Woody native and exotic species respond differently to New Zealand dryland soil nutrient and moisture gradients

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Abstract: In many New Zealand dryland grass and shrubland areas, native and exotic woody species are invading, but it is unclear what environmental factors favour native dominance. One possibility is that differences in soil nutrients and moisture, or a combination of these factors, differentially affect the growth and hence invasive potential of native and exotic woody dryland species. We tested the prediction that native woody species outperform exotic woody species under low-nutrient and dry soil conditions. In a pot experiment, we measured the relative growth rate and root:shoot ratio of six exotic and eight native species across moisture and field-derived soil nutrient gradients. Using plot survey data from the South Island, New Zealand, we then modelled the relative occurrence of exotic woody species, using derived measures of temperature, soil nitrogen, moisture and disturbance. All seedling growth responses we measured were affected by soil moisture and nutrient status, and the same set of species were fastest-growing across treatments. Contrary to predictions, native and exotic woody species performed similarly in low-nutrient soils, and native species grew faster than exotic species in soils with higher total nitrogen levels. Two native woody species (*Ozothamnus leptophyllus* and *Kunzea ericoides*) performed better than all woody exotics across all nutrient and moisture levels. Survey data showed that a higher proportion of exotic woody species were present at warm, dry sites with low levels of soil nitrogen. This study suggests that exotic woody species in New Zealand drylands are not necessarily superior in their growth rates, and that rehabilitation efforts favouring high-performing native woody species may stand the best chance of creating a native-dominated shrubland.

Keywords: invasive potential; rehabilitation; relative growth rate; RGR; root:shoot ratio; seedling growth rate; soil nitrogen

Introduction

Invasion by a species into a new environment is influenced by the traits of the invader, the attributes of the receiving community, and the conditions of the environment (e.g. Crawley 1987; Rejmánek & Richardson 1996; Tecco et al. 2010). The most successful plant invaders commonly have traits that enhance success in disturbed habitats, such as rapid growth rate, early maturity, high seed production, and ready dispersal (Grotkopp & Rejmánek 2007; Pysek & Richardson 2007). In general, exotic invasive species appear to be disadvantaged over native species in low-resource systems, and invasion by exotic species is therefore more common in high- than low-resource ecosystems (e.g. Huenneke et al. 1990; Stohlgren et al. 2002; Daehler 2003). However, there is increasing evidence that this pattern does not always hold (e.g. see Funk & Vitousek 2007; Maron & Marler 2007; Funk 2008; Ordonez et al. 2010; Ordonez & Olff 2013), and many species do invade low-resource ecosystems, including grasslands and arid shrublands (Funk 2013).

Although there are many different potential nutrient limitations, nitrogen (N) and phosphorus (P) limitations are the most common. In many ecosystems, plant species may be differentially limited by N and P. In regions where water is not limited, plant invasions may be constrained by the soil nutrients (Eskelinen & Harrison 2014), but in semi-arid regions, the availability of water itself can be limiting or co-limiting by reducing the nutrient availability (see review by Funk 2013). In response to declining soil moisture, plants generally increase their relative allocation of assimilates to root compared with shoot growth (root:shoot ratio) to increase their potential water uptake and to ease transpiration loss (McDonald & Davies 1996; Funk 2013). While a higher root:shoot ratio may result in persistence during periods of scarce resources and hence provide a competitive advantage when establishing in a dry environment (Li & Wilson 1998; Chaves et al. 2003), high productivity (e.g. high growth rate) is more directly a strategy for successful competition and invasion (Vilà & Weiner 2004; Stastny et al. 2005).

In this study, we focus on the effect of soil nutrients and moisture and their interaction on the performance of native relative to exotic woody species in the New Zealand drylands. This zone lies primarily in the east of the South and North islands, and is highly influenced by the mountain rain-shadow effect, which causes low rainfall relative to evapotranspiration (Rogers et al. 2005). About half of the New Zealand dryland zone can be classed as 'arid', with the rest 'semi-arid', according to the global aridity index based on both rainfall and evapotranspiration (Kassas 1999). Originally forested, this zone was irreversibly altered by successive waves of human settlement, and related regimes of fire and grazing resulted in extensive grasslands (McGlone 2001), which have become progressively invaded by non-native species (Treskonova 1991; Rose et al. 2004). Today, woody communities are beginning to re-establish. About 28% of remaining undeveloped land in South Island drylands now supports seral shrublands that have developed without deliberate human intervention (Walker et al. 2009b). The emerging plant communities are

novel assemblages of both native and exotic woody species filtered by disturbances such as fire and mammalian grazing (e.g. rabbits, hares, possum, sheep and cattle). However, this reinvasion by native and/or exotic woody species does not occur to the same extent everywhere, and the processes governing these patterns in dryland regions remain poorly understood (Walker et al. 2009a, b).

As elsewhere, native grass and woody species in New Zealand have been suggested to be adapted to low-fertility conditions (Craine et al. 2006). This has been exemplified in shrub and forest reserves, where higher soil fertility was significantly correlated with higher exotic species richness (Timmins & Williams 1991). Hence, we predicted that in low-nutrient soils and under dry conditions, native woody species would outperform exotic species. We tested this prediction using soils and woody species from the New Zealand drylands.

