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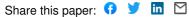**Institutions:** University of Cape Town, University of Colorado Boulder, Stellenbosch University, University of Western Australia

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BIODIVERSITY REVIEW

Ecophysiological traits associated with the competitive ability of invasive Australian acacias

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ABSTRACT

Aim We explored morphological and ecophysiological traits that enable invasive Australian acacias to compete with native species for resources (light, water and nutrients) necessary to support the substantial growth associated with successful invasions.

Location Global.

Results Invasive Australian acacias grow large and seed prolifically in invaded regions. The greater capacity for vegetative growth is underpinned by their ability to acquire and efficiently use resources in non-native habitats. Key biological traits that enhance acquisition include (1) rapid and substantial allocation to root mass (up to 6-fold more than co-occurring native species) directed towards deep roots (at least 50% longer than those of natives) and to extensive shallow root networks; (2) heteroblasty, in most species, conferring high relative growth rates as bipinnate seedlings but long-lived, nutrient-conserving phyllodes as adults and (3) strong N_2-fixation abilities.

Main conclusions The ecophysiological traits that govern the competitive interaction of invasive Australian acacias with native species are an important component of the recognized suite of factors including introduction history, human use and enemy release that combine to produce successful invasions. Traits interact to give Australian acacias competitive advantage over many native species. One such interaction is that of N_2 fixation, which when coupled with slow decomposition of sclerophyllous phyllodes results in alteration of soil nutrient cycling. The lasting legacy of soil N-enrichment hinders the competitive ability of native species and further enhances invasions. The importance of edaphic factors and competitive interactions in determining invasive success should be considered in predictive modelling of species distributions.

Keywords
Biological invasions, Cape Floristic Region, fynbos, phyllodes, relative growth rate, water-use efficiency.

INTRODUCTION

The ability of alien species to establish, grow and survive in non-native environments is highly dependent on their ability to compete with native species for the essential resources of light, water and nutrients. Australian acacias (1012 species in the subgenus *Phyllodineae* DC native to Australia; Miller *et al.*, 2011; Richardson *et al.*, 2011) are some of the most successful and prolific invasive species globally (Lowe *et al.*, 2000; Henderson, 2007; Richardson & Rejmánek, 2011). Invasive Australian acacias successfully compete for resources in non-native environments (Werner *et al.*, 2008), enabling them to realize their potential to grow larger than native vegetation (Table 1). Success of invaders is irrefutably also contingent on several other factors (Rejmánek *et al.*, 2005; Thuiller *et al.*, 2006). For example, the history of introduction (both frequency and magnitude) and the human use of the introduced species play an important role in the subsequent scale of invasion (Lockwood *et al.*, 2005; Wilson *et al.*, 2007; Carruthers *et al.*, 2011; Castro-Díez *et al.*, 2011; Griffin *et al.*, 2011;

Table 1 Height, above-ground biomass and normalized difference vegetation index (NDVI) of invasive Australian acacia stands in comparison with native vegetation in the Cape Floristic Region (CFR), South Africa. Values indicate means ± SE, where available.

Acacia spp.	Measure	Acacia	Native	Reference
A. saligna	Height (m)	6.0	2.5	van Wilgen & Richardson, 1985
A. cyclops & A. saligna	Biomass (kg m^{-2})	10.4	2.0–3.5	Milton & Siegfried, 1981
A. saligna	Biomass (kg m^{-2})	5.8	1.8	van Wilgen & Richardson, 1985
A. cyclops & A. saligna	NDVI	0.63 ± 0.01	0.51 ± 0.01	Fatoki, 2007

Kull *et al.*, 2011; van Wilgen *et al.*, 2011). Reproductive and dispersal strategies can also influence the likelihood of invasion success (Gibson *et al.*, 2011). Furthermore, the absence of pests and pathogens of alien species in their new range also enhances the competitiveness of alien species (Williamson, 1996; Crawley, 1997). In this article, however, we focus on identifying ecophysiological traits and mechanisms enabling acquisition and conservation of resources that contribute to competitive success of Australian acacias in non-native ranges.

