

Relationship between Maximum Leaf Photosynthesis, Nitrogen Content and Specific Leaf Area in Balearic Endemic and Non-endemic Mediterranean Species

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Gas exchange parameters, leaf nitrogen content and specific leaf area (SLA) were measured *in situ* on 73 C₃ and five C₄ plant species in Mallorca, west Mediterranean, to test whether species endemic to the Balearic Islands differed from widespread, non-endemic Mediterranean species and crops in their leaf traits and trait inter-relationships. Endemic species differed significantly from widespread species and crops in several parameters; in particular, photosynthetic capacity, on an area basis (A), was 20 % less in endemics than in non-endemics. Similar differences between endemics and non-endemics were found in parameters such as SLA and leaf nitrogen content per area (N_a). Nevertheless, most of the observed differences were found only within the herbaceous deciduous species. These could be due to the fact that most of the non-endemic species within this group have adapted to ruderal areas, while none of the endemics occupies this kind of habitat. All the species—including the crops—showed a positive, highly significant correlation between photosynthetic capacity on a mass basis (A_m), leaf nitrogen content on a mass basis (N_m) and SLA. However, endemic species had a lower A_m for any given SLA and N_m . Hypotheses are presented to explain these differences, and their possible role in reducing the distribution of many endemic Balearic species is discussed. © 2003 Annals of Botany Company

Key words: Balearic endemic species, leaf nitrogen content, Mediterranean climate, photosynthesis, specific leaf area.

INTRODUCTION

Relationships between the growth capacity of a species and morphological and physiological leaf traits have been established (Poorter *et al.*, 1990; Poorter and Bergkotte, 1992; Cornelissen *et al.*, 1996, 1997; Grime *et al.*, 1997). These traits include photosynthetic capacity (A_m), leaf nitrogen content (N_m), both on a mass basis, leaf life span and specific leaf area (SLA). Species with high SLA and N_m usually show high potential relative growth rates (Hunt and Cornelissen, 1997). A_m has been positively correlated with N_m and SLA (Poorter *et al.*, 1990; Reich *et al.*, 1994, 1997).

According to Reich *et al.* (1999), these patterns are common to all species, because significant nitrogen per unit mass accumulation would be required in leaves to achieve a high A_m . Nitrogen accumulation requires thicker leaves, i.e. a lower SLA (Abrams *et al.*, 1994; Niinemets, 1999). However, thick leaves with low SLA show a low A_m , probably due to a limited diffusion of light and CO₂ to the site of carboxylation (Lloyd *et al.*, 1992; Terashima and Hikosaka, 1995; Hanba *et al.*, 1999). Thus, biophysical constraints place a limit on the maximum photosynthetic rate that can be achieved by a leaf with a given SLA or N_m . Species with a lower A_m for a given SLA or N_m are possible from a biophysical point of view. However, they would be potentially less competitive (Reich *et al.*, 1999).

Of all the species, crops are the most likely to have overcome these biophysical constraints since they have been intensely selected to maximize production over hundreds of years. Other species that are likely to have overcome these biophysical constraints are C₄ species, which have evolved a more efficient photosynthetic pathway than C₃ plants. On the other hand, if species exhibiting a lower A_m for a given SLA or N_m were to be found, those having evolved under low competitive pressure would be the primary candidates. Species endemic to the Balearic Islands could meet these conditions, since they have evolved under pre-human ecological conditions characterized by a high pressure by herbivores (Alcover *et al.*, 2000) and, presumably, relatively low competition between plants. Palynological data clearly show that there was a strong change in the vegetation composition of the islands after the arrival of humans (Burjachs *et al.*, 1994; Yll *et al.*, 1994), which has been dated to approx. 5000 years ago (Alcover *et al.*, 2000). Indeed, in Hawaii, another insular system with a high percentage of endemism, native species have lower A_m , SLA and relative growth rate than invasive species, and this fact has been related to the competitive and invasive ability of the later species (Pattison *et al.*, 1998; Baruch and Goldstein, 1999; Durand and Goldstein, 2001).

Net photosynthesis, leaf nitrogen content and specific leaf area were measured on 78 species, including crops, endemic and non-endemic species, growing in a Mediterranean climate. The objectives of the present work were (a) to test

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TABLE 1. List of species considered in this study and several of their traits

