Similarities in recruitment but differences in persistence in two related native and invasive trees: relevance of regenerative and vegetative attributes

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Abstract. Ecological theory predicts that the success of exotic plants in new environments depends on a combination of both regenerative and vegetative attributes. Identifying those attributes may benefit from approaches that specifically compare related exotic and native species, thereby overcoming strong habitat dependence and phylogenetic bias. *Gleditsia triacanthos* L. (Fabaceae) is described as an aggressive woody invader in a broad range of ecosystems of Argentina, where it coexists with other leguminous trees. In the present study, we assessed whether the success of *G. triacanthos* in the lower areas of Chaco woodlands of central Argentina is determined (1) by differences from the dominant native, *Prosopis alba*, in its combination of several attributes that enhance the invader's competitive ability, (2) by differences from *P. alba* in few key attributes that facilitate its spread, or (3) by strong functional similarities in response to environmental filtering by the invaded system. Our comparison of 19 functional traits of both species showed that regenerative and vegetative trends may vary independently, and that two contrasting strategies seem to underlie the success of *G. triacanthos* in this region. On the one hand, the invader might benefit by sharing regenerative attributes with the native relative that dominates the community, which is evidently a successful way of recruiting in the system. On the other hand, as recruitment is ensured, the species differs in several vegetative attributes, which may enhance its competitive ability in terms of growth rates and nutrient uptake.

Introduction

Invasion of new areas by exotic species is a global phenomenon, with economic, social and ecological consequences for biodiversity and ecosystem processes (Mack *et al*. 2000; Pimentel *et al*. 2000; Cohen 2002; Walther *et al*. 2009; Le Maitre *et al*. 2011). One of the major goals of research on invasive species is to understand the mechanisms involved in the invasion process. To meet that goal, studies generally focus on two aspects: the degree of invasibility of certain ecosystems or communities (i.e. characteristics of the community that enhance or hinder their susceptibility to get invaded by exotic species; Davies *et al*. 2007; Compagnoni and Halpern 2009; Milbau *et al*. 2009), and the attributes that confer invasiveness to certain species (i.e. functional differences between exotic invasive species and native or non-invasive congeners; Daehler 2003; Pratt and Black 2006; van Kleunen *et al*. 2010).

It is well known that the success of exotic plants in new environments depends largely on their functional attributes (Leishman *et al*. 2007; Pyšek and Richardson 2007; van Kleunen *et al*. 2010). The relevance of regenerative and/or vegetative features might vary during the different stages of the invasion process (Lloret *et al*. 2005; Dietz and Edwards 2006; Theoharides and Dukes 2007). Seed longevity and ability to recruit and germinate in broad ranges of conditions

might be crucial for the species to enter the new community (Crawley *et al*. 1996; Kudoh *et al*. 2007; Pyšek and Richardson 2007). In turn, vegetative traits might be critical to allow successful competition, survival and growth, once the plant has established (Funk and Vitousek 2007; Leishman *et al*. 2007; van Kleunen *et al*. 2010). Finally, a combination of both regenerative and vegetative attributes might aid in the final rates of spread and dominance in the invaded system. A comprehensive comparative study of functional traits in coexisting exotic and native species should therefore include traits relevant to both the regenerative and the established phases of the plant life cycle (McAlpine *et al*. 2008).

In line with Darwin's naturalisation hypothesis (Darwin 1859), assessments of invasiveness that take phylogeny into account suggest that exotic genera are more successful in new ranges than genera with native representatives (Lockwood *et al*. 2001; Ricciardi and Atkinson 2004; Strauss *et al*. 2006). Accordingly, knowledge of invasiveness may benefit from the analysis of differences and similarities between phylogenetically related native and exotic species (Darwin 1859; Lockwood *et al*. 2001; Ricciardi and Atkinson 2004).