First, we report the growth responses of native and exotic woody seedlings along moisture and field-derived soil nutrient gradients under glasshouse conditions. Second, using plot-based field data compiled from a variety of surveys across the South Island drylands (see Walker et al. 2009b), we modelled the relative occurrence of exotic woody species in relation to climatic factors, soil N, and disturbance. The aims were to determine: (1) how differences in soil nutrients, moisture, or a combination of these factors affect the growth and hence invasion potential of native *versus* exotic woody dryland species; (2) which native woody species are more likely to outperform exotic woody species, and under which conditions; and (3) whether the patterns of exotic woody species proportion in the field matched the patterns we expect from theory and our experimental results.

Methods

Species

We selected 16 woody plant species for the experiment on the basis of the distribution and trait data of woody species occurring in the New Zealand drylands (Walker et al. 2009b). The traits used include aspects of vigour or competitive ability, reproduction and dispersal, and tolerance of light, fire and herbivory; known to have functional relationships to patterns of occurrence in dry environments (see appendix 3 of Walker et al. (2009b) for full details). The 16 selected species represented the two most commonly recorded native and exotic woody species from each of eight principal functional groups derived from a hierarchical cluster analysis (Ward 1963) on the traits of 236 woody species (EC unpubl. data). This process ensured we (1) included the most common dryland woody species, (2) included species with diverse traits, and hence potentially different responses to treatments, and (3) minimised the similarity in traits among individuals within the exotic and native groups. All selected woody species are able to survive drought to some degree, by virtue of their commonness in the New Zealand drylands. Of this initial list of species, 14 species germinated and were included in the experiment (six exotic and eight native woody species; see Table 1).

Soils

Soils were collected in the field from six South Island sites (Fig. 1) in spring 2006, representing four orders in the New Zealand Soil Classification (Hewitt 1993). The sites were chosen to be topographically similar (slope ranging from 10 to 15°; aspect between NW and NE) and lie along the isohyet corresponding with a 600-mm annual Penman water deficit (Penman 1948; Leathwick et al. 2002). All had sparse ground cover consisting of herbaceous vegetation. At each site, we collected the top 10 cm of 'A' horizon soil from an area of approximately 1 m² from five locations, positioned c. 20 m apart in a line along the isohyet. We discarded the top centimetre of topsoil and any plant material, and measured bulk density. The samples were then amalgamated and transported to the laboratory, where they were sieved of roots and rocks to <4 mm. Soils were sterilised by autoclave and the soil microbial communities were then standardised by adding 25 ml of inoculation mix to each pot. The inoculation was obtained by aqueous extraction from samples of our seedling-raising medium, and our six non-sterilised soils, and hence contained a mixture of their soil microbial communities. Subsamples of soil from each site were analysed by the Environmental Chemistry Laboratory, Landcare Research, Palmerston North, for total soil N and plant-available P (Olsen P) (Blakemore et al. 1987).

Table 1. Details of the species used in this study, and summary of dry weights at harvest (root plus shoot biomass) for each species across all treatments. Plants were grown in 450-ml pots.

| Species	Species code	Native / Exotic	Dry weight (g)		
			Minimum	Mean	Maximum
Acer pseudoplatanus	Acepse	Exotic	0.069	1.182	4.200
Carmichaelia petriei	Carpet	Native	0.031	0.400	1.980
Coprosma propinqua	Coppro	Native	0.014	0.862	2.880
Cytisus scoparius	Cytsco	Exotic	0.022	1.444	4.340
Discaria toumatou	Distou	Native	0.028	0.688	2.400
Kunzea ericoides	Kuneri	Native	0.001	0.711	2.530
Lupinus arboreus	Luparb	Exotic	0.300	3.000	11.030
Olearia odorata	Oleodo	Native	0.350	2.119	5.350
Ozothamnus leptophylla	Ozolep	Native	0.008	2.421	7.660
Pinus radiata	Pinrad	Exotic	0.150	1.309	3.161
Pittosporum tenuifolium	Pitten	Native	0.0121	0.755	2.450
Rosa rubiginosa	Rosrub	Exotic	0.008	1.421	10.501
Sophora microphylla	Sopmic	Native	0.180	0.899	2.300
Ulex europaeus	Uleeur	Exotic	0.200	1.891	5.760
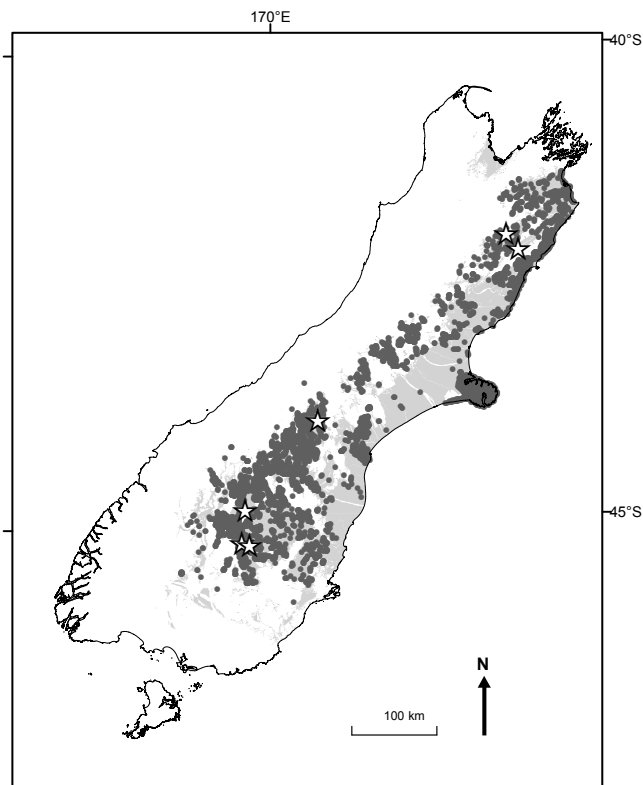
Figure 1. South Island of New Zealand showing the extent of the drylands area (light grey shading), the 3383 plots included in the analysis of the distribution of exotic woody species (grey points), and the six sites from which soils were taken for the shade-house experiment (white stars).