Species	Family	Evolutionary history	Leaf habit	Life form	Photosynthetic pathway	Habitat
<i>Acer opalus</i> Mill. subsp. <i>granatense</i> (Boiss.) F.Q. & Rothm.	Aceraceae	E	WD	MP	C ₃	R
<i>Ailanthus altissima</i> (Mill.) Swingle	Simaroubaceae	NE	WD	MP	C ₃	RS
<i>Amaranthus blitoides</i> S. Watson	Amaranthaceae	NE	HD	Th	C ₄	AF
<i>Amaranthus retroflexus</i> L.	Amaranthaceae	NE	HD	Th	C ₄	AF
<i>Anagyris foetida</i> L.	Fabaceae	NE	WD	NP(MP)	C ₃	MS
<i>Arbutus unedo</i> L.	Ericaceae	NE	E	MP	C ₃	OF
<i>Atriplex halimus</i> L.	Chenopodiaceae	NE	E	NP	C ₄	SM
<i>Avena sativa</i> L.	Poaceae	C	HD	Th	C ₃	AF
<i>Avenula crassifolia</i> (F.Q.) Holub	Poaceae	E	HD	Th	C ₃	R
<i>Beta vulgaris</i> L.	Chenopodiaceae	NE	HD	H(Th)	C ₃	AF
<i>Brassica napus</i> L.	Brassicaceae	C	HD	Th	C ₃	AF
<i>Brassica oleracea</i> L.	Brassicaceae	C	HD	Ch	C ₃	AF
<i>Capparis spinosa</i> L.	Capparidaceae	C	WD	NP	C ₃	AF
<i>Capsicum annuum</i> L.	Solanaceae	C	HD	Th	C ₃	AF
<i>Cephalaria squamiflora</i> (Sieber) Greuter subsp. <i>balearica</i> (Willk.) Greuter	Dipsacaceae	E	E	Ch.	C ₃	R
<i>Ceratonia siliqua</i> L.	Caesalpiniaceae	C	E	MP	C ₃	AF
<i>Cistus albidus</i> L.	Cistaceae	NE	SD	NP	C ₃	MS
<i>Cistus monspeliensis</i> L.	Cistaceae	NE	SD	NP	C ₃	MS
<i>Cistus salviifolius</i> L.	Cistaceae	NE	SD	NP	C ₃	MS
<i>Cneorum tricoccon</i> L.	Cneoraceae	NE	E	NP	C ₃	MS
<i>Convolvulus arvensis</i> L.	Convolvulaceae	NE	HD	H(G)	C ₃	AF
<i>Crepis triasii</i> (Camb.) Nyman	Asteraceae	E	E	H	C ₃	R
<i>Cichorium intybus</i> L.	Asteraceae	NE	HD	H	C ₃	AF
<i>Chenopodium album</i> L.	Chenopodiaceae	NE	HD	Th	C ₃	AF
<i>Datura stramonium</i> L.	Solanaceae	NE	HD	Th	C ₃	AF
<i>Delphinium pictum</i> Willd.	Scrophulariaceae	E	HD	Th	C ₃	MS
<i>Dianthus rupicola</i> Biv. subsp. <i>bocchoriana</i> L. Llorens & Gradaille	Caryophyllaceae	E	E	Ch	C ₃	R
<i>Dittrichia viscosa</i> (L.) Greuter	Asteraceae	NE	WD	NP	C ₃	AF
<i>Euphorbia margalidiana</i> Kühbier & Lewej.	Euphorbiaceae	E	E	NP(Ch)	C ₃	RC
<i>Euphorbia pithyusa</i> L.	Euphorbiaceae	NE	E	Ch	C ₃	MS
<i>Ficus carica</i> L.	Moraceae	C	WD	MP	C ₃	AF
<i>Fraxinus angustifolia</i> Vahl	Oleaceae	NE	WD	MP	C ₃	FWS
<i>Globularia cambessedesii</i> Willk.	Globulariaceae	E	E	Ch	C ₃	R
<i>Helianthus annuus</i> L.	Asteraceae	C	HD	Th	C ₃	AF
<i>Helleborus foetidus</i> L.	Ranunculaceae	NE	E	Ch	C ₃	MS
<i>Helleborus lividus</i> Ait.	Ranunculaceae	E	E	Ch	C ₃	MS
<i>Hypericum balearicum</i> L.	Hypericaceae	E	E	NP	C ₃	MS
<i>Hypericum hircinum</i> L. subsp. <i>cambessedesii</i> (Coss. ex Barceló) Sauvage	Hypericaceae	E	WD	NP	C ₃	FWS
<i>Lactuca sativa</i> L.	Asteraceae	C	HD	Th	C ₃	AF
<i>Lavandula dentata</i> L.	Lamiaceae	NE	E	Ch	C ₃	MS
<i>Lavatera cretica</i> L.	Malvaceae	NE	HD	NP(Ch)	C ₃	AF
<i>Ligusticum huteri</i> Porta	Apiaceae	E	E	Ch	C ₃	R
<i>Limonium migjornense</i> L. Llorens	Plumbaginaceae	E	E	Ch	C ₃	SM
<i>Lycopersicon esculentum</i> Mill.	Solanaceae	C	HD	Th	C ₃	AF
<i>Olea europaea</i> L. var. <i>sylvestris</i> (Mill.) Brot.	Oleaceae	NE	E	MP	C ₃	MS
<i>Paeonia cambessedesii</i> Willk.	Paeoniaceae	E	HD	G	C ₃	MS
<i>Pastinaca lucida</i> L.	Apiaceae	E	HD	H	C ₃	MS
<i>Phlomis italica</i> L.	Lamiaceae	E	SD	Ch	C ₃	MS
<i>Phillyrea latifolia</i> L.	Oleaceae	NE	E	MP	C ₃	MS
<i>Pinus halepensis</i> Mill.	Pinaceae	NE	E	MP	C ₃	MS
<i>Pistacia lentiscus</i> L.	Anacardiaceae	NE	E	MP	C ₃	MS
<i>Pistacia terebinthus</i> L.	Anacardiaceae	NE	WD	MP	C ₃	MS
<i>Pisum sativum</i> L.	Fabaceae	C	HD	Th	C ₃	AF
<i>Populus alba</i> L.	Salicaceae	NE	WD	MP	C ₃	FWS
<i>Populus nigra</i> L.	Salicaceae	NE	WD	MP	C ₃	FWS
<i>Pteridium aquilinum</i> (L.) Kuhn	Hypolepidaceae	NE	HD	G	C ₃	OF
<i>Quercus coccifera</i> L.	Fagaceae	NE	E	NP(MP)	C ₃	MS
<i>Quercus ilex</i> L.	Fagaceae	NE	E	MP	C ₃	OF
<i>Quercus humilis</i> Mill.	Fagaceae	NE	WD	MP	C ₃	OF
<i>Rhamnus alaternus</i> L.	Rhamnaceae	NE	E	P(Ch)	C ₃	MS
<i>Rhamnus ludovici-salvatoris</i> R. Chodat	Rhamnaceae	E	E	P(Ch)	C ₃	MS
<i>Rosa agrestis</i> Savi	Rosaceae	NE	WD	NP	C ₃	MS
<i>Silene mollissima</i> (L.) Pers.	Caryophyllaceae	E	E	Ch	C ₃	R
<i>Solanum melongena</i> L.	Solanaceae	C	HD	Th(Ch)	C ₃	AF

