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Relative growth rate in phylogenetically related deciduous and evergreen woody species

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Abstract Relative growth rate (RGR) and other growth parameters were studied in eight pairs of closely related deciduous and evergreen species (within the same genus or family). The main objective of this study was to test the association between leaf turnover rate and RGR, specific leaf area (SLA, leaf area/leaf dry weight) and other growth variables. Plants were grown for 6 months in a greenhouse under favourable water and nutrient conditions. Variation in RGR among the 16 woody species was due mainly to differences in morphological parameters such as leaf area ratio (LAR, whole plant area/whole plant dry weight) and SLA). However, temporal variation in RGR within species was due mainly to variation in net assimilation rate. When phylogeny was not taken into account, analyses showed that deciduous species grew faster than evergreens. In contrast, when phylogeny was taken into account, the data analysis showed that a faster RGR is not consistently associated with the deciduous habit (in five pairs it was, but in the other three it was not). The faster growth of the deciduous trees (in the five positive contrasts) could be explained by their higher LAR and higher SLA relative to evergreens. The lack of differences in RGR between deciduous and evergreens (in three pairs) was due to the higher leaf mass ratio (LMR, leaf dry biomass/total dry biomass) for the evergreens, which offset the higher SLA of the deciduous species, resulting in a similar LAR in both functional groups (LAR=LMR×SLA). Deciduous species had consistently higher SLA than evergreens. We suggest that SLA, more than RGR, could be an important parameter in determining adaptive advantages of deciduous and evergreen species.

Keywords Biomass allocation · Leaf longevity · RGR · SLA · Specific leaf area

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Introduction

Plant species with different leaf life spans (for example, deciduous and evergreen trees) frequently occupy different habitat types. Several hypotheses have been proposed for the advantages of having a longer or shorter leaf life span (Chabot and Hicks 1982; Kikuzawa 1991; Aerts 1995), most notably those related to drought and freezing resistance, resource conservation (carbohydrates and/or nutrients), control of nutrient recycling and time to amortise the leaf construction cost. Kikuzawa (1991) put forward a model based on cost-benefit analysis in relation to carbon which appears to explain the global distribution of evergreens and deciduous species. However, this model does not explain the distribution at smaller spatial scales or the coexistence of deciduous and evergreen species in some habitats.

Most studies to date have found that deciduous woody species show higher potential growth rates, higher specific leaf areas (SLAs) and higher photosynthetic rates than evergreen speices (Reich and Walters 1992; Cornelissen et al. 1996, 1998; Reich et al. 1997; Reich 1998). The greater relative growth rate (RGR) of deciduous species has been considered an important determinant of their distribution in productive habitats (i.e. with high availability of nutrients and water) through greater competitive ability (Cornelissen et al. 1996, 1998).

The greater RGR of deciduous species seems to be determined by their higher leaf area ratio (LAR, plant area/plant dry weight), which in turn is accounted for by their higher SLA (leaf area/leaf dry mass) (Cornelissen et al. 1996, 1998). Other characteristics such as biomass allocation to leaves (LMR, leaf mass ratio) or net assimilation rate (NAR) account for much less of the RGR variation between deciduous and evergreen species.

Nevertheless, most comparative studies concerning deciduous and evergreen species have not controlled for phylogeny (Coley 1988; Reich et al. 1997) or have been based on comparisons at higher taxonomic levels (family, order) (Cornelissen et al. 1996). Closely related spe-

cies would be expected to show similar characteristics because they share a relatively recent common ancestry, and this should be taken into account when making any comparisons between species (Harvey and Pagel 1991; Saverimuttu and Westoby 1996; Swanborough and Westoby 1996; Villar et al. 1998).

One of the more frequently used methods to control for phylogeny in comparative studies is phylogenetic independent contrasts (PICs) (Harvey and Pagel 1991; Saverimuttu and Westoby 1996; Swanborough and Westoby 1996). PICs compare attributes of species differing in a specific phenotype (e.g. deciduous vs evergreen) within a given taxon level. Each PIC is a different fork in the evolutionary tree, so the comparison within a PIC is independent of the comparison in another PIC.

In the present study, we test the association between leaf life habit (deciduous and evergreen) and other characteristics (e.g. RGR, SLA) by employing a PIC-based comparative analysis, selecting pairs for comparison a priori (Armstrong and Westoby 1993). Specifically, we compare eight pairs of deciduous and evergreen woody species (1) to examine whether there are differences in RGR between deciduous and evergreen species; if so, (2) to identify the causes of these differences, and (3) to determine which characteristics of deciduous and evergreen species could confer important advantages in some habitats and explain their different distributions in nature.

Materials and methods

Plant material

Eight pairs of deciduous and evergreen phylogenetically related species (i.e. in the same genus or family) were selected (Table 1). Four of the 16 species studied were not native to the Iberian Peninsula: *Gleditsia triacanthos* (central and eastern North America, although it is naturalised in central and southern Europe), *Ficus retusa* (South Asia), *Sterculia platanifolia* (Asia) and *S. diversifolia* (Australia). Nomenclature follows Valdés et al. (1987), except for the non-native species which follow Romero (1984). Deciduous and evergreen species of the three pairs in the Fagaceae family were selected at random (Table 1); other combinations produced similar results.

Seeds of the species were collected from several plants in autumn 1996 (Table 1). We discarded the smaller and bigger seeds in those species showing high variability in seed weight (i.e. species from the Fagaceae family) to homogenise initial seedling weight. This increases the reliability of RGR estimates (Poorter and Garnier 1996).

Germination tests, following Catalán Bachiller (1991) were conducted to determine the time required for seed germination and thus have all species growing at the same time. The seeds were placed in plastic trays with a substratum of sand and peat (3:1). The trays were watered twice per week with 100 ml of nutrient solution (modified Hoagland solution; Poorter and Remkes 1990) and with tap water once a week. Due to germination problems in *Pistacia lentiscus*, *Pistacia terebinthus* and *Olea europaea*, seedlings of these species were acquired at a local plant nursery (Viveros Sierra Norte, Villanueva del Río y Minas, Seville).

