

Ecological characteristics of the flora of the Northwest Iberian Peninsula

Maria Luisa Buide, José María Sánchez & Javier Guitián
Departamento de Biología Vegetal, Universidad de Santiago, 15706, Spain

Received 23 December 1996; accepted in revised form 23 October 1997

Key words: Dioecy, Dispersal, Flora of Galicia, Life forms, Northwest Iberian Peninsula, Pollination

Abstract

An analysis of the ecological characteristics (life form, seed-dispersal mode, pollination mode, and reproductive mode) of about 1800 species of the flora of northwest Spain indicates that the most frequent characteristics are hemicryptophyte or therophyte life form, semachorous or barochorous seed dispersal, entomophilous pollination, and hermaphroditism. Following binary classification of the above characteristics (herbaceous versus woody life form, animal-assisted versus abiotic seed dispersal, animal-assisted versus abiotic pollination, dioecous versus hermaphrodite reproductive mode), statistically significant associations were found for all pairs of characteristics except pollination mode and reproductive mode (in disagreement with the results of previous studies which have detected significant associations between dioecy and abiotic pollination) and pollination mode and life form. To investigate the evolutionary plasticity of the different characters, we used nested analysis of variance with (in the case of life form, for example) percentage of species in genus with herbaceous life form as response variable, and with genus, family, order and subclass as nested factors and class as crossed factor. The results of this analysis indicated that higher-level grouping (class or subclass) accounted for the majority of total variance only in the case of pollination mode, suggesting either that pollination mode was typically determined early in evolutionary history and that there is currently little plasticity in this characteristic (i.e., phylogenetic constraints), or that this characteristic has been subject to stabilizing selection (i.e., phylogenetic niche conservatism). The other ecological characters, by contrast, showed high variability at lower levels in the taxonomic hierarchy.

Introduction

The morphological characteristics which distinguish some organisms from others are used by taxonomists to group organisms into species, and to group these species into higher-level units that should ideally reflect their origin and evolution. However, groups that are taxonomically unrelated may show great similarity in their ecological characteristics, such as life form, mode of dispersal or pollination mode. This is of interest because characteristics of this type may have played a key role in the diversification of such groups: specifically, some authors have argued that rapid diversification is facilitated by short-lived life form and animal-assisted modes of dispersal and pollination, though others have attributed greater importance to morphological and physiological plasticity (see Tiffney & Mazer 1995, and references therein).

In recent years there has been a considerable research effort aimed at cataloguing ecological characteristics in local floras (see for example Fitter & Peat 1994) and in particular taxonomic groups (Eriksson & Bremer 1992; Ricklefs & Renner 1994). The resulting databases have allowed identification both of relationships between characters and of geographical patterns in their distribution (see, for example, Fox 1985; Muenchow 1987; Gentry 1988; Renner & Ricklefs 1995). This information has also made a decisive contribution to the debate on the causes of diversification in angiosperms (Herrera 1989; Midgley & Bond 1991; Eriksson & Bremer 1992; Tiffney & Mazer 1995).

Information on the ecological characteristics of local floras is thus of interest for testing existing hypotheses and as a basis for the development of more general models. Here, we report a study of the ecological characteristics of the flora of Galicia, a region

occupying the northwest corner of the Iberian Peninsula. Specifically, we aimed (a) to collate information on the frequency of particular ecological characteristics among the species of the Galician flora, (b) to identify possible associations between characteristics, and (c) to quantify the variability of each characteristic within taxonomic groupings of varying level. An absence of variation in a given characteristic within a particular taxonomic grouping may be due either to phylogenetic constraints (i.e., low plasticity) or to stabilizing selection ('niche conservatism' see Lord et al. 1995). Phylogenetic constraints have been defined as taxon-specific limitations that impose a particular combination of characters regardless of selective pressures (Herrera 1992). In accordance with this view, a characteristic that shows considerable variation among high-level taxa (e.g., classes) but relatively little variation among lower-level subtaxa within each class (e.g., families) can be assumed to have become fixed in most families at an early stage in their evolutionary history, and to show relatively little plasticity in response to selective pressure.