TABLE 1. Continued

Species	Family	Evolutionary history	Leaf habit	Life form	Photosynthetic pathway	Habitat
<i>Solanum tuberosum</i> L.	Solanaceae	C	HD	G	C ₃	AF
<i>Sorghum bicolor</i> (L.) Moench	Poaceae	C	HD	Th	C ₄	AF
<i>Trifolium subterraneum</i> L.	Fabaceae	C	HD	Th	C ₃	AF
<i>Triticale</i> sp.	Poaceae	C	HD		C ₃	AF
<i>Urginea maritima</i> (L.) Baker	Liliaceae	NE	HD	G	C ₃	MS
<i>Urtica atrovirens</i> Req. ex Loisel. subsp. <i>bianorii</i> (Knoche) F.Q. & Garcias	Urticaceae	E	HD	Th	C ₃	MS
<i>Verbascum sinuatum</i> L.	Scrophulariaceae	NE	HD	H	C ₃	AF
<i>Vicia faba</i> L.	Fabaceae	C	HD	Th	C ₃	AF
<i>Viola x balearica</i> Rosselló, Mayol & Mus	Violaceae	E	E	H	C ₃	R
<i>Viola jaubertiana</i> Marès & Vigin	Violaceae	E	E	H	C ₃	R
<i>Viola stolonifera</i> J.J. Rodr.	Violaceae	E	E	H	C ₃	MS
<i>Vitex agnus-castus</i> L.	Verbenaceae	NE	WD	MP	C ₃	RC
<i>Vitis vinifera</i> L. cv Manto Negro	Vitaceae	C	WD	P	C ₃	AF
<i>Zea mays</i> L.	Poaceae	C	HD	Th	C ₄	AF

Evolutionary history: E, endemic species; NE, non-endemic species; C, crops. Leaf habit: HD, deciduous herbaceous; WD, woody deciduous; SD, semi-deciduous; E, evergreen. Life form: P, phanerophyte; NP, nano-phanerophyte; MP, macro-phanerophyte; Ch, chamaephyte; G, geophyte; H, hemi-cryptophyte. Photosynthetic pathway: C₃ or C₄. Habitat: RC, rocky coast; SD, sandy dunes; SM, saltmarshes; MS, Mediterranean shrub-land; OF, oak forests; R, rupicolous; AF, agricultural fields; FWS, freshwater streams; RS, roadsides.

whether Balearic endemic species have lower A_m , N_m and SLA than other Mediterranean species; and (b) to determine if crops and endemic species overcome, respectively, the biophysical and ecological limitations suggested for the relationships between these leaf traits.

MATERIALS AND METHODS

Plant selection and classification into functional groups

Seventy-three C₃ species and five C₄ species (Table 1), which represent more than 5.5 % of the Balearic flora (De Bolòs, 1997), were randomly chosen from different habitats to represent different growth forms, leaf habits and evolutionary histories. The species were classified into leaf habits (herbaceous deciduous, woody deciduous, semi-deciduous and evergreens). Deciduous species comprise all species that shed their leaves outside the growing season. This group was divided into herbaceous and woody deciduous species. Semi-deciduous species were defined as all woody species that shed some of their leaves outside the growing season, depending on its length and severity, and evergreen species, all woody species that maintain their leaf canopy year round.