Growth conditions and harvests

In April 1997, the seedlings were planted in black polyethylene plastic bags (20 cm diameter, 35 cm height) with a capacity of 3.5 l. Bags were filled with the same substratum used for germination. Approximately 100 seedlings of similar size per species were selected to homogenise individual size and increase the reliability of RGR estimates (Poorter and Garnier 1996).

Plants were grown in the University greenhouse (Campus Universitario Rabanales) with the temperature maintained between 19.5 and 34.2°C. Radiation inside the greenhouse was 85% of irradiance in the open. Plants were placed at random to control for potential environmental heterogeneity within the greenhouse. A slow-release fertiliser (Compo Nitrophoska; Basf) with 12% N, 12% P_2O_5, 1.2% Mg, 6% S, 0.1% Mn, 0.05% B, 0.02% Zn and other micronutrients in smaller proportions was used. From the beginning of the experiment to 27 June, the plants were fertilised weekly with 0.14 g of fertiliser. From 27 June to the end of the experiment, a weekly dose of 0.34 g was used. During the experiment, the plants were watered abundantly every other day.

There were three harvests per species (harvest 1: day 0; harvest 2: day 44±11; harvest 3: day 95±12). The first harvest (day 0) was carried out 2 weeks after seedlings were planted, having allowed them some time to acclimatise. There were only 1- to 2-day differences in harvest dates of the deciduous and evergreens within each

Table 1 Species studied, code of the phylogenetic independent contrast (*PIC*) and species, and origin of seeds. Species leaf habit: *D* deciduous, *E* evergreen

Family	PIC code	Species code	Species	Seed origin
Anacardiaceae	1	A	*Pistacia terebinthus* (D)	Sierra Norte (Seville)
		a	*Pistacia lentiscus* (E)	Sierra Norte (Seville)
	2	B	*Castanea sativa* (D)	Aracena (Huelva)
		b	*Quercus coccifera* (E)	Osuna (Seville)
Fagaceae	3	C	*Quercus pyrenaica* (D)	Cardeña (Córdoba)
		c	*Quercus rotundifolia* (E)	Osuna (Seville)
	4	D	*Quercus robur* (D)	Vigo (La Coruña)
		d	*Quercus suber* (E)	Aracena (Huelva)
Leguminoseae	5	E	*Gleditsia triacanthos* (D)	María Luisa Park, Seville
		e	*Ceratonia siliqua* (E)	Linares Stream (Córdoba)
Moraceae	6	F	*Ficus carica* (D)	Osuna (Seville)
		f	*Ficus retusa* (E)	María Luisa Park, Seville
Oleaceae	7	G	*Fraxinus angustifolia* (D)	Santo Domingo (Córdoba)
		g	*Olea europaea* (E)	Sierra Norte (Seville)
Sterculiaceae	8	H	*Sterculia platanifolia* (D)	María Luisa Park, Seville
		h	*Sterculia diversifolia* (E)	María Luisa Park, Seville

PIC. For each harvest, an average of 11±2 plants per species were selected at random. Roots were separated from the soil. Subsequently, roots, stems, leaves and petioles were separated and their fresh weight obtained. To calculate SLA (m^2/kg leaf dry weight), a subsample of the leaves was photocopied and the leaf area was calculated using the area/weight ratio of a piece of paper. For a few cases in the last harvest, SLA was calculated taking 20 leaf punches from each plant harvested. Finally, the samples were dried at 70°C for at least 48 h to obtain the dry weight. During data processing, the petioles were included with the stems, as both have similar functions. Leaf-related variables (SLA and LMR) were calculated excluding the petiole weight. The proportions of leaves, stems and roots were calculated as the ratio plant fraction dry weight/whole plant dry weight. Dry matter content was calculated as the ratio dry weight/fresh weight.

Statistical analysis

We compared the attributes of deciduous and evergreen species using two different approaches. First, we carried out an across-species analysis for each growth parameter (one-way ANOVA) assuming the species to be independent. All the species were analysed together, thus phylogeny was not taken into account. Second, we considered the phylogenetic relationships between species, conducting eight one-way ANOVAs (one per PIC) for each variable using the type of species (deciduous or evergreen) as the independent variable. For all the variables studied, except RGR, ANOVAs were carried out using the GLM procedure (SAS 1985). RGR was calculated by linear regression of the ln dry weight versus time (Hunt 1982). To obtain RGR, the weight of any attached cotyledons was excluded from total plant dry weight (RGR sensu stricto; Cornelissen et al. 1996). Differences in RGR between deciduous and evergreen species were analysed comparing the slopes of the linear regressions (RGR) using a covariance analysis (GLM procedure). Regression and correlation analyses were done with Statistica (StatSoft 1996). Variables based on percentages were arcsine transformed prior to analysis (Zar 1997). Throughout the paper we use total plant dry matter content as it was very well correlated (r>0.86) with the dry matter content of other plant fractions (leaf, stem or root).

We estimated the temporal changes in RGR, LAR and NAR for each species by calculating the values of the three parameters using the data of period 1 (harvest 1 and 2; giving RGR_1, LAR_1 and NAR_1) and period 2 (harvest 2 and 3; giving RGR_2, LAR_2 and NAR_2). To identify the causes of the temporal differences in RGR (RGR_2–RGR_1), we correlated them with the differences in LAR (LAR_2–LAR_1) and NAR (NAR_2–NAR_1) for the same periods.

Results

Comparison between deciduous and evergreen species without taking phylogeny into account

There were significant differences between deciduous and evergreen species for all the variables studied when phylogeny was not taken into account (Table 2). Deciduous species showed a significantly higher RGR than evergreen ones. This was largely due to the higher LAR of deciduous species and also partly to their higher NAR (Table 2).

The higher LAR of deciduous species was determined by their higher SLA and not by LMR, which was lower in deciduous species. Deciduous species also showed higher stem proportions (SMR) and higher root proportions (RMR) (Table 2). Deciduous species showed a lower dry matter content than evergreens (Table 2).