Gleditsia triacanthos, a deciduous leguminous plant native to North America, has been described as an aggressive woody invader in different parts of the world (Global Compendium

of Weeds, available at http://www.hear.org/gcw/species/gleditsia_triacanthos, verified 11 October 2011). In Argentina, *G. triacanthos* invades a broad range of ecosystems, including subtropical mountain forests, temperate–humid palm savannas, Pampas grasslands and xerophytic Chaco mountain forests (Grau and Aragón 2000; Marco and Páez 2000; Ghersa *et al.* 2002; Zalba and Villamil 2002; Ruiz Selmo *et al.* 2007; Giorgis *et al.* 2011). In woody communities of central Argentina, *G. triacanthos* coexists with several native leguminous trees (e.g. *Prosopis alba*, *P. nigra*, *P. chilensis*, *P. torquata*, *P. flexuosa*, *P. caldenia*, *Acacia aroma*, *A. caven* and *A. praecox*; Mazia *et al.* 2001; Ferreras and Galetto 2010; Giorgis *et al.* 2011). In particular, at lower altitudes in Córdoba mountain woodlands, the invader seems to share both habitat (Giorgis 2011) and dispersal features with *P. alba*. Both species have indehiscent fruits, mostly dispersed by large vertebrates, such as livestock. To our knowledge, no studies have explored similarities or differences between *G. triacanthos* and this native relative in terms of both regenerative and vegetative attributes. A broad trait comparison between vegetative traits of several exotic and native woody species of the study area suggested an overall acquisitive syndrome among all woody exotic species (i.e. large, soft, thin, nutrient-rich leaves, and low-density wood; all related to rapid growth and resource capture) as compared with the native species of the Chaco mountains (Tecco *et al.* 2010). Although *P. alba* and *G. triacanthos* were included in that study, the approach lacked specific comparisons between related native and exotic species, because their species selection was not clade-based but rather community-based. Also, there is some evidence that *G. triacanthos* has better regenerative performance than another coexisting relative (*Acacia aroma*), aided by a higher number of seeds per plant, percentage germination of scarified seeds and seedling recruitment (Ferreras and Galetto 2010). Here, we attempt to evaluate whether the success of *G. triacanthos* is determined: (1) by differences from the dominant native, *P. alba*, in its combination of several attributes that enhance the invasive species' competitive ability (van Kleunen *et al.* 2010); (2) by differences from *P. alba* in few key attributes that facilitate its spread (Gurvich *et al.* 2005); or alternatively (3) by strong functional similarities in response to environmental filtering by the invaded system (Thompson *et al.* 1995, 2010; Thompson and Davis 2011). We address this still unresolved question by comparing both species in terms of 19 functional traits relevant to the regenerative and established phases of their life cycle (Cornelissen *et al.* 2003).

Materials and methods

Individuals of the species studied were distributed in the Chaco woodland of central Argentina, in the contact zone between the mountain and the plain areas, where *G. triacanthos* invades woodlands dominated by *P. alba*. The natural vegetation of the area is a seasonally dry woodland dominated by trees such as *Lithraea molleoides*, *Aspidosperma quebracho-blanco*, *Prosopis* spp., *Geoffroea decorticans*, *Zanthoxylum coco*, *Celtis* spp., thorny shrubs, such as *Acacia caven*, *Condalia* spp., *Schinus fasciculatus*, cacti, herbs, as well as epiphytes and vines (Luti *et al.* 1979; Cabido and Zak 1999). In addition to *Gleditisa triacanthos*, other exotic woody species

are present in the area, such as *Ligustrum lucidum*, *Melia azederach*, *Morus alba*, *Pyracantha angustifolia* and *Ulmus pumila*. Mean annual temperature is 16°C, with frosts commonly occurring from May to October (De Fina 1992). Mean annual rainfall is ~850 mm, mainly concentrated in the warm season (October to April) (Capitanelli 1979).

The Fabaceae is a large, complex and highly diverse family which grows across a very wide range of environments and has some extraordinarily widely distributed genera. Conventional taxonomy places *G. triacanthos* and *P. alba* in separate subfamilies (i.e. Caesalpinioideae and Mimosoideae) and recent phylogenetic studies show that the relationship is a distant one (Lavin *et al.* 2005). Still, some convergent evolution based on similar selective pressures and ecological drivers in their native environments might have occurred. The latter, as well as the present coexistence and dominance in the study area, allows the use of this pair of species to address our study questions.

Regenerative characterisation

Both species were characterised in terms of the following five regenerative traits: seed mass, water permeability of seed coat, germination at different photo- and thermo- periods, seed response to different water potentials and seed longevity. Mature dry seeds of *Prosopis alba* and *Gleditsia triacanthos* were collected from 15 individuals randomly distributed in the study area. Seeds were stored in the laboratory at room temperature for 30 days, before the start of the experiments.

