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Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings?

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Abstract. Research into interspecific variation in functional traits is important for our understanding of trade-offs in plant design and function, for plant functional type classifications and for understanding ecosystem responses to shifts in species composition. Interspecific rankings of functional traits are a function of, among other factors, ontogenetic or allometric development and environmental effects on phenotypes. For woody plants, which attain large size and long lives, these factors might have strong effects on interspecific trait rankings. This paper is the first to test and compare the correspondence of interspecific rankings between laboratory grown seedlings and field grown adult plants for a wide range of functional leaf and stem traits. It employs data for 90 diverse woody and semi-woody species in a temperate British and a (sub)Mediterranean Spanish flora, all collected according to a strict protocol. For 12 out of 14 leaf and stem traits we found significant correlations between the species ranking in laboratory seedlings and field adults. For leaf size and maximum stem vessel diameter > 50 % of variation in field adults was explained by that in laboratory seedlings. Two important determinants of plant and ecosystem functioning, specific leaf area and leaf N content, had only 27 to 36 and 17 to 31 % of variation, respectively, in field adults explained by laboratory seedlings, owing to subsets of species with particular ecologies deviating from the general trend. In contrast, interspecific rankings for the same traits were strongly correlated between populations of field adults on different geological substrata. Extrapolation of interspecific trait rankings from laboratory seedlings to adult plants in the field, or *vice versa*, should be done with great caution.

Keywords: Allometry; Interspecific variation; Intraspecific variation; Ontogeny; Shrub; Trait; Tree.

Nomenclature: Castroviejo et al. (1986-2000); Stace (1991).

Abbreviations: DM/SM = Leaf dry mass/saturated mass ratio; LD = leaf density; PAR = Photosynthetically active radiation; SLA = Specific leaf area; SSLM = Specific saturated leaf mass; SVD_{max} = Maximum stem vessel diameter.

Introduction

The study of interspecific variation in functional traits of plants has provided, and will continue to provide, important insights into (1) fundamental patterns and trade-offs in plant design and functioning (e.g. Poorter & Bergkotte 1992; Reich et al. 1992; Von Willert et al. 1992; Grime et al. 1997; Lambers et al. 1998; Craine et al 2001); (2) the classification of plant species into 'functional types' or strategies (e.g. Von Willert et al. 1990, 1992; Diaz & Cabido 1997; Lavorel et al. 1997; Westoby 1998; Gitay et al. 1999; Semenova & van der Maarel 2000); (3) the effects of (changing) species composition on ecosystem functions (e.g. Schulze et al. 1994; MacGillivray et al. 1995; Wardle et al. 1998; Díaz et al. 1999). But how are interspecific trait rankings obtained? Three different approaches have been frequently used, each with their own advantages and disadvantages, i.e. field sampling, 'common garden' studies and laboratory screening.

1. Field sampling. Interspecific trait rankings of (adult) plants in the field have the obvious advantage of not needing extrapolation to natural conditions, but the drawback is that the causes of this variation are difficult to unravel. Many of the important traits of adult plants in the field, particularly numerically continuous ones, show ample variability within a given species, which may affect species rankings for these traits. Such variability may result from a combination of (onto-)genetic differences within and between populations, environmental effects on phenotypes and measurement error (e.g. Grimshaw & Allen 1987; Huante et al. 1995; Thompson et al. 1997; Wright et al. 2001; Garnier et al. 2001a, b).

2. Common garden studies. One way to reduce variability due to environmental factors is to grow plants of a range of species or genotypes in a 'common garden' (see Reich et al. 1996), i.e. an outdoor site of limited size with relatively little environmental heterogeneity. For woody plants, however, this approach requires much space over a long period of time, while environmental heterogeneity remains an important source of variability. This approach can be seen as intermediate between 1 and 3.

3. Laboratory screening. An alternative is to derive interspecific rankings in functional traits from those of young plants grown under relatively favourable controlled environmental conditions, such as in laboratory growth chambers. This 'laboratory screening' approach has been widely used because of the relative ease of standardization of ontogeny/allometry and the plants' environment (e.g. Poorter & Bergkotte 1992; Grime et al. 1997). In such studies interspecific trait variation may be largely interpreted as inherent (genetically determined).

The question arises whether, and to what extent, interspecific trait rankings of young plants in laboratory screenings can be used as reliable predictors of interspecific trait rankings of adult plants in the field, and *vice versa*. In other words, how robust are interspecific trait rankings to a combination of ontogenetic, allometric (*sensu* Niklas 1994) and environmental factors? This is a very important question given the recent push to combine interspecific trait databases (1) to reveal trans-regional and even global trait linkages and trade-offs and (2) as a tool for predicting responses to global environmental changes (Díaz et al. 2002).

Some preliminary studies tackled this question for a small number of leaf traits, but with a bias towards herbaceous species (Garnier & Freijsen 1994; Fenner et al. 1999; Poorter & de Jong 1999; Poorter & Garnier 1999). For woody plants, some data are available for specific leaf area (SLA, leaf area / leaf dry mass) and leaf N content (Cornelissen et al. 1997; Poorter & Garnier 1999), relative growth rate (Cornelissen et al. 1998), leaf size (Cornelissen 1999) and stomatal conductance (Kolb et al. 1997), but a comprehensive picture has been lacking. There is ample evidence of drastic ontogenetic or allometric shifts in particular plant taxa for various functional traits from the seedling phase to adulthood of woody plants, for example in leaf structural traits (Groom et al. 1997; King 1999) and leaf chemistry and palatability (Fenner et al. 1999). The temperate leguminous shrub *Ulex* provides an obvious example of an extreme shift in leaf morphology, from broad leaves on young seedlings to photosynthetic spines on adult plants. Such shifts for particular species are likely to upset the correspondence of trait rankings between seedlings and adult plants.