Comparison between deciduous and evergreen species controlling for phylogeny

In general, when phylogeny was accounted for, the differences between deciduous and evergreen species were not as clear as suggested in the above analysis. The mean values for each variable and species are shown in the Appendix.

In five out of eight PICs, the deciduous species showed a higher RGR than evergreens (Fig. 1A). The other three PICs with no significant differences in RGR were: *P. terebinthus-P. lentiscus; Quercus robur-Q. suber* and *S. platanifolia-S. diversifolia*.

As for RGR, the differences in LAR and NAR between deciduous and evergreen species were not so clear after controlling for phylogeny: in four out of eight PICs, deciduous species had a higher LAR (Fig. 1B) and in only three out of eight PICs did the deciduous species have a higher NAR (Fig. 1C).

For SLA, we found that for all eight PICs, the deciduous species had a higher value than the evergreens (Fig. 1D), in agreement with the results from the across-species analyses (Table 2).

With respect to biomass allocation, deciduous and evergreen species showed no clear differences. For five out of eight PICs, evergreens showed a higher LMR than deciduous species, but for another two PICs the trend was opposite (Fig. 2A). Only three out of eight PICs showed a higher SMR for deciduous species, but this variable was higher for evergreens in one PIC (Fig. 2B). Five out of eight PICs showed a higher RMR for deciduous species, but the opposite trend was found for two other PICs (Fig. 2C).

For two out of eight PICs, deciduous species showed a lower dry matter content, whereas for another PIC,

Table 2 Mean values (±SD) of the study variables for the eight deciduous and eight evergreen species using data from all three harvests: relative growth rate (*RGR*); net assimilation rate (*NAR*); leaf area ratio (*LAR*); specific leaf area (*SLA*); leaf mass ratio, considering only the limb (*LMR*), stems and petiole mass ratio (*SMR*), root mass ratio (*RMR*), and plant dry matter content (*DM*). Phylogeny is not controlled for in this statistical analysis (ANOVA). *Asterisks* show the level of significance of differences between mean values of deciduous and evergreen species (*P<0.05; **P<0.01; ***P<0.001)

Growth habit	RGR (mg g^{-1} day^{-1})	NAR (g m^{-2} day^{-1})	LAR (m^2 kg^{-1})	SLA (m^2 kg^{-1})	LMR	SMR	RMR	DM (%)
Deciduous	41.1±2.4 ***	3.58±2.07 *	12.3±8.9 ***	26.8±11.0 ***	0.43±0.14 ***	0.25±0.12 **	0.32±0.16 **	23.9±7.0 **
Evergreen	31.3±2.5	2.98±2.47	8.4±5.1	16.5±8.5	0.50±0.11	0.22±0.09	0.28±0.14	26.0±8.4

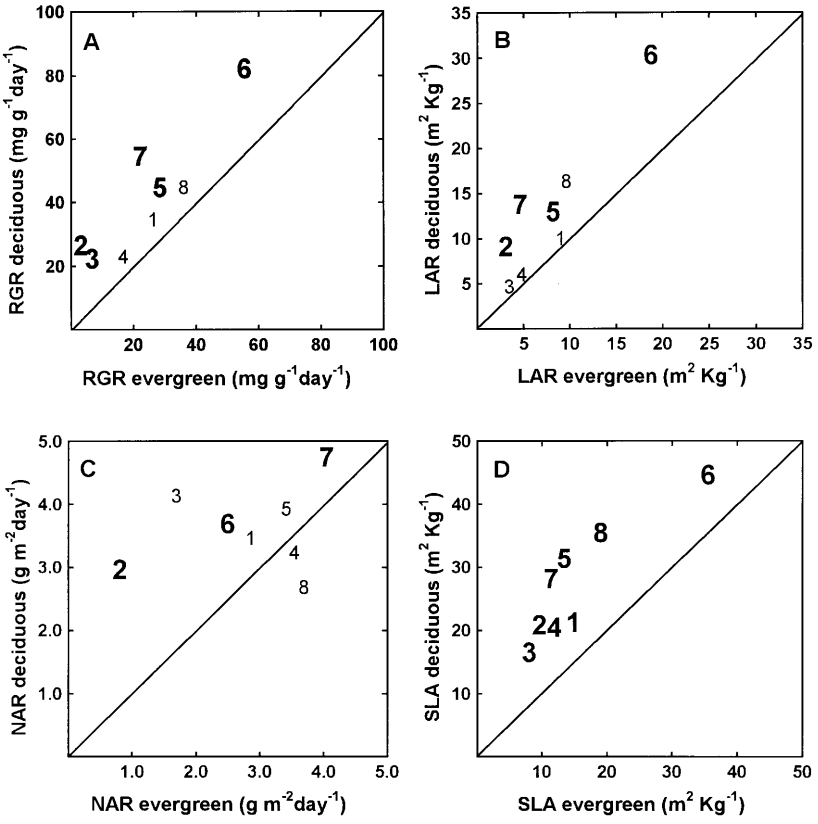

Fig. 1 Relationship between the mean values of the variables in deciduous and evergreen species of each phylogenetic independent contrast (PIC) for relative growth rate (*RGR*) (**A**), leaf area ratio (*LAR*) (**B**), net assimilation rate (*NAR*) (**C**) and specific leaf area (*SLA*) (**D**). For PIC codes see Table 1. The *straight line* represents the 1:1 ratio between deciduous and evergreen. *Numbers in bold* and *larger font* represent significant differences between the values for deciduous and evergreens within each PIC