Material and methods

Information sources

A total of 1718 species – those covered by the Flora of Galicia of Merino (1905–1909) and the published volumes of the Flora of Iberia of Castroviejo et al. (1989–1993) – were considered. These species represent about 85% of those currently accepted for Galicia (Soñora, unpublished estimate); however, most of the more recent additions are rare or sporadic, and for many Galicia is at the limit of their range; we thus consider the 1718 species considered here to be representative of the region. The taxonomic classification of species was as per Cronquist (1981).

The classification of species by life form was derived from De Langhe et al. (1978), Amaral Franco (1971–1984), Amaral Franco & Da Rocha (1994) and Pignatti (1982). The following Raunkiaer life forms (Raunkiaer 1934) were present in the data set: phanerophyte, nanophanerophyte, chamaephyte, hemicryptophyte, helophyte, hydrophyte, geophyte and therophyte. A total of 102 species could not be unequivocally classified by life form and were excluded from the corresponding analyses. For statistical analyses, life form was classified as woody (phanerophyte, nan-

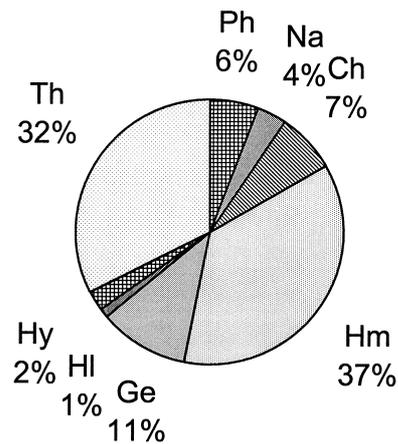


Figure 1. Percentages of species of the Galician flora with different Raunkiaer life forms (Ph = phanerophytes, Na = nanophanerophytes, Ch = chamaephytes, Hm = hemicryptophytes, Ge = geophytes, HI = helophytes, Hy = hydrophytes, Th = therophytes).

ophanerophyte or chamaephyte) or herbaceous (other life forms).

Seed-dispersal mode was determined on the basis of published data (Luftensteiner 1982; Murray 1986; Ridley 1930; Van der Pijl 1982), or was inferred from fruit morphology and in view of our experience in the field, as endozoochorous, exozoochorous, myrmecochorous, autochorous, hydrochorous, anemochorous due to small size, anemochorous due to pappi, anemochorous due to wings, autochorous, or semachorous/barochorous (i.e., no evident morphological adaptations for seed dispersal). Note that some authors (for example, Willson et al. 1990) do not consider anemochory due to small size to be a specific adaptation for dispersal, and classify seeds of this type together with those that display no evident adaptations for dispersal; however, we have followed Luftensteiner (1982) in considering anemochory due to small size to be a mode of dispersal. A total of 94 species could not be readily classified and were excluded from the corresponding analyses. For statistical analyses, dispersal mode was classified as biotic (endozoochores, exozoochores and myrmecochores) or abiotic (all other categories).

Pollination mode was determined as either biotic or abiotic on the basis of published reports (Heywood 1978; Faegri & Van der Pijl 1979) or our own experience in the field. Since we lack field data on many of the species considered, our classification may in many cases fail to reflect complex relationships between plants and their pollinators (see Her-

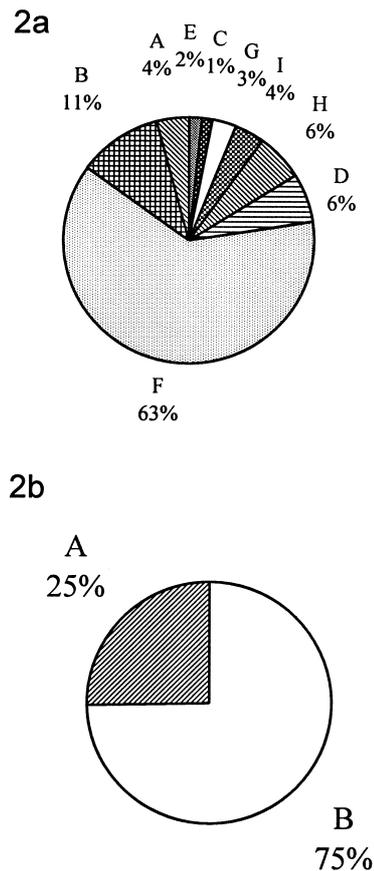


Figure 2. (a) Percentages of species of the Galician flora with biotic seed-dispersal mechanisms (G = myrmecochory, I = exozoochory, H = endozoochory) and abiotic seed-dispersal mechanisms (D = autochory, C = anemochory due to small size, A = anemochory due to wings, B = anemochory due to pappi, E = hydrochory, F = semachory/barochory). (b) Percentages of species of the Galician flora with biotic (B) and abiotic (A) modes of pollination.

ra 1996); however, we consider that the classification used is probably broadly valid.

