Oecologia (1999) 118:248–255

J.H.C. Cornelissen

A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy

Received: 2 March 1998 / Accepted: 15 October 1998

Abstract A hypothesized relationship between seed weight and leaf size was investigated for 58 diverse British (semi-)woody species. Interspecific variation in leaf size of adult plants corresponded allometrically with interspecific variation in the weight of an infructescence (seed-bearing inflorescence). The relationship between seed size and leaf size of adult plants was triangular. The corners of the triangle were interpreted in terms of ecological strategy. Medium-sized infructescences, small seeds and large leaves were seen among medium-sized, fast-growing, earlier-successional, mostly deciduous shrubs and trees; small infructescences, small seeds and small leaves mostly among low, slow-growing evergreens from stress-prone, proclimax habitats; and large infructescences, large seeds and large leaves among slow-growing, later-successional trees of potential competitive vigour. The hypothesis that the combination of large seeds and small leaves is allometrically unlikely was supported by the data. The roles of ontogeny and taxonomic relatedness in the seed size-leaf size relationship were examined by correlative and taxonomic analyses of seed, plant and leaf size during the unfolding of the life history from seed through two seedling phases to adulthood. Deciduous versus evergreen leaf habit was a source of deviation from the otherwise linear allometric relationships during ontogenetic development, none of which were, individually, confounded significantly with taxonomy.

Key words Allometric · Ecological strategy · Leaf area · Ontogenetic · Seed weight

Introduction

Interspecific variation in the size of leaves can partly be explained by climatic variation (Raunkiaer 1934). Environmental stress factors associated with climate, geology, altitude or latitudinal position, notably heat, cold, drought and radiation load, have been shown to select for smaller leaves (Orians and Solbrig 1977; Parkhurst and Loucks 1972; Givnish 1987; Körner et al. 1989). However, within areas of similar macroclimatic conditions great interspecific variation in leaf size is usually seen, even within plant communities. This may be explained by three main factors which may interact. First, microclimatic variation among the species' usual habitats may account for similar leaf size selection as above but on a micro-geographical scale. Such variation could be connected with the ecological strategy and successional position of different species in ecosystems. A second explanation could be that leaf sizes themselves do not affect the species' success in a local flora, but are merely a neutral trait confounded phylogenetically with other traits of the particular higher taxon they belong to. Third, and possibly related to such phylogenetic constraints, leaf size may be an allometric consequence of plant size, anatomy and architecture. This implies that it may also change between juvenile and adult phases of a given species. Knowing the possible constraining effects of allometry, ontogeny and phylogeny on leaf size may help us interpret the adaptive significance of present-day variation in leaf size among species in their natural environments.

Corner (1949) proposed general "rules" of allometry in terrestrial plants, one of which was a correspondence in the size of axes (e.g. stems, branches) and their appendages (e.g. leaves, inflorescences). This rule could be a consequence of vascular, meristematic and/or biomechanical demands on the axes to equip them for supplying and supporting their appendages. The correspondence between axis diameter (or cross-sectional area) and leaf size is supported by empirical evidence for

---

J.H.C. Cornelissen (✉)
Sheffield Centre for Arctic Ecology and
Unit of Comparative Plant Ecology,
Department of Animal and Plant Sciences,
The University, 26 Taptonville Road,
Sheffield S10 5BR, UK
e-mail: h.cornelissen@sheffield.ac.uk,
Fax: +44-114-2682521

temperate zone deciduous trees (White 1983a; Niklas 1994), evergreen trees (White 1983b) and South African shrubs of the genus *Leucadendron* (Bond and Midgley 1988). Axis diameter and size of reproductive appendages were positively related within *Leucadendron* (Midgley and Bond 1989) and among temperate species throughout the plant kingdom (Niklas 1993). Midgley and Bond (1989) reasoned that if both leaf and inflorescence size were positively related to axis diameter, they should be connected with one another as well, at least in plants which bear leaves and inflorescences on the same axes. They supported this hypothesis with evidence from several South African genera and families. Continuing the same line of reasoning, seed size and leaf size should theoretically be connected among species if infructescence (seed-bearing inflorescence) size and individual seed size were positively related. In the real world, however, the "pioneer's" regenerative strategy of large infructescences with numerous small seeds (MacArthur and Wilson 1967; Grime 1977) has given rise to deviations from the latter relationship. I therefore hypothesize that small-seededness is seen in combination with either small or large leaves of mature woody plants. However, since (very) large seeds result by definition in an infructescence of medium to large size, allometric theory should make the combination of large seeds and small leaves unlikely.

If the hypothesized allometric constraints on leaf size and seed size exist in mature plants, another question to be addressed is whether and how allometric rules also apply during the ontogenetic development from seed to adulthood. Do large (small) seeds generally produce large (small) seedlings with large (small) leaves? Does a large-leaved (small-leaved) seedling generally grow into a large-leaved (small-leaved) adult plant? This paper attempts to answer these questions using laboratory and field data from 58 (semi-)woody species in a temperate-zone flora, representing a wide range of functional types and taxa. The dependence of the relationships studied on phylogenetic constraints is evaluated through additional analyses that account for the taxonomic relatedness of the species involved.