Of the c. 300 Australian *Acacia* spp. introduced around the world, 23 have become highly invasive (Richardson & Rejmánek, 2011), particularly in Mediterranean-type ecosystems that are often water- and/or nutrient limited such as the South African Cape Floristic Region (CFR) or Portuguese dune ecosystems (Groves & di Castri, 1991; Witkowski, 1991a; Stock *et al.*, 1995; Marchante *et al.*, 2003; Rouget *et al.*, 2003; Werner *et al.*, 2010) and disturbed environments such as riparian and post-fire environments (Henderson, 2007; Richardson *et al.*, 2007). The effects of Australian acacia invasions on native ecosystems have been widely documented with a range of recorded impacts (reviewed in van Wilgen *et al.*, 2008; Le Maitre *et al.*, 2011) including declines in native species diversities (Richardson *et al.*, 1989; Holmes & Cowling, 1997; Marchante *et al.*, 2003), reductions in stream flows because of increased water use (Enright, 2000; Dye *et al.*, 2001), alterations to nutrient cycling (Yelenik *et al.*, 2004) and modifications to fire regimes (van Wilgen & Richardson, 1985). Many of these impacts are linked with the propensity of the Australian acacias to grow much larger, in both height and total biomass, than the native vegetation in invaded ranges (e.g. Table 1). The vigorous vegetative growth of these plants also supports prolific production of nutrient-rich seeds, leading to large, persistent seed banks (Milton, 1980; Holmes, 1989; Gibson *et al.*, 2011), which are a major factor contributing to their successful invasion and persistence (Richardson & Kluge, 2008).

Competition for the resources to support this growth capacity depends on characteristics of both the invaded region and the invader's biological traits (Thuiller *et al.*, 2006). Disturbance and the native plant community matrix in the invaded region strongly influence the distribution and availability of resources to alien plants. The 'Empty Niche Hypothesis' suggests that alien plants are able to establish, persist and invade in novel environments by accessing resources not utilized by native flora (Elton, 1958; MacArthur, 1970). This was expanded upon by Davis *et al.* (2000) in the 'Fluctuating Resource Hypothesis', which proposes that invasions are facilitated only when resources fluctuate (as a result of excess inputs into the system or reduced use by native flora) and temporarily become available for acquisition by invasive species.

Whether the invader can capitalize on the availability of resources is governed by its biological traits. Researchers have, over several decades, investigated which biological traits confer success of invaders over native species (Baker, 1974; Rejmánek & Richardson, 1996; Pyšek & Richardson, 2007). One key trait commonly recognized to support successful invasions is the ability of aliens to better acquire limiting resources or to use resources more efficiently than native species (e.g. Vitousek, 1986; Cordell *et al.*, 2002; Funk & Vitousek, 2007). Here, we review key ecophysiological traits and mechanisms that enable invasive Australian acacias to acquire the resources (light, water and nutrients) necessary to support the greater vegetative growth and meet the reproductive costs associated with successful invasions.

RESOURCE ACQUISITION AND USE BY INVASIVE AUSTRALIAN ACACIAS

Light

Competition for light is likely to be most fierce during germination. Invasive Australian acacia seedlings grow taller (*Acacia mangium* 50% taller than a common heath-forest species in Borneo, *Melastoma beccarianum*, Osunkoya *et al.*, 2005; *A. saligna* 123% taller than a fynbos biome species in South Africa, *Protea repens*, Witkowski, 1991b) and faster than native species (Witkowski, 1991b; Peperkorn *et al.*, 2005; Osunkoya *et al.*, 2005). Once established, the fast-growing Australian acacias overtop native vegetation, out-competing native species for light (Rutherford & de Bösenberg, 1988). As a consequence, native vegetation most often cannot survive under the dense invasive Australian acacia canopies, leaving the understory bare (Holmes & Cowling, 1997). If native vegetation is able to persist, it is often only at the acacia canopy edge or at low levels in the understory (Midgley *et al.*, 1992). The high growth rates of Australian acacias are most likely supported by the superior abilities of Australian acacia seedlings to obtain necessary water and nutrients.

Water

Water depletion in invaded ecosystems is considered one of the most significant impacts of Australian acacia species (Le Maitre

et al., 1996, 2000; Enright, 2000; Le Maitre, 2004). Several studies provide evidence for increased water use by Australian acacias in invaded regions. In a Portuguese pine forest, stand water use increased by 6.5% because of *Acacia longifolia* invasions (Table 2). Evapotranspiration (ET) was 13–51% higher in *A. mearnsii* stands compared with native vegetation in southern African grassland and CFR sites (Table 2). Furthermore, invasive Australian acacias decreased the water yield of sampled South African river catchments by up to 5% (Table 2), a value predicted to increase dramatically with the projected spread of invasions (Le Maitre *et al.*, 2002). Increased water use is likely a result of larger above-ground biomasses (*c.* 3-fold greater) of Australian acacia stands compared with native vegetation (Table 1). Larger above-ground biomass yields an associated higher leaf area for transpiration as indicated using normalized difference vegetation index data (NDVI) as a proxy for leaf area index (Turner *et al.*, 1999), which was 25% greater in invasive Australian acacia stands compared with native CFR vegetation (Table 1).