For seed mass, a sample of 100 seeds of each species was weighed with a precision balance (0.1 mg). Seed-coat permeability to water was estimated by a water imbibition experiment. Two treatments were considered for each species: scarified seeds (individually with sandpaper) and non-scarified seeds. Each treatment consisted of three replicates of 20 seeds per species. Seeds were placed in 9-cm-diameter Petri dishes on filter paper moistened with distilled water. Dishes were placed in a chamber at $22 \pm 1°C$, 12/12 daily photoperiod of ~38 μmol m^{-2} s^{-1} cool white fluorescent light tubes. Initial seed weight was measured at the beginning of the experiment (i.e. Time 0). Water imbibition was then measured at two times (at 8 and 24 h of imbibition). On each occasion, seeds were removed from the moist paper, blotted dry, weighed with a precision balance (0.1 mg), and returned to the Petri dishes. The amount of water uptake was determined as the actual increase in seed weight expressed as a percentage (see Baskin *et al.* 2004; Funes and Venier 2006). Seed germination percentage following the treatments was also measured in both species.

Seed germination of both species was evaluated across different photo-thermo periods. Seeds were incubated in a chamber under light (12/12 h daily photoperiod of ~38 μmol m^{-2} s^{-1}, provided by cool white fluorescent light tubes) and darkness (dishes wrapped with a layer of aluminum foil). Three different temperature regimes of 15/5°C, 25/15°C and 35/20°C were used, alternating each temperature every 12 h. Scarified seeds were used for the experiment to overcome the physical dormancy observed with the water imbibition experiments (see Results). Seeds were placed for 15 days in 9-cm-diameter Petri dishes, with filter paper moistened with distilled water when necessary. Germination of

seeds incubated in darkness was checked at the end of each experiment.

Response to water potential was tested following Cony and Trione (1998). The following four treatments were used: 0 (control), –0.2, –0.7 and –1.2 MPa (Polietilenglicol 6000). Scarified seeds were placed in 9-cm-diameter Petri dishes on filter paper moistened with the four solutions. Petri dishes were incubated in a chamber with light (12/12 h daily photoperiod of ~38 μmol m^{-2} s^{-1}, provided by cool white fluorescent light tubes) at 25/15°C, which corresponds to the optimal thermo-period of most woodland species in the region (Funes *et al.* 2009). Seed germination percentage was measured for 30 days.

Germination of 1-year-old seeds was tested on both species to estimate seed longevity. Scarified seeds were placed in 9-cm-diameter Petri dishes on filter paper and incubated in a chamber at 25/15°C during 30 days, as in the previous experiments.

In all germination experiments, three replicates of 20 seeds were used for each treatment. Protrusion of the radicle was the criterion for germination.

Vegetative characterisation

We considered 14 vegetative morpho-functional traits (Table 1), all of them with direct functional implication in resource capture, retention and release for adult plants under different environmental conditions (Weiher *et al.* 1999; Westoby *et al.* 2002; Cornelissen *et al.* 2003; Díaz *et al.* 2004; Lloret *et al.* 2005). All traits were measured in the field on healthy, sexually mature plants growing in unshaded habitats; reported values are the average of at least six replicates per species. For details on ecological interpretation and measurements of traits, see Appendix 1, Hendry and Grime (1993), Díaz and Cabido (1997), Grime *et al.* (1997), Westoby (1998) and Cornelissen *et al.* (2003).

Data analysis

Differences in regenerative and vegetative traits between *G. triacanthos* and *P. alba* were assessed with Mann–Whitney tests, except seed-coat permeability, which was compared using ANOVA, followed by l.s.d. Fisher test (Sokal and Rohlf 1995).

Results

Regenerative attributes

The evaluation of seed-coat permeability revealed that, like for many members of Fabaceae, seeds of both *P. alba* and *G. triacanthos* have physical dormancy, as evidenced by strong increases in their rates of water imbibition following scarification (Fig. 1). Despite the variation in final imbibition rate, no significant differences were found in the subsequent germination percentages between species, neither for scarified and nor non-scarified seeds (Table 2). Accordingly, germination percentage tended to be similar in most of the germination assays, including the 1-year-old seeds. The exceptions were at the coldest thermo-period (i.e. 15/5°C light and dark) and under slight osmotic stress (i.e. –0.2 MPa), where the exotic tree species exhibited lower germination percentages than did *P. alba*. Significant differences in seed mass were observed between species, with *G. triacanthos* having a much heavier seed than *P. alba* (Table 2).

