbos	Acacia	Grass	Lupine
Soil organic matter (%)	$0.8\pm0.02a$	$2.5\pm0.34b$	$1.4 \pm 0.28a$	$1.1 \pm 0.29a$
Soil pH	$4.6 \pm 0.1$	$4.8 \pm 0.1$	$4.8 \pm 0.1$	$4.9 \pm 0.1$
Soil $Ca^{2+}$ ( $\mu g/g$ )	$105.2 \pm 13.8a$	$363.8 \pm 63.8 b$	$214.2 \pm 36.1b$	$192.4 \pm 49.2 ab$
Soil $Mg^{2+}$ (ppm)	$18.6 \pm 1.3a$	$111.1 \pm 26.9b$	$41.8 \pm 8.5 ab$	$37.6 \pm 14.2a$
Soil Na <sup>+</sup> (ppm)	$10.9 \pm 0.5$	$15.9 \pm 3.2$	$19.2 \pm 4.5$	$12.6 \pm 2.7$
Soil K <sup>+</sup> (ppm)	$17.0\pm1.7$	$29.8\pm3.8$	$20.6\pm4.2$	$25.9\pm4.9$

Table 1. Soil and litter properties sampled for exotic and native species.

Letters represent significant differences ( $P \le 0.05$ ) for one-way ANOVAS with post-hoc Tukey tests.

and net N mineralization rates (Melillo et al. 1982; Wedin and Tilman 1990; Vinton and Burke 1995; Evans et al. 2001). Thus, although more



*Figure 3.* Litter nitrogen concentration for fynbos, acacia, lupine, and grass vegetation types. Letters represent significant differences among vegetation types for one-way ANOVA with post-hoc Tukey tests (F = 20.65,  $P \le 0.01$ ).



*Figure 4.* Cumulative decomposition, measured as  $CO_2$  release by soil microbes, for fynbos, grass, lupine, acacia litter, and a control (soil only). Letters represent significant differences among litter types for repeated measures ANOVA with post-hoc Tukey tests (F = 111.22,  $P \le 0.01$ ).

nitrogen is returning to the soil under lupine, and inorganic nitrogen is increasing, total soil N may not increase under lupine due to the fast rate at which it decomposes and moves into the next generation of plants.

When comparing the magnitude of effects that acacia and lupine have on reference vegetation types, it becomes clear that both N-fixing alien plants increase available nitrogen (Figure 1a, b), but only acacia increases total N pools (Figure 2). This is despite the fact that lupine deposits larger quantities of litter each year than acacia. While it is possible that different microbial communities, differential plant uptake, or slightly different abiotic conditions may have been responsible for this difference, we believe that faster decomposition rates of lupine litter are responsible. Microcosm studies demonstrated that lupine litter caused more  $CO_2$  to be respired than acacia, in spite of similarly high N concentrations relative to non-fixing N litter (Figures 3 and 4). It is probable that highly labile N is causing faster decomposition and higher rates of nitrogen cycling through the lupine system, whereas the high N concentrations in acacia litter are tied up in low quality carbon, thereby adding to the organic N pool in the acacia soil. It might be the different life history strategies of the two species (herbaceous annual vs. woody perennial) that explain why lupine has much higher quality litter, from the decomposers point of view, than acacia.

Previous studies of litter decomposition in the fynbos have shown that acacia litter does not immobilize nitrogen, at least in the first year (Witkowski 1991). This suggests that microbial N limitation should not slow the rates of decomposition and N mineralization in acacia litter. Rather, microbial C limitation, due to low carbon quality in the litter, may create a lag in organic

123

N decomposition under acacia stands. Secondary carbon compounds, lignins, or polyphenols slow litter decomposition even when microbes are not N limited (Melillo et al. 1982; Hättenschwiler and Vitousek 2000), and this type of low quality carbon may lead to the slower decomposition rates in acacia litter. Knops et al. (2002) postulate that large inputs of low quality carbon can cause nitrogen to be tied up in the microbial biomass pool, leading to high soil total N. This mechanism may be responsible for the lack of soil total N seen in the lupine soil as compared to acacia, despite more organic N being returned each year through litter inputs. This pattern was also seen under Hieracium pilosella patches in New Zealand: although the exotic had higher tissue N, it was postulated that higher levels of polyphenols and lignin led to an increase in soil and microbial C pools and a decrease in N mineralization (Scott et al. 2001).

The efficacy of restoration attempts that include N-fixing invader removal in low N adapted systems such as fynbos will depend on how long elevated levels of nitrogen persist. Native species in low-N systems frequently have slow growth rates that do not respond to elevated nutrient levels (Stock and Lewis 1984; Witkowski et al. 1990) and may actually be negatively affected by added nitrogen (Lamb and Klaussner 1988; Witkowski 1989). Therefore, higher levels of available N in soil may be facilitating secondary invasions by weedy nitrophilous grass species at Riverlands (P. Holmes, personal communication) such as Ehrharta calycina, which was found to be N-limited in a previous study (Yelenik et al. 2004). This trend was also observed with different species of weedy annual grasses in California after the clearing of N-fixing Lupinus arboreus individuals (Maron and Conners 1996).