Apart from water loss because of greater above-ground biomass, leaf-specific water loss (i.e. transpiration rates) of invasive Australian acacias is also an important consideration, although relatively poorly documented. Rutherford & de Bösenberg (1988) reported that *A. cyclops* generally had higher transpiration rates per leaf area than indigenous fynbos species. Further studies would thus be useful in determining whether increased water use is mostly owing to larger above-ground biomass or also partially because of increased transpiration rates per leaf area. What is of interest is how invasive Australian acacias access these significant volumes of water.

Water acquisition

Plant water acquisition is dependent on the size, surface area and depth of its roots as well as how these roots are spatially distributed through the soil profile (Shenk & Jackson, 2002). Invasive Australian acacias generally have a higher investment in rootstocks (measured by root mass ratio; RMR) than native species, yielding a higher biomass of roots (Table 3) with a surface area 2- to 6-fold greater than that of native species (Werner *et al.*, 2010). Australian acacia seedlings also develop

roots 1.5- to 4-fold longer than co-occurring native species (Table 3), which penetrate deeper into the soil profile (Witkowski, 1991b). This occurs at significantly faster rates than that of native vegetation with no associated reduction in above-ground biomasses (Witkowski, 1991b; Musil, 1993; Peperkorn *et al.*, 2005). The substantial and rapid root growth of acacia seedlings enables these plants to out-compete native species for water, especially during water-limited periods, a trait that has also been recognized as an advantage for other invasive species (Roché *et al.*, 1994). Data on rooting patterns of larger, mature Australian acacias are sparse. However, considering the substantial initial root investment and strong correlations between above-ground and below-ground biomass of trees (e.g. Robinson, 2004), it is likely that large adult invasive Australian acacias also have substantially greater root investment than native species. One study described how *A. saligna,* when grown in a mixed stand with *Eucalyptus* and *Atriplex,* had roots as deep as 6 m within 4 years of planting and at one site had roots up to 16 m deep after several additional years (Knight *et al.*, 2002). Further information about rooting depth is imperative for understanding the capacity of invasive Australian acacias to access deep water (and associated nutrient sources) possibly facilitating competitive exclusion of native species.

The spatial distribution of root biomass is also of great importance in determining the success of sustained water acquisition. A dimorphic root system comprising both deep roots enabling water acquisition during dry periods and a dense shallow network of surface roots that obtain water from the upper soil horizon in wetter periods is of great benefit (Pate *et al.*, 1995; Canadell *et al.*, 1996; Joffre *et al.*, 2007). Juvenile *A. saligna* and *A. cyclops* show dimorphic roots in the invaded CFR, South Africa (Hoffman & Mitchell, 1986), whereas the native Fabaceae species compared, *Aspalathus albens*, *A. flexuosa* and *Rafnia angulata*, have significantly fewer surface lateral roots, with no lateral roots at all in the dry summer (Hoffman & Mitchell, 1986).

Overall, invasive Australian acacias show substantial initial below-ground investment producing bigger root systems that penetrate deeper into the soil in comparison with native species. Both the size and the spatial distribution of roots

Acacia spp.	Country	Vegetation type	Measurement	Effect	Reference
A. longifolia	Portugal	Pine forest	Stand water use	6.5% increase	Rascher *et al.*, 2009
A. mearnsii	South Africa	CFR vegetation	ET	13% increase	Dye *et al.*, 2001
A. mearnsii	South Africa	Grassland	ET	51% increase	Dye *et al.*, 2001
Acacia spp.*	South Africa	Native vegetation	Water yield of catchment	1–5% reduction	Le Maitre *et al.*, 2002

Table 2 The effect of Australian acacia invasions on stand level water use (scaled up from individual tree sap flows derived using Granier's constant heat method), modelled evapotranspiration (ET) derived using the Bowen ratio energy balance technique, and estimated water yields of sampled catchment areas (based on biomass-based regression models) when compared to native uninvaded vegetation.

*Mixed species including *A. cyclops, A. dealbata, A. longifolia, A. mearnsii, A. melanoxylon* and *A. saligna.*

Table 3 Comparison of root mass ratios (RMR), root biomass and root length indicated by a ratio of the measure comparing invasive Australian acacia seedlings to co-occurring native species in invaded ranges. Data are for vegetation varying from 6 to 18 months in age.

Acacia spp.	Region	Native spp.	Vegetation age (months)	RMR	Root biomass	Root length	Reference
A. longifolia	Portugal	Halimium halimifolium	7	1.5×	3.0×	1.6×	Peperkorn et al., 2005
		Pinus pinea		0.7×	0.9×	4.1×	
A. saligna	CFR	Protea repens	6	1.6×	15.0×	1.8×	Witkowski, 1991b
A. saligna	CFR	Ericoid spp.	18	1.6×	3.3×	1.7×	Musil, 1993
		Restioid spp.		0.5×	1.8×	1.9×	
		Proteoid spp.		1.5×	2.5×	1.5×	

provide an early competitive advantage for water acquisition, particularly in water-stressed periods.