This paper is the first to test and compare the correspondence of interspecific rankings between laboratory grown seedlings and field grown adult plants for a wide range of functional leaf and stem traits. Most of these traits are widely accepted as being critical for plant functioning, and some (e.g. SLA, foliar N content, leaf size) have a key position in ecosystem carbon and nutrient cycling or response to environmental change (e.g. Schulze et al. 1994; Box 1996; Cornelissen et al. 1999, 2001). For those traits we also test the sensitivity of interspecific rankings to environmental (edaphic) factors to which adult plants are exposed in the field. Since evergreen and deciduous species are known to vary consistently in many of the traits investigated (Reich et al. 1992; Cornelissen et al. 1996, 1997; Castro-Díez et al. 1998a, 2000), these leaf habits are also considered as a possible source of deviation from interspecific trait rankings of laboratory seedlings vs field adults. We employ data for 90 woody and semi-woody species in a temperate British and a (sub) Mediterranean Spanish flora, all collected according to a strict protocol.

Methods

Study areas and species

The study comprised 62 woody and semi-woody species from a temperate atlantic flora in central England and 42 (including two *Quercus ilex* subspecies) from a Mediterranean and sub-Mediterranean flora in northern Spain (Table 1). For 14 of these species adult plants in the field were sampled both in England and in Spain.

The English species were from within a 25 km radius around Sheffield (53°20' N, 1°50' W) at altitudes between 50 and 350 m a.s.l. Here, mean annual rainfall ranges between ca. 600-1200 mm, distributed throughout the year but with a winter maximum. Mean annual temperature is ca. 10 ºC, while frost may occur in 6-8 months of the year. Evapotranspiration only exceeds precipitation in none to two months each year. The main semi-natural ecosystems in which woody plants were sampled are broad-leaved woodland, heathland, low management grassland, coniferous plantations and ruderal habitats. These ecosystems cover several geological substrata (see below). Some additional species, most of which are naturalised in the British Isles (Table 1; Stace 1991), were sampled in parks and gardens in Sheffield. Seeds for the laboratory seedling assay were generally collected from this region, but some species were from other British or Dutch provenances (App. 1 in Cornelissen 1996).

Table 1. The study species sampled in the field, life form and leaf habit. Life forms: T = tree; S = shrub; SS = subshrub (dwarf shrub); C = climber; SC = scrambler. Leaf habits: D = deciduous; E = evergreen. *L. vulgare* and *R. fruticosus* are deciduous or semi-evergreen, but treated here as deciduous species. * sampled in garden or park.

British species	Family	Life form	Leaf habit	Spanish species	Family	Life form	Leaf habit
*Acer platanoides**	Aceraceae	T	D	*Arbutus unedo*	Ericaceae	S	E
Acer pseudoplatanus	Aceraceae	T	D	*Atriplex halimus*	Chenopodiaceae	S	E
*Aesculus hippocastanum**	Hippocastanaceae	T	D	*Buxus sempervirens*	Buxaceae	S	E
Alnus glutinosa	Betulaceae	T	D	*Celtis australis*	Ulmaceae	T	D
*Arbutus unedo**	Ericaceae	S	E	*Cistus albidus*	Cistaceae	SS	E
Berberis vulgaris	Berberidaceae	S	D	*Cistus clusii*	Cistaceae	SS	E
Betula pendula	Betulaceae	T	D	*Cistus laurifolius*	Cistaceae	S	E
Buddleja davidii	Buddlejaceae	S	D	*Clematis vitalba*	Ranunculaceae	C	D
Buxus sempervirens	Buxaceae	S	E	*Cornus sanguinea*	Cornaceae	S	D
Calluna vulgaris	Ericaceae	SS	E	*Corylus avellana*	Betulaceae	S	D
Castanea sativa	Fagaceae	T	D	*Crataegus monogyna*	Rosaceae	S	D
Cornus sanguinea	Cornaceae	S	D	*Daphne gnidium*	Thymeleaceae	S	E
Corylus avellana	Betulaceae	S	D	*Fraxinus angustifolius*	Oleaceae	T	D
Crataegus monogyna	Rosaceae	S	D	*Globularia alypum*	Globulariaceae	SS	E
Cytisus scoparius	Fabaceae	S	E	*Hedera helix*	Araliaceae	C	E
*Daphne mezereum**	Thymeleaceae	S	D	*Helianthemum hirtum*	Cistaceae	SS	E
Dryas octopetala	Rosaceae	SS	E	*Helianthemum nummularium*	Cistaceae	SS	E
Empetrum nigrum	Empetraceae	SS	E	*Helianthemum squamatum*	Cistaceae	SS	E
Erica cinerea	Ericaceae	SS	E	*Lavandula angustifolia*	Lamiaceae	SS	E
Fagus sylvatica	Fagaceae	T	D	*Lavandula latifolia*	Lamiaceae	SS	E
Frangula alnus	Rhamnaceae	S	D	*Ligustrum vulgare*	Oleaceae	S	D
Fraxinus excelsior	Oleaceae	T	D	*Linum suffruticosum*	Linaceae	SS	E
*Hebe × franciscana**	Scrophulariaceae	S	E	*Lonicera implexa*	Caprifoliaceae	C	E
Hedera helix	Araliaceae	C	E	*Phillyrea angustifolia*	Oleaceae	S	E
Helianthemum nummularium	Cistaceae	SS	E	*Pinus halepensis*	Pinaceae	T	E
*Hippophae rhamnoides**	Eleagnaceae	S	D	*Pinus sylvestris*	Pinaceae	T	E
Ilex aquifolium	Aquifoliaceae	T	E	*Pistacia lentiscus*	Anacardiaceae	S	E
*Juglans regia**	Juglandaceae	T	D	*Pistacia terebinthus*	Anacardiaceae	S	D
*Laburnum anagyroides**	Fabaceae	T	D	*Prunus spinosa*	Rosaceae	S	D
Larix decidua	Pinaceae	T	D	*Quercus coccifera*	Fagaceae	S	E
Ligustrum vulgare	Oleaceae	S	D	*Quercus faginea*	Fagaceae	T	D
Lonicera periclymenum	Caprifoliaceae	C	D	*Quercus ilex* ssp. *ballota*	Fagaceae	T	E
Malus sylvestris	Rosaceae	T	D	*Quercus ilex* ssp. *ilex*	Fagaceae	T	E
Picea sitchensis	Pinaceae	T	E	*Retama sphaerocarpa*	Fabaceae	S	E
Pinus sylvestris	Pinaceae	T	E	*Rhamnus alaternus*	Rhamnaceae	S	E
*Prunus laurocerasus**	Rosaceae	S	E	*Rhamnus lycioides*	Rhamnaceae	S	E
*Prunus lusitanica**	Rosaceae	S	E	*Rosmarinus officinalis*	Lamiaceae	S	E
Prunus spinosa	Rosaceae	S	D	*Sambucus nigra*	Caprifoliaceae	S	D
*Quercus cerris**	Fagaceae	T	D	*Santolina chamaecyparissus*	Asteraceae	SS	E
Quercus ilex ssp. *ilex*	Fagaceae	T	E	*Solanum dulcamara*	Solanaceae	SC	D
Quercus petraea	Fagaceae	T	D	*Ulmus minor*	Ulmaceae	T	D
Quercus robur	Fagaceae	T	D	*Viburnum tinus*	Caprifoliaceae	S	E
*Quercus rubra**	Fagaceae	T	D				
Rhamnus catharticus	Rhamnaceae	S	D				
Rhododendron ponticum	Ericaceae	S	E				
*Ribes nigrum**	Glossulariaceae	S	D				
Ribes uva-crispa	Glossulariaceae	S	D				
Rosa arvensis	Rosaceae	SC	D				
Rubus fruticosus s.l.	Rosaceae	SC	D				
Salix caprea	Salicaceae	T	D				
Sambucus nigra	Caprifoliaceae	S	D				
Solanum dulcamara	Solanaceae	SC	D				
Sorbus aucuparia	Rosaceae	T	D				
Taxus baccata	Taxaceae	T	E				
Thymus polytrichus	Lamiaceae	SS	E				
Ulex europaeus	Fabaceae	S	E				
Ulex gallii	Fabaceae	S	E				
Ulmus glabra	Ulmaceae	T	D				
Vaccinium myrtillus	Ericaceae	SS	D				
Vaccinium vitis-idaea	Ericaceae	SS	E				
Viburnum opulus	Caprifoliaceae	S	D				
*Viburnum tinus**	Caprifoliaceae	S	E				