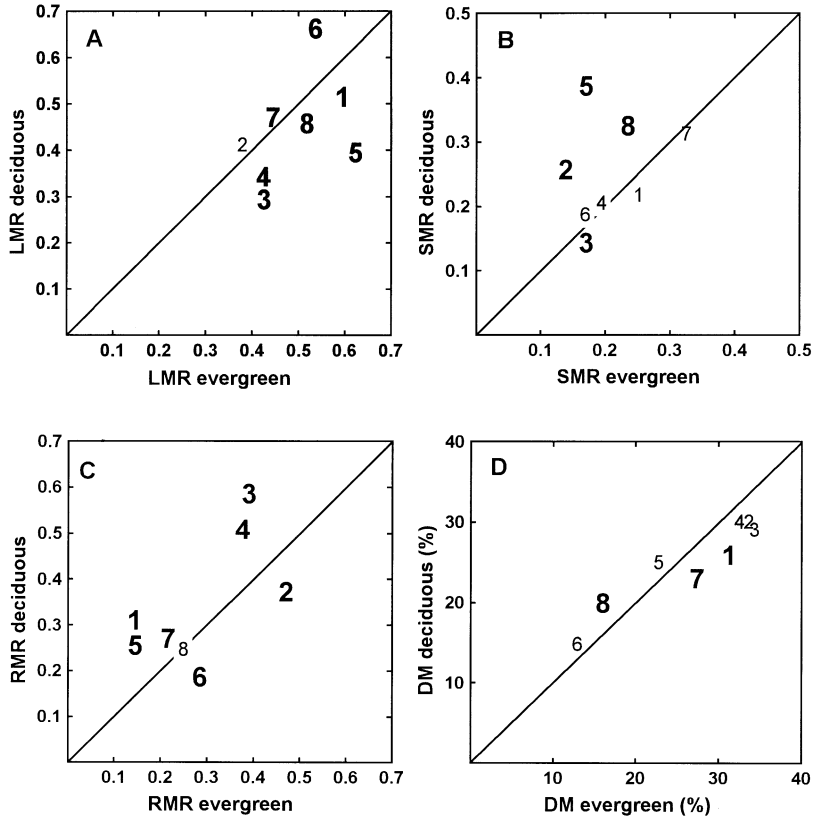

Fig. 2 As in Fig. 1 for leaf mass ratio (*LMR*) (**A**), stem mass ratio (*SMR*) (**B**), root mass ratio (*RMR*) (**C**) and plant dry matter content (*DM*) (**D**)

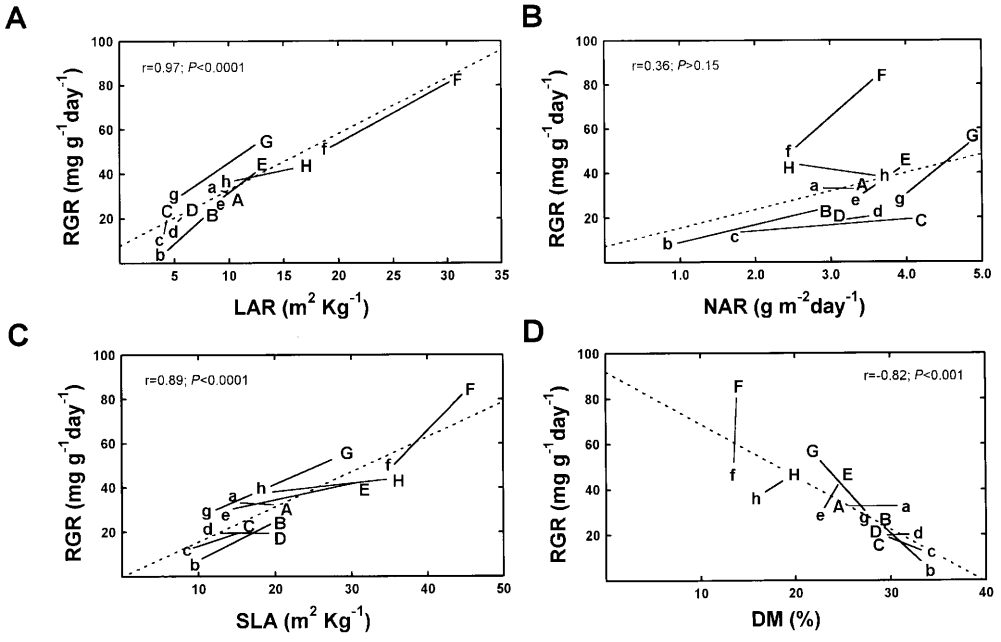

Fig. 3 Relationship between *RGR* and leaf area ratio (*LAR*) (**A**), net assimilation rate (*NAR*) (**B**), specific leaf area (*SLA*) (**C**) and plant dry matter content (*DM*) (**D**). *Upper-* and *lowercase letters* represent the deciduous and evergreen species, respectively, of each PIC, linked by a *solid line*. The *dashed line* represent the regression line calculated for all data (*r* and *P* are also shown)

evergreens had a lower dry matter content; the other four PICs showed no significant differences (Fig. 2D).

Causes of the differences in RGR between species

Variation in RGR between species was explained by the variation in LAR (Fig. 3A; $P<0.001$) and not by NAR (Fig. 3B; $P>0.15$). Much of the variation in LAR was explained by SLA ($r=0.93$, $P<0.001$) and to a lesser extent by LMR ($r=0.65$, $P<0.01$).

Taking phylogeny into account, four out of five PICs in which there were differences in RGR (pairs B-b, E-e, F-f, G-g) also showed significant differences in LAR (Figs. 1B, 3A). For PICs B-b, F-f and G-g, the differences in RGR were also related to significant differences in NAR (Figs. 1C, 3B).

RGR was highly correlated with SLA (Fig. 3C; $P<0.001$). The five PICs showing differences in RGR (Fig.°1A) also showed differences in SLA (Figs. 1D, 3C). Although there were differences in SLA in the other three PICs (pairs A-a, D-d and H-h), they did not show differences in RGR. This can be explained by the lack of significant differences in LAR, suggesting that differences in SLA were counteracted by LMR (LAR=LMR×SLA; Figs. 1D, 2A).

RGR was positively correlated with LMR in an across-species analysis (Fig. 4A; $P<0.01$). However, after controlling for phylogeny, this trend was observed for only one PIC (F-f; Fig. 4A).