Similarly, three evolutionary groups were distinguished: crops, endemic and non-endemic species. Crop species are those currently being farmed. Endemic species are defined as those with a distribution limited to the Balearic Islands, with the addition of *Delphinium pictum* and *Acer opalus* ssp. *granatense*. *Delphinium pictum* also occurs on Corsica and Sardinia, and is considered a Balearic–Tyrrhenic species (Contandriopoulos and Cardona, 1984), and *A. opalus* ssp. *granatense* also occurs in the south-east of the Iberian Peninsula and in North Africa, and is considered an Ibero-Magreb-Balearic species (De Bolòs *et al.*, 1993). A classification of the species according to life form, following Raunkiaer (1934), is provided (Table 1).

All plants were field-grown except *Quercus humilis*, which was grown outdoors in 90 l pots. The study was carried out in 1999 and 2000 on the island of Mallorca, in the western Mediterranean basin, with dry, hot summers and cool winters. The mean annual precipitation varies from 300 mm on the southern coast, to above 1000 mm in the north-western mountains, and the rain falls mainly from autumn to spring. The drought period lasts for 2–6 months, with considerable variation between sites and years.

Gas exchange and nitrogen content measurements

Leaf gas exchange rates were measured when water availability was not limiting and maximum photosynthetic rates were expected. That was mostly in spring and, in a few cases, autumn. Measurements were made on well-developed sun-exposed leaves of healthy plants using a Li-6400 infra-red gas-exchange analyser (Li-Cor Inc., Lincoln, NE, USA). To avoid the midday depression of photosynthesis, measurements were made during mid-morning on sunny days. Cuvette temperatures were set at levels approximating the air temperature on each sampling occasion. Light intensity was held constant at 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ to ensure light-saturated photosynthesis, and the CO₂ partial pressure was set to 360 $\mu\text{mol mol}^{-1}$. The gas-exchange parameters were obtained by direct measurements of net CO₂ assimilation rate per unit leaf area (A), and computations of stomatal conductance (g), sub-stomatal CO₂ concentration (C_i) and intrinsic water use efficiency (A/g) were based on conventional formulae (von Cammerer and Farquhar, 1981). Single leaves on six to eight different individuals per species were sampled. After measurements, they were collected and the projected one-sided fresh area was measured using an AM-100 area meter (Analytical Development Co., Hoddesdon, UK). After drying for 48 h at 70 °C, the SLA was calculated as the ratio of leaf area to

TABLE 2. Effect of leaf habit, evolutionary history and their interaction (LH × EH) on net CO₂ assimilation rate on an area basis (A), stomatal conductance (g), sub-stomatal CO₂ concentration (C_i), intrinsic water use efficiency (A/g), specific leaf area (SLA), net CO₂ assimilation rate on a mass basis (A_m), leaf nitrogen content on a mass basis (N_m) and leaf nitrogen content on an area basis (N_a)—only P values are shown

	A	g	C _i	A/g	SLA	A _m	N _m	N _a
Leaf habit	<0.001	<0.001	0.20	0.02	<0.001	<0.001	<0.001	0.78
Evolutionary history	0.11	0.15	0.80	0.79	0.09	0.93	0.52	0.06
LH × EH	0.06	0.02	0.47	0.14	0.02	0.01	0.01	0.50

TABLE 3. Mean values and their standard error (when more than one species was available) for all the parameters studied (abbreviations as in Table 2) for each possible combination of leaf habit and evolutionary history