The Spanish species were from a ca. 25000 km² area which extends from the middle Ebro Basin near Zaragoza north up the foothills of the Pyrenees near Jaca and northwest to the Atlantic coast near Bilbao (41° 21' - 43° 16' N, 0° 21'E - 2° 53' W), at altitudes between 170 and 1030 m a.s.l. Mean annual rainfall ranges from 350 mm in the Ebro Basin to 1200 mm at the Atlantic coast, spring and autumn being the wetter seasons. Mean annual temperature is ca. 11 °C near the Atlantic coast and at higher altitudes and 15 °C towards the Ebro Basin and frost may only occur in three to five winter months. Evapotranspiration exceeds precipitation during two to four months in the drier parts. We sampled many of the species in xerophytic shrubland, xerophytic woodland and riverine vegetation, but mesic shrubland and woodland were also significantly represented, both in lowland and upland areas. The underlying geology is generally limestone and partly marls, but a few populations of some species grew on gypsum substrata. For those species that were sampled in the field in both countries, seeds for the laboratory seedling assay were mostly collected in England, but *A. unedo*, *B. sempervirens*, *Q. ilex* ssp. *ilex* and *V. tinus* seeds were from Spain (Table 1).

Collecting from adult plants in the fields

England

Between 5 July and 8 August 1995, between one and four (in most species two or three) adult plants of each species were sampled, each from a different geological substratum with associated differences in soil characteristics. The main substrata were acidic sandstone, carboniferous limestone, magnesium limestone and slightly acidic loamy deposits with coal strata ('Coal Measures'). For each plant 15 undamaged, fully expanded sun leaves were cut off and stored in wet tissue at 5 °C until measurement. For evergreen species we took both a 15-leaf subsample of the current year's cohort and a 15-leaf subsample of the previous year's cohort. In the heteroblastic species, *H. helix*, *I. aquifolium* and *L. decidua*, we took 15 leaf subsamples of each leaf type. For all leaf traits (see below) we took the mean for each plant (in the evergreen and heteroblastic species calculated as the mean for the two cohort means) and subsequently the mean for all plants, to obtain one species mean value for further data analysis.

Spain

Samples were collected between July and September, mostly in 1992 and partly in subsequent years. We sampled nine species out of the 42 in 5-16 localities distributed throughout the whole climatic gradient, selecting one plant per site. The remaining species were collected just in one or a few sites (Castro-Díez 1996; Castro-Díez et al. 1997, 1998b; Villar-Salvador et al. 1997). Stem vessel diameters of field adults were measured on two 3 yr old branch segments per plant at mid height at the southern side of the crown. From the same branches, 25 fully expanded and hardened sun leaves were sampled from the current year cohort and stored in the freezer until analysis. Stem (wood) density of field adults was measured on three 0.1- 0.2 m segments of branches which were at least six years old, each segment coming from a different site within the study area. Mean trait values were first calculated per plant, then per population and then over all populations to obtain the species mean.