Vegetative attributes

The species exhibited important differences in terms of their vegetative attributes (Table 3). *G. triacanthos* showed significantly higher specific leaf area and leaf and leaflet area, thinner and softer leaves, and higher leaf nutrient contents than did the native tree. In addition, the exotic tree showed clonal spread, whereas *P. alba* lacked this vegetative reproduction ability. There were also differences in the water-use traits between species. *P. alba* showed lower values of leaf water potential and leaf area/shoot area than did *G. triacanthos*, which indicates a more stress-tolerant strategy of the former species. The only similarities observed between species in terms of vegetative traits were in canopy height, wood density and wood saturated water content.

Table 1.   Vegetative traits measured on the exotic species *Gleditsia triacanthos* and its native relative *Prospis alba*
For details on ecological meaning and measurement procedures, see Appendix 1, Cornelissen *et al.* (2003) and references therein

| Trait	Type of variable
Plant height	Continuous (cm)
Stem specific density	Continuous (oven dry mass of a section of a plant third main stem divided by the volume of the same section when still fresh; g mm^{-3})
Wood saturated water content	Continuous (g g^{-1})
Specific leaf area	Continuous (mm^2 leaf area per mg leaf mass)
Leaf area	Continuous (mm^2)
Leaflets area	Continuous (mm^2)
Leaf area/shoot area	Continuous (m^2 leaf area per cm^2 shoot area)
Leaf water potential	Continuous (–MPa)
Leaf thickness	Continuous (mm)
Leaf toughness	Continuous (= leaf tensile strength; N mm^{-1} leaf width)
Leaf phosphorous mass	Continuous (foliar P concentration per unit leaf mass)
Leaf nitrogen mass	Continuous (foliar N concentration per unit leaf mass)
Leaf phenology	Ordinal: 1 = deciduous; 2 = semi-deciduous; 3 = evergreen
Clonal spread	Binary: 0 = no clone expansion; 1 = clone expansion
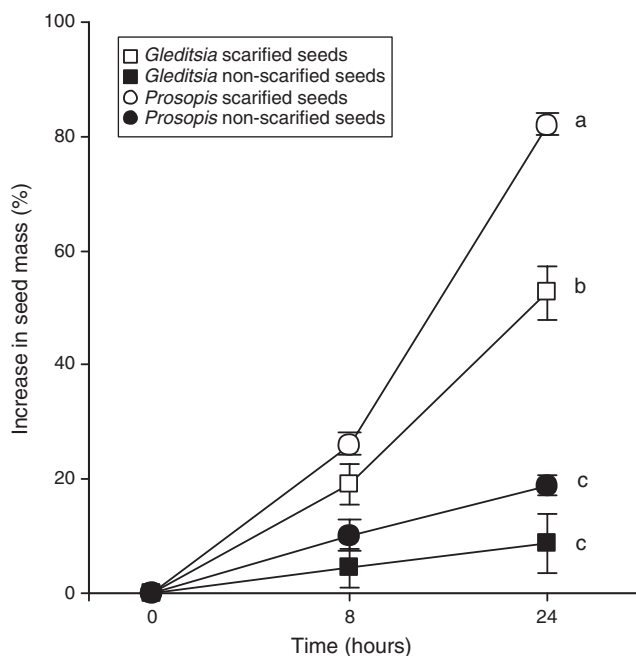
Fig. 1. Water permeability of *Gleditsia triacanthos* and *Prosopis alba* seeds, estimated by a water imbibition test on scarified and non-scarified seeds. Although water imbibition rates showed strong increases following scarification in both species, differences were observed after 24 h between species ($F = 32.81$, $P = 0.0004$) and scarification treatments ($F = 242.36$, $P < 0.0001$), with significant interactions ($F = 7.84$, $P = 0.0232$).

Discussion

Regenerative attributes

Gleditsia triacanthos and *P. alba* had more similarities than differences in terms of regenerative traits, as was also observed for different groups of regenerative traits in other pairs of native–exotic species (Thompson *et al.* 2001; Thompson and McCarthy 2008). These shared traits could be attributed to the presence of physical dormancy in both species,

Table 2. Comparison of regenerative traits between the exotic species *Gleditsia triacanthos* and its native relative *Prospis alba*

Means and standard errors are provided for seed mass and for percentages of seed germination following different experiments (i.e. coat permeability, contrasting photo/thermo periods, osmotic stress and longevity). Asterisks indicate significant differences between species following Mann–Whitney test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s., $P > 0.05$