Group	No. of species	A	g	C _i	A/g	SLA	A _m	N _m	N _a
Herbaceous deciduous endemic	5	15.6 ± 1.3 ^a	294.2 ± 45.9 ^a	230.4 ± 6.3 ^a	57.0 ± 5.8 ^b	143.6 ± 25.4 ^a	230.9 ± 48.3 ^a	29.2 ± 4.6 ^a	2.0 ± 0.1 ^a
Herbaceous deciduous non-endemic	10	20.8 ± 2.0 ^b	625.4 ± 106.5 ^b	239.3 ± 7.3 ^a	43.5 ± 6.9 ^{ab}	178.7 ± 19.7 ^a	393.8 ± 57.2 ^b	38.5 ± 4.0 ^{ab}	2.6 ± 0.4 ^a
Herbaceous deciduous crops	13	21.7 ± 1.3 ^b	608.3 ± 60.1 ^b	241.8 ± 4.6 ^a	37.7 ± 2.9 ^a	185.3 ± 10.1 ^a	405.1 ± 32.1 ^b	47.6 ± 1.3 ^b	2.6 ± 0.1 ^a
Woody deciduous endemic	2	12.4 ± 5.0 ^a	210.9 ± 98.7 ^a	228.6 ± 2.4 ^{ab}	62.3 ± 5.2 ^a	210.0 ± 33.2 ^b	280.3 ± 146.4 ^a	34.4 ± 1.7 ^a	1.7 ± 0.2 ^a
Woody deciduous non-endemic	9	19.0 ± 1.1 ^a	321.3 ± 32.3 ^a	213.7 ± 3.9 ^a	62.1 ± 2.9 ^a	107.7 ± 9.8 ^a	204.6 ± 15.2 ^a	28.2 ± 1.6 ^a	2.7 ± 0.3 ^a
Woody deciduous crops	3	19.8 ± 4.0 ^a	461.1 ± 157.7 ^a	237.0 ± 8.3 ^b	48.2 ± 8.5 ^a	140.3 ± 15.6 ^a	276.9 ± 52.1 ^a	33.5 ± 6.9 ^a	2.3 ± 0.7 ^a
Semi-deciduous endemic	1	20.0 ^a	419.3 ^a	238.0 ^a	48.6 ^a	90.8 ^a	182.1 ^a	20.9 ^a	2.3 ^a
Semi-deciduous non-endemic	3	20.1 ± 2.2 ^a	421.9 ± 74.3 ^a	249.3 ± 26.8 ^a	54.3 ± 17.3 ^a	79.9 ± 5.7 ^a	163.4 ± 12.2 ^a	19.6 ± 0.7 ^a	3.2 ± 0.6 ^a
Evergreen endemic	14	14.0 ± 0.7 ^a	246.7 ± 25.5 ^a	227.5 ± 6.6 ^a	62.0 ± 4.1 ^a	132.0 ± 18.1 ^c	185.2 ± 25.3 ^c	28.4 ± 2.4 ^b	2.4 ± 0.3 ^a
Evergreen non-endemic	12	12.7 ± 1.3 ^a	201.6 ± 35.1 ^a	212.3 ± 9.3 ^a	77.7 ± 6.6 ^a	75.3 ± 8.1 ^b	101.8 ± 21.3 ^b	18.0 ± 1.6 ^a	2.4 ± 0.2 ^a
Evergreen crops	1	13.2 ^a	277.5 ^a	241.3 ^a	48.2 ^a	39.6 ^a	52.4 ^a	14.3 ^a	3.6 ^a

Values within the same evolutionary history group with a different superscript letter differ at $P < 0.05$.

dry mass. From A and SLA values, A_m was calculated as the CO₂ fixed per unit time per unit leaf dry mass. Because the photosynthetic rates were measured at near optimum conditions, they should approach the maximum photosynthetic capacity of the species under field conditions.

Total N_m was determined in the same leaves as those measured for A_m, using an elemental analyser (model EA 1108; Carlo Erba Instruments, Milan, Italy). After drying, the leaves of each species were pooled, and the N content was measured as the average of two analyses per sample. The nitrogen data are shown both on a mass (N_m) and area (N_a) basis.

Statistical analysis

All the parameters (A, g, C_i, A/g, SLA, A_m, N_m and N_a) were analysed by a multifactor ANOVA using the multiple range test of statgraphics (Manugistics, 1998). Least square means of the effects and their standard errors were calculated according to Searle (1971) and Snedecor and Cochran (1980), using a linear model that included the effects of evolutionary history (endemic, non-endemic and

crop) and leaf habit (herbaceous deciduous, woody deciduous, semi-deciduous and evergreen). Regression adjustments and the interaction between factors were analysed by multiple regression techniques (Draper and Smith, 1981), using the multiple regression procedure of statgraphics (Manugistics, 1998).

All these methods solve models with unbalanced data, which cannot be solved by crude means. Least square means yield values of the dependent variable for every level of each factor from an orthogonal decomposition of the information. This means that, for instance, least square means for leaf habit are calculated as if all the individuals had the same evolutionary history.

RESULTS

Effects of leaf habit and evolutionary history on leaf traits

Means and the standard error of all the variables studied for each species are available on the *Annals of Botany* website [Supplementary Information; <http://aob.oupjournals.org>]. A first analysis of the variance including the three

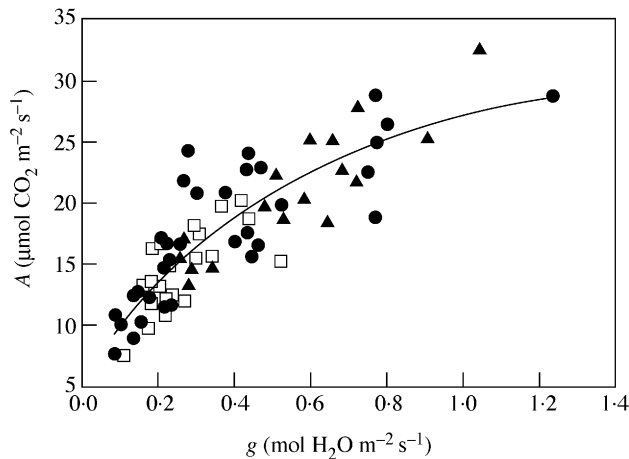


FIG. 1. Relationship between net photosynthetic rate on an area basis (A) and stomatal conductance (g). Filled circles correspond to non-endemic species, empty squares to endemic species and filled triangles to crops. Values correspond to means of six to eight replicates. The curve of best fit is shown as a hyperbolic adjustment ($A = 4.80 + 35.75g/(0.62 + g)$; $r^2 = 0.75$). C_4 species were excluded from the relationship.