Materials and methods

Choice of species

The (semi-)woody species (Table 1) were chosen mostly according to their prominence in the landscape in the British Isles, with some additional less common species, in order to achieve a wide range of life-forms, leaf habits and taxa. The list included natives, naturalized plants and a few forestry favourites. Seed size or leaf size themselves were no criterion for species choice. The common shrubs *Cytisus scoparius* and *Ulex* spp. were not included in this paper, because in these species only the small seedlings have substantial leaves, whilst the older plants have no or rudimentary leaves and depend for photo-assimilation mostly on the stems. Nomenclature in this paper follows Stace (1991).

Table 1 The study species and their life history. Nomenclature follows Stace (1991). Species marked with * are not native to the British Isles, but do grow and reproduce well there (leaf habit categories: *D* deciduous, *SE* semi-evergreen, *E* evergreen; life form categories: *T* tree, *S* shrub, *SS* subshrub, *PS* procumbent subshrub, *C* climber, *SC* scrambler). The species groups *A–E* correspond with those in Fig. 3

	Leaf habit	Life form	Species group
*Acer platanoides**	D	T	D
*A. pseudoplatanus**	D	T	D
*Aesculus hippocastanum**	D	T	C
Alnus glutinosa	D	T	A
Arbutus unedo	E	S/T	D
Berberis vulgaris	D	S	E
Betula pendula	D	T	A
*Buddleja davidii**	D	S	A
Buxus sempervirens	E	S	E
Calluna vulgaris	E	SS	B
*Castanea sativa**	D	T	C
Cornus sanguinea	D	S	D
Daphne mezereum	D	S	E
Dryas octopetala	E	PS	B
Empetrum nigrum	E	PS	B
Erica cinerea	E	SS	B
Fagus sylvatica	D	T	D
Frangula alnus	D	S	E
Fraxinus excelsior	D	T	D
*Hebe × franciscana**	E	S	A
Hedera helix	E	C	D
Helianthemum nummularium	E	PS	B
Hippophae rhamnoides	D	S	E
Ilex aquifolium	E	T	D
*Juglans regia**	D	T	C
*Laburnum anagyroides**	D	T	D
*Larix decidua**	D	T	E
Ligustrum vulgare	SE	S	E
Lonicera periclymenum	D	C	E
Malus sylvestris	D	T	E
*Picea sitchensis**	E	T	E
Pinus sylvestris	E	T	E
*Prunus laurocerasus**	E	S	D
*P. lusitanica**	E	S/T	D
P. spinosa	D	S	E
*Quercus cerris**	D	T	C
*Q. ilex**	E	T	D
Q. petraea	D	T	C
Q. robur	D	T	C
Rhamnus cathartica	D	S	E
*Rhododendron ponticum**	E	S	A
*Ribes nigrum**	D	S	A
R. uva-crispa	D	S	D
Rosa arvensis	D	SC	D
Rubus fruticosus	SE	SC	D
Salix caprea	D	T	A
Sambucus nigra	D	S	D
Solanum dulcamara	D	SC	D
Sorbus aucuparia	D	T	D
Taxus baccata	E	T	E
Thymus polytrichus	E	PS	B
Ulmus glabra	D	T	D
Vaccinium myrtillus	D	SS	B
V. vitis-idaea	E	SS	B
Viburnum opulus	D	S	D
*V. tinus**	E	S	D

Seeds and seedlings

Seeds of most species were collected from within a 25-km radius around Sheffield, United Kingdom, and a small proportion from elsewhere in Europe (details in Cornelissen et al. 1996). Mean dry weight of the seed (sensu stricto), determined after 48 h at 80°C, was based on samples ranging from 10 (very large) to 100 (very small) seeds. A subpopulation of each species was germinated and the seedlings treated in a standard indoor growth environment following a standard procedure for analysis of mean relative growth rate (RGR), as described in detail by Cornelissen et al. (1996). The following details are directly relevant for this study. Seedlings were grown in quarried sand at 135 μmol m^{-2} s^{-1} of photosynthetically active radiation for 14 h each day (at 20–22°C; night 15–17°C), and, after an initial stepwise build-up, at full Rorison's nutrient solution (Hendry and Grime 1993) and a continuous supply of bottom-water. The first half of each population ("initial seedlings") was harvested once the modal group of seedlings of the population had just opened (but not necessarily expanded) the first true leaf. This ontogenetically defined start of the growth analysis period allowed comparison of species differing by orders of magnitude in size. The total dry weight of the seedlings as defined here excluded any thick storage cotyledons without a photosynthetic function (cf. Cornelissen et al. 1996). The remaining half of the population ("3-week seedlings") was grown in the same standard environment for another 3 weeks, then also harvested. Samples consisted of 8–30 plants (average 16). In this paper, "leaf" is defined strictly and includes a rachis and its leaflets in the case of compound leaves. Mean leaf size was calculated as the quotient of the total leaf area of a plant (excluding petiole area) and the number of expanded leaves. In most species leaf area was determined using a Delta-T area meter (Burwell, Cambridge, UK), but the areas of tiny leaves were assessed visually against a 1-mm paper grid. In some species, for instance those with enrolled leaves, the true one-sided leaf area was calculated by multiplying the projected area by a conversion factor derived from foliar cross-sections. Dry weights of leaves and whole plants were determined as for seedlings.