Laboratory seedlings

Woody species vary greatly in their requirements for dormancy breaking and germination. The (fresh, cleaned) seeds of many species, including most of the bird dispersed and some large seeded species, were pretreated in a greenhouse as long as necessary by burying them in a moist 50:50 sand and compost mixture at ca. 20 °C (4 - 20 wk) and then in the same medium, also moist, at 2 - 5 °C (stratification). In some species with weaker dormancy

only the latter pretreatment was required. For a few ericaceous species (e.g. *Empetrum nigrum*) an additional warm-cold cycle was applied, while a few other species (e.g. *Fagus sylvatica*) were pretreated in sand only. After pretreatment, germination was promoted at ca. 20°C. Seeds of many other, often small seeded species, were germinated on moist filter paper, with or without (e.g. *Salix caprea*) previous dormancy breaking pretreatment. Such dormancy pretreatment could be either scarification in the case of hard seed coats (e.g. *Cistaceae*, *Fabaceae*) or a dark stratification at 2-5°C (2-8 wk) on the same moist filter paper (e.g. *Pinus sylvestris*). Again, germination was invoked at 20°C. A few species with notoriously deep dormancy (*Crataegus monogyna*, *Fraxinus excelsior*, *Ilex aquifolium*, *Taxus baccata*) were collected from the field just after germination, in the cotyledon phase without true leaves. Once the new root system of any germinated seedling was considered strong enough, the seedling was transplanted into the plant containers for further growth and subsequent screening tests, with gradual acclimation of light and nutrient availability before the start of the actual screening. Details of seedling growing conditions are in Cornelissen et al. (1996). Essentially, the seedlings grew in quarried sand, at non limiting water and nutrient availability in a growth chamber, with photosynthetically active light supplied during 14 hr days at 130 ± 5 µmol m^{-2} s^{-1} (at 20-22°C; night temperature 15-17°C). We standardized the ontogenetic phase among all species by growing the seedlings for 21 days from the day that the modal plant of the population had just opened (but not necessarily expanded) its first true leaf (i.e. not counting leaf like cotyledons), at which time the plants were assumed to commence the transition from the cotyledon dependent phase to independent photosynthetic assimilation. On day 21 the plants were harvested. We pickled three or four random plants (details in Castro-Díez et al. 1998a) for anatomical and stomatal analyses. The remainder (8-30 plants, usually 16 per species) were separated into leaves, cotyledons, stems and (washed) roots.

Traits and measurements

The functional and/or ecological significances of the traits investigated here have been well documented and reviewing these in detail is beyond the scope of this paper. Stomatal traits are linked with foliar conductance for CO_2 and water transport (e.g. Salisbury 1927; Carpenter & Smith 1975; Woodward 1987; Von Willert et al. 1992; Beerling & Kelly 1996; Gutschik 1999); epidermal cell size to nuclear DNA amount, phenology and drought tolerance (e.g. Cutler et al. 1977; Grime et al. 1985; van Arendonk & Poorter 1994). Specific leaf

area (SLA), specific saturated leaf mass (SSLM; leaf saturated mass / leaf area), leaf dry mass / saturated mass ratio (DM/SM), leaf thickness and leaf density (LD = leaf dry mass / fresh volume) are all interrelated and feature in the trade-off between inherent relative growth rate and protection against abiotic stress, pathogen attack or herbivory (e.g. Lambers & Poorter 1992; Reich et al. 1992; Garnier & Laurent 1994; Cornelissen et al. 1996; Castro-Díez et al. 1997, 2000; Westoby 1998; Poorter & De Jong 1999; Poorter & Garnier 1999; Weiher et al. 1999; Wilson et al. 1999; Wright et al. 2001). Leaf size has important consequences for the leaf energy and water balance. Interspecific variation in leaf size has been connected with climatic variation, geology, altitude or latitude where heat stress, cold stress, drought stress and high radiation stress all tend to select for relatively small leaves (e.g. Raunkiaer 1934; Parkhurst & Loucks 1972; Orians & Solbrig 1977; Givnish 1979; Box 1996). Foliar nutrient contents tend to be closely connected with photosynthetic capacity, but also to palatability to herbivores and litter decomposability (e.g. Field & Mooney 1986; Reich et al. 1992; Cornelissen & Thompson 1997; Castro-Díez et al. 1997; Cornelissen et al. 1997; Castro-Díez et al. 1998b; Aerts & Chapin 2000; Wright et al. 2001). Stem vessel diameter (SVD_{max}) has been associated with plant water transport capacity and growth rate as well as (inversely) to drought and cold tolerance (e.g. Zimmermann 1983; Baas & Schweingruber 1987; Tyree & Sperry 1989; Gartner 1990; Villar-Salvador et al. 1997; Castro-Díez et al. 1998a), while high stem densities (SD) have been related to structural strength, protection and carbon storage and lower growth rates (e.g. Gartner 1990; Favrichon 1994; Castro-Díez et al. 1998a; Roderick & Berry 2001).

The methodology followed for the measurement of all 14 traits is described in App. 1. Stomatal area fraction (SAF) is defined as the total stomatal area on both leaf surfaces divided by the one-sided leaf area (see App. 1).

Data analysis

Data analyses were carried out separately for the British and the Spanish species subsets, because (1) the different climates and soils of both regions could have caused both inherent and phenotypical overall differences in traits and trait rankings of the two woody floras involved and (2) the two woody floras, differing greatly in their lower and higher level taxonomy, served as one large and powerful independent phylogenetic contrast (*sensu* Harvey & Pagel 1991; Freckleton 2000). Since each of the two woody species sets also featured a wide range of genera, families (Table 1) and higher taxa (see Castro-Díez et al. 1998a) within itself, it was not necessary to perform separate 'taxonomic relatedness

tests' (e.g. Kelly & Beerling 1995) on the interspecific ranking analyses described below.

Interspecific rankings of trait variation of laboratory seedlings and field adults were principally compared by Spearman's rank correlation (*r*). Subsequently we also employed Pearson's (parametric) product-moment correlation, after data transformation (see below). Pearson's correlation (ρ) provides information on the relative amount of scatter around the linear trend line. It also enabled us to interpret the determination coefficient ρ^2 (as in linear regression) as the fraction of trait variation in field adults explained by that of laboratory seedlings (given a significant relationship). This would also provide a link with previous data in the literature. Stomatal and epidermal traits, SLA and SSLM were ln-transformed prior to analysis and leaf sizes log_{10}-transformed to meet the requirement of normality of the frequency distributions. Differences in stomatal distributions between upper and lower leaf surfaces (classes H, A and He; see above) between laboratory seedlings and field adults were tested using a χ^2 test. Gymnosperms were excluded from this analysis because it was difficult to define and interpret upper and lower surface in these species given the combination of leaf shape (*Picea* and *Pinus*) and their variable position in relation to vertical light gradients.