Reproductive mode was determined on the basis of the floras cited above (Merino 1905–1909; Castroviejo et al. 1989–1993) or our own experience in the field. Since the information available is incomplete, species were simply defined as either hermaphrodite or dioecious, without considering systems such as gynodioecy and heterostyly.

Data analysis

All analyses were carried out with the simplified binary variables (herbaceous versus woody life form, biotic versus abiotic dispersal, biotic versus abiotic pollin-

ation, hermaphroditism versus dioecy). Possible relationships between characteristics were investigated by heterogeneity analysis of 2×2 contingency tables (by chi-square tests, or Fisher's exact test where one or more cells contained only a small number of cases). The units compared were genera, not species: there was thus some loss of information, but this disadvantage is outweighed by the greater probability of independence between units (see Harvey & Pagel 1991). A genus was considered to exhibit a given characteristic if more than 80% of the species of that genus present in the study region exhibited that characteristic. In order to investigate phylogenetic variation in the different characters, a procedure based on nested analysis of variance was used. We first calculated the percentage of species within each genus displaying the characteristic in question (e.g., herbaceous life form), and then performed a nested analysis of variance with this percentage as response variable, and with the crossed factor *class* and the nested factors *subclass*, *order* and *genus*. Genera with fewer than five species in the Galician flora were excluded from the analysis. To correct for the effect of number of species in each grouping, percentages were subjected to the Freeman-Tukey transformation (Zar 1996). The proportion of variance explained by each taxonomic level was calculated as per Sokal & Rohlf (1979). Unless otherwise indicated, statistical significance is taken to be indicated by *p* values of less than 5%.

Results and discussion

Characteristics of the flora

Life form. The majority of species of the Galician flora are hemicryptophytes and therophytes (Figure 1). This high proportion of annuals and perennials, as opposed to woody species, is characteristic of temperate regions (see Crawley 1986). The proportion of therophytes (32%) is intermediate between the proportions previously reported for temperate and Mediterranean regions, in accordance with the 'submediterranean' climate of the study region (Rivas-Martínez, unpublished classification). In general, the life-form spectrum is similar to that reported for floras of other regions of similar latitude (see, for example, Pignatti 1994).

Dispersal. The proportions of species in each of the nine seed-dispersal categories are shown in Fig-

Table 1. Results of heterogeneity analysis of contingency tables cross-classifying the various ecological characters considered in the present study. The binary classifications used in this part of the study were *herbaceous* (H) or *woody* (W) for life form, *abiotic* (A) or *biotic* (B) for seed-dispersal mode and for pollination mode, and *dioecious* (D) or *within-plant monoecious* (M) for reproductive mode. Heterogeneity analysis was by the chi-square test or Fisher's exact test (when one or more cell frequencies were low).

Life form	Dispersal mode		Life form	Pollination mode		Life form	Reproduction mode	
	A	B		A	B		M	D
H	384	37	H	103	345	H	441	4
W	45	39	W	14	71	W	77	10
	$\chi^2 = 74.7, P < 0.001$			$\chi^2 = 1.4, P = 0.23$			$\chi^2 = 27.8, P < 0.001$	

Dispersal mode	Pollination mode		Dispersal mode	Reproduction mode		Pollination mode	Reproduction mode	
	A	B		M	D		M	D
A	111	350	A	456	4	A	118	3
B	8	69	B	68	9	B	437	12
	$\chi^2 = 6.4, P < 0.001$			$\chi^2 = 28.3, P < 0.01$			$\chi^2 = 0.01, P = 0.9$	

ure 2a. Only about 13% of species use biotic methods. The largest category (63% of species) is semachorous/barochorous. Species with wind-dispersed seeds bearing wings or pappi account for 16.4% of the total; this figure is similar to that reported in previous studies of temperate-zone floras (Willson et al. 1990). Again as reported by Willson et al. (1990), and by Sorensen (1986), the proportion of species whose seeds are dispersed by exozoochory is extremely low; this is likewise in accordance with the low proportion of exozoochoric taxa in the world flora as a whole (less than 5% of angiosperm species).