Mature plants in the field

Between 5 July and 8 August 1995, between one and four (in most species two or three) sexually mature plants of each species were sampled within a 25-km radius around Sheffield, each plant growing on a different geological substratum. The four main substrata (all at altitudes <300 m) were: MG, millstone grit (acidic sandstone); CL, carboniferous limestone; ML, magnesium limestone; CM, coal measures (slightly acidic, loamy). The great majority of the samples were from semi-natural sites, but a minor proportion was from parks and gardens. A sample consisted of 15 typical, fully expanded, undamaged (simple or compound) sun leaves. The leaves were kept fresh (in wet tissue at 5°C) for up to 24 h until their area was measured (as above). Mean leaf size ("adult leaf size" in this paper) was based on the 15 leaves or, as in most evergreen species, it was the average based on the means for a 15-leaf sample from the present year's cohort and a 15-leaf sample from the previous year's cohort. In *Larix decidua* it was based on 15-leaf samples from both brachyblasts and twig apices. The dry weight of each leaf was determined as above.

Normal maximum plant height (excluding exceptional values for individuals) of self-supporting woody plants in the British Isles (excluding climbers and scramblers) are according to Stace (1991). In the autumns of 1996 and 1997, between 10 and 50 typical, ripe infructescences per species were collected from 47 of the same species (excluding the coniferous gymnosperms) in and around Sheffield. Mean infructescence dry weight (including stalks) was determined as for other plant parts.

Data analysis

Relationships among species between two parameters were tested using linear regression and product-moment correlation analysis. Because of the range of several orders of magnitude, all parameters were $\log_{10}$-transformed before analysis. Additionally, some key positive relationships were tested taking into account the taxonomic relatedness of the species involved, following a method derived from Kelly and Beerling (1995) and using the taxonomic classification by Cronquist (1981). For each set of two or more subtaxa belonging to the same taxon (e.g. three species of the same genus), it was recorded whether the relationship concerned (e.g. seedling weight vs seedling mean leaf size) showed a positive or negative trend. The average value of the lower taxa could subsequently be employed for a similar comparison of the next level up (e.g. genera within families), up to the level of classes. Combining the results at all taxonomic levels, chi-squared tests were carried out to investigate whether these trends were positive significantly more often than expected by chance.

Results

Although not presented as such for brevity, all relationships below refer to $\log_{10}$-transformed parameters. In this paper leaf size can also be interpreted as leaf dry weight, as both parameters were tightly correlated among seedlings as well as among adults across all species (in both cases: $r = 0.99$, $P < 0.001$). Eight of the species in this study had compound leaves. There were strong interspecific correlations between the sizes of whole leaves (used in this paper because these are appendages sensu Corner 1949) and those of functional leaf analogues (leaflets in the case of compound leaves): $r = 0.996$, $P < 0.001$ among seedlings; $r = 0.96$, $P < 0.001$ among adult plants. Linear regressions for mean leaf sizes of adult plants revealed that in none of the four combinations of geologies that shared more than 10 species was there a significant deviation from the 1:1 line due to site: (1) MG versus CL, $n = 26$ species, $r^2 = 0.93$ between substrata, slope = 1.02; (2) MG versus ML, $n = 26$, $r^2 = 0.94$, slope = 0.99; (3) CL versus ML, $n = 29$, $r^2 = 0.92$, slope = 0.98; (4) MG versus CM, $n = 15$, $r^2 = 0.99$, slope = 1.00. Given such correspondence of leaf sizes among geological substrata, I used the mean value over the sampling sites. In adult plants, an overall correlation of mean leaf size with maximum plant height ($r = 0.54$, $P < 0.001$) was much improved if the gymnosperms were excluded ($r = 0.76$, $P < 0.001$; Fig. 1). Another possible allometric partner, infructescence weight, was closely connected with leaf size (Fig. 2) and this relationship stood up to a taxonomic relatedness test (17 contrasts showing a positive and 3 a negative trend: $\chi^2_{(1)} = 5.58$, $P < 0.05$). There was a significant but triangular correlation of adult leaf size with seed weight (Fig. 3). The plants in corner A in Fig. 1, with small (<1 mg) seeds, medium-sized infructescences and large (>1000 mm^2) adult leaves, were, on average, fast growers (Table 2; seedling RGR data from Cornelissen et al. 1996). *Rhododendron ponticum* was a slow-growing exception. In contrast, the species in corner B in Fig. 1, with small (<1 mg) seeds, small infructescences and small (<1000 mm^2) adult leaves, had relatively low seedling mean RGRs, as did the species (C in Fig. 1) with large (>1000 mg) seeds, large infructescences and large