Trait	*Gleditsia triacanthos*	*Prosopis alba*	*P*
Seed mass (mg)	179.5 ± 11	49.9 ± 2.4	***
Seed germination (%)			
Imbibition test			
Scarified seeds	86.6 ± 3.3	88.3 ± 1.6	n.s.
Non-scarified seeds	10 ± 0	13.3 ± 6	n.s.
Temperature/light			
15/5°C Light	$44b \pm 6.1$	85 ± 2.8	*
15/5°C Dark	0	81.6 ± 7.2	**
25/15°C Light	97.3 ± 2.6	91.6 ± 1.6	n.s.
25/15°C Dark	97.3 ± 2.6	96.6 ± 3.3	n.s.
35/20°C Light	90.6 ± 1.3	98.3 ± 1.6	n.s.
35/20°C Dark	85.3 ± 8.7	98.3 ± 1.6	n.s.
Water potential			
Control	80 ± 0.2	100 ± 0	n.s.
–0.2 MPa	48.3 ± 1.63	100 ± 0	*
–0.7 MPa	$0c$	5 ± 2.9	n.s.
–1.2 MPa	$0c$	$0c$	n.s.
Germination after 1 year	91.65 ± 4.4	100 ± 0	n.s.

which is expected to be related to similar seed characteristics, such as hard seed coats that are impermeable to water. Specific assessment of biotic and abiotic factors that could break seed dormancy and modify seed germination (such as passage through the digestive tract of dispersers, fire; Baskin and Baskin 1998; Baskin *et al.* 2000; Ortega Baes *et al.* 2002) would certainly complement the present findings.

Despite the overall similarity of both species in germination performance, seed mass of *G. triacanthos* was more than three times larger than that of the seeds of the native relative. This finding contrasts with the pattern usually described for invasive

Table 3. Comparison of vegetative traits between the exotic species *Gleditsia triacanthos* and its native relative *Prospis alba*

Means and standard errors are provided for continuous variables. Asterisks indicate significant differences between species following Mann–Whitney test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s., $P > 0.05$

Trait	*Gleditsia triacanthos*	*Prosopis alba*	*P*
Plant height (cm)	840 ± 57.88	816.667 ± 65.41	n.s.
Stem specific density (g mm^{-3})	0.703 ± 0.015	0.765 ± 0.031	n.s.
Wood saturated water content (g g^{-1})	0.80	0.82	n.s.
Specific leaf area (mm^2 mg^{-1})	24.811 ± 2.6	10.2 ± 0.479	**
Leaf area (mm^2)	12553.43 ± 1861	2671.997 ± 790.8	***
Leaflets area (mm^2)	76.93 ± 15.64	15.84 ± 1.99	**
Leaf area/shoot area (m^2 cm^{-2})	1.134 ± 0.164	0.231 ± 0.034	**
Leaf water potential	-2.94 ± 0.18	-3.74 ± 0.2	**
Leaf thickness (mm)	0.167 ± 0.013	0.321 ± 0.021	***
Leaf toughness (N mm^{-1})	0.836 ± 0.052	2.138 ± 0.121	***
Leaf phosphorous mass (%)	0.208 ± 0.027	0.126 ± 0.003	*
Leaf nitrogen mass (%)	2.872 ± 0.172	2.324 ± 0.076	*
Leaf phenology	Deciduous	Semi-deciduous	–
Clonal spread	Yes	No	–

species, i.e. that invasive species have a smaller seed mass than do non-invasives, which is generally related to rapid colonisation of disturbed habitats (Rejmànek and Richardson 1996; Hamilton *et al*. 2005). Alternatively, as observed in mature plant communities, a large seed mass might benefit seedling performance through high reserve contents (e.g. positive correlation with shade tolerance; Rejmànek *et al*. 2005). Whether seed-mass differences are related to differential seedling performance between *G. triacanthos* and its native counterpart is unknown, and deserves further study. Previous findings in the region have described higher seedling recruitment for *G. triacanthos* than for another native Fabaceae species with smaller seeds, *Acacia aroma* (Ferreras and Galetto 2010).

The remaining few regenerative traits that differed between species appeared to be more limiting than favourable for the exotic species. *G. triacanthos* had lower performance than *P. alba* in terms of seed germination at low temperatures and under low water stress (–0.2 MPa). However, this should not affect the invader success in the study area. In Chaco woodlands, water availability is highest during the warm period of the year, so both species seem to have the same chances to germinate. Whether water stress explains the absence of records of *G. triacanthos* in drier eco-regions of Argentina is beyond the scope of the present study; however, it represents an interesting avenue for exploring experimentally (see http://www.uns.edu.ar/inbiar for *G. triacanthos* distribution in Argentina, verified 11 October 2011).