There was no significant correlation between RGR and proportion of stems (SMR; Fig. 4B; $P>0.10$); how-

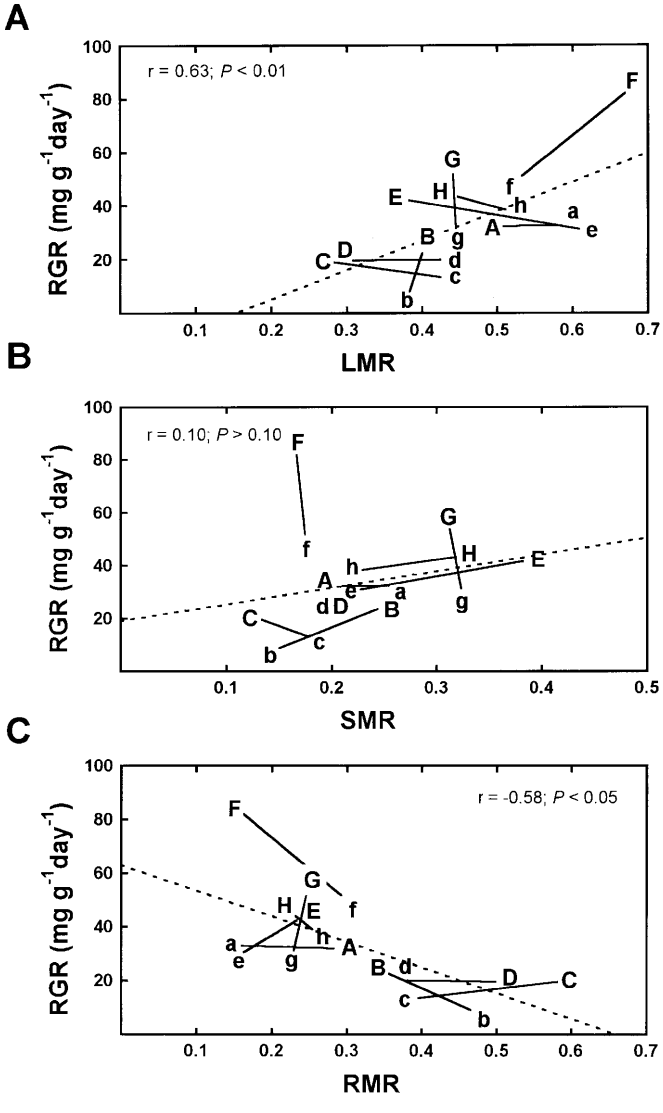

Fig. 4 Relationship between *RGR* and leaf mass ratio (*LMR*) (**A**), stem mass ratio (*SMR*) (**B**), and root mass ratio (*RMR*) (**C**). *Symbols* as in Fig. 3

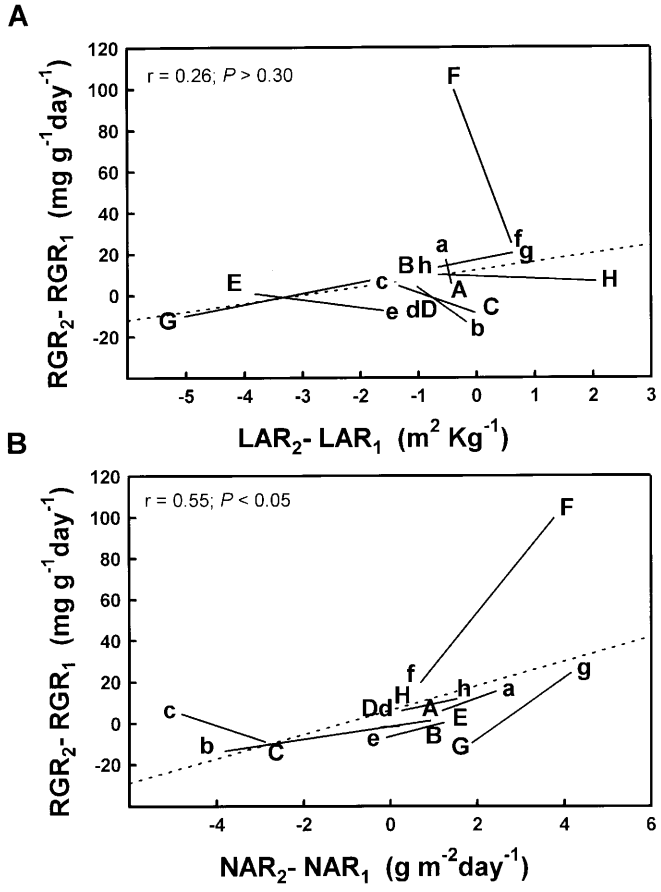

Fig. 5 Relationship between the temporal variation in RGR (RGR_2–RGR_1) and in LAR (LAR_2–LAR_1) (**A**) and NAR (NAR_2 –NAR_1) (**B**). *Symbols* as in Fig. 3. For more details, see text

ever, the correlation became significant after excluding the PIC F-f (r=0.80, P <0.001). After controlling for phylogeny, there was no positive trend between RGR and SMR, because for five PICs (A-a, C-c, D-d, F-f and G-g), there was no positive relationship between RGR and SMR.

There was a negative correlation between RGR and the proportion of roots (RMR; r=–0.58, P<0.05), but after controlling for phylogeny, this trend was only shown by two of eight PICs (B-b and F-f; Fig. 4C).

RGR was negatively correlated with the total dry matter content (P<0.001). Similar results were obtained with the dry matter content of plant fractions (leaf, stem or root). However, considering phylogeny, we only found two PICs with this negative trend (B-b and G-g; Fig. 3D).

Temporal variation in RGR

The RGR values discussed in the preceeding text corresponded to mean values for the whole study period (harvest 1, 2 and 3). However, RGR was not constant through time, showing substantial variation in some species (Appendix). Six species showed a decrease in RGR through time, whereas the other 10 showed an increase. Averaged overall, the mean value of RGR_1 (harvest 1 and 2) was 31.1 mg g^{-1} day^{-1}, whereas the mean value for RGR_2 (harvest 2 and 3) was 39.9 mg g^{-1} day^{-1}, a circa 30% increase. RGRs for the different periods (RGR_1, RGR_2) or mean RGR (for all the periods) were very well correlated with each other (r>0.7).