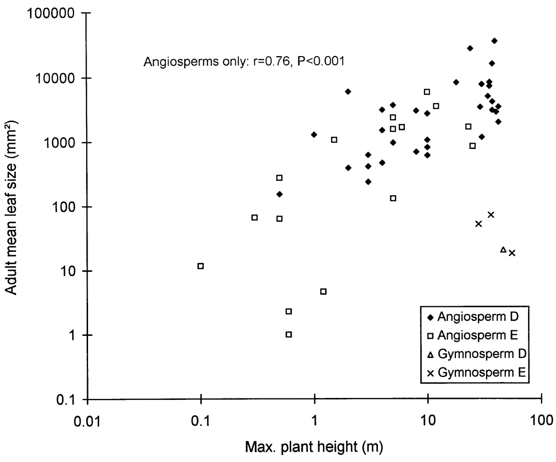

Fig. 1 The relationship between maximum plant height and adult mean leaf size in woody angiosperms and gymnosperms (*D* deciduous, *E* evergreen). The correlation analysis refers to $\log_{10}$-transformed data

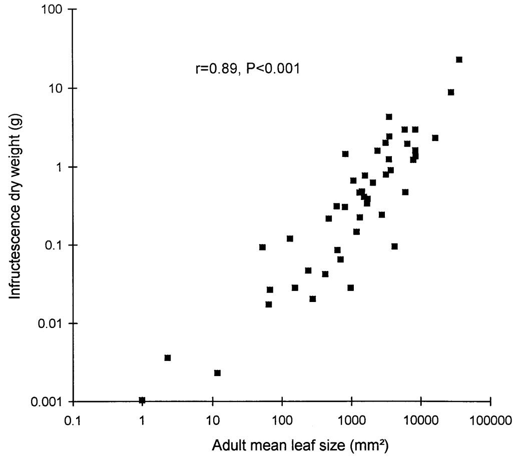

Fig. 2 The relationship between leaf size of adult plants and infructescence dry weight among 47 woody species (excluding coniferous gymnosperms). The correlation analysis refers to $\log_{10}$-transformed data

(> 1000 mm^2) adult leaves (Table 2). The species (D, E in Fig. 1) of intermediate seed weight also had intermediate seedling RGRs (Table 2). The results were very similar if leaflets rather than whole leaves were used for compound-leafed species (Table 2). The combination of large seeds and small leaves did not occur in the entire species set. On average, adult leaves of deciduous species (4775 ± 1184 mm^2) were larger than those of evergreens (1057 ± 338 mm^2; *t*-test on $\log_{10}$-transformed data: $P < 0.001$).

The relationship between seed weight and adult leaf size can be considered in four steps that follow the ontogenetic development of woody plants. Firstly, the total weight of initial seedlings was correlated closely with seed weight (Fig. 4A). Among all species, initial seedling weight corresponded also with that of 3-week seedlings (Fig. 4B), but at a given initial seedling weight (X) deciduous species (D) had a higher 3-week seedling weight (Y) than evergreens (E) (linear regressions of the form $Y = aX + b$ on $\log_{10}$-transformed data; a = 0.71 (D) and 0.87 (E), not significant; b = 1.25 (D) and 0.66 (E), $P < 0.01$). Plant weight and mean leaf size of 3-week seedlings were closely correlated (Fig. 4C), deciduous species again displaying larger leaves than evergreens (*t*-test on $\log_{10}$-transformed data: $P < 0.001$). Mean leaf size of seedlings and adult plants were also correlated rather closely among all 58 species (Fig. 4D). A very similar relationship emerged if leaflets rather than whole leaves were used for the eight compound-leafed species ($r = 0.85$, $P < 0.001$). All of these four positive relationships were also significant when taxonomic relatedness was accounted for. Indeed, positive trends for these relationship emerged both at lower and higher levels of taxonomy, except for that between initial seedling weight and 3-week seedling weight at the species level (Table 3). Overall, the relationship between seed weight and adult leaf size appeared somewhat confounded with taxonomy (Table 3).

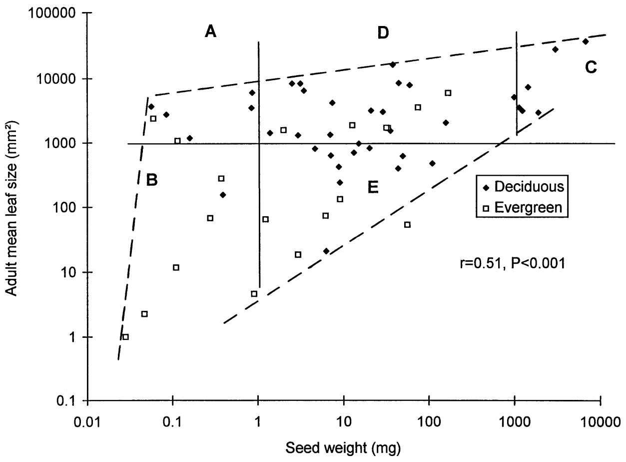

Fig. 3 The relationship between mean seed dry weight and adult mean leaf size in a range of woody species. Arbitrary class boundaries are 1 and 1000 mg for seed weight and 1000 mm^2 for leaf size. The correlation analysis refers to $\log_{10}$-transformed data. The arbitrary *dashed triangle* includes all species except the gymnosperm *Taxus baccata*

Discussion

The results of this analysis support the hypothesized triangular relationship between seed size and adult leaf size in a temperate-zone woody flora (Fig. 3), with major variation in leaf size particularly at the small-seeded side of the range. The triangle depends on the absence of species that combine large seeds with small leaves, as hypothesized. It appears that, indeed, Corner's rule of appendage allometry has constrained the evolutionary options open to woody species to vary both traits in combination. The challenge is now to unravel the individual roles that allometry, ontogeny, ecology and phylogeny play in the seed size – leaf size relationship and to identify possible overlap between these four roles.