evolutionary histories revealed that most of the parameters differed significantly (data not shown). However, *post hoc* tests showed that the differences among evolutionary histories were due only to the differences between crops and the other two groups (not shown). A second analysis excluding crops revealed that all the studied parameters except C_i and N_a differed significantly among leaf habits (Table 2). By contrast, no parameter differed significantly among endemic and non-endemic species. However, for some parameters, in spite of the lack of significance, the differences were not negligible. For instance, A averaged $18.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in non-endemic species, but only $15.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in endemic species, which is proportionally the same difference as that observed between non-endemic species and crops ($20.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Also, g , SLA and N_a differed by 25 % between endemic and non-endemic species. In addition, the analysis revealed a significant interaction between leaf habit and evolutionary history for A , g , SLA, A_m and N_m (Table 2). This implies that some of the differences observed among leaf habits are modulated by evolutionary history.

Table 3 shows mean values and their standard errors of all the studied parameters for each interaction among leaf habit and evolutionary history. Clearly, the effect of evolutionary history was most marked in herbaceous deciduous species. Within this group, strong differences were observed between endemics and both non-endemics and crops in A , g , A/g , A_m and N_m . No effect of evolutionary history was observed in semi-deciduous and woody deciduous species, except that SLA tended to be higher in endemic species. Nevertheless, it should be noted that the small number of species in some of these interactions may affect the significance of the differences observed for some parameters. Within evergreen species, there was no effect of evolutionary history in either A , g , C_i , A/g or N_a . However, there was a strong effect of SLA, which was involved in strong effects in both A_m and N_m (Table 3).

As expected, comparing leaf habits, evergreen species were more clearly separated from the other three groups, showing 30–40 % lower A and g values and a significantly higher A/g (Table 3).

Relationships between leaf traits

Figure 1 shows that the 73 C_3 species fitted a single positive curvilinear relationship between g and A ($r = 0.91$, $P < 0.001$). The endemic species lay mainly in the linear part of the regression, as did most of the typical Mediterranean species. Only some crops and weeds (*Beta*, *Chenopodium*, *Cychorium*, *Datura*, *Lavatera* and *Verbascum*) were in the saturated part of the regression (i.e. at g above $0.6 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$).

Considering all the species, A_m and N_m were positively correlated with SLA (not shown). However, endemic species showed a significant ($P < 0.05$), somewhat reduced, A_m for high SLA (Fig. 2). According to a covariance analysis of the regression coefficients, the slopes of A_m – N_m relationships differed marginally ($P = 0.07$) between endemic and non-endemic species (Fig. 2). By contrast, crop relationships were closer to the general ones observed in non-endemics. The five C_4 species were also close to the general pattern described for the 73 C_3 species (Fig. 2), but some of them showed a slightly higher A_m than expected for their N_m and SLA. The five species included here may not be enough to determine whether the whole C_4 species group shares the same regression pattern as the C_3 species. On an area basis, A showed no significant correlation with N_a ($r = 0.22$, n.s.).

DISCUSSION

Differences in photosynthetic capacity between Balearic endemic and non-endemic species

On average, endemic species showed a 20 % lower net photosynthetic capacity on an area basis than non-endemics and crops. Baruch and Goldstein (1999) and McDowell (2002) have reported similar results in Hawaii and Oregon, respectively. In the study by Baruch and Goldstein (1999), native species had a 30 % lower net CO_2 assimilation than invasive species. These differences were even larger (50 %) in a comparison of two invasive and two non-invasive *Rubus* species (McDowell, 2002). It is noticeable that the differences observed in the present study are of a similar order of magnitude, regardless of the fact that only a few of the species studied exhibit invasive behaviour.

Although Balearic endemics also had a lower stomatal conductance than the other evolutionary groups, the similarity of the average C_i for all the groups suggests that reduced g was not the cause of photosynthetic limitation, but rather a consequence of it (Wong *et al.*, 1979). Therefore, it is likely that a non-stomatal factor is responsible for the lower photosynthetic capacity of endemics. Possibilities include a higher mesophyll resistance in endemics than in other species (i.e. a larger difference between C_i and the actual CO_2 concentration in the chloroplasts), a reduced