Moisture

Plants were grown in one of two contrasting water treatments. Each plant was in a separate pot, with a water dripper attached to an automated watering system. Controlled quantities of water were applied every 1 or 2 days. A 'dry' treatment remained close to permanent wilting point (PWP) throughout the experiment, while a 'wet' treatment was maintained at close to field capacity (FC). To facilitate accurate water application and control, FC and PWP of each potted (i.e. disturbed and processed) soil was determined (see Monks et al. (2012) for method). Unplanted pots scattered throughout the experimental set-up were weighed at least twice weekly to enable adjustment of the watering rate to compensate for day-to-day fluctuations in atmospheric moisture levels. Bulk density of the processed experimental soils was determined by measuring the volume and dry weight for each of the naturally compacted soils in pots after several dry–wet cycles. Processed soil bulk density was within 10% of the bulk density of the undisturbed soils in the field (see Monks et al. 2012).

Experimental design and harvest

The experiment was situated in a plastic-roof windbreak-walled 'shade-house' at Lincoln, New Zealand (43°38.4′ S, 172°28.6′ E). The plastic roof excluded rainfall, but the windbreak walls allowed free air movement while limiting wind speed. Light levels were at c. 60% of ambient. The experiment followed a randomised complete split-plot block design. Five blocks were installed; main plots were trays within which a full set

of species was grown in one soil with one water regime, and each individual pot within a tray was an experimental unit. Each treatment was replicated five times giving five seedlings per species per treatment combination.

Dryland-sourced seeds of all species were germinated in commercial potting mix, and seedlings at the cotyledon stage, or soon after, were washed and planted into 8 × 8 cm (450 ml) pots of all soils. Up to 3 weeks after the start of the experiment dead seedlings were replaced. After 6 months (July 2007), each seedling was cut at the root collar, and the roots were hand-washed free of soil. Roots and shoots were oven-dried at 60°C for 72 h and weighed. Pretreatment biomass was determined for a subsample of 10 representative seedlings of each species (except *Ozothamnus leptophyllus*) harvested at the set-up of the experiment, cut and oven-dried as above. For each plant harvested at the end of the experiment, relative growth rates (RGR; Bellingham et al. 2004) and root:shoot ratios were calculated. Pretreatment biomass values for *Ozothamnus leptophyllus* were constrained by lack of material and so were conservatively set to the smallest biomass at final harvest (0.008 g) for RGR calculations.

Statistical analysis

Two response variables (RGR and root:shoot ratio) were modelled using linear mixed-effects models with a Gaussian error distribution, where soil type, block, tray, and plant species were random intercepts. Soil was specifically included as a random effect to ensure that the degrees of freedom for the soil chemistry (total N and Olsen P, hereafter referred to as N and P, respectively) relationships were correctly estimated, because the soil chemistry was estimated from one-off assays on bulked soil samples ($n = 6$). We checked graphically for adherence to model assumptions, including homoscedasticity of residuals, and inspected ratios of residual sums of squares to degrees of freedom to check for overdispersion.

In each analysis a set of candidate models was used to test the fixed effects of soil moisture and nutrients. These models reflected plausible hypotheses about the relationships between the response of native and exotic species to soil moisture, soil N, and soil P. The models were primarily distinguished by the inclusion or exclusion of different interactions between soil moisture, soil nutrient status, and the indigenous or exotic origin of the species, which we sought to understand. Soil moisture was included in all RGR and root:shoot ratio models as we expected it to be a strong determinant of growth at the driest level in the experiment. We hypothesised that:

1. Soil resource limitation of any kind (whether N, P, or water) increases root:shoot ratio and decreases relative growth rates.
2. Soil moisture affects the availability of soil nutrients (N or P) and the growth response to it (Water:N interaction; Water:P interaction).
3. Native species grow faster than exotic species in low-resource soils (Native:N or Native:P interaction) or where low soil moisture causes co-limitation of nutrients (Native:N:Water or Native:P:Water interaction).

We ran a similar set of linear mixed-effect models to assess whether certain native species were more likely to outperform exotic species, and under which conditions this would occur. In these models, the response variable was RGR, Species (if present in the candidate model) was a fixed (rather than random) effect, and the Native status was removed as a fixed effect.

The plot-based distribution data (n = 3383) were analysed with a logistic generalised additive model. We modelled the proportion of woody species that were exotic species in each plot as a function of the environmental predictors mean annual temperature, mean annual rainfall, annual soil moisture deficit, and soil N in the top (0–10 cm) mineral horizon. The proportion of woody species that were exotic represented the most informative measure of exotic species 'success' that could be applied over all data, and that is comparable across environmental and ecosystem gradients. While the abundance of exotic woody species would be a better measure of their 'success' across the landscape, this could not be modelled because, in the compiled data, abundance was measured using a variety of incompatible methods (e.g. grassland, shrubland and forest methods) and a meta-analytical framework would suffer from the inherent spatial biases of different methodologies.

As discussed above, water availability and nutrient availability may affect the distribution of exotic species. In temperate regions, including New Zealand, exotic species richness has been shown to increases with temperature (Sax 2001; Stohlgren et al. 2002; Wiser & Allen 2006). The distance to the nearest road and to the nearest indigenous forest were also included in the model as they have previously been shown to affect the richness of exotic species (Moles et al. 2008; Sullivan et al. 2009).