Most workers have found endozoochory to be very frequent in particular types of community, most notably woodland and woodland fringe communities (see Guitián & Sánchez 1992, and references therein). However, this dispersal mode is much less frequent when entire floras are considered. We found endozoochorous species to account for about 5.9% of the total; this figure is similar to that of 6.3% reported for the British flora, and slightly higher than the figure of 3.7% reported for the flora of Europe as a whole (Kay 1992).

Pollination. Of the 1718 species, 75% are pollinated biotically (i.e., insect-pollinated) (Figure 2b). This 3:1 ratio is similar to that previously found in a study of Mediterranean areas of southeastern Galicia (Guitián & Sánchez 1992). Biotic pollination is typically dominant in temperate regions (Ricklefs & Renner 1994), and appears to become less frequent with increasing latitude (Midgley & Bond 1991).

Reproductive mode. Dioecious species account for only 2.5% of the Galician flora. Dioecy occurs in many higher-level taxa, but mostly in dicotyledons. The proportion of dioecious species reported in previous studies has varied widely (for example, 27.7% in Hawaii and 2.5% in southern California; see Bawa 1980 and Richards 1986), but our figure is similar to that reported for the British Isles (Kay & Stevens 1986). The high variability between different floras probably reflects the fact that the proportion of dioecious species is largely a function of the taxonomic composition of the flora, and is relatively independent of local selective pressures (Renner & Ricklefs 1995); this would also explain the similarity between the proportion of dioecious species in Galicia and in the British Isles.

Associations between characters

Life form (herbaceous or woody) was significantly associated with seed-dispersal mode (biotic or abiotic) (Table 1). Endozoochory was dominant among phanerophytes and nanophanerophytes (Figure 3), as reported for angiosperms in general by Fleming (1991), for woody species in temperate communities by Howe & Smallwood (1982), and for woodland and thomscrub communities in the Iberian Peninsula by Guitián & Sánchez (1992); indeed, the high incidence of animal-assisted seed dispersal among woody plants of temperate and tropical regions is well known. By contrast, herbaceous plants typically use less specialized mechanisms or are semachorous/barochorous (Figure 3).

Statistically significant associations were also detected between pollination mode and seed-dispersal