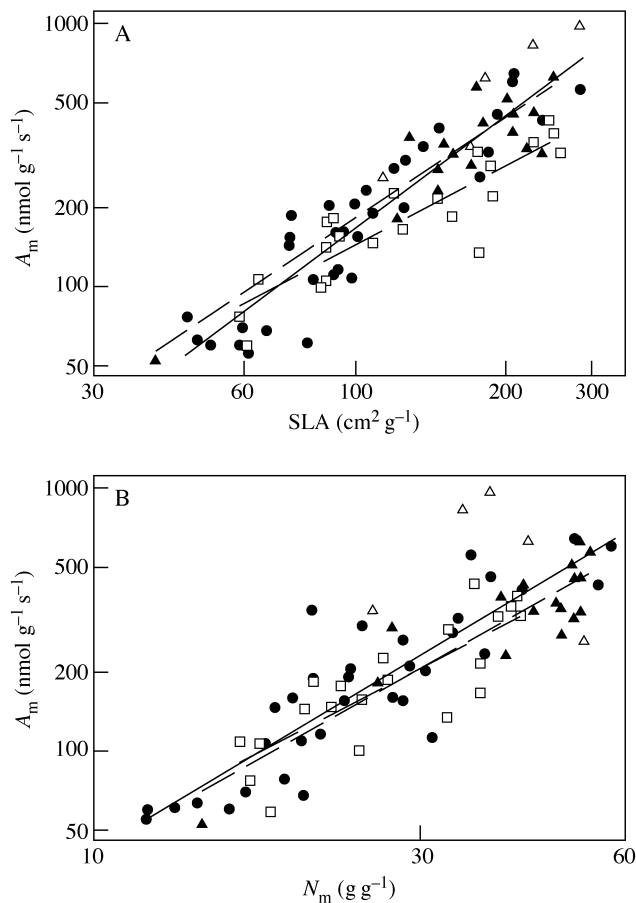


FIG. 2. Relationship between log net photosynthetic rate on a mass basis (A_m) and log specific leaf area (SLA) (A), and log A_m and log leaf nitrogen content on a mass basis (N_m) (B). Filled circles correspond to non-endemic species, empty squares to endemic species, filled triangles to crops, and empty triangles to C_4 species. Regression fits are shown as solid lines (non-endemic), short dashed lines (crops) and long dashed lines (endemic). For non-endemic species, $\log_{10} A_m = 1.41 \log_{10} SLA - 0.60$ ($r^2 = 0.84$) and $\log_{10} A_m = 1.56 \log_{10} N_m + 0.06$ ($r^2 = 0.77$). For crops, $\log_{10} A_m = 1.25 \log_{10} SLA - 0.24$ ($r^2 = 0.84$) and $\log_{10} A_m = 1.46 \log_{10} N_m + 0.15$ ($r^2 = 0.79$). For endemic species, $\log_{10} A_m = 0.99 \log_{10} SLA + 0.17$ ($r^2 = 0.79$) and $\log_{10} A_m = 1.37 \log_{10} N_m + 0.29$ ($r^2 = 0.69$). C_4 species were not included in regressions. Values correspond to means of six to eight replicates.

Rubisco content, activity and/or specificity factor, and/or higher respiration rates.

A higher mesophyll resistance in woody plants than in herbs, and in sclerophylls than in mesophytes, has been reported (Lloyd *et al.*, 1992; Evans and von Caemmerer, 1996). However, the effects of leaf habit were taken into account in our statistical analysis, and thus cannot be responsible for the observed differences between endemics and non-endemics. Mesophyll resistance of endemic species has not been evaluated, so this possibility should be addressed in future studies.

Variations in the Rubisco specificity factor, i.e. the relative affinity of Rubisco for CO_2 and O_2 , have been reported for C_3 plants. A few Balearic endemic species have been analysed in this regard. Their specificity factor is 15–20 % lower than that for other common species

(Delgado *et al.*, 1995) which, according to the model of Laing *et al.* (1974), would result in 10–20 % less CO_2 assimilation in endemic species, consistent with the present observations. The Rubisco specificity factor would need to be determined for a larger number of endemic and non-endemic species to confirm this trend.

Respiration rates were determined in only one endemic species, *Rhamnus ludovici-salvatoris* (Gulías *et al.*, 2002). This has twice the respiration rate of its relative *R. alaternus*. Similar results were observed by McDowell (2002) in *Rubus* species. Further studies are needed to elucidate the role of each of these possible limitations to photosynthesis in Balearic endemic species.

Interactions between leaf habit and evolutionary history in photosynthetic capacity and related parameters

Besides the overall differences between endemic and non-endemic species, most of these differences were found within the herbaceous deciduous group. The high proportion of rupicolous species within the endemics could have been responsible for this, since this type of species has evolved in a resource-limiting environment. Nevertheless, no significant differences were found for any parameter between rupicolous and non-rupicolous endemic species in a separate ANOVA (data not shown). Another possible explanation for the observed differences between endemic and non-endemic herbaceous deciduous species is a differential specialization for habitat among the two groups. While a high proportion of the non-endemic herbaceous deciduous species usually live in ruderal areas, only a few endemic species share this kind of habitat. This fact could account for the higher photosynthetic capacity and nitrogen content of the former, which could be the result of adaptation to a high-resource habitat.

Endemic species showed lower SLA than non-endemic species in the herbaceous deciduous group, but this was higher in all the other leaf habit groups. Similarly, SLA for invasive and non-invasive species yielded opposite results in the studies of Baruch and Goldstein (1999) and McDowell (2002).