The temporal changes in RGR can be explained by changes in LAR and/or NAR. We found that the changes in RGR (RGR_2–RGR_1) were mainly explained by changes in NAR (NAR_2–NAR_1, P<0.05; Fig. 5B) and not by changes in LAR (LAR_2–LAR_1, P>0.3; Fig. 5A). We obtained similar results after controlling for phylogeny.

Discussion

Relative growth rate and SLA

Mean RGRs varied widely across species, ranging from 81.7 mg g^{-1} day^{-1} in *F. carica* to 8 mg g^{-1} day^{-1} in *Q. coccifera*. What mechanisms could have brought about such large differences in RGR? Considering all the species without taking into account phylogeny, variation in RGR was explained by the variation in LAR and mostly in SLA. Similar results have been found in many studies of both herbaceous plants (Garnier 1992; Lambers and Poorter 1992; Poorter and Van der Werf 1998) and woody species (Reich and Walters 1992; Huante et al. 1995; Cornelissen et al. 1996, 1998; Lusk et al. 1997).

Our study shows that the patterns in RGR and other growth components in deciduous and evergreens species are influenced by phylogeny. In an across-species analysis (not controlling for phylogeny), deciduous species have a higher RGR than evergreens, due to their higher LAR and also partly to their higher NAR. These results agree with those of Cornelissen et al. (1996, 1998).

However, if we consider phylogenetic relationships between species, the differences between deciduous and evergreen species were not clear for many of the growth components studied. In five pairs, the deciduous species had a higher RGR than evergreens, but there were no differences in three pairs. The reason why there were no differences in these three PICs is that the LMR showed an opposite trend to SLA, the evergreens having a higher LMR and a lower SLA than the deciduous species. As a result, there were no differences in LAR (LAR=SLA×LMR) between evergreens and deciduous species in these three PICs, explaining the similar RGR between the two functional groups.

Therefore, we cannot generalize that deciduous species always grow faster than evergreens. This contrasts with the findings of other studies (Reich and Walters 1992; Cornelissen et al. 1996, 1998). One possible explanation is that the comparisons between these functional groups in other studies used higher taxonomic levels than genera. These species would be expected

to differ due to phylogenetic separation. Significant differences in RGR tended to be found in taxonomically distant pairs (Appendix). Another possible explanation is that most of the species studied belong to Mediterranean ecosystems, where water stress might have constrained RGR in both evergreen and deciduous species.

The only attribute consistently associated with the evergreen habit for all eight PICs was a low SLA. Thus, our study shows that there is not a general association between evergreens and low RGR, but there is a clear association between low SLA and evergreens, suggesting that SLA could have adaptive value. This would be in accordance with the hypothesis of Poorter (1991), which suggests that RGR is not the target variable for selection, but other variables such as SLA could be more important for conferring advantages in certain habitats. Thus, the association between RGR and type of habitat found in several studies (Grime and Hunt 1975; Poorter and Remkes 1990) could be caused by SLA, simply because SLA and RGR are closely related.

SLA is associated with a number of morphological, physiological and biochemical traits. Species with a low SLA (or with evergreen habit) show relatively high construction costs (Merino 1987; Poorter and Villar 1997; Villar and Merino 2001) and low protein concentrations (Reich and Walters 1992; Cornelissen et al. 1997). The latter associates with a lower photosynthetic rate (Sobrado 1994; Villar et al. 1995; Reich et al. 1997; Reich 1998). This may result in the longer leaf longevity of low-SLA species, as more time is necessary to amortize the construction costs of the leaf. Several studies support this hypothesis (Sobrado 1994; Reich et al. 1997). Our results support this notion, because the NARs of evergreens (Fig. 1C) were often lower than those of deciduous species. This would explain the association between low SLA and extended leaf longevity (evergreens).

In addition, a low SLA value signifies a high leaf weight per leaf area, which is caused by thicker leaves (Castro-Díez et al. 2000). Most of the native evergreens studied (*P. lentiscus*, *Q. coccifera*, *Q. rotundifolia*, *C. siliqua* and *O. europaea*) are characterised by a thick cuticle and several layers of partially lignified epidermal cells (Lillis 1991), which would explain their low SLA. In dry Mediterranean ecosystems, a thick cuticle in native evergreens can be a mechanism for reducing water loss. In fact, these species are classified as xerophytic and sclerophyllous and occupy warm habitats where water is a limiting factor for several months per year (Blanco et al. 1997). In addition, the low protein (N) concentration of their tissue (Reich and Walters 1992; Cornelissen et al. 1997) may indicate a lower need for N and other nutrients, which would be advantageous in nutrient-poor habitats (Aerts 1995). In fact, several authors have found a higher proportion of evergreens in habitats with nutrient-poor soils (Loveless 1962; Monk 1966).

Therefore, species with a low SLA (Mediterranean evergreens in our study) could be more successful in occupying resource-poor (water and/or nutrient) habitats, which would explain their distribution in these habitats.

In contrast, most of the native deciduous species studied (*Castanea sativa*, *Q. pyrenaica*, *Q. robur*, *Fraxinus angustifolia*, *F. carica*) are frequently found in wet habitats (riverside, shade habitats or in the north part of the Iberian Peninsula) (Blanco et al. 1997), which also have soils containing a large proportion of organic matter and are rich in nutrients. In these resource-rich habitats, the possession of a high SLA (more area per unit dry weight) and the associated high protein concentrations would allow greater efficiency in acquiring light and in photosynthesis, leading to better competitive ability. In fact, species with high SLA are usually found in nutrient-rich and productive habitats (Nielsen et al. 1996; Lusk et al. 1997). In addition, other important factors such as higher tolerance to both shade and/or frost can also be important for explaining the distribution of deciduous species.

Causes of temporal variations in RGR

RGR was not uniform through the study period (Appendix). What caused these changes over time? Are changes in NAR or LAR responsible for the changes in RGR?