Water-use efficiency

Water-use efficiencies (WUE) of invasive Australian acacias do not show significant differences in comparison with native vegetation in invaded areas (instantaneous gas exchange measures and long-term measures using foliar $\delta^{13}C$ ratios as a proxy; Table 4). The WUE of invasive Australian acacias may however be situation- and species dependent, particularly when considering the differences in foliar types. One of the distinguishing characteristics of majority of the Australian acacias (c. 95%; Maslin & Stirton, 1997) is the fact that different foliar types exist between seedling and adult life stages (termed heteroblasty). Seedlings develop bipinnate compound leaves, which are replaced within weeks to years of emergence by modified petioles that enlarge and flatten to form simple leaf-like structures termed phyllodes (Walters & Bartholomew, 1984; Boland et al., 2006). In water-limited conditions when a higher WUE would be desirable, phyllodes may be of particular advantage as these are thought to confer tolerance to drought because of their sclerophyllous nature (Elias, 1981; Pasquet-

Kok et al., 2010). Additionally, the sensitivity of stomatal closure in phyllodinous Australian acacias in response to increased vapour pressure deficits could contribute to phyllodes being more drought-tolerant in water-limited areas (Ullmann, 1989; Brodribb & Hill, 1993; Pasquet-Kok et al., 2010). Low WUE, on the other hand, would exist when water is abundant and transpiration can occur freely. Thus, WUE is likely to be highly plastic. However, available data are from contexts in which water was readily available and hence marked differences between the WUE of Australian acacias and native species cannot be expected. Thus, investigations into the response of WUE of Australian acacias in comparison with native species under varying water availabilities are still needed.

Nutrition

Alien plant invasions can occur in a range of nutritional environments including low-resource environments (Funk & Vitousek, 2007). This is also true of Australian acacias, which are often highly competitive in nutrient-poor Mediterranean-type ecosystems such as the CFR and Portuguese dune systems (Groves & di Castri, 1991). Invasive Australian acacias are able to effectively acquire nutrients and have been shown to have

Table 4 Instantaneous water-use efficiency (WUE) measured by gas exchange analysis and long-term WUE determined from foliar $\delta^{13}C$ of invasive Australian acacias in comparison with native species. Data collected by Kraaij & Cramer (1999) are from a non-riparian field site in the high-rainfall season (August–September 1998) in the Cape Floristic Region (CFR), South Africa. Peperkorn et al. (2005) provide data from a greenhouse study in which plants were irrigated. Data derived from Crous (2010) are from riparian field sites located in the CFR, South Africa. Relative to natural vegetation, + indicates a higher WUE of Australian acacias, 0 indicates no significant difference and − indicates a lower WUE.

Acacia spp.	Native spp.	Water availability	Measure	Comparison	Reference
A. longifolia	Protea repens	High – wet season	WUE	0	Kraaij & Cramer, 1999
	Chrysanthemoides monilifera	High – wet season	WUE	+	
	Dodonaea viscosa	High – wet season	WUE	0	
	Leucadendron salignum	High – wet season	WUE	+	
A. longifolia	Halimium halimifolium	High – irrigated	WUE	0	Peperkorn et al., 2005
A. mearnsii	Brabejum stellatifolium	High – riparian	$\delta^{13}C$	0	Crous, 2010
	Metrosideros angustifolia	High – riparian	$\delta^{13}C$	−	
A. saligna	Protea repens	High – wet season	WUE	0	Kraaij & Cramer, 1999
	Chrysanthemoides monilifera	High – wet season	WUE	0	
	Dodonaea viscosa	High – wet season	WUE	0	
	Leucadendron salignum	High – wet season	WUE	+	

greater leaf N concentrations than native species in invaded regions, while P concentrations are slightly more variable (Table 5). Musil (1993) found that *A. saligna* also exhibited greater concentrations of K, Ca and Mg than native fynbos species. Considering that Australian acacias themselves originate from some of the most nutrient-poor soils in the world (Young & Young, 2001), it is not surprising that these species are able to effectively compete for nutrients, leading us to question whether these plants possess particular traits or mechanisms that enhance their competitive ability for nutrient acquisition and conservation.