Climatic predictor variables for each plot were obtained from modelled surfaces (mean annual temperature and soil moisture deficit from Land Environments New Zealand (Leathwick et al. 2002; mean annual rainfall from J. Leathwick unpubl., held by Landcare Research). Predicted soil N for each plot was obtained from Monks et al. (2012). For each plot, the distance to the nearest road was calculated in a geographical information system using LINZ topographical map data. The land cover database (LCDB version 3.3; Pairman 2013) was used to calculate the distance from each plot to the nearest

land parcel with indigenous forest cover in 2001 (polygons classed as 'Indigenous forest' and 'Broadleaved indigenous hardwoods'). Both distance measures were log-transformed. Correlation between any pair of variables was less than 0.8.

All models in each candidate set were fitted and then compared using the corrected Akaike Information Criterion (AICc) to determine the Kullback–Leibler (KL) best model (Burnham & Anderson 2002). The KL best model is the most parsimonious model (best fit to the data for the fewest parameters) given the candidate model set. Additional models were considered to receive substantial support if the difference between model i AICc value and that of the KL best model (ΔAICc i) was <2 (Burnham & Anderson 2002). The explained variance (r^2) is provided in the text for the KL best model only as an indication of the model fit.

All analyses were performed in R (R Core Team 2014); experimental and distribution model fitting included use of the packages *nlme* (Pinheiro et al. 2014) and *mgcv* (Wood 2011), respectively. Models are presented in graphical form by averaging the observed and fitted response variables across all levels of random effects, using the package *effects* (Fox 2003).

Results

Plants at harvest ranged from 1 mg to 11 g dry weight (Table 1) and were between 2 and 55 cm tall (data not shown). The best model for root:shoot ratio was the two-way interaction between native status and soil water (r^2 = 0.55) (Table 2). While all species had lower root:shoot ratios at higher soil moisture, the effect of soil moisture was greatest for native species. The root:shoot ratio of exotic species was higher than that of native species, regardless of soil moisture status (Fig. 2).

The two-way interaction model between native status and soil N plus an additive moisture component (r^2 = 0.68) was

Table 2. Summary of the model fits for the root:shoot ratio.

Model[1]	K[2]	AICc[3]	ΔAICc[4]	AICcWt[5]	LL[6]	Rank[7]
Nat*W	9	1134.16	0	0.55	−557.97	1
Nat*N*W	13	1137.65	3.49	0.10	−555.61	2
Nat*P*W	13	1138.05	3.89	0.08	−555.80	3
Nat+W	8	1138.40	4.24	0.07	−561.11	4
N+W	8	1138.64	4.48	0.06	−561.23	5
W	7	1138.73	4.57	0.06	−562.30	6
Nat*N+W	10	1139.49	5.32	0.04	−559.61	7
N*W	9	1139.91	5.75	0.03	−560.85	8
Nat*P+W	10	1140.21	6.05	0.03	−559.97	9
Nat*N*P+W	14	1145.00	10.84	0	−558.25	10
Nat*N*P*W	21	1149.39	15.23	0	−553.13	11

[1]For model specification, 'Nat' indicates the native/exotic status, 'N' soil nitrogen, 'W' soil water treatment, and 'A*B' is shorthand for A + B + interaction between A and B.
[2]K indicates the number of estimated parameters for each model.
[3]The Akaike Information Criterion corrected for small samples (AICc) for each model
[4]The delta AICc compared with the top-ranked model
[5]The Akaike weights ('model probabilities' sensu Burnham & Anderson (2002)). These measures indicate the level of support (i.e. weight of evidence) in favour of any given model being the most parsimonious among the candidate model set.
[6]The log-likelihood of each model
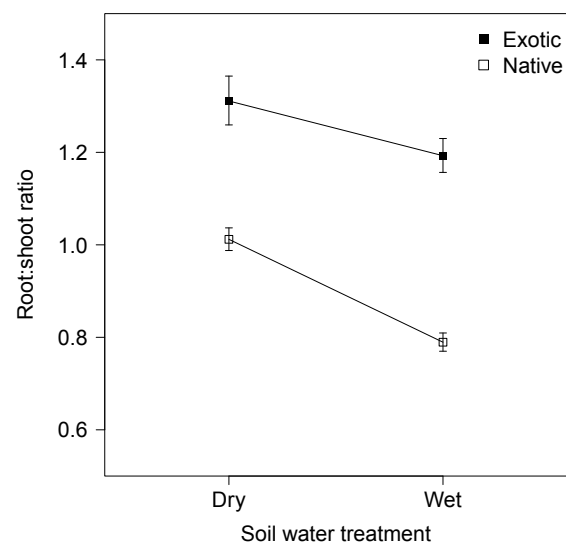[7]The rank of each model based on AICc

Figure 2. Observed and fitted root:shoot ratios for native (open squares) and exotic (black squares) woody species in the dry and wet treatments for the NativeExotic * Water model. Data (means ± 1 SE) are presented averaged across the random-effects terms in the model.

a more parsimonious description of the relative growth rates than the alternative models (Table 3). All species grew faster at higher soil N levels, and native species were more responsive to soil N (increased their growth rates more) than exotic species (Fig. 3a). At low soil N, the RGR of native species was equal to, or slightly higher than, the growth rates of exotics. Dry conditions resulted in a similar decrease in growth rates for exotic and native species (Fig. 3a). However, there was also reasonable support for a second model, which contained the three-way interaction between native status, soil N and soil moisture effect ($r^2 = 0.68$) (Table 2; Fig. 3b).