Table 2 Mean trait values (± SE) for species groups A–E in Fig. 3. For leaf size, values in parentheses refer to leaf analogues (i.e. leaflets in the case of compound leaves). One-way ANOVAs revealed significant heterogeneity among the five species groups in log infructescence size (F = 32.5, P < 0.001) and in seedling mean RGR (F = 3.71, P = 0.01)

	Log seed weight (mg)	Log adult leaf size (mm^2)	Log infructescence dry weight (g)	Seedling RGR (day^{-1})
Group A				
Mean	−0.77	3.40 (3.40)	−0.25	0.138
SE	0.19	0.10 (0.10)	0.14	0.020
Group B				
Mean	−0.75	1.22 (1.22)	−2.14	0.070
SE	0.21	0.36 (0.36)	0.25	0.011
Group C				
Mean	3.31	3.89 (3.63)	0.81	0.068
SE	0.12	0.20 (0.07)	0.23	0.006
Group D				
Mean	1.28	3.53 (3.33)	−0.089	0.098
SE	0.16	0.07 (0.07)	0.099	0.011
Group E				
Mean	1.08	2.35 (2.35)	−0.98	0.084
SE	0.13	0.15 (0.15)	0.15	0.007

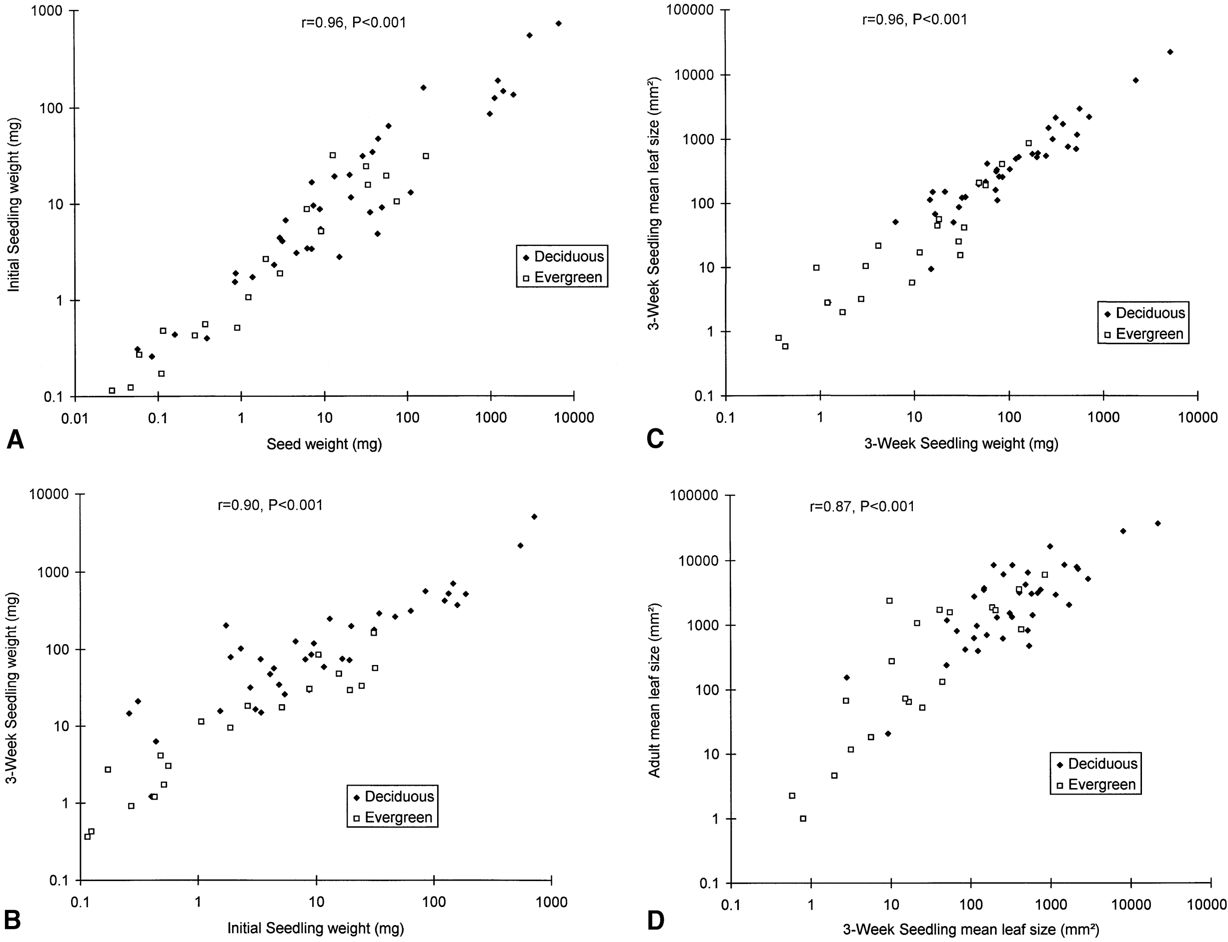

Fig. 4 The relationships between **A** mean seed dry weight and plant dry weight (excluding thick storage cotyledons) of initial seedlings (definition see text); **B** plant dry weight of 3-week seedlings (defined in Methods) and that of initial seedlings; **C** mean leaf size and plant dry weight (excluding thick storage cotyledons) of 3-week seedlings; and **D** mean leaf size of adults and that of 3-week seedlings. The correlation analyses refer to $\log_{10}$-transformed data for all species