Nutrient acquisition

Nutrient acquisition by plants is influenced by three major factors: root structure (including biomass, surface area and spatial distribution), soil nutrient availability and the ability of the plant to form specialized associations for nutrient acquisition (Lambers *et al.*, 2008a). Root biomass can be preferentially allocated to enriched shallow soils and/or towards growing deeper roots to tap unused nutrient resources (Jobbágy & Jackson, 2001; Lambers *et al.*, 2008a; Craine, 2009). As discussed earlier, invasive Australian acacias allocate a greater percentage of biomass to both deep and shallow roots in comparison with native species in invaded regions (Table 3). Acacia roots may also be more plastic in response to soil nutrient availability than other species. For example, the RMR of *A. longifolia* almost doubled when nutrient concentrations were reduced compared with native Mediterranean dune species *Halimium halimifolium* and *Pinus pinea* (Peperkorn *et al.*, 2005).

The availability of soil nutrients to a plant is dependent on soil moisture and the ability of the plant to increase available nutrient concentrations through the use of root exudates. Soil moisture strongly influences the diffusive flux of nutrients into the rhizosphere. Plants can alter soil moisture by redirecting available water resources via hydraulic redistribution (Burgess *et al.*, 1998; Hawkins *et al.*, 2009), potentially increasing the solubility and hence availability of nutrients to plant roots

(Jackson *et al.*, 2000; Ryel, 2004; Hawkins *et al.*, 2009). However, very little direct evidence for nutrient acquisition via hydraulic redistribution is available (Lambers *et al.*, 2006), and this remains an untested possibility for invasive Australian acacias. Furthermore, transpirational water use by plants also drives nutrient mass flow (Barber, 1995), and transpiration is thus partially regulated by nutrient availability, particularly N (Raven *et al.*, 2004; Cramer *et al.*, 2008, 2009; Cernusak *et al.*, 2010). Mass flow of nutrients requires adequate soil water to supply transpirational demand and hence operates at the expense of WUE (Barber, 1995; Tinker & Nye, 2000; Raven *et al.*, 2004; Cramer *et al.*, 2009). For many species, a decrease in nutrient availability decreases WUE (Raven *et al.*, 2004), as has also been observed for *A. longifolia* (Peperkorn *et al.*, 2005) suggesting that a water-nutrient trade-off may occur. The fact that water is required for both diffusive and mass-flow mobility of nutrients in soil provides a powerful explanation for the interaction of these two resources in determining plant growth.

Soil nutrient concentrations can also be altered by plants actively extracting nutrients that are not readily available, through the release of root exudates such as carboxylates and phosphatases (Lambers *et al.*, 2008a). In the highly invaded South African CFR, well-represented families such as Proteaceae and the Restionaceae commonly produce specialized cluster roots, which increase surface area for diffusion and exudate release (Lamont, 1982; Lambers *et al.*, 2006). Cluster roots are efficient at acquiring nutrients, particularly P from low-concentration and sparingly soluble sources (Lambers *et al.*, 2006). Invasive Australian acacias lack cluster roots and are thus unlikely to be able to access these more recalcitrant forms of soil P. Despite this, invasive Australian acacias still compete effectively for nutrients in the intrinsically nutrient-poor soils of the CFR (Table 5). This competition may be enhanced through the ability of plants to form symbiotic mycorrhizal associations for nutrient acquisition (Lambers *et al.*, 2008a).

Mycorrhizal associations occur in 82% of higher land plants (Brundrett, 2002) and enhance nutrient (particularly P)

Table 5 Foliar N and P concentrations (mean mg g^{-1} ± SE) of Australian acacia species in comparison with native species from the invaded region. Significantly larger values ($P < 0.05$) in comparisons are in bold. ND indicates no available data. Available data stem from studies in the Cape Floristic Region (CFR), South Africa.

Acacia spp.	[N]	[P]	Native spp.	[N]	[P]	Reference
A. cyclops	**18.5 ± 0.71**	2.58 ± 0.10	*Pterocelastrus tricuspidatus*	9.70 ± 0.26	**6.31 ± 0.47**	Witkowski, 1991a
A. longifolia	**9.94 ± 0.98**	ND	*Protea repens*	2.38 ± 0.56	ND	Kraaij & Cramer, 1999
A. saligna	**13.31 ± 2.66**	ND	*Chrysanthemoides monilifera*	4.06 ± 0.42	ND	
			Dodonaea viscosa	5.04 ± 0.56	ND	
			Leucadendron salignum	1.82 ± 0.28	ND	
A. saligna	**20.50 ± 0.77**	1.01 ± 0.07	*Leucospermum parile*	7.90 ± 0.31	0.93 ± 0.04	Witkowski, 1991a
A. saligna	25.00 ± 3.57	**1.48 + 0.16**	*Protea repens*	18.00 ± 2.04	0.65 + 0.21	Witkowski, 1991b
A. saligna	**14.29 ± 0.14**	**0.7 ± 0.01**	Ericoid	12.75 ± 0.7	0.59 ± 0.06	Musil, 1993
			Restioid	7.56 ± 0.14	0.31 ± 0.03	
			Proteoid	8.82 ± 0.42	0.59 ± 0.03	