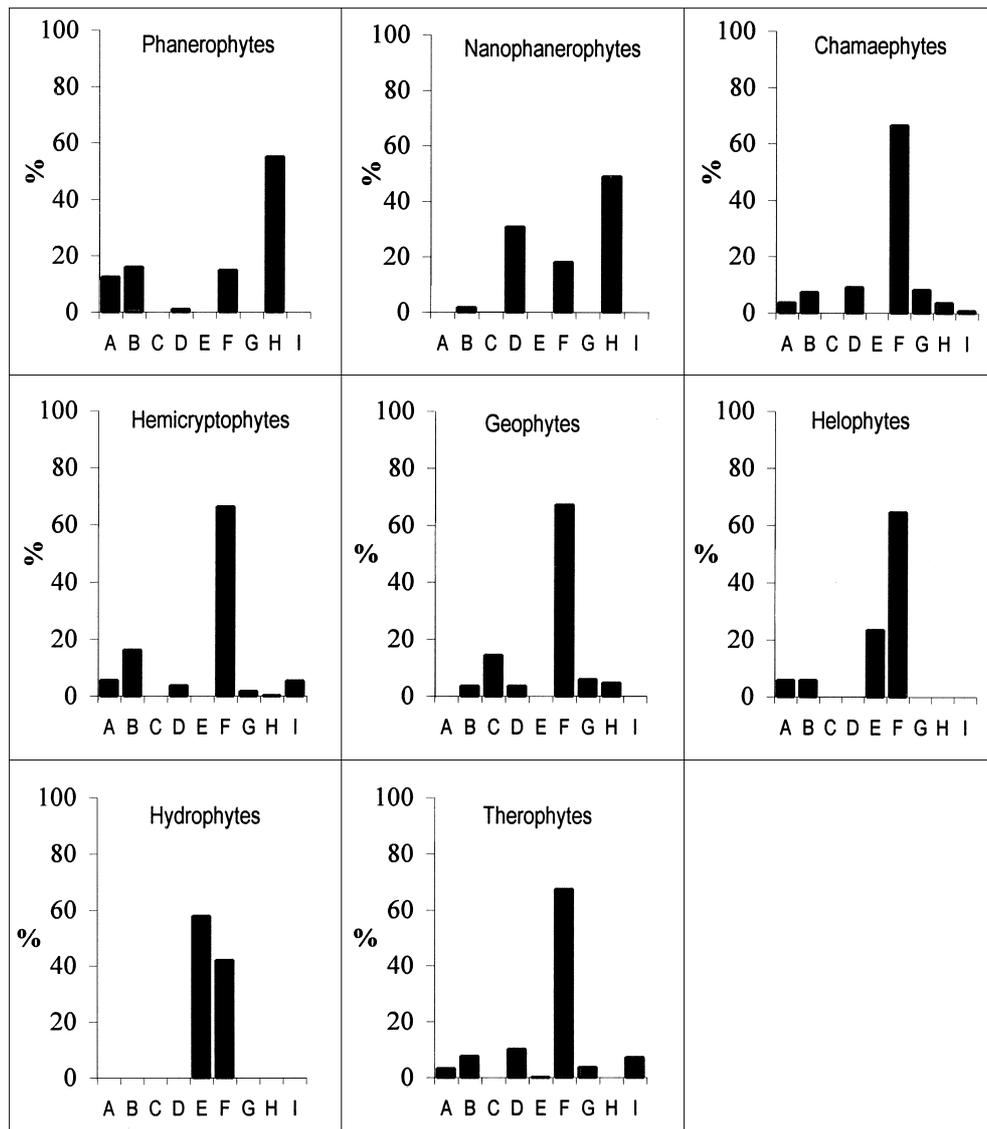


Figure 3. Frequency distribution of seed-dispersal mode within each life-form category for species of the Galician flora. (D = autochory, C = anemochory due to small size, A = anemochory due to wings, B = anemochory due to pappi, E = hydrochory, F = semachory/barochory, G = myrmecochory, H = endozoochory, I = exozoochory).

mode (Table 1). Specifically, a species with biotic seed-dispersal has a higher-than-expected probability of being animal-pollinated. Such associations have been reported previously in a study of angiosperm families (Ricklefs & Renner 1994). Unlike these authors, however, we did not detect any relationship between pollination mode and life form, possibly because we compared genera while Ricklefs & Renner compared families.

Dioecy has been reported to be associated with various characteristics (see Renner & Ricklefs 1995, for a review), though particularly with woodiness, animal-assisted seed dispersal and fleshy fruits (Bawa 1980; Givnish 1980; Muenchow 1987). The results of the present study likewise reveal significant associations between dioecy and these characteristics (Table 1). However, dioecy was not significantly associated with abiotic pollination, and thus our data for the Galician flora do not support the hypothesis that dioecy is more

Table 2. Percentage of among-genus variance in relative frequencies of the different ecological characters explained by different taxonomic levels, as estimated by nested analysis of variance (see Methods).

	Percentage variance			
	Class	Subclass	Order	Genus
Life form	5.9	5.8	21.1	67.2
Dispersal	3.0	1.0	8.3	87.7
Sex	8.4	5.1	33.7	52.8
Pollination	16.6	34.5	5.3	43.6

frequent in species with inefficient pollination mechanisms (Wilson 1979; Bawa 1980), and more specifically with wind pollination (Fox 1985; Renner & Ricklefs 1995).

Taxonomic composition and ecological characteristics

The best-represented families in the Galician flora are the Poaceae, Asteraceae and Fabaceae, which together account for 29% of the 1718 species considered. These three families are likewise the most important in other local floras at similar latitudes (see for example Devesa 1995), in what appears to be a common pattern in Holarctic floras.