In keeping with the results for the native-status models, the model that best described the species-level growth rates across the nutrient and soil moisture gradients again included the three-way interaction between species, soil N and soil moisture ($r^2 = 0.73$) (Table 4). The growth rates of several species increased to various degrees with increases in soil moisture and soil N. The only negative growth response was seen for *Acer pseudoplatanus* under higher soil N in the wet treatment. Regardless of nutrient and moisture content, some species consistently grew faster than others, as can be seen in plots of the growth-rate ranks (Fig. 4). Moreover, one of two native species (*Ozothamnus leptophyllus* or *Kunzea ericoides*) consistently had the fastest growth rates, beating the fastest-growing exotic species (*Cytisus scoparius*) in both the wet and dry treatments (Fig. 4). Other species showed strong increases or decreases in the rank of their growth rate across nitrogen and water levels (e.g. *Pittosporum tenuifolium* and *Coprosma propinqua* strongly increased in rank with higher soil N, whereas *Discaria toumatou* and *Pinus radiata* decreased in rank; Fig. 4).

The experimental results predicted that exotic woody species grow slower and thus potentially should perform worse and be rarer than natives, in sites of higher fertility, irrespective of water availability. We tested this prediction by modelling the proportion of exotic woody species, using a plot-based dataset compiled for the New Zealand South Island drylands. These field observations concur with the shade-house experiment (Fig. 5). Predicted soil N in the first mineral soil horizon, mean annual temperature, mean annual rainfall, soil moisture deficit and distance to the nearest road and indigenous forest were all significant predictors (all $P < 0.0001$) of the proportion of exotic woody species (overall deviance explained by the model was 44.8%). A greater proportion of exotic species were found at sites with lower soil N (Fig. 5a). Exotic species were also more common at warmer sites with low annual rainfall (Fig. 5b, d). Sites with low soil moisture deficit, however, also had high proportions of exotic species (Fig. 5c). Variables indicating increased disturbance and/or more intensive land use (closer to road and further to the nearest indigenous forest, respectively) corresponded with a higher proportion of exotic woody species (Fig. 5e, f).

Discussion

All seedling growth responses we measured were affected by soil moisture and nutrient status. However, contrary to predictions of increased productivity of exotic species at high resource availability, in our experiment the native woody species grew faster than the exotic woody species in soils with higher total N levels. Moreover, while moisture and nutrient

Table 3. Summary of the model fits for the relative growth rates. For details on the various table components, see Table 2.

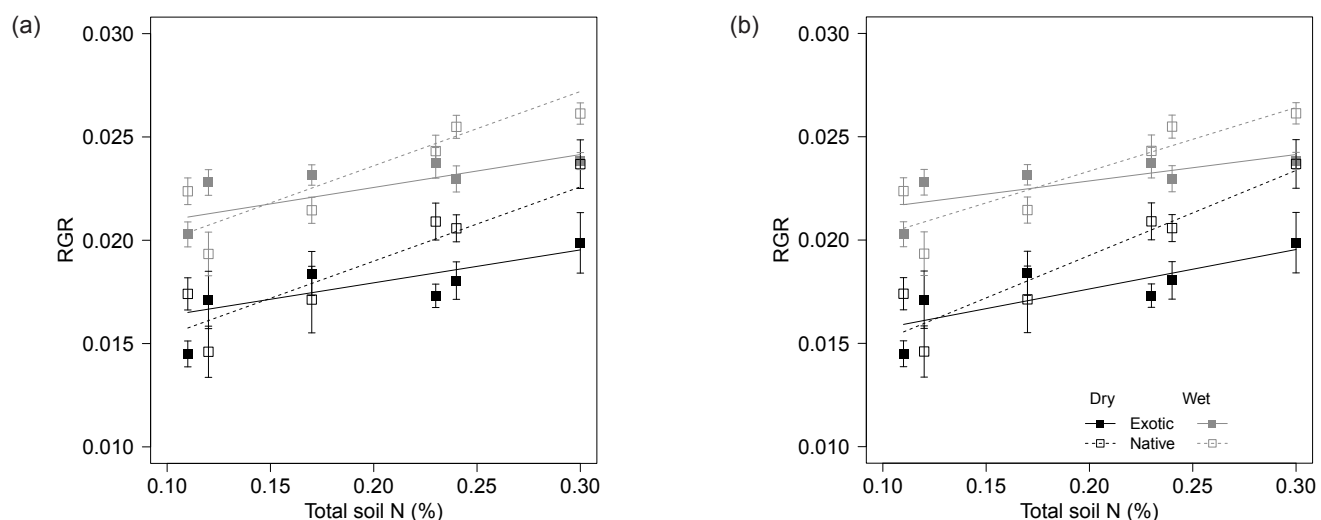| Model	K	AICc	ΔAICc	AICcWt	LL	Rank
Nat*N+W	10	−6258.50	0	0.61	3139.38	1
Nat*N*W	13	−6256.98	1.52	0.29	3141.71	2
Nat*N*P+W	14	−6253.26	5.24	0.04	3140.88	3
Nat*P+W	10	−6252.72	5.78	0.03	3136.49	4
N*W	9	−6250.39	8.12	0.01	3134.30	5
N+W	8	−6250.09	8.41	0.01	3133.13	6
Nat*P*W	13	−6249.02	9.48	0.01	3137.73	7
Nat*N*P*W	21	−6244.66	13.84	0	3143.89	8
W	7	−6241.96	16.54	0	3128.05	9
Nat*W	9	−6240.05	18.46	0	3129.13	10
Nat+W	8	−6239.98	18.53	0	3128.08	11