acquisition (Lambers *et al.*, 2008b; Smith & Read, 2008). Both arbuscular mycorrhizas (AM) and ectomycorrhizas (EM) are able to take up soluble P from the soil, but only EM are able to chemically release P from sorbed and organic complexes (Smith & Read, 2008). Most Australian acacia species are able to form AM and possibly also EM associations (Reddell & Warren, 1987). However, the relative importance of these associations for P uptake in acacias remains unclear. Hoffman & Mitchell (1986) showed a positive correlation between AM colonization with plant biomass accumulation and P content of *A. saligna* seedlings in the CFR. In contrast, Rodríguez-Echeverría *et al.* (2009) found that despite significant colonization of *A. longifolia* roots by AM fungi in Mediterranean dune systems, no advantage in P acquisition was conferred. The benefits of EM and AM associations in Australian acacias must depend on the form and availability of P in the soil. The formation of mycorrhizal associations and the lack of cluster roots are likely to restrict the invasive Australian acacias to dependence on organic P and the more soluble forms of inorganic P. This inability to acquire the sparingly soluble forms of P that cluster-rooted species (particularly Proteaceae, Restionaceae and Fabaceae) of the invaded CFR do may serve to limit invasions of Australian acacias on some extremely nutrient-impoverished sandstone-derived soils of the CFR.

Australian acacias are well known for their N_2-fixation abilities (Levine *et al.*, 2003). N_2-fixing associations occur in most Australian acacias (Lawrie, 1981; Lee *et al.*, 2006), which usually nodulate with common, but slow-growing *Bradyrhizobium* species (Lafay & Burdon, 2001; Rodríguez-Echeverría *et al.*, 2011). Associations with other nodulating species have also been reported, including *Rhizobium, Ensifer, Mesorhizobium, Burkholderia, Phyllobacterium* and *Devosia* species (Marsudi *et al.*, 1999; Lafay & Burdon, 2001; Hoque *et al.*, 2011). Associations between acacias and their nodulating symbionts are highly complex and can be influenced by several biotic and abiotic factors (Thrall *et al.*, 2000, 2007; Murray *et al.*, 2001; Rodríguez-Echeverría *et al.*, 2011). Nonetheless, invasive Australian acacias nodulate readily in both their native and non-native regions (reviewed in this volume by Rodríguez-Echeverría *et al.*, 2011) and are considered prolific N_2-fixing species (Lawrie, 1981). In coastal dunes of Portugal,

A. longifolia was more efficient at forming symbiotic associations with bacteria and fixed greater amounts of N than other co-occurring N_2-fixing legumes (*Ulex eurpaeus* and *Cytisus grandiflorus*; Rodríguez-Echeverría *et al.*, 2009). Similarly, comparing the $\delta^{15}N$ of N_2-fixing plants to others with N_2 fixation disrupted by O_2 fumigation, Stock *et al.* (1995) found that *A. saligna* in the CFR relied almost completely on symbiotic N_2 fixation, while *A. cyclops* growing on slightly more nutrient-rich soil obtained only 51% of its N budget from N_2 fixation. The long-term post-fire persistence of invasive Australian acacias in the CFR is somewhat puzzling because few native N_2-fixing legumes (especially reseeders) persist beyond their post-fire dominance (Kruger, 1983; Hoffmann *et al.*, 1987; Cocks, 1994; Cramer, 2010). This lack of indigenous legume reseeder persistence has been ascribed to the post-fire decline in P availability (Power *et al.*, 2010). These authors suggested that deep roots and excessive water consumption may contribute to Australian acacia persistence.

The N_2-fixing capabilities of Australian acacias and their ability to persist in invaded regions result in a substantial inputs of N-enriched litter, leading to an elevated soil N status (Table 6). However, the ability of an invader to fix N_2 in itself does not necessarily translate to immediate alteration of the invaded system's nutrient cycling (Corbin & D'Antonio, 2004). Instead, Yelenik *et al.* (2007) demonstrated that with Australian acacias, the combination of N_2 fixation coupled with the slow decomposition rates associated with sclerophyllous phyllodes led to elevated soil N pools with long-term impacts for ecosystem nutrient cycling. Australian acacias are thus strong ecosystem engineers, and the lasting legacy of increased soil N following Australian acacia invasion often results in reinvasion by the same or other alien species (Stock *et al.*, 1995; Marchante *et al.*, 2004, 2008, 2009; Yelenik *et al.*, 2004).