Table 3 Taxonomic analysis of some hypothesized allometric relationships. Taxonomic classification follows Cronquist (1981). Given a proposed relationship, it is indicated for each contrast (two or more taxa of the same taxon of the next level up) whether the trend (in linear regression) was positive or negative. The null hypotheses state that these trends are positive no more often than expected if by chance in one-tailed chi-squared tests. Numbers of positive contrasts are before and total numbers of contrasts after the slash (n/N)

	Seed weight vs initial seedling weight	Initial seedling weight vs 3-week seedling weight	3-Week seedling weight vs 3-week seedling leaf size	3-Week seedling leaf size vs adult leaf size	Seed weight vs Adult leaf size
Species within genus	5/6	2/6	6/6	5/6	3/6
Genera within family	6/8	7/8	8/8	7/8	6/8
Families within order	5/5	5/5	4/5	3/5	4/5
Orders within subclasses	4/4	4/4	4/4	4/4	3/4
Subclasses within class	2/2	2/2	2/2	2/2	2/2
All contrasts	22/25	20/25	24/25	21/25	18/25
$\chi^2_{(1)}$	8.4 ($P < 0.01$)	4.9 ($P < 0.05$)	13.4 ($P < 0.001$)	6.5 ($P < 0.05$)	2.5 (NS)

NS Not significant

Focusing first on the allometrics of leaf size, the latter was positively connected with plant height in the self-supporting subset of the angiosperms studied here. The same relationship has previously been reported for 85 Estonian woody angiosperms (Niinemets and Kull 1994) and within two Finnish birches and their hybrid (Senn et al. 1992). In all three studies the relationship appeared to act principally at the life-form level between sub-shrubs, shrubs and trees as groups. This may be explained to some extent by the fact that smaller woody life-forms have thinner trunks that cannot support a heavy crown (Niklas 1994). Considering the biomechanically determined centrifugal tapering of axis diameter (Cannell et al. 1988), and given a minimum branching intensity for efficient leaf display, a small woody plant could not support sufficiently thick outer twigs to support large leaves (White 1983a; Niklas 1994). A large-leafed crown has been considered efficient in humid temperate zones because of relatively small woody support investments per unit of light intercepting area (Givnish 1979). Thus, larger woody plants should bear larger leaves than small plants. The relationship between adult plant height and adult leaf size appeared not to hold for gymnosperms. If vessel diameters play an important role in tree allometry (see next paragraph), the narrow tracheids of gymnosperms may allow them to develop a crown with relatively small leaves borne on narrow twigs, whilst the tall trunk needs to be thick for structural strength. Both tracheids (Woodward 1995) and small leaves have been considered adaptive in the boreal climates where gymnosperms tend to predominate (Chabot and Hicks 1982).

More direct evidence in support of Corner's rule, and particularly the hypothesis derived from it by Midgley and Bond (1989), was provided by the general correspondence of the sizes of reproductive appendages (infructescences in this paper) and leaves across a broad range of British woody species. This relationship was robust to the higher taxonomic identity of the species involved. Thus, this apparently fundamental relationship has now been demonstrated for a range of woody taxa in both the northern and the southern hemisphere. The actual mechanism of this allometry is still unclear. On the one hand it may depend simply on the biomechanics of mass load versus length and angle of the lever arm of the different organs, or of total cross-sectional vessel or meristem area needed to support organs of a certain size (Castéra and Morlier 1991; Niklas 1993). On the other hand, it may result from balanced source-sink relations of photosynthates between leaf and reproductive appendage. Plants tend to be built up from a number of small semi-autonomous "integrated physiological units", for instance combinations of a leaf and a particular reproductive structure through a vascular connection (Waller and Steingraeber 1995). This seems to contrast with Hiura et al. (1996), who found a slight negative relationship between seed size and adult leaf size within *Fagus crenata*, and interpreted this in terms of a tradeoff between reproductive and vegetative investments of biomass. However, their ranges in seed size and $\log_e$ leaf size were only twofold, which is very little compared to the interspecific ranges in this study.