Figure 3. Observed and fitted relative growth rates (RGR) of native and exotic woody species across soil N and water gradients for the two top-ranked models. Observed relative growth rates are represented by squares (means ± 1 SE); lines are fitted using (a) the best (NativeExotic * Nitrogen + Water) and (b) the second-best (NativeExotic * Nitrogen * Water) model. All data are presented averaged across the random-effects terms in the model. Solid lines and filled squares indicate exotic species; dotted lines and open squares indicate native species. Lines and symbols in grey and black show the dry and wet treatments, respectively.

Table 4. Summary of the model fits for the relative growth rates at the species level (Spp). For details on the various table components, see Table 2.

| Model	K	AICc	ΔAICc	AICcWt	LL	Rank
Spp*N*W	60	−6362.32	0	0.74	3245.86	1
Spp*N*W+P	61	−6360.21	2.11	0.26	3245.97	2
Spp*P*W	60	−6343.08	19.24	0	3236.24	3
Spp*W	32	−6342.70	19.61	0	3204.66	4
Spp+N+W	33	−6322.42	39.90	0	3195.60	5
Spp*N+P+W	34	−6320.46	41.85	0	3195.71	6
Spp*P+N*W	35	−6319.41	42.90	0	3196.27	7
Spp*N+P*W	35	−6318.64	43.68	0	3195.89	8
Spp*P+W	33	−6314.62	47.69	0	3191.70	9
Spp+N*W	21	−6303.27	59.04	0	3173.20	10
Spp+N+W	20	−6303.00	59.31	0	3172.01	11
Spp+N+P+W	21	−6301.12	61.20	0	3172.12	12
Spp*N*P+W	61	−6300.17	62.14	0	3215.95	13
Spp+N+P*W	22	−6299.34	62.97	0	3172.29	14
Spp+P+W	20	−6296.58	65.74	0	3168.80	15
Spp+P*W	21	−6294.81	67.51	0	3168.97	16
Spp+W	19	−6293.32	69.00	0	3166.12	17
N+W	7	−5485.29	877.02	0	2749.71	18
N*W	8	−5484.11	878.20	0	2750.14	19
P+W	7	−5478.73	883.58	0	2746.43	20
P*W	8	−5476.82	885.50	0	2746.49	21
W	6	−5475.35	886.97	0	2743.72	22
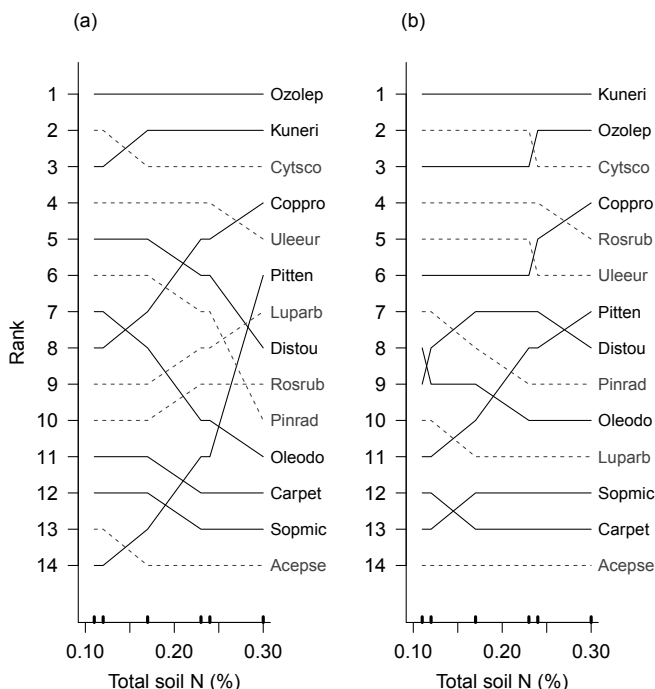
Figure 4. Relative growth rate ranking of all woody species in response to total soil nitrogen (N), plotted for (a) dry and (b) wet treatments. Native species are indicated by solid lines and bold species codes, and exotic species are indicated by dashed lines (for species codes, see Table 1). The species *Kunzea ericoides* and *Ozothamnus leptophyllus* are consistently the fastest-growing native species regardless of soil nutrient and moisture status, and they often perform better than the top exotic species (*Cytisus scoparius*). Tick marks on the *x*-axis indicate the total N levels of the six soils in this study.

status affected growth rates overall, the relative success of the fastest-growing species was not affected and two native woody species consistently performed better than the woody exotics. The distribution of exotic woody species in the field broadly supported our experimental findings. We discuss the results and implications for dryland rehabilitation and succession.

Native and exotic growth is affected differentially by soil and moisture

Under water-limited conditions, plants generally increase their root:shoot ratio to increase potential water uptake and to reduce loss through transpiration (Chaves et al. 2003; but see also Padilla & Pugnaire 2007). While the native species in this study appeared to have greater growth plasticity in response to drought, the exotic species allocated a much greater proportion of their biomass to roots even under wet conditions (Fig. 2). It appears that the exotic woody weed species in New Zealand drylands are morphologically (but not necessarily physiologically; see Kissel et al. 1987) better adapted to exploit low soil moisture than the native species. These results concur with similar findings for woody species in Australia (Leishman & Thomson 2005) and for grasses in New Zealand (Meurk 1978; Lee et al. 2000).