Vegetative attributes

The differences in performance associated with the vegetative traits of this pair of species are consistent with the results reported for a group of native and exotic species in this region (Tecco *et al*. 2010) and in other parts of the world (Leishman *et al*. 2007). *G. triacanthos* has been shown to have key elements of an acquisitive syndrome of resource use (i.e. those related to higher growth rate and nutrient uptake; Díaz *et al*. 2004), along with some attributes often associated with higher competitive ability (e.g. larger leaf area; Grime 1979; Lloret *et al*. 2005). For example, differences in leaf water potential indicate that water transport is more efficient in *G. triacanthos*, but it is less resistant to drought than *P. alba* (Sperry *et al*. 2008). This higher conductivity would lead to higher transpiration and hence higher photosynthesis and growth in *G. triacanthos*. This invasive species would avoid the dry season by being deciduous, whereas *P. alba* maintains some of its leaves year round. Sprouting behaviour is a key trait for persistence in which allocation of resources to storage to support regrowth is expected to carry a cost traded off against growth or reproduction (Bond and Midgley 2001). However, in the case of *G. triacanthos*, by having such acquisitive leaf attributes, this invader seems to benefit both in terms of rapid growth and persistence.

The overall acquisitive syndrome of *G. triacanthos* may not only permit it so succeed in the presence of a dominant native relative, such as *P. alba*, in relatively well conserved woodlands, but also might favour its spread into the increasingly disturbed areas (i.e. areas affected by forest fragmentation, fire, logging and urbanisation) that characterise the remaining Chaco

woodlands of the region (Zak *et al*. 2008). Moreover, the sprouting behaviour is expected to alter woodland dynamics by favouring self-replacement after stem death (i.e. sprouts grow much faster than seedlings and can quickly reoccupy their own gaps), even if the tree is not shade tolerant (Bond and Midgley 2001).

Final remarks: being similar in recruiting but different in persisting

A considerable amount of research has been devoted to identifying attributes of invasive species that confer advantages over natives (Daehler 2003; Pratt and Black 2006; van Kleunen *et al*. 2010). Both regenerative and vegetative attributes are expected to influence final rates of spread and dominance of an invader in the new system. Going back to the original questions of the present study and on the basis of a comparison of 19 functional regenerative and vegetative traits in a pair of species, we suggest that by being similar to the dominant native, *P. alba*, in regenerative features (i.e. recruitment), but differing in its combination of attributes that enhance competitive ability (i.e. persistence and eventually dominance), may enable *Gleditsia triacanthos* to succeed as an invader in the Chaco woodlands of central Argentina. Whether having larger seeds (i.e. higher storage of resources) favours seedling survival and performance is not known, but could give it a critical advantage during the regeneration phase of an invasion, an aspect that should be explored in future studies.

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Appendix 1.   Description and brief information about the ecological context for 17 functional traits recognised as critical for tackling ecological questions of plant strategies

LA/SA, leaf area/shoot area; LNC, leaf N concentration; LPC, leaf P concentration; L_{th}, leaf thickness; SLA, specific leaf area