The results of nested analysis of variance (Table 2) indicate that, of the four characteristics considered, only variance in mode of pollination was principally explained by higher-level taxonomic grouping (class or subclass), indicating that this character is relatively ancient, which might be related to its strong dependence on basic floral structure (Peat & Fitter 1994; see however Herrera 1996) or alternatively to stabilizing selection (Lord et al. 1995). By contrast, variance in mechanism of seed dispersal was largely explained by lower-level grouping (family or genus), suggesting that this character is much more plastic and responsive to selective pressure, or that it is not subject to stabilizing selection. Note that the two possible explanations (i.e., phylogenetic constraints and niche conservatism) are not mutually exclusive (see Lord et al. 1995). Variance in life form and reproductive mode was explained by both mid-level grouping (order) and lower-level grouping; similar results in previous studies have been interpreted to indicate that such characteristics have been acquired independently in numerous lineages, becoming fixed at different stages in each lineage's evolutionary history (Peat & Fitter 1994). In the present study,

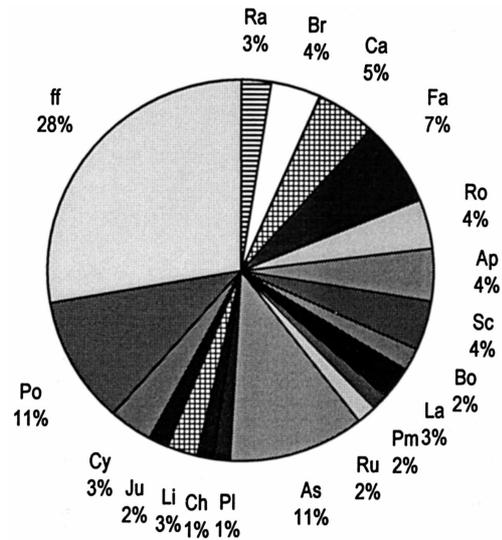


Figure 4. Percentage of species of the Galician flora within each of the major families (Ra = Ranunculaceae, Br = Brassicaceae, Ca = Caryophyllaceae, Fa = Fabaceae, Ro = Rosaceae, Ap = Apiaceae, Sc = Scrophulariaceae, Bo = Boraginaceae, La = Lamiaceae, Pm = Plumbaginaceae, Ru = Rubiaceae, As = Asteraceae, Pl = Polygonaceae, Ch = Chenopodiaceae, Li = Liliaceae, Ju = Juncaceae, Cy = Cyperaceae, Pc = Poaceae, ff = families with less than 25 species).

for example, all orders present contain both herbaceous and woody species, while individual genera may be exclusively herbaceous (e.g., *Ranunculus*), exclusively woody (e.g., *Quercus*) or mixed (*Helianthemum*).

Conclusions

- The most frequent characteristics of species of the Galician flora are herbaceous (hemicytrophyte or therophyte) life form, abiotic seed-dispersal mechanism (semachory or barochory), biotic pollination, and within-plant hermaphroditism.
- A number of between-character associations were detected, but there was no association between abiotic pollination mechanism and dioecy, or between pollination and life-form.
- Our results suggest that pollination mode has typically been determined early in evolutionary history, unlike life form, seed-dispersal mode and reproductive mode.
- Our results likewise suggest that particular ecological characters of the Galician flora have often appeared independently in the different phylogenetic groups, which explains why many taxonomically unrelated groups show common characteristics.

Acknowledgements

Santiago Ortiz and Javier Amigo supplied information on some of the species considered. The comments of Mónica Medrano, Luis Navarro and Pablo Guitián improved the manuscript. We thank two anonymous referees for their critical comments on an early version of this paper. M. Luisa Buide is in receipt of a research grant from the Consellería de Educación e Ordenación Universitaria de the Xunta de Galicia.