Nutrient conservation

The sclerophyllous nature of Australian acacia phyllodes translates to long-lived leaves and evergreen trees (Loveless, 1961; Turner, 1994a). The evolutionary drivers for this adaptation, whether drought tolerance or nutrient conservation, have been subject to much debate (Givnish, 1979; Turner,

Table 6 Litter biomass, litter N concentrations and soil N concentrations of Australian acacia invasions compared to uninvaded native vegetation in Portugal and in the Cape Floristic Region (CFR). Data for longer (20+ years) and shorter (10 years) invasion periods are shown for Portugal. A + indicates a significantly ($P < 0.05$) greater value associated with Australian acacias in comparison with native vegetation, 0 indicates no significant difference and ND indicates no data available.

Acacia spp.	Region	Litter Biomass	[N]	Soil [N]	Reference
A. cyclops	CFR	+	+	+	Witkowski, 1991b
	CFR	ND	ND	+	Stock *et al.*, 1995
A. longifolia	Portugal (20+ years)	+	+	+	Marchante *et al.*, 2008
	Portugal (10 years)	+	+	0	
	Portugal	ND	ND	+	Rodríguez-Echeverría *et al.*, 2009
A. saligna	CFR	+	+	+	Witkowski, 1991b
	CFR	ND	ND	+	Musil, 1993
	CFR	ND	ND	+	Stock *et al.*, 1995
	CFR	+	+	+	Yelenik *et al.*, 2004, 2007

1994b; Pasquet-Kok *et al.*, 2010). In nutrient-rich environments, the common drought-tolerance adaptation is drought deciduousness (Mooney & Dunn, 1970). However, in nutrient-poor environments, drought deciduousness would lead to the costly loss of limited nutrients. Thus, it is thought that sclerophyllous, long-lived phyllodes evolved to enhance nutrient conservation in response to nutrient limitations (Beadle, 1966; Specht & Rundel, 1990) with drought tolerance and unpalatability being associated with the sclerophyllous nature of phyllodes.

Extended leaf longevity of Australian acacias would, however, not be a marked advantage when invading other sclerophyllous vegetation with similar nutrient-retention characteristics. For example, leaf longevity of Australian acacias (mean years ± SE; 1.84 ± 0.28; Wright *et al.*, 2002) did not differ significantly ($P > 0.05$) from that of native CFR vegetation (mean ± SE; 2.62 ± 0.31; Midgley & Enright, 2000). Sclerophylly, although not different from that of the invaded flora, when coupled with other traits such as N_2 fixation may contribute to the success of Australian acacias. Interestingly, the non-phyllodinous and relatively non-sclerophyllous (i.e. high SLA) invasive Australian acacia, *A. mearnsii*, has particularly long-lived bipinnate leaves, which turn brown during drought but recover subsequent to the onset of rain (Orians & Milewski, 2007) possibly acting to conserve nutrients over multiple seasons.

Heteroblasty thus confers the advantage of different growth strategies between juvenile and adult life stages and between different environmental circumstances (Pasquet-Kok *et al.*, 2010). As young seedlings, acacias benefit from the high relative growth rate associated with bipinnate leaflets (Witkowski, 1991b; Hansen, 1996; Evans *et al.*, 2000; Pasquet-Kok *et al.*, 2010). The phyllodinous species then switch to slower-growing, longer-lived and hence nutrient-conserving phyllodes (Ullmann, 1989; Orians & Milewski, 2007; Pasquet-Kok *et al.*, 2010). Using acacia invasions in South Africa as a case study,

the distinct advantage of phyllodes in nutrient-poor and summer-drought regions can be inferred by the relative success of phyllodinous species in the mediterranean climate and nutrient-poor fynbos biome (Rouget *et al.*, 2004; Table 7, e.g. *A. pycnantha*). In contrast, the non-phyllodinous species (e.g. *A. mearnsii* and *A. dealbata*) are more successful as invaders in more mesic environments or along water courses (Rouget *et al.*, 2004; Table 7) where nutrients and water are not as limiting.

Plants can also conserve nutrients through the remobilization of limiting nutrients prior to leaf abscission (Eckstein *et al.*, 1999; Wright *et al.*, 2002), acting to increase the mean residence time of nutrients in the plant. Australian acacias remobilize nutrients prior to leaf abscission, especially when the specific nutrient is limiting in the system (Witkowski, 1991a). In the South African CFR, *A. saligna* remobilized a large proportion (71%) of its leaf P, an amount significantly greater than that of the comparison native species *Leucospermum parile* (48%; Witkowski, 1991a). However, studies assessing remobilization efficiencies of these plants in comparison with natives in invaded regions are scarce. Specht (1981) and Langkamp & Dalling (1982) showed that remobilization of nutrients by invasive Australian acacias was not particularly different to that of other Australian species from nutrient-impoverished areas (e.g. *Banksia ornata* and *Acacia holosericea*) and is thus not a trait unique to the invasive Australian acacias.