We found that the temporal changes in RGR were mainly due to variation in NAR (Fig. 5B). This can be partly explained by an increase in the photoperiod of about 11% during the period in which the experiment was carried out (between April and August). Several studies have found a positive effect of increasing radiation on both NAR and RGR (Hunt and Cornelissen 1997; Poorter and Van der Werf 1998; Meziane and Shipley 1999). Therefore, the temporal changes in NAR could be determined by a higher CO_2 fixation due to increasing length of photoperiod.

Interestingly, the differences in RGR between species were caused by morphological parameters (LAR), while the temporal changes in RGR were caused by physiological parameters (NAR). This could be due to the more plastic nature of the physiological relative to the morphological parameters.

As far as we know, there is no comparative study including several species in which both the causes of differences in RGR between species and the causes of the temporal changes in RGR have been investigated. Most investigations have been carried out in optimal conditions and resources, using growth chambers with low variation in those factors. Introducing some temporal and natural variation in some resources would add to the realism of the experiments.

Conclusion

In summary, our study shows that the variation in RGR between woody species was explained by variation in LAR (particularly the SLA component), but the differ-

ences in RGR and other growth components between deciduous and evergreen species depend on whether or not phylogeny is controlled for in the analysis. When phylogeny was taken into account, the differences between these two functional groups were not consistant for many of the growth components studied. Therefore, we cannot make the generalization that deciduous species always grow faster than evergreens. The only attribute consistently associated with the evergreen habit was a lower SLA. This suggests that SLA, more than RGR, could be an important parameter in determining the adaptive advantages of evergreens in dry and/or nutrient-poor habitats and deciduous species in resource-rich habitats.

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Appendix

Mean values (±SD) of the study variables for each pair (PIC) of deciduous and evergreen species

Abbreviations as in Table 2. Values for RGR at different periods are shown: RGR_1 (calculated between the harvest 1 and 2), RGR_2 (harvest 2 and 3) and mean RGR (harvest 1, 2 and 3). The periods for the different harvests were: harvest 1 (0 days), harvest 2 (44±11 days) and harvest 3 (95±12 days). RGR was calculated as the slope of ln dry weight against time. The differences in LMR, SMR, RMR and DM were calculated using arcsine-transformed data. *Asterisks* show the level of significance of differences between the mean values of the deciduous and evergreen species in each PIC studied (+ $0.05<P<0.10$; *$P<0.05$; **$P<0.01$; ***$P<0.001$; *n.s.* not significant)

Species	RGR_1 (mg g^{-1} day^{-1})	RGR_2 (mg g^{-1} day^{-1})	RGR) (mg g^{-1} day^{-1}	NAR) (g m^{-2} day^{-1}	LAR (m^2 kg^{-1})	SLA (m^2 kg^{-1})	LMR	SMR	RMR	DM (%)
Pistacia terebinthus	29.2±5.0 n.s.	34.4±3.3 n.s.	33.0±1.8 n.s.	3.47±1.75 n.s.	9.4±4.2 n.s.	19.3±5.4 *	0.50±0.10 **	0.21±0.05 n.s.	0.29±0.08 ***	25.1±4.8 ***
Pistacia lentiscus	20.7±6.9	36.7±3.1	32.4±2.1	2.88±1.87	9.2±2.5	15.6±3.6	0.59±0.08	0.25±0.08	0.16±0.07	31.2±5.8
Castanea sativa	22.6±4.9 n.s.	23.6±4.6 **	23.1±2.4 ***	2.89±1.63 *	7.3±2.7 ***	18.9±4.2 ***	0.41±0.08 n.s.	0.23±0.09 ***	0.36±0.10 ***	29.7±4.6 +
Quercus coccifera	13.4±5.9	–0.1±7.0	8.1±2.8	0.60±3.06	4.0±1.5	10.6±3.7	0.39±0.07	0.15±0.07	0.46±0.08	33.7±3.2
Quercus pyrenaica	23.8±3.2 +	14.5±7.0 n.s.	21.0±2.1 **	4.00±2.55 n.s.	4.3±1.5 +	15.1±2.0 ***	0.28±0.08 ***	0.13±0.05 *	0.58±0.06 ***	29.7±4.8 n.s.
Quercus rotundifolia	19.2±4.7	0.2±6.3	13.1±2.7	1.91±3.77	4.1±1.7	9.4±2.1	0.43±0.11	0.17±0.06	0.39±0.14	33.2±5.0
Quercus robur	20.1±4.2 n.s.	18.1±5.4 n.s.	19.2±2.2 n.s.	3.18±2.17 n.s.	5.4±1.9 n.s.	19.4±3.5 ***	0.30±0.07 ***	0.19±0.07 n.s.	0.50±0.09 ***	29.5±5.1 +
Quercus suber	20.8±3.3	18.9±5.2	20.0±2.0	3.53±2.45	5.5±1.4	13.0±2.5	0.42±0.08	0.19±0.06	0.38±0.11	32.4±4.9
Gleditsia triacanthos	41.5±3.4 +	42.2±3.4 ***	42.0±1.7 ***	3.89±1.17 n.s.	12.2±4.2 ***	31.1±6.9 ***	0.38±0.07 ***	0.38±0.07 ***	0.23±0.13 *	24.2±5.9 n.s.
Ceratonia siliqua	34.6±2.4	26.5±1.7	29.2±1.0	3.41±0.71	8.9±1.9	14.5±2.5	0.61±0.06	0.18±0.06	0.16±0.09	22.9±5.5
Ficus carica	58.6±5.8 +	157.9±22.5 **	81.7±6.4 ***	3.68±3.01 *	29.7±9.1 **	43.9±10.2 *	0.67±0.09 ***	0.17±0.06 n.s.	0.16±0.06 ***	14.0±2.8 n.s.
Ficus retusa	46.0±5.1	66.5±18.3	50.7±4.2	2.52±1.60	18.7±5.4	35.3±7.9	0.53±0.10	0.18±0.07	0.29±0.09	13.6±1.8
Fraxinus angustifolia	60.5±8.6 ***	49.8±4.7 *	53.0±2.5 ***	4.94±2.00 *	12.4±5.3 ***	27.3±6.4 ***	0.44±0.12 ***	0.31±0.05 n.s.	0.25±0.10 ***	22.6±5.2 ***
Olea europaea	12.8±5.2	37.1±2.6	30.3±1.9	3.99±2.97	5.7±1.1	12.4±1.5	0.44±0.08	0.33±0.07	0.23±0.08	27.2±3.6
Sterculia platanifolia	40.1±6.1 n.s.	46.6±6.5 n.s.	44.1±3.0 n.s.	2.58±1.15 n.s.	15.3±6.0 n.s.	34.9±7.2 ***	0.44±0.14 ***	0.33±0.15 *	0.23±0.12 n.s.	18.8±3.3 **
Sterculia diversifolia	33.1±3.8	43.0±2.8	39.3±1.5	3.66±1.19	10.20±2.9	19.7±4.1	0.51±0.07	0.24±0.15	0.25±0.11	16.6±2.3