High productivity is a strategy for successful competition and invasion (Vilà & Weiner 2004; Stastny et al. 2005). Invasive, non-native plants are usually more productive than co-occurring native species because of a set of functional traits including relatively rapid growth, high foliar nutrient contents, and high reproductive output (Sutherland 2004; Mitchell et al. 2006; Grotkopp & Rejmánek 2007; Leishman et al. 2007; Pysek & Richardson 2007). However, contrary to expectations, native and exotic woody species had similar growth rates at low N levels, and native woody species grew faster than exotic woody species at high soil N (Fig. 3). These results join an increasing body of evidence that invasive species do not always perform better than resident native species under high resource availability (e.g. Funk 2008, 2013; Ordonez et al. 2010; Ordonez & Olff 2013). However, exotic woody species had consistently higher root:shoot ratios than native woody species, which may result in persistence during periods of scarce resources (water and/or nutrients) and hence provide a competitive advantage when establishing in a dry environment (see below; Chaves et al. 2003; Funk 2013).

Some natives consistently perform better than exotics

Although relative growth rates of seedlings differed along soil moisture and nutrient gradients, the ranks of the fastest species' growth rates were similar across these gradients (Fig. 4). Two native species (*Ozothamnus leptophyllus* and *Kunzea ericoides*) consistently equalled or exceeded growth rates of invasive exotic species such as broom (*Cytisus scoparius*) and sweet briar (*Rosa rubiginosa*). These results concur with Lambers and Poorter's (1992) assertion that the relative growth rate of all species is lower when nutrient availability is limited, but potentially fast-growing species will still grow faster than potentially slow-growing species. We note that, since this experiment was conducted, Poorter et al. (2012) published a meta-analysis into the effect of pot size, suggesting that the ratio of biomass to pot volume should not exceed 1 g/L to ensure that growth is not constrained by pot size. This may have affected several species in our study (see Table 1) and likely moderated our growth estimates for high growth rate treatments (e.g. higher soil N). The species ranks in the wet treatment were similar to the more growth limited dry treatment
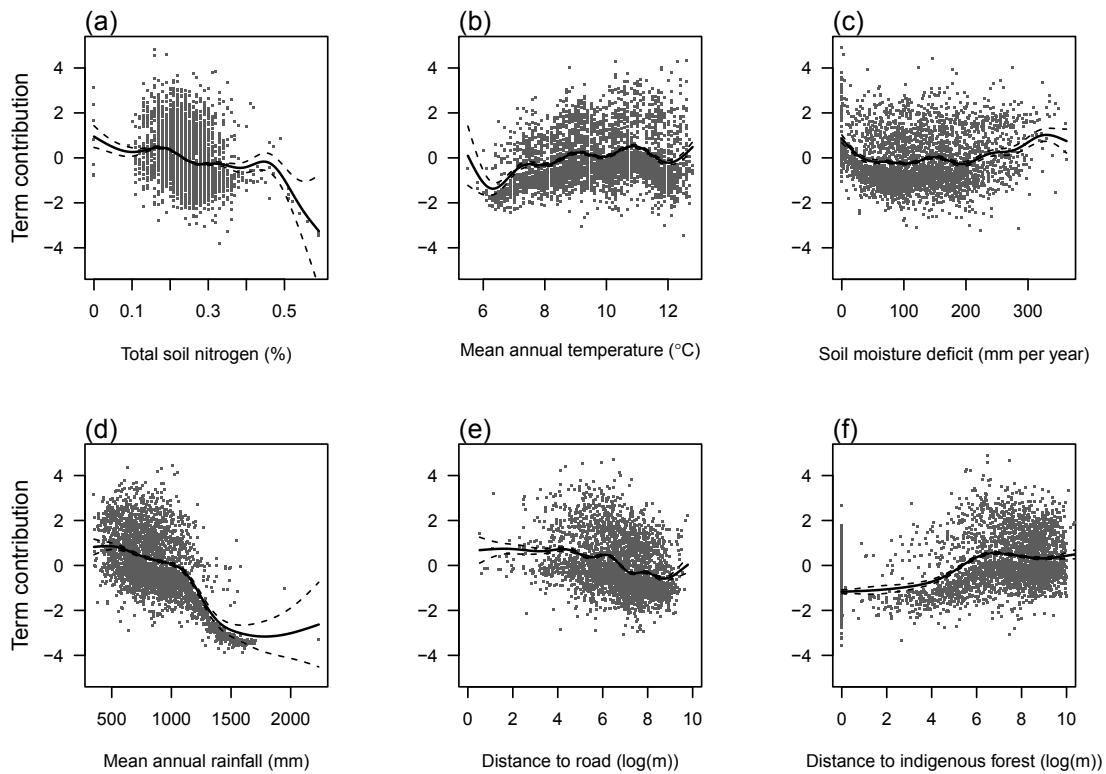
Figure 5. Contribution of the individual terms from the model of proportion of woody species that is exotic in 3383 field plots in the New Zealand drylands. A variable's (a–f) term contribution is the additive contribution of the modelled variable to the fitted model of the proportion of exotic woody species. Solid lines indicate the mean contribution of the fitted term. Dashed lines indicate the standard errors on the predictions. The points indicate the partial residuals (residuals from the fitted model plus the contribution of the individual term).

(Fig. 4) suggesting that the different species were similarly affected by pot size as productivity increased. Hence we do not think our conclusions were unduly influenced by pot size constraints.