Trait	Description	Ecological meaning
Vegetative trait		
Plant height (cm)	The shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) on a plant and the ground level, expressed in cm.	Is associated with growth form, position of the species in the vertical light gradient of the vegetation, competitive vigour, reproductive size, whole plant fecundity, potential lifespan, and whether a species is able to establish and attain reproductive size between two disturbance events (e.g. fire, storm, ploughing, grazing). Within species, and among plants closely related within lineages, and across diverse species as well as in broad interspecific comparisons, height tends to correlate allometrically with other size traits, for instance aboveground biomass, stem diameter, rooting depth, lateral spread and leaf size (Cornelissen *et al.* 2003).
Stem-specific density ($g\,mm^{-3}$)	The oven-dry mass of a section of a plant's main stem divided by the volume of the same section, when still fresh.	Stem-specific density is a core functional trait because of its importance for the stability, defence, architecture, hydraulics, carbon (C) gain and growth potential of plants. Stem density partly underlies the growth–survival trade-off; a low stem density (with large vessels) leads to a fast growth, because of cheap volumetric construction costs and a large hydraulic capacity, whereas a high stem density (with small vessels) leads to a high survival, because of biomechanical and hydraulic safety, resistance against pathogens, herbivores and physical damage (Cornelissen *et al.* 2003).
Wood saturated water content ($g\,g^{-1}$)	The ratio between water-saturated fresh mass (g) of a terminal twig and its oven-dry mass (g). It is calculated as: (saturation mass – dry mass) dry mass.	Considered a critical component of species' potential to store water in plant tissues. Is associated to transpiration and photosynthesis efficiency (Stratton *et al.* 2001). This trait should be positively correlated with potential relative growth rate but this has, to our knowledge, not been tested explicitly.
SLA ($mm^2\,mg^{-1}$)	The one-sided area of a fresh leaf divided by its oven-dry mass.	SLA is frequently used in growth analysis because it is often positively related to potential relative growth rate across species. SLA scales positively with the mass-based light-saturated photosynthetic rate and leaf N concentration, and negatively with leaf longevity and C investment in secondary compounds. In general, species in permanently or temporarily (e.g. deserts during the rainy season) resource-rich environments tend to have higher SLA than those in resource-poor environments, although there are exceptions (Cornelissen *et al.* 2003).
Leaf and leaflets area (mm^2)	The one-sided projected surface area of a single leaf or leaf lamina, expressed in mm^2.	Leaf size and has important consequences for the leaf energy and water balance. Interspecific variation in leaf area has been related to climatic variation, geology, altitude or latitude, where heat stress, cold stress, drought stress, nutrient stress, and high-radiation stress all tend to select for relatively small leaves. Within climatic zones, variation in leaf area may also be linked with allometric factors (plant size, twig size, anatomy and architecture, leaf number, number of lateral buds produced) and ecological strategy with respect to environmental nutrient stress and disturbances, and phylogenetic factors can also play an important role. When measuring leaf area on compound-leaved species, either the leaflet area or the whole leaf area can be measured. For the heat balance the leaflet area is important, which is functionally analogous to a simple leaf. When analysing total light capture, the whole leaf should be measured. For compound-leaved species both the leaflet area and whole leaf area should be measured, as this allows one to address more questions and to compare the results with other studies (Cornelissen *et al.* 2003).

Appendix 1.   (*continued*)

Trait	Description	Ecological meaning
LA/SA	The amount of leaf area a species produces per unit cross-section of sapwood (the inverse of Huber value, expressed in $m^2 cm^{-2}$).	Also defined as leaf : sapwood area ratio. This trait is crucial for both water transport (with related effects on photosynthetic rate) and mechanical strength (Cornelissen *et al.* 2003). This trait is an indicator of leaf water status; lower values of LS/SA allow constant provision of water to the leaves which might buffer any increase in leaf transpiration (Wright *et al.* 2004).
Leaf water potential	Measured with a pressure chamber, or Scholander bomb.	Species facing soil water shortage can avoid water stress to a degree by dropping leaves, or delay water stress in their tissues by rooting deeply, or shutting stomata and losing stored water slowly through their cuticle. Alternatively, tissues may tolerate physiological desiccation. The bulk leaf water potential (Ψ_L; unit MPa) is a simple indicator of leaf water status; the more negative the value, the more dehydrated the leaf. When measured in the dry season, the midday Ψ_L can provide a useful index of the degree of drought experienced. Thus, the minimum value for Ψ_L that a plant reaches, usually at midday at the driest, hottest time of year, can be used as an index of the tolerance to water shortage that the species demonstrates (assuming that the plants are still healthy and not drought-injured) (Stratton *et al.* 2001; Cornelissen *et al.* 2003; Wright *et al.* 2004).
L_{th}	The thickness of a single leaf or leaf lamina, expressed in mm.	L_{th} plays a key role in determining the physical strength of leaves. Optimisation theory, balancing photosynthetic benefits against C costs of respiration and transpiration, predicts that L_{th} should be higher in sunnier, drier, and less fertile habitats, as well as in foliage with longer leaf lifespan. Both within- and among-species, the strongest anatomical driver of variation in leaf thickness is the number and thickness of mesophyll layers. Consequently, L_{th} is a strong driver of leaf N per area. Although higher L_{th} should lead to faster photosynthetic rates per unit leaf area (via higher N : area), this relationship is often weak in inter-specific studies, for a combination of reasons. First, because of covariance of SLA and % N, thicker leaves often have lower %N and longer leaf-lifespan (which are associated with lower photosynthetic rate per unit leaf mass). Second, thicker-leaved species may have slower CO_2 diffusion (lower mesophyll conductance) via longer diffusion pathways, greater internal self-shading of chloroplasts, or higher optical reflectivity in combination with lower internal transmittance. Thick leaves are also a feature of succulents (Cornelissen *et al.* 2003).
Leaf toughness ($N mm^{-1}$)	Leaf toughness or tensile strength is estimated as the force needed to tear a leaf or leaf fragment, divided by its width, expressed in $N mm^{-1}$.	Physically stronger leaves are better protected against abiotic (e.g. wind, hail) and biotic (e.g. herbivory, trampling) mechanical damage, contributing to longer leaf lifespans. Physical investment in leaf strength is a good indicator of C investment in structural protection of the photosynthetic tissues (Cornelissen *et al.* 2003).
Leaf N and P mass (%)	LNC and LPC are the total amounts of N and P, respectively, per unit of dry leaf mass, expressed as %dry leaf mass (or in $mg g^{-1}$).	Interspecific rankings of LNC and LPC are often correlated. Across species, LNC tends to be closely correlated with mass-based maximum photosynthetic rate and with SLA. High LNC or LPC is generally associated with high nutritional quality to the consumers in food webs. However, LNC and LPC of a given species tend to vary significantly with the N and P availability in their environments. The LNC : LPC (N to P) ratio is used as a tool to assess whether the availability of N or P is more limiting for C cycling processes in ecosystems. Legumes and other N-fixing plants tend to have higher LNC : LPC ratios than other plants growing at the same site (Cornelissen *et al.* 2003; Wright *et al.* 2004).