Within the British flora we tested the robustness of species rankings in the field for three adult traits of particular interest (SLA, leaf size, leaf N) by comparing site pairs taken from the four predominant geological substrata. Following Garnier et al. (2001a), the geology with the largest number of species, the acidic sandstone, was used as the standard to correlate against.

Results

Interspecific rankings of seedlings vs field adults

Table 2 and Figs. 1 and 2 show that the best correspondence (Spearman's $r \geq 0.79$, i.e. determination coefficient > 0.62) between species rankings of laboratory seedlings and field adults was for leaf size (in both floras) and max. stem vessel diameter (SVD_{max}; Spain only). Well below that ($0.67 \geq r > 0.50$) followed DM/SM, Stomatal Index, Stomatal Density, SAF, SSLM (all traits Britain only), SD (Spain only) and SLA (both floras). Interspecific ranking correlations were still (marginally) significant but much weaker for leaf N ($r = 0.33$; mean for both floras) and leaf P ($r = 0.50$; mean for both floras). Leaf thickness (both floras) and leaf density (LD; Spain only) showed no significant correspondence between rankings for laboratory seedlings and field adults.
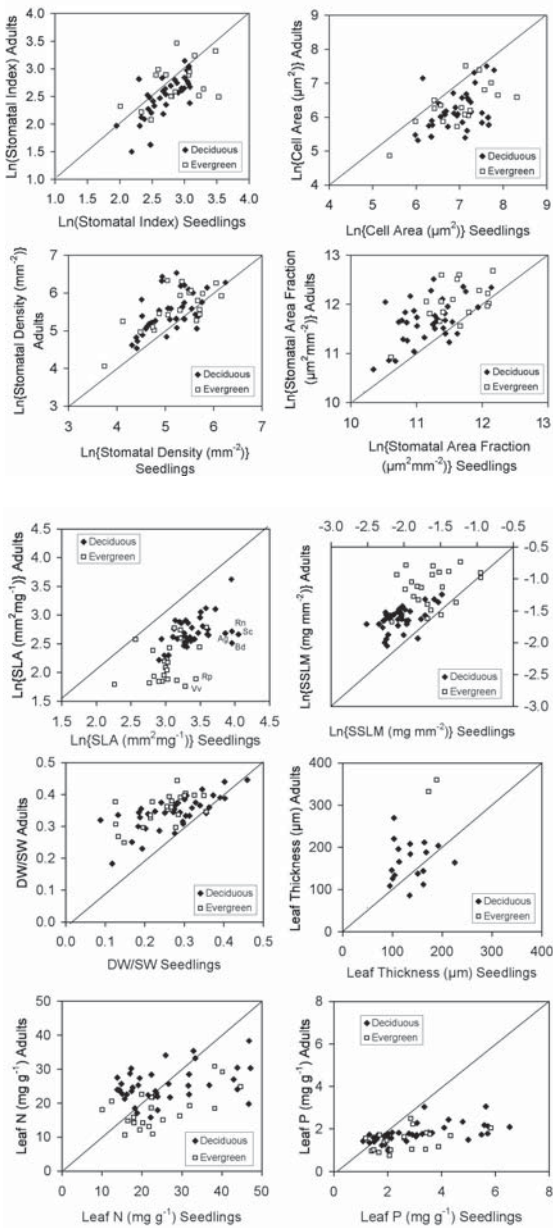
Fig. 1. Comparisons of interspecific trait variation in laboratory seedlings and field adults in British woody species, where each data point represents the two means for one species. The 1:1 line is shown for reference. The leaf size figure is in Cornelissen (1999). Species codes for SLA: Ag = *Alnus glutinosa*; Bd = *Buddleja davidii*; Rn = *Ribes nigrum*; Rp = *Rhododendron ponticum*; Sc = *Salix caprea*; Vv = *Vaccinium vitis-idaea*.

For most traits the interspecific patterns around the overall trend line (not shown) did not differ between deciduous and evergreen species. However, for SLA, leaf N and leaf P, field adults of deciduous species seemed to achieve higher values at common seedling value than evergreens, while the opposite pattern was apparent for leaf thickness and SVD_{max} (Figs. 1 and 2).
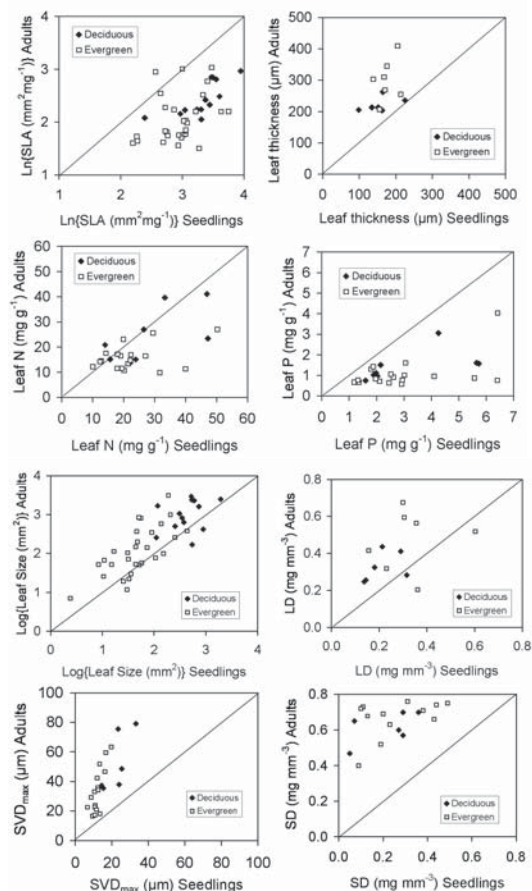
Fig. 2. Comparisons of interspecific trait variation in laboratory seedlings and field adults in Spanish woody species, where each data point represents the means for one species. The 1:1 line is shown for reference.