IMPLICATIONS FOR FUTURE INVASION RISK

Global change is expected to alter resource distribution and availabilities through changes to climate, nutrient cycling (through nutrient deposition), disturbance regimes and land-use practices. These changes are generally predicted to favour the increase and impacts of alien plant invasions around the globe (Dukes & Mooney, 1999; Thuiller *et al.*, 2007; Vilà

Table 7 Percentage of records of the eight most widespread invasive Australian acacia species found in each biome in South Africa. Species are ranked from most prevalent to least prevalent according to the percentage of quarter degree squares occupied, as recorded in the South African Plant Invaders Atlas (SAPIA; Henderson, 2007). The percentage of the total records that were found along water courses is also listed. Foliage indicates whether adult plants have leaves (L) or phyllodes (P). The biome in which each species had the highest occurrence is in bold.

Acacia spp.	Foliage	QDS (%)	Percentage of records found in each biome*					
			Savanna	Fynbos	Grassland	Nama karoo	Succulent karoo	Water courses
A. mearnsii	L	21	27	33	**38**	0	1	36
A. dealbata	L	12	12	2	**85**	0	0	50
A. saligna	P	8	9	**83**	0	0	7	35
A. cyclops	P	8	16	**74**	0	0	10	19
A. melanoxylon	P	7	15	**62**	23	0	0	27
A. longifolia	P	5	18	**73**	9	0	1	36
A. decurrens	L	5	16	**0**	84	0	0	13
A. pycnantha	P	2	3	**97**	0	0	0	4

*Biomes classified according to Rutherford, 1997.

Table 8 Response of net assimilation rate (NAR), relative growth rate (RGR), total plant biomass, stomatal conductance and total N fixed of invasive Australian acacias under elevated CO_2 levels (700 ppm). Foliage indicates whether adult plants have leaves (L) or phyllodes (P). + indicates an increase, 0 indicates no significant difference and − indicates a decrease in comparison with current ambient CO_2 levels (350 ppm), while ND is no data available.

Acacia spp.	Foliage	NAR*†	RGR*†	Biomass*†	Conductance‡	Total N fixed†
A. dealbata	L	+	+	+	0	0
A. implexa	P	+	+	+	+	+
A. irrorata	L	+	+	+	−	+
A. mearnsii	L	+	+	+	−	+
A. melanoxylon	P	+	+	+	−	+
A. saligna	P	+	+	+	0	ND

*Atkin et al., 1999; †Schortemeyer et al., 2002; ‡Evans et al., 2000.

et al., 2007), although there are exceptions (Richardson et al., 2000, 2010). Invaders may be able to benefit from these changes either by being stronger competitors for resources or because of decreased competition from stressed native species (Thuiller et al., 2007), as suggested by Davis et al. (2000) in the 'Fluctuating Resource Hypothesis'. Under elevated $[CO_2]$ environments, Australian acacias have higher net assimilation rates, leading to increased relative growth rate and plant biomass (Table 8). Plants also showed a decrease conductance and hence increased WUE (Table 8). Moreover, Australian acacias also fixed greater amounts of N_2 under elevated $[CO_2]$ (Table 8) as has also been shown for several other N_2-fixing species (Thomas et al., 1991; Vogel & Curtis, 1995; Polley et al., 1997). These studies indicate that with continuing global change, Australian acacia species may well have increased invasive competitive abilities for resource acquisition, further enhancing their invasion success.

CONCLUSION

To synthesize, the height and biomass of invasive Australian acacias in invaded ranges far exceeds that of the native species both as seedlings and as adults. Initial high relative growth rates allow acacias to overtop the native vegetation and out-compete natives for light. Greater below-ground investment combined with mycorrhizal and N_2-fixing symbioses enables access to both water and nutrients needed to sustain growth. Furthermore, sclerophylly and the greater ability to remobilize limiting nutrients enable efficient nutrient conservation. Thus, no one ecophysiological or morphological trait can be identified as the primary driver of invasion success. Instead, it would appear that multiple traits act synergistically to confer competitive advantage. Understanding the traits used by invasive Australian acacias to acquire, utilize and conserve essential resources will allow us to better understand how resource distribution and availability influence invasions across a landscape. Incorporating greater edaphic and biotic components of the invaded environments into current species distribution models would thus enhance predictive power of models that are currently mostly limited to the use of only abiotic factors and limited soil characteristics (Meier et al.,

2010). This is vital for predicting alien plant distributions, under both current and future global change scenarios.

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BIOSKETCH

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Author contributions: T.L.M., M.D.C., K.J.E. and N.N.B. conceptualized the paper, the writing of which was led by T.L.M.

Editor: David Richardson