Appendix 1.   (*continued*)

Trait	Description	Ecological meaning
Leaf phenology	Proportion of the year that the leaf canopy is green, and thus able to perform photosynthesis.	Certain groups of competition avoiders may have very short periods of foliar display outside the main foliar peak of the more competitive species. Species that colonise gaps after major disturbance events may belong to this group too. Deciduous species avoid losing precious foliar resources by resorbing them and then dropping the leaves before the onset of a drought season or winter. Evergreen species have the advantage of a year-round ability to photosynthesise and they manage important growth at the beginning of the favourable season, before seasonally green species start competing for light (Cornelissen *et al.* 2003).
Clonal spread	Clonality is the ability of a plant species to reproduce or regenerate itself vegetatively, thereby producing new 'ramets' (aboveground units) and expanding horizontally.	Clonality can give plants competitive vigour and the ability to exploit patches rich in key resources (e.g. nutrients, water, light). Clonal behaviour may be an effective means of short-distance migration under circumstances of poor seed dispersal or seedling recruitment. Clonality also gives a plant the ability to form a bud bank, which can be a very important determinant of recovery and persistence after environmental disturbances. The bud bank consists of all viable axillary and adventitious buds that are present on a plant and are at its disposal for branching, replacement of shoots, regrowth after severe seasons (winter, dry season, fire season), or for vegetative regeneration after injury (Cornelissen *et al.* 2003).
Regenerative trait		
Seed mass (mg)	The species' average dry mass of a seed, expressed in mg. Also called seed size.	Stored resources in large seeds tend to help the young seedling to survive and establish in the face of environmental hazards (e.g. deep shade, drought, herbivory). Smaller seeds can be produced in larger numbers with similar reproductive effort. Smaller seeds also tend to be buried deeper in the soil, particularly if their shape is close to spherical, which aids their longevity in seed banks (Baskin and Baskin 1998).
Seed germination (%) following		
Imbibition test		Indicates the rate of water uptake in seeds. Comparisons of water uptake between scarified and no scarified seeds are indicative of physical seed dormancy (Funes and Venier 2006).
Temperature and light test		Gives information about the range of temperature and light conditions in which a species could germinate (Baskin and Baskin 1998). A broad range of germination conditions must be related to broad possibilities for species establishment.
Water potential test		Useful to understand the probability of seed germination in environments with different water availability. Higher percentage of seed germination as water potential becomes more negative is related to higher probabilities of germination in environments with increasing water stress (Bradford 1990).
Longevity test		Gives information of species' seed viability (i.e. potential to germinate) after a certain period from its production. Higher longevity is expected to give species higher probabilities of waiting for proper germination conditions in the environment, thereby increasing the likelihood of seedling establishment (Baskin and Baskin 1998). For several species, having seed longevity is one of the prerequisites to form persistent seed banks (Schwienbacher *et al.* 2010).