Overall trait shifts from seedling phase to adulthood

Across all species, field adults generally had lower Stomatal Index and smaller epidermal cell size, higher Stomatal Density and SAF than laboratory seedlings, as shown by the deviations from the 1:1 line (Fig. 1). SLA was generally lower in field adults than in laboratory seedlings. The same pattern emerged for leaf P and, less consistently, leaf N, except that leaf N and P of field adults often exceeded those in laboratory seedlings at the lower end of the range (Fig. 1). Field adults generally had thicker (SSLM, leaf thickness), denser (LD) and less juicy leaves (DM/SM) than laboratory seedlings, while their stems were generally denser (SD) with wider vessels (SVD_{max}) (Figs. 1 and 2). For 52 angiosperm species, laboratory seedlings had a relatively high proportion of stomata on the upper leaf surface compared to field adults. Seedlings had 14 hypostomatous, 24 intermediate (He) and 14 amphistomatous species, respectively, whilst adults had 20, 25 and seven species in these categories (see Table 3; $\chi^2_{(2)} = 6.11$, $P < 0.05$).

Table 2. Linear trend lines ($Y = aX + b$) for plant traits of field adults (Y) on the same traits of laboratory seedlings (X). For units see Figs. 1 and 2. For each relationship the significance of the Spearman correlation coefficient (r) is given: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Pearson's correlation coefficients (ρ, for transformed data) are given in parentheses. Climbers and scramblers were excluded from stem traits (see text). If included, SVD_{max} had $r = 0.794$ ($N = 25$, $P < 0.001$) for Spearman, while SD had $r = 0.528$ ($N = 20$, $P < 0.05$). Part of the results for leaf sizes in Great Britain were previously published (Cornelissen 1999).

	Great Britain	r (ρ)	N	Signif.	Spain	r (ρ)	N	Signif.
Ln(Stomatal Index)	$Y = 0.73\,Y + 0.48$	0.626 (0.633)	53	***				
Ln(Stomatal Density)	$Y = 0.64\,Y + 2.26$	0.583 (0.631)	53	***				
Ln(Stomatal Area Fraction)	$Y = 0.63\,Y + 4.63$	0.539 (0.597)	53	***				
Ln(Epidermal Cell Area)	$Y = 0.54\,Y + 2.51$	0.470 (0.520)	53	***				
Ln(SLA)	$Y = 0.69\,Y + 4.78$	0.613 (0.604)	62	***	$Y = 0.57X + 0.43$	0.527 (0.521)	42	***
Ln(SSLM)	$Y = 0.63\,Y + 0.11$	0.670 (0.654)	61	***				
DM/SM	$Y = 0.42\,Y + 0.24$	0.623 (0.649)	61	***				
Leaf Thickness	$Y = 0.59\,Y + 102$	0.352 (0.312)	20	$P = 0.13$	$Y = 0.76X + 138$	0.512 (0.408)	13	$P = 0.07$
[10]Log(Leaf Size)	$Y = 0.88\,Y + 1.08$	0.798 (0.871)	58	***	$Y = 0.88X + 0.64$	0.793 (0.785)	42	***
Leaf N	$Y = 0.26\,Y + 16.2$	0.319 (0.418)	60	*	$Y = 0.41X + 8.48$	0.348 (0.556)	26	$P = 0.08$
Leaf P	$Y = 0.18\,Y + 1.14$	0.604 (0.540)	59	***	$Y = 0.24X + 0.48$	0.391 (0.507)	25	*
Leaf Density (LD)					$Y = 0.47X + 0.27$	0.319 (0.400)	13	$P = 0.29$
Stem Vessel Diameter (SVD_{max})					$Y = 2.23X + 5.03$	0.790 (0.789)	22	***
Stem Density (SD)					$Y = 0.36X + 0.56$	0.535 (0.497)	18	*

Intraspecific variation in trait rankings of field adults

The cross species comparisons of adult SLA, leaf size and leaf N between site pairs differing in geology revealed generally much stronger correlations than those between laboratory seedlings and field adults (Table 4). The determination coefficients for site comparisons (derived from Pearson's ρ^2) were 0.74 for SLA, 0.95 for leaf size and 0.61 for leaf N. The correlations were generally strongest between the acidic sandstone and 'Coal Measures' sites, both of which host acidic soils. The carboniferous and magnesium limestone sites, both with higher pH soils, had strong mutual correlations (data not shown).

Table 3. Position of stomata in laboratory seedlings and field adults in British woody species. H = Hypostomatous; A = Amphistomatous; He = Hypostomatous with occasional stomata on upper side; S = Stem stomata. Relative change towards more stomata on lower as compared to upper side from seedling to adult phase: 0 = No change; + = Small change; ++ = Moderate change, +++ = Large change; -- = change towards relatively more on upper side.

	Seedlings	Adults	Change		Seedlings	Adults	Change
Acer platanoides	H	H	0	*Lonicera periclymenum*	He	He	0
Acer pseudoplatanus	H	H	0	*Malus sylvestris*	He	He	0
Aesculus hippocastanum	He	H	+	*Picea sitchensis*	A	He	++
Alnus glutinosa	He	He	0	*Pinus sylvestris*	A	A	0
Arbutus unedo	H	H	0	*Prunus laurocerasus*	He	H	+
Berberis vulgaris	H	H	0	*Prunus lusitanica*	He	He	0
Betula pendula	He	He	0	*Prunus spinosa*	H	H	0
Buddleja davidii	A	He	++	*Quercus cerris*	H	H	0
Buxus sempervirens	He	He	0	*Quercus ilex* ssp. *ilex*	H	H	0
Calluna vulgaris	A	He	++	*Quercus petraea*	H	H	0
Castanea sativa	He	He	0	*Quercus robur*	H	H	0
Cornus sanguinea	He	He	0	*Rhododendron ponticum*	A	He	++
Corylus avellana	He	He	0	*Ribes nigrum*	He	He	0
Crataegus monogyna	He	He	0	*Ribes uva-crispa*	He	He	0
Cytisus scoparius	A,S	A,S	0	*Rosa arvensis*	He	He	0
Empetrum nigrum	H	H	0	*Rubus fruticosus*	A	He	++
Fagus sylvatica	H	H	0	*Salix caprea*	H	H	0
Frangula alnus	He	H	+	*Sambucus nigra*	He	He	0
Fraxinus excelsior	H	H	0	*Solanum dulcamara*	A	A	0
Hebe x franciscana	A	He	++	*Sorbus aucuparia*	He	He	0
Hedera helix	He	He	0	*Taxus baccata*	He	He	0
Helianthemum nummularium	A	A,(S)	0	*Thymus polytrichus*	A	A	0
Hippophae rhamnoides	A	H	+++	*Ulex europaeus*	A,S	A,S	0
Ilex aquifolium	He	H	+	*Ulex gallii*	A,S	A,S	0
Juglans regia	He	He	0	*Ulmus glabra*	He	He	0
Laburnum anagyroides	He	He	0	*Vaccinium myrtillus*	A,S	A,S	0
Larix decidua	He	A	--	*Vaccinium vitis-idaea*	A	H	+++
Ligustrum vulgare	H	H	0	*Viburnum opulus*	He	He	0