Whilst allometric principles may determine which combinations of traits are "mandatory" and which impossible, they appear to leave ample opportunities for ecologically relevant trait differentiation within these constraints. In the case of the leaf size-infructescence size relationship in this woody flora, interspecific differentiation particularly in infructescence type has important significance for the ecological strategy of different species groups. In their most outspoken expressions, three combinations of traits can be recognised as corners of the seed size-leaf size triangle (Fig. 3). The first combination (group A, cf. Tables 1, 2) of large infructescences with numerous small seeds and large adult leaves is associated with fast-growing, mostly deciduous, relatively early-successional shrubs and small trees. The seeds are dispersed over large distances mostly by wind (and in some cases birds) for effective colonisation of relatively bare ruderal (*Betula*, *Buddleja, Hebe*) or flooding-prone soils (*Alnus*, *Ribes nigrum*, *Salix*) (cf. Rodwell 1991a; Stace 1991; Schütt et al. 1995). Fast seedling growth may allow these plants to escape overshading in a rapidly closing canopy. Once established they appear to put more of their resources into long-term (woody) structures and in competitive vigour through a more substantial crown of larger-sized leaves. Most of these species are relatively shade-intolerant and will gradually succumb as succession progresses. Secondly, the combination (group B) of small infructescences with small seeds and small adult leaves is typical of the slow-growing, mostly evergreen subshrubs in this study. These plants occur in stressed habitats (heathland, calcareous grassland) of low nutrient availability and a proclimax phase of succession due to regular grazing or other landuse (cf. Rodwell 1991b; Stace 1991). These conditions inhibit the accumulation of a substantial biomass and promote evergreenness as a nutrient conservation strategy (Monk 1966). As mentioned above, the small leaves and rather low reproductive effort in absolute terms may be an allometric consequence of the small size of these plants. The third corner (group C) of the triangle consists of mid- to late-successional tree species with very large seeds (and therefore large infructescences) and large leaves. Their growth is slow, but their large biomass investments in woody support structures eventually allow tall stature. These large plants can develop wide crowns with large leaves for optimized light interception per unit branch biomass. This, together with their tall stature, should give them competitive vigour in the woodland or forest canopies they occur in naturally (cf. Rodwell 1991a; Stace 1991; Schütt et al. 1995).

These results suggest that there is some overlap of the three seed size-leaf size corners A, B and C (Fig. 3) with the ruderal, stress-tolerant and competitive strategies, respectively, as defined by Grime (1977) and adapted for trees by Brzeziecki and Kienast (1994) and Cornelissen et al. (1998). It is important to realize that none of the woody species come close to the extreme ruderal strategy. The central parts of the triangle (groups D and E), appear to consist of a mixture of species in terms of ecological strategies, with growth rates on average intermediate between those of the other species groups (Table 2). The distributions within these groups appear to be consistent with the strategies of the adjacent corners of the triangle. Within group D, the relatively early-successional, bird-dispersed scrambler and shrub species from fertile sites tend to be towards the left, close to group A (e.g. *Rosa*, *Rubus*, *Sambucus*, *Solanum*) and the big, competitive, later-successional trees (e.g. *Acer* spp., *Fagus*, *Fraxinus*) towards the right. Group E, like A, seems linked with stress-prone habitats. It contains all four gymnosperms and 9 out of 12 of the angiosperms in this group are shrubs generally associated with relatively infertile sites (e.g. *Buxus*, *Crataegus*, *Frangula*, *Hippophae*).

The data presented here have shed light on the roles of allometry, ecology and taxonomy on the seed size-leaf size relationship during the ontogenetic development from seed to adulthood. The interspecific correspondence between the weight of the seeds and that of the seedlings at the transition from cotyledon-dependent to leaf-dependent phase was paramount and was seen both within lower and higher taxa. This relationship among woody species has also been found by other authors, who have interpreted large seed resources ecologically as an adaptive strategy to help seedlings survive and establish in stressed environments (Salisbury 1942; Grime and Jeffrey 1965; Piper 1986; Seiwa and Kikuzawa 1991; Jurado and Westoby 1992; Saverimuttu and Westoby 1996).

Generally, among the woody species studied here, large (small) seedlings after the seed-dependent phase remained relatively large (small) when grown on for three more weeks in a standard environment. However, there was considerable scatter due mainly to the faster growth of deciduous as compared to evergreen species (Cornelissen et al. 1996), which was linked to the shorter leaf lifespans and higher specific leaf area (leaf area:leaf dry weight) of the former rather than to their leaf size (Reich et al. 1992; Cornelissen et al. 1996). This was also apparent from a taxonomic relatedness analysis which, although yielding an overall independence of the relationship on taxonomy, suggested that the relationship did not occur among congeneric species. Indeed, three out of the four negative contrasts at this taxonomic level contained congeneric deciduous and evergreen species. Consistent with the different mean RGRs and the resulting larger seedlings after 3 weeks of autotrophic growth, the larger leaves of deciduous species as compared to the evergreens already manifested themselves at that stage. The fundamental validity of the allometric relationship between plant weight and leaf size of 3-week seedlings is supported by its occurrence at all taxonomic levels.

Finally, these differences in leaf size between large and small and between deciduous and evergreen 3-week seedlings were broadly maintained up to adulthood, again within higher as well as lower taxa. Following from the above relationships between plant size and mean leaf size both in the seedling and the mature phase, it follows that "once a large plant with large leaves, always a large plant with large leaves" in comparison with other species of a temperate woody flora.

I conclude that there are limits to the possible combinations of plant size, infructescence size, seed size and leaf size in the different phases of the life history of woody plants, and the underlying allometric rules appear to have operated throughout the phylogenetic history. Within the limits of these rules, there has been ample opportunity for important ecological specialization among woody species. Such specialization can be observed in a present-day flora, for instance among species of different natural habitat, life-form, leaf habit and regenerative strategy.