References

- Amaral Franco, J. 1971–1984. Nova Flora de Portugal (Continente e Açores), vols 1–2. Sociedade Astória, Lisbon.
- Amaral Franco, J. & Da Rocha Afonso, M. L. 1994. Nova Flora de Portugal (Continente e Açores), vol 3. Escolar Editora, Lisbon.
- Bawa, K. S. 1980. Evolution of dioecy in flowering plants. *Ann. Rev. Ecol. Syst.* 11: 15–39.
- Castroviejo, S., Laínz, M., López González, G., Monserrat, P., Muñoz Garmendía, F., Paiva, J. & Villar, L. (eds). 1989–1993. Flora Ibérica: plantas vasculares de la Península Ibérica e Islas Baleares. Real Jardín Botánico, C.S.I.C., Madrid.
- Crawley, 1986. The structure of plant communities. In: Crawley, M. J. (ed.). *Plant ecology*. Blackwell Scientific Publications, Oxford.
- Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York.
- De Langhe, J. E., Delvosalle, L., Duvigneaud, J., Lambinon, J. & Vanden Berghen, C. (eds). 1978. Nouvelle flore de la Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des Régions voisines (Ptéridophytes et Spermatophytes). Deuxième édition. Patrimoine du Jardin Botanique National de Belgique, Meise.
- Devesa, J. A. 1995. Vegetación y flora de Extremadura. Universitas Ed., Badajoz.
- Eriksson, O. & Bremer, B. 1992. Pollination systems, dispersal modes, life forms, and diversification rates in angiosperm families. *Evolution* 46: 258–266.
- Faegri, K. & van der Pijl, L. 1979. The principles of pollination ecology. 3rd edition. Pergamon Press, Oxford.
- Fitter, A. H. & Peat, H. J. 1994. The ecological flora database. *J. Ecol.* 82: 415–425.
- Fleming, T. H. 1991. Fruiting plant-frugivore mutualism: the evolutionary theater and the ecological play. Pp. 119–144. In Price P. W., Lewinsohn, T. M., Fernandes, G. W. & Benson, W. W. (eds), *Plant-Animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley & Sons, New York.
- Fox, J. F. 1985. Incidence of dioecy in relation to growth form, pollination and dispersal. *Oecologia* 67: 244–249.
- García Rollán, M. 1981–1983. Claves de la Flora de España (Península y Baleares), 2 vols. Ediciones Mundi-Prensa, Madrid.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographic gradients. *Ann. Missouri Bot. Garden* 75: 1–34.
- Givnish, T. J. 1980. Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. *Evolution* 34: 959–972.
- Guitián, J. & Sánchez, J. M. 1992. Seed dispersal spectra of plant communities in the Iberian Peninsula. *Vegetatio* 98: 157–164.
- Harvey, P. H. & Pagel, M. D. 1991. The comparative method in evolutionary biology. Oxford series in Ecology and Evolution. Oxford University Press, Oxford.
- Herrera, C. 1989. Seed dispersal by animals: a role in angiosperm diversification. *Am. Natur.* 133: 309–322.
- Herrera, C. 1992. Interspecific variation in fruit shape: allometry, phylogeny and adaptation to dispersal agents. *Ecology* 73: 1834–1841.
- Herrera, C. 1996. Floral traits and plant adaptation to insect pollinators: A Devil's advocate approach. Pp. 65–87. In: Lloyd, D. G. & Barret, S. C. H., (eds), *Floral biology*, Chapman & Hall, New York.
- Heywood, V. H. 1978. Flowering plants of the World. Oxford University Press, Oxford.
- Howe, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. In: Murray, D. R. (ed.), *Seed dispersal*. Academic Press, Australia.
- Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201–228.
- Kay, Q. O. N. 1992. Edible fruits in a cool climate: the evolution and ecology of endozoochory in the European flora. Pp. 217–250. In: Marshall, C. & Grace, J. (eds), *Fruit and seed production*. Cambridge University Press, Cambridge.
- Kay, Q. O. N. & Stevens, D. P. 1986. The frequency, distribution and reproductive biology of dioecious species in the native flora of Britain and Ireland. *Bot. J. Linnean Soc.* 92: 39–64.
- Kremer, P. & Van Andel, J. 1995. Evolutionary aspects of life forms in angiosperm families. *Acta Bot. Neerl.* 44: 469–479.
- Lord, J., Westoby, M. & Leishman, M. 1995. Seed size and phylogeny in six temperate floras. Constraints, niche conservatism, and adaptation. *Am. Nat.* 146: 349–364.
- Luftensteiner, H. W. 1982. Untersuchungen zur Verbreitungsbiologie von Pflanzengemeinschaften an vier Standorten in Niederösterreich. *Bibliotheca Botanica*, Stuttgart.
- Merino, B. 1905–1909. Flora descriptiva e ilustrada de Galicia, 3 vol. Editorial la Voz de Galicia, La Coruña.
- Midgley, J. J. & Bond, W. J. 1991. Ecological aspects of the rise of angiosperms: a challenge to the reproductive superiority hypotheses. *Biol. J. Linnean Soc.* 44: 81–92.
- Muenchow, G. E. 1978. Is dioecy associated with fleshy fruit? *Am. J. Bot.* 74: 287–293.
- Murray, D. R. (ed.) 1986. *Seed dispersal*. Academic Press, Australia.
- Peat, H. J. & Fitter, A. H