Leaf trait relationships: ecological implications

A highly significant hyperbolic correlation was obtained between A and g (Fig. 1), consistent with other reports using a single species (Farquhar *et al.*, 1987) or various species (Field and Mooney, 1986). Most of the typically Mediterranean species lay on the linear part of the A – g relationship (i.e. the region of highest A/g) suggesting that low water availability in a Mediterranean climate has exerted an important evolutionary pressure on both endemic and non-endemic species.

The present data clearly support the general correlation between N_m , A_m and SLA described by Reich *et al.* (1997) for six biomes and different plant life forms (Fig. 2). Even the slopes of the regressions among these parameters were similar to those described by Reich *et al.* (1997). Leaf habit does not modify these general relationships, as described by Reich *et al.* (1997, 1999).

As expected, crops had higher A_m and lower A/g than the other groups because they have been selected to maximize plant production but not to improve the efficiency of resource use (Boyer, 1982, 1996). Despite these differences, crops lay close to the general relationships between A_m , N_m and SLA, in agreement with the hypothesis of Reich *et al.* (1999) that no species can improve A_m without increasing SLA, due to biophysical limitations. Similar results were observed by Schulze *et al.* (1994).

Endemic species, and some of them in particular, did not follow the general relationships between SLA, N_m and A_m (Fig. 2). The differences between endemic and non-endemic species were maximal at high SLA and N_m , whereas the reduced number of existing endemic species with low SLA and N_m precludes the establishment of clear differences in that region of the relationship. These differences may imply that a higher proportion of the leaf biomass is made up of non-photosynthetic compounds and structures in the endemics than in non-endemics, which could be a consequence of the prevailing conditions during the evolution of these species. If endemic species were evolving under low niche competition, as commonly observed on islands (Cox and Moore, 1993), a low photosynthetic capacity would not be as unfavourable as it is under high competitive pressure. On the other hand, the reduced competitive ability of endemics could be a consequence of devoting high amounts of resources to the synthesis of defensive compounds, a likely consequence of evolution under (a well-described) high pressure by herbivores on these islands (Bover and Alcover, 2000). Indeed, high photosynthetic nitrogen-use efficiency has been related to a high nitrogen investment in photosynthetic compounds and to a high Rubisco specific activity (Poorter and Evans, 1998).

Competition among plants may have increased due to the introduction of continental plant species by humans (Burjachs *et al.*, 1994; Yll *et al.*, 1994). Owing to their lower competitive ability (among other possible factors), the distribution of endemic species should have been reduced since humans arrived on the islands. Indeed, there is palynological evidence to show that some of the genera that are now extinct or that have a very narrow distribution were widespread before humans arrived on the islands (Burjachs *et al.*, 1994; Yll *et al.*, 1994). Remarkably, some of the endemic species with a more restricted distribution (namely *Acer*, *Ligusticum*, *Paeonia* or *Rhamnus ludovici-salvatoris*) actually fall in the lower part of the A -SLA relationship. A similar situation can be found at present in Hawaii, where invasion of plant species is much more recent. In these islands, native species have been shown to have some disadvantageous traits compared with invasive species, which means that they are less able to capture resources efficiently and have a lower growth capacity (Pattison *et al.*, 1998; Baruch and Goldstein, 1999; Durand and Goldstein, 2001).

Concluding remarks

Prior to the present study, different plant traits that were related to a low competitive ability, and resulted in a shrinking distribution range of these species, were

suggested to be present in species endemic to islands. Among these traits, pollination and seed dispersal limitations have been suggested (Givnish, 1998). Also, it has been suggested that species endemic to islands synthesize fewer chemical defences (Carlquist, 1970), although the opposite has been proposed as well (Bohm, 1998). Recently, Hawaiian native species have been shown to have lower A_m and SLA than invasive ones, and this has been related to their lower competitive and invasive ability (Baruch and Goldstein, 1999). The present results support the hypothesis that photosynthetic capacity is another important factor contributing to the limited distribution of some endemic species. Moreover, the similarity of the present results and those reported in Hawaii, a group of islands recently invaded by alien species and with a tropical climate, suggests a convergence pattern of photosynthetic traits in native species on islands.

The observed differences between endemic and non-endemic species support the hypothesis presented here that evolution in a low competitive environment may allow the occurrence of species with a low A_m for a given SLA. According to the ecological interpretation of Reich *et al.* (1999), these leaf traits may be disadvantageous for competition with other plant species, suggesting a possible cause for the decline in the distribution of many Balearic endemic species after the introduction of allochthonous species (Alomar *et al.*, 1997). Interestingly, characters negatively affecting competition have also been described in animals endemic to islands (Sondaar, 1977; McNab, 1994), including the extinct Balearic bovid *Myotragus* (Alcover *et al.*, 1999; Bover and Alcover, 1999).

SUPPLEMENTARY INFORMATION

Mean values of gas exchange parameters (net CO₂ assimilation rate on an area basis, stomatal conductance, substomatal CO₂ concentration, intrinsic water use efficiency and net CO₂ assimilation rate on a mass basis), specific leaf area and leaf nitrogen content (on a mass and on an area basis) for each species are available on the *Annals of Botany* website (<http://aob.oupjournals.org>).

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