References

Aerts R (1995) The advantages of being evergreen. Trends Ecol Evolut 10:402–415

Armstrong DP, Westoby M (1993) Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. Ecology 74:1092–1100

Blanco E, Casado MA, Costa M, Escribano R, Garcia M, Genova M, Gomez A, Gomez F, Moreno JC, Morla C, Regato P, Sainz H (1997) Los bosques ibéricos. Planeta, Barcelona

Castro-Díez P, Puyravaud JP, Cornelissen JHC (2000) Leaf structure and anatomy as related to leaf mass per area variation in seedlings of a wide range of woody plant species and types. Oecologia 124:476–486

Catalán Bachiller G (1991) Semillas de árboles y arbustos forestales. Icona (M.A.P.A.), Madrid

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annu Rev Ecol Syst 13:229–59

Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defence. Oecologia 74:531–536

Cornelissen JHC, Castro Díez P, Hunt R (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. J Ecol 84:755–765

Cornelissen JHC, Werger MJA, Castro-Díez P, Van Rheenen JWA, Rowland AP (1997) Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. Oecologia 111:460–469

Cornelissen JHC, Castro-Díez P, Carnelli AC (1998) Variation in relative growth rate among woody species: scaling up. In: Lambers H, Poorter H, Vuuren M van (eds) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 363–392

Garnier E (1992) Growth analysis of congeneric annual and perennial grass species. J Ecol 80:665–675

Grime JP, Hunt R (1975) Relative growth-rate: its range and adaptive significance in a local flora. J Ecol 63:393–422

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford

Huante P, Rincón E, Acosta I (1995) Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. Funct Ecol 9:849–858

Hunt R (1982) Plant growth curves: the functional approach to plant growth analysis. Arnold, London

Hunt R, Cornelissen JHC (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytol 135:395–417

Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. Am Nat 138:1250–1263

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Lillis M (1991) An ecomorphological study of the evergreen leaf. Braun-Blanquetia 7

Loveless AR (1962) Further evidence to support a nutritional interpretation of sclerophylly. Ann Bot 26:551–561

Lusk CH, Contreras O, Figueroa J (1997) Growth, biomass allocation and plant nitrogen concentration in Chilean temperate rainforest tree seedlings: effects of nutrient availability. Oecologia 109:49–58

Merino JA (1987) The costs of growing and maintaining leaves of mediterranean plants. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC (eds) Plant response to stress. NATO ASSI Ser G15. Springer, Berlin Heidelberg New York, pp 553–564

Meziane D, Shipley B (1999) Interacting components of interespecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. Funct Ecol 13:611–622

Monk CD (1966) An ecological significance of evergreenness. Ecology 47:504–505

Nielsen SL, Enríquez S, Duarte CM, Sand-Jensen K (1996) Scaling maximum growth rates across photosynthetic organisms. Funct Ecol 10:167–175

Poorter H (1991) Interspecific variation in the relative growth rate of plants: the underlying mechanisms. PhD thesis, Utrecht University, The Netherlands

Poorter H, Garnier E (1996) Plant growth analysis: an evaluation of experimental design and computational methods. J Exp Bot 47:1343–1351

Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553–559

Poorter H, Van der Werf A (1998) Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers H, Poorter H, Vuuren M van (eds) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 309–336

Poorter H, Villar R (1997) The fate of acquired carbon in plants: chemical composition and construction costs. In: Bazzaz FA, Grace J (eds) Resource allocation in plants. Academic Press, San Diego, pp 39–72

Reich PB (1998) Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers H, Poorter H, Vuuren M van (eds) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 467–487

Reich PB, Walters MB (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecol Monogr 62:365–392

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734

Romero P (1984) Itinerario botánico por el parque de María Luisa de Sevilla. Instituto de Ciencias de la Educación, Universidad de Sevilla

SAS (1985) SAS/STAT guide for personal computers, version 6 edition. SAS Institute, Cary, NC

Saverimuttu T, Westoby M (1996) Components of variation in seedling potential relative growth rate: phylogenetically independent contrasts. Oecologia 105:281–285

Sobrado MA (1994) Leaf age effects on photosynthetic rate, transpiration rate and nitrogen content in a tropical dry forest. Physiol Plant 90:210–215

StatSoft (1996) Statistica for Windows 5.1. StatSoft Inc, Tulsa, Okla

Swanborough, P, Westoby M (1996) Seedling relative growth rate and its components in relation to seed size: phylogenetically independent contrasts. Funct Ecol 10:176–184

Valdés B, Talavera S, Fernández-Galiano E (1987) Flora vascular de Andalucía Occidental. Ketres, Barcelona

Villar R, Merino J (2001) A comparison of leaf construction cost in woody species with differing leaf life-spans in contrasting ecosystems. New Phytol (in press)

Villar R, Held AA, Merino J (1995) Dark leaf respiration in light and darkness of an evergreen and a deciduous plant species. Plant Physiol 107:421–427

Villar R, Veneklaas EJ, Jordano P, Lambers H (1998) Relative growth rate and biomass allocation in 20 *Aegilops* (Poaceae) species. New Phytol 140:425–437

Zar JH (1997) Biostatistical analysis. Prentice-Hall, London