Acknowledgements I thank Bruno Cerabolini, who played a major role in the collecting of leaves in the field; Stuart Band and the Forestry Commission, Alice Holt Lodge, Farnham, for kindly supplying some of the seeds; Philip Grime, Dylan Gwynn-Jones, John Hodgson, Rod Hunt, Ken Thompson and two anonymous referees, for stimulating discussions and/or comments on an early draft. This work was supported by an EC Human Capital and Mobility fellowship.

References

Bond WJ, Midgley JJ (1988) Allometry and sexual differences in leaf size. Am Nat 131:901–910

Brzeziecki B, Kienast F (1994) Classifying the life-history strategies of trees on the basis of the Grimian model. For Ecol Manage 69:167–187

Cannell MR, Morgan J, Murray MB (1988) Diameters and dry weights of tree shoots: effects of Young's Modulus, taper deflection and angle. Tree Physiol 4:219–231

Castéra P, Morlier V (1991) Growth patterns and bending mechanisms of branches. Trees 5:232–238

Chabot BF, Hicks DJ (1982) The ecology of leaf lifespans. Annu Rev Ecol Syst 13:229–259

Cornelissen JHC, Castro-Diez 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, Castro-Díez P, Carnelli AL (1998) Variation in relative growth rate among woody species. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 363–392

Corner EJH (1949) The durian theory and the origin of the modern tree. Ann Bot 13:367–414

Cronquist A (1981) An integrated system of classification of flowering plants. Columbia University Press, New York

Givnish TJ (1979) On the adaptive significance of leaf form. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in plant population biology. Columbia University Press, New York, pp 375–407

Givnish TJ (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytol 106 [Suppl]:131–160

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Grime JP, Jeffrey DW (1965) Seedling establishment in vertical gradients of sunlight. J Ecol 53:621–642

Hendry GAF, Grime JP (1993) Methods in comparative plant ecology. Chapman and Hall, London

Hiura T, Koyama H, Igarashi T (1996) Negative trend between seed size and adult leaf size throughout the geographical range of *Fagus crenata*. Ecoscience 3:226–228

Juradó E, Westoby M (1992) Seedling growth in relation to seed size among species of arid Australia. J Ecol 80:407–416

Kelly CK, Beerling DJ (1995) Plant life form, stomatal density and taxonomic relatedness: a reanalysis of Salisbury (1927). Funct Ecol 9:422–431

Körner C, Neumayer M, Pelaez Menendez-Riedl S, Smeets-Scheel A (1989) Functional morphology of mountain plants. Flora 182:353–383

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Midgley J, Bond W (1989) Leaf size and inflorescence size may be allometrically related traits. Oecologia 78:427–429

Monk CD (1966) An ecological significance of evergreenness. Ecology 63:571–584

Niinemets Ü, Kull K (1994) Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. For Ecol Manage 70:1–10

Niklas KJ (1993)The allometry of plant reproductive biomass and stem diameter. Am J Bot 80:461–467

Niklas KJ (1994) Plant allometry: the scaling of form and process. The University of Chicago Press, Chicago

Orians GH, Solbrig OT (1977) A cost-income model of leaves and roots with special reference to arid and semi-arid areas. Am Nat 111:677–690

Parkhurst DF, Loucks OL (1972) Optimal leaf size in relation to environment. J Ecol 60:505–537

Piper JK (1986) Germination and growth of bird-dispersed plants: effects of seed size and light on seedling vigor and biomass allocation. Am J Bot 73: 959–965

Raunkiaer C (1934) The life forms of plants and plant geography. Oxford University Press, New York

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

Rodwell JS (1991a) British plant communities, vol 1. Woodlands and scrub. Cambridge University Press, Cambridge

Rodwell JS (1991b) British plant communities, vol 2. Mires and heaths. Cambridge University Press, Cambridge

Salisbury EJ (1942) The reproductive capacity of plants. Bells, London

Saverimuttu T, Westoby M (1996) Seedling longevity under deep shade in relation to seed size. J Ecol 84:681–690

Schütt P, Schuck HJ, Aas G, Lang UM (1995) Enzyklopädie der Holzgewächse. Ecomed, Landsberg

Seiwa K, Kikuzawa K (1991) Phenology of tree seedlings in relation to seed size. Can J Bot 69:532–538

Senn J, Hanhimäki S, Haukioja E (1992) Among-tree variation in leaf phenology and morphology and its correlation with insect performance in the mountain birch. Oikos 63:215–222

Stace CA (1991) New flora of the British Isles. Cambridge University Press, Cambridge

Waller DM, Steingraeber DA (1995) Opportunities and constraints in the placement of flowers and fruits. In: Gartner BL (ed) Plant stems, physiology and functional morphology. Academic Press, San Diego, pp 51–73

White PS (1983a) Corner's rules in eastern deciduous trees: Allometry and its implications for the adaptive architecture of trees. Bull Torrey Bot Club 110:203–212

White PS (1983b) Evidence that temperate east North American evergreen woody plants follow Corner's rules. New Phytol 95:139–145

Woodward FI (1995). Ecophysiological controls of conifer distribution. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 79–94