After these species are removed, the equivalent amount of additional  $NH_4^+$  and  $NO_3^-$  in the soil from acacia and lupine (Figure 1a, b) will have similar effects on community processes in the short term. In the long term, however, acacia and lupine will have differential effects, related to whether or not total soil N has been elevated. Corbin and D'Antonio (2004) suggest that species which alter N fluxes and soil N pools simultaneously, such as *Acacia saligna*, will leave the longest legacy after exotic plant removal. This is due to the lag effect resulting in the slow, steady release of available N from the large organic N pool in the soil. Conversely, after a species such as *Lupinus luteus* is cleared, available N levels will dissipate more quickly, especially if aboveground biomass is removed in subsequent years mechanically or by fire.

Our results from comparing two species identify patterns that may be true for N-fixing invaders more generally. Woody N-fixing species may, in general, have longer lasting effects on soil N than shorter lived herbaceous species. This is due to their higher likelihood of having low quality C litter that would bind organic N for longer periods of time in microbial pools, whereas annuals or herbaceous N-fixers should have more decomposable litter (Wardle et al. 1998). Vinton and Burke (1995), in studies of non N-fixing plants, found that grouping species as annual vs. perennial predicted their effects on N cycling in soils. Indeed, we have found that all woody perennial N-fixing alien plants for which data is available increase both total N and available N in soils (Table 2). In addition, there is evidence that the effects of woody perennial invasive persist after they are cleared: Lupinus arboreus removal plots still showed higher levels of total soil nitrogen 5 years after clearing (Maron and Jeffries 1999). Nitrogen mineralization rates in stands cleared of Acacia saligna did not differ from rates under intact stands 1 year post-clearing (Yelenik et al. 2004). Our results, however, only include two species of N-fixing plant, and our compiled results for alien N-fixers only include one annual species (Table 2). Therefore a more complete survey of alien N-fixing species will be needed before we can definitively show that these traits ultimately lead to differential long term effects of soil nitrogen inputs.

Our data demonstrate that two alien species, both of which are N-fixers, can have differential effects on ecosystem function. In this system, both N-fixers altered nitrogen cycling, but the long term effects of the two species after they are cleared will probably be very different. This study therefore supports the emerging idea that multiple plant traits, particularly ones that do not covary, provide better predictors of ecosystem level effects of plant species (Eviner and Chapin 2003; Eviner 2004). In this case, the

Species	Growth form	Location	Total soil N	Available N
Myrica faya	Woody perennial	Hawaii, USA	Increased <sup>1</sup>	Increased <sup>1</sup>
Lupinus arboreus	Woody perennial	California, USA	Increased <sup>2</sup>	Increased <sup>2,3,4</sup>
Cytisus scoparius	Woody perennial	California, USA	Increased <sup>5</sup>	Increased <sup>5</sup>
Acacia cyclops	Woody perennial	Western Cape, South Africa	Increased <sup>6,7</sup>	Increased <sup>7</sup>
Acacia saligna	Woody perennial	Western Cape, South Africa	Increased <sup>6,7,8,9</sup>	Increased <sup>8,9</sup>
Lupinus luteus	Annual herb	Western Cape, South Africa	No difference <sup>9</sup>	Increased <sup>9</sup>

Table 2. Invasive N-fixing plants for which data on total soil total N and available N (under invasive relative to native vegetation) could be obtained.

References: (1) Vitousek and Walker (1989), (2) Maron and Jefferies (1999), (3) Pickart et al. (1998), (4) Maron and Conners (1996), (5) Haubensak and Parker (2004), (6) Witkowski (1991), (7) Stock et al. (1995), (8) Yelenik et al. (2004) and (9) present study.

annual or perennial nature of nitrogen fixing plants seems to delineate those exotic species which will have effects lasting longer.

#### Acknowledgements

We thank P. Holmes, W. de Vlam, and D. Rousseau for help with the field project, K. Wienand for help in the lab, as well as J. Levine, P. Adler, J. Hille Ris Lambers, and M. Cadotte for help with the manuscript. Funding for this work was provided by the University of Cape Town Research Committee and the National Research Foundation (W.D. Stock and D.M. Richardson) and the Institute for Plant Conservation (D.M. Richardson). D.M.R. acknowledges support from the DST Centre of Excellence for Invasion Biology.