Table 4. Comparisons of interspecific rankings of functional traits between sites in the Sheffield area differing in geological substratum, for subsets of the woody flora. Spearman's correlation coefficients (r) are given first, Pearson's correlation coefficient (ρ) are in parentheses. Leaf size data were $\log_{10}$-transformed prior to Pearson's correlation. Significance for Spearman's r: ** = $P < 0.01$, *** = $P < 0.001$. n = number of species. Part of the results for leaf size were published previously (Cornelissen 1999).

		n	r	(ρ)	
Specific leaf area					
Acidic Sandstone vs	Carboniferous Limestone	27	0.781	(0.831)	***
	Magnesium Limestone	28	0.749	(0.942)	***
	Coal Measures	15	0.821	(0.807)	***
Leaf size					
Acidic Sandstone vs	Carboniferous Limestone	26	0.895	(0.965)	***
	Magnesium Limestone	26	0.968	(0.972)	***
	Coal Measures	15	0.968	(0.993)	***
Leaf N content					
Acidic Sandstone vs	Carboniferous Limestone	22	0.665	(0.723)	**
	Magnesium Limestone	23	0.566	(0.747)	**
	Coal Measures	12	0.937	(0.868)	***

Discussion

When discussing patterns of interspecific variation in functional traits, it is important to separate overall shifts in trait values from seedling to adult across species from ontogenetic trends in the trait *rankings* of species. In the following we will discuss the most important results for both, including the possible contributions of allometric, environmental and methodological factors to the patterns found.

Overall trait shifts

In our study overall trait shifts from laboratory seedlings to field adults across species were the norm rather than the exception. SD and SVD_{max} were among the most obvious examples, field adults consistently having much higher values than laboratory seedlings. These may be allometric relationships, since tall plants require more dense stem tissues to provide more biomechanical strength (Givnish 1995; Castro-Díez et al. 1998a) and a relatively high water transport capacity, which is facilitated by wider conduits (Castro-Díez et al. 1998a). There was also a clear syndrome of leaf trait shifts from the seedling phase to adulthood, involving stomatal, other morphological, structural and nutrient traits. Essentially, they resulted in a shift from emphasis on leaf productiveness in seedlings (thinner and less dense leaves with larger epidermal cells of greater SLA, more relative stomatal area for water and gas exchange, higher water content and foliar nutrient contents) to increasing robustness of leaves in the face of environmental pressures and hazards in adults (also involving time needed to build up structural defence), or as an allometric consequence of the greater

size of adults (see Cornelissen 1999 for leaf size). It is beyond the scope of this paper to discuss in detail all individual trait shifts between laboratory seedlings and field adults. However, in the following we shall give examples of strong relative differences in such shifts among species, which affect interspecific trait rankings.

Factors affecting interspecific rankings of laboratory seedlings versus field adults

While significant correlations between interspecific rankings of laboratory seedlings and field adults were demonstrated for 12 out of 14 traits studied here, the most remarkable finding was that the strength of these correlations is weak (i.e. determination coefficients < 0.45) also for 12 out of 14 traits (see below). So, which are the main factors that 'upset' the correspondence of interspecific trait rankings of laboratory seedlings and field adults? Or, in other words, why is it that particular species deviate from the expected overall ontogenetic trait shift? Below we discuss (1) allometry, (2) methodology, (3) different environments of seedlings and adults, (4) leaf habit and (5) variability in the field as possible explanatory factors.

• Allometric rules might dictate that species or life forms with a relatively large size difference between seedlings and adults (e.g. trees) may also have a greater ontogenetic shift in functional leaf and stem traits than smaller ones (e.g. herbs or small shrubs). SD, which has a strong allometric component (see above), could be an example of this. Indeed, this trait had major scatter in interspecific rankings of seedlings versus adults.

• Low correlation may also be attributed to methological issues. For example, in seedlings stem measurements included the xylem pith and cortical parenchyma. At early development stages, pith and cortical parenchyma represent a high portion of the stem volume, while in adult plants stems mainly consist of lignified xylem. Whilst in seedlings the whole stem cross-section was used, only wood was included in field adults. Such combinations of ontogenetic and methodological factors may interfere with species rankings of stem density. Another possible methodological source that may account for differences between seedling and adult traits within species is, that for a small proportion, the seed provenance for seedling screening was different from the sampling site for field adults. In a few cases (*Frangula alnus*, *Juglans regia*, *Larix decidua*, *Quercus rubra*, *Tilia cordata*) seed provenances were from mainland Europe, while adult traits were measured on British plants.

• Young and old plants of the same species may effectively grow in different environments. For woody species, environmental conditions experienced by tall plants with high canopies are often very different from those encountered by seedlings. An obvious example is

the regeneration of tree seedlings in the forest. Seedlings of species that regenerate in forest gaps will encounter more exposed conditions, while the older trees of the same species will encounter shade as the new forest canopy closes up (see Platt & Strong 1989 for a review). In such species, leaves and stems of seedlings would be expected to be very different from those of adult plants. On the other hand, in shade-tolerant species that regenerate in the forest understorey and remain below the upper forest canopy, foliar and stem traits would be expected to remain relatively similar in structure, morphology and chemistry.