Dryland current and future woody communities

The distribution of exotic woody species in the field supported our experimental findings of increased relative performance of exotic woody species at low soil N. In the South Island dryland zone, exotic woody species made up a larger proportion of species in warmer, drier environments where soil N in the top mineral horizon was low. While we found only a small effect of water availability on the differential relative growth rates of exotic and native woody species in our pot experiment, the field distribution suggests a strong effect of annual rainfall on the proportion of exotic woody species present (Fig. 5). Exotic woody species are relatively more common in areas of lower rainfall; however, this is combined with an increase in exotic proportion in areas of low soil moisture deficits, suggesting that exotic species may dominate in areas where both rainfall and evaporative demand are low. The positive relationship between mean annual temperature and the relative species richness of exotic species follows trends seen in temperate regions, including New Zealand (Sax 2001; Stohlgren et al. 2002; Wiser & Allen 2006).

An increasing body of evidence suggests that native species do not always have a competitive advantage over exotic invasive species in low-resource environments (e.g. see Funk & Vitousek 2007; Maron & Marler 2007; Funk 2008; Ordonez et al. 2010; Ordonez & Olff 2013). Under these

conditions, invading species possess traits associated with high resource acquisition or high resource conservation, or both (Funk 2013). The resource acquisition abilities of exotic woody species compared with native woody species may be indicated by their consistently higher root:shoot ratios (Fig. 2), demonstrating enhanced water acquisition, which may also convey a relative advantage in N acquisition (Chaves et al. 2003; Funk 2013). Interestingly, the response of root:shoot ratio of native woody species to water availability was more plastic compared with exotic woody species. While increased phenotypical plasticity is generally associated with invasive exotic species (Richards et al. 2006), this does not always result in an improved fitness (Davidson et al. 2011). More work on the phenotypical plasticity and water relationships of native and exotic species (e.g. water use efficiency) and whether this results in improved fitness in these drylands may shed more light on the physiological adaptations and mechanisms that the root:shoot ratio and other traits provide under dry and low-nutrient conditions.

The selection of species used to assess determinants of invasiveness is critical as it affects the interpretation of the results (van Kleunen et al. 2010). The pot experiment described here used an objective approach to select the most common native and exotic woody species from each of eight clusters of species based on a cluster analysis of 14 morphological and life history traits and using 3383 plots from throughout the South Island dryland zone. This means both the native and exotic woody species are common (and/or invading) across the drylands and that they share similar traits. We suggest that this, in combination with the lack of representation across the lower end of the soil fertility gradient in previous studies, may

explain the deviation of our results with previous New Zealand studies that found that native grasses and woody species are better adapted to low-fertility conditions than exotic grasses (Craine et al. 2006) and that exotic species richness increases with soil fertility (Timmins & Williams 1991).

Other characteristics of the receiving habitats also affected the proportion of exotic woody species. For example, areas with frequent disturbance (e.g. by fire, agriculture or roadside mowers) are often dominated by introduced species (Moles et al. 2012). In our model, disturbance was only very indirectly captured by the distance to the roads and forests. In addition, the measure of distance to the nearest indigenous forests was a significant contributor and captured an element of disturbance (management intensity of the habitat matrix), while also incorporating the findings that fewer exotic species can establish in the shaded understorey of intact forest systems (Jesson et al. 2000; Moles et al. 2008).

Some exotic species (most notably *Rosa rubiginosa, Cytisus scoparius, Ulex europaeus*) are predicted to be among the most frequently occurring woody species in most dryland environments with low richness (Walker et al. 2009b). While exotic woody species will be important components of future woody communities, the results of this study suggest that management can be used to tip the balance toward increasing native woody dominance. Exotic woody species are not necessarily superior in their growth rates, but rather they may dominate because of a legacy of a prior disturbance regime. Rehabilitation efforts favouring high-performing native species, like *Kunzea ericoides* and *Ozothamnus leptophyllus,* may stand the best chance of creating a native-dominated shrubland. Indeed, the result that these two species are potential high performers across soil nutrient and moisture gradients is supported by the fact they have long been regarded as 'scrubweeds' in New Zealand drylands, along with undesirable exotics like sweet briar, gorse and scotch broom (Leonard 1962; Bascand & Jowett 1982). While this provides opportunities for rehabilitation, the social dimension of species performance in restoration ecology is also an important consideration (e.g. low-intensity restoration projects may not be successful if the candidate species are unacceptable to the public).

Predicting future state-transitions and community compositions of woody New Zealand dryland vegetation (Walker et al. 2009a, b) will depend on understanding both fundamental and realised responses to environment (King & Wilson 2006; Moles et al. 2012). The shade-house pot experiment represented a simplification of the field in order to assess some of the underlying potential limitations to woody establishment in New Zealand drylands. This experiment suggests that, regardless of soil moisture and nutrients, the ranking of the fastest-growing species is similar. So, while soil type will influence the speed at which woody invasion occurs, it can probably be discounted as a major mediator of the relative competitive abilities of potential invaders. In the field, the (realised) distribution of species is affected by many other factors and their interactions, including climate, herbivory, seed availability, competition with other species and human interactions (Aerts 1999; Pugnaire & Luque 2001; Ganade & Brown 2002; Bellingham et al. 2004; Lockwood et al. 2005). However, this work provides a vital starting point to comprehend fundamental responses, and in combination with other experiments looking at regeneration and competition, both in the field and laboratory, will provide an increased understanding of the role of native and exotic woody species in the drylands of New Zealand.

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