#### References

- Callaway RM, Thelen GC, Rodriguez A and Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731–733
- Chapin FS III (1993) Functional role of growth forms in ecosystem and global processes. In: Ehleringer JR and Field CB (eds) Scaling Physiological Processes: Leaf to Globe, pp 287–312. Academic Press, San Diego, CA
- Chapin FS III, Reynolds HL, D'Antonio CM and Eckhart VM (1994) The functional role of species in terrestrial ecosystems. In: Walker B and Steffen W (eds) International Geosphere–Biosphere Programme Book Series, Vol. 2: Global Change and Terrestrial Ecosystems, pp 403–428. Cambridge University Press
- Corbin JD and D'Antonio CM (2004) Effects of exotic species on soil nitrogen cycling: implications for restoration. Weed Technology 18: 1464–1467
- Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M and Knops J (2002) Functional traits, productivity and effects on

nitrogen cycling of 33 grassland species. Functional Ecology 16: 563–574

- D'Antonio CM and Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63–87
- Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6: 503–523
- Evans RD, Rimer R, Sperry L and Belnap J (2001) Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecological Applications 11: 1301–1310
- Eviner VT (2004) Plant traits that influence ecosystem processes vary independently among species. Ecology 85: 2215–2229
- Eviner VT and Chapin FS (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology Evolution and Systematics 34: 455–485
- Gill RA and Burke IC (1999) Ecosystem consequences of plant life form changes at three sites in the Semiarid United States. Oecologia 121: 551–563
- Hättenschwiler S and Vitousek PM (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends in Ecology and Evolution 15: 238–243
- Haubensak KA and Parker IM (2004) Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington (USA). Plant Ecology 175: 71–79
- Hooper DU and Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecological Monographs 68: 121–149
- Knops JMH, Bradley KL and Wedin DA (2002) Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecology Letters 5: 454–466
- Lamb AJ and Klaussner E (1988) Response of the fynbos shrubs *Protea repens* and *Erica plukenetii* to low-levels of nitrogen and phosphorus applications. South African Journal of Botany 54: 558–564
- Le Maitre DC, van Wilgen BW, Chapman RA and Mckelly DH (1996) Invasive plants and water resources in the Western Cape province, South Africa: modeling the consequences of a lack of management. Journal of Applied Ecology 33: 161–172
- Maron JL and Conners PG (1996) A native nitrogen-fixing shrub facilitates weed invasion. Oecologia 105: 302–312
- Maron JL and Jefferies RL (1999) Bush lupine mortality, altered resource availability, and alternative stable states. Ecology 80: 443–454

- Melillo JM, Aber JD and Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621–626
- Moll EJ, Campbell BM, Cowling RM, Bossi L, Jarman ML and Boucher C (1984) A description of the major vegetation categories in and adjacent to the fynbos biome. South African National Scientific Programmes Report No. 83. CSIR, Pretoria, South Africa
- Pickart AJ, Miller LM and Duebendorfer TE (1998) Yellow bush lupine invasion in northern California coastal dunes – I. Ecological impacts and manual restoration techniques. Restoration Ecology 6: 59–68
- Rowell DL (1994) Air in soils supply and demand. In: Soil Science: Methods and Applications. Longman Scientific and Technical, Essex, pp 109–129
- Scott NA, Saggar S and McIntosh PD (2001) Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. Ecological Applications 11: 1311–1322
- Stock WD and Lewis OAM (1986) Atmospheric input of nitrogen to a coastal fynbos ecosystem of the Southwestern Cape province, South Africa. South African Journal of Botany 52: 273–276
- Stock WD and Lewis OAM (1984) Uptake and assimilation of nitrate and ammonium by an evergreen fynbos shrub species *Protea repens* L (Proteaceae). New Phytologist 97: 261–268
- Stock WD, Wienand KT and Baker AC (1995) Impacts of invading N<sub>2</sub>-fixing Acacia species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and <sup>15</sup>N natural abundance values. Oecologia 101: 375–382
- van Wilgen BW, Le Maitre DC and Cowling RM (1998) Ecosystem services, efficiency, sustainability and equity: South Africa's Working for Water Programme. Trends in Ecology and Evolution 13: 378
- Vinton MA and Burke IC (1995) Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76: 1116–1133

- Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16
- Vitousek PM and Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59: 247–265
- Wardle DA, Barker GM, Bonner KI and Nicholson KS (1998) Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects. Journal of Ecology 86: 405– 420
- Wardle DA, Yeates GW, Williamson W and Bonner KI (2003) The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups. Oikos 102: 45–56
- Wedin DA and Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433–441
- Williamson M and Fitter A (1996) The varying success of invaders. Ecology 77: 1661–1666
- Witkowski ETF and Mitchell DT (1987) Variations in soil phosphorus in the fynbos biome, South Africa. Journal of Ecology 75: 1159–1171
- Witkowski ETF (1989) Effects of nutrients on the distribution of dry mass, nitrogen and phosphorus in seedlings of *Protea repens* (L) L (Proteaceae). New Phytologist 112: 81–487
- Witkowski ETF (1991) Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. Journal of Applied Ecology 28: 1–15
- Witkowski ETF, Mitchell DT and Stock WD (1990) Response of a Cape fynbos ecosystem to nutrient additions – shoot growth and nutrient contents of a proteoid (*Leucospermum parile*) and an ericoid (*Phylica cephalantha*) evergreen shrub. Acta Oecologica-International Journal of Ecology 11: 311–326
- Yelenik SG, Stock WD and Richardson DM (2004) Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. Restoration Ecology 12: 44–51