For particular species subsets in our study we also encountered occasional extreme trait switches between seedlings and adults, beyond the expected overall trait shift, that could be interpreted as a result of highly contrasting environments during the seedling and adult phases. For instance, adult SLA for the six species marked in Fig. 1 were ca. four times lower than seedling SLAs (untransformed data) and strongly deviated from the interspecific trend. All of these species regenerate and establish after disturbances such as urban soil perturbations (*B. davidii*), floods (*A. glutinosa, R. nigrum, S. caprea*) or fire (*R. ponticum, V. vitis-idaea*), aided by productive, high SLA leaves (Lambers et al. 1998). Some of these (*B. davidii, R. ponticum, V. vitis-idaea*) had amphistomatous seedling leaves (vs hypostomatous or intermediate in adults; Table 3), which may facilitate gas exchange associated with fast growth in such environments. Once grown up, these six species appear to develop lower-SLA leaves, equipped to avoid herbivory, pathogens or other environmental hazards that might reduce their lifespan (Reich et al. 1992). Valladares et al. (2000) have shown that species that depend on disturbances to establish have a more plastic SLA response to shifts in light conditions than understorey species, as experienced by seedlings growing up into adult plants. Such a plastic response can result in large variation of SLA interspecific ranking. An additional source of variation in our study, was that laboratory seedlings of British species received approximately a fifth of daily total photosynthetically active radiation (PAR) in a large forest clearing at full sunlight in summer (Cornelissen et al. 1998), which was probably also well below the mean daily PAR that exposed field adults receive throughout a normal growing season. The contrast between seedling and field environment may have been stronger in the Mediterranean species, which generally experience higher irradiance and stronger water and nutrient limitations in the field than British species.

• Leaf habit also interfered with the correspondence of interspecific rankings between laboratory seedlings and field adults. For instance, at common seedling foliar N or P, evergreens generally had lower foliar N or P than deciduous species. This could indicate that seedlings of evergreens, which tend to be conservative with nutrients (Aerts 1995), take up and store surplus N, i.e. N supplied above the growth requirement, in the leaves: 'luxury' consumption, (Chapin 1980; see also Cornelissen et al. 1997). In the field, evergreens are mostly limited to sites with nutrient stress, which may explain the relatively low leaf N and P of field adults compared to deciduous species.

• In contrast, cross site correlations for SLA, leaf size and foliar N in the British woody flora had little variation of interspecific trait ranking in adults due to geology and population origin. Among these, leaf N had much greater deviations than SLA or leaf size. It is possible that foliar nutrient contents are affected more strongly by intensive land use and higher soil nutrient availability in the lowland sites with higher soil base status, compared to the poor, acidic upland sites (Thompson et al. 1997). At the same time, interspecific species rankings for leaf N varied less in relation to geological substrata in a large set of herbs and dwarf shrubs from the Sheffield flora (Thompson et al. 1997). Our results for the woody species of the Sheffield flora confirm a recent report for a Mediterranean flora in southern France, where the interspecific ranking for SLA in field adults was also robust to site factors and considerably less so for leaf N (Garnier et al. 2001a). While the importance of variability in soil nutrient availability and other environmental effects (e.g. water and light availability) on intraspecific trait variation should not be underestimated, a picture is beginning to emerge of a stronger contribution of interspecific variation in allometry and ecology to shifts in trait rankings between laboratory seedlings and field adults.

Predicting traits of field adults from laboratory seedlings?

To what extent do interactions of ontogenetic development with (1) allometry, (2) methodology, (3) environment, (4) leaf habit as well as (5) site differences in growth conditions of adult plants, upset interspecific rankings of functional traits? Or, can we reliably predict interspecific rankings for different traits of adult woody plants in the field from those of laboratory grown seedlings and *vice versa*? Through significant correlations we have shown here for a wide range of functional leaf and stem traits, both in a British and a Spanish woody flora, that such predictions are possible to some extent (see also Cornelissen et al. 1997 and Poorter & Garnier 1999 for SLA and leaf N). However, the predictive power is only strong, i.e. explains well over half of the variation in field adults, in two morphological traits; leaf size and SVD_{max} (determination coefficients > 0.6). For two key traits

with respect to ecosystem carbon and nutrient cycling, SLA and leaf N content, interspecific variation among laboratory seedlings explained only 27 to 36 and 17 to 31 %, respectively, of the interspecific variation among field adults. This contrasts with 53 % reached for SLA in a similar comparison among a range of herbaceous and woody species in The Netherlands (Poorter & de Jong 1999). Perhaps this higher percentage reflects the relatively modest overall ontogenetic shift among the larger herbaceous subset in the latter study. Leaf thickness and leaf density did not even reach significant correlations in our study, although this may have been due partly to the low numbers of species participating in our study; Poorter & Garnier (1999) did find a significant correlation for LD in the above species set in The Netherlands.

Conclusion

Whether or for which traits these results justify extrapolation from laboratory seedlings to field adults, will depend on the type and scale of study, but it is clear that caution is advisable. For instance, among 97 western European woody species mean RGRs of young laboratory seedlings had good correspondence with SLA measured from the same plants ($\rho^2 = 0.51$; $P < 0.001$; Cornelissen et al. 1998). However, seedling RGRs explained only a third of the variation in SLA in field adults in a subset of 58 of the same species ($\rho^2 = 0.33$, $P < 0.001$; Cornelissen unpubl.).

It is also clear that further data are needed to test the robustness of interspecific trait rankings, both for herbaceous and woody plants. It would help our understanding of these rankings greatly if the different factors governing them could be unravelled, particularly the individual and interactive contributions of allometry (Niklas 1994; Brouat et al. 1998) and environmental influences (Garnier et al. 2001a; Wright et al. 2001) on ontogenetic trait patterns. To achieve this we would need to investigate interspecific trait variation in combinations of both seedlings and adult plants, both in laboratory or 'common garden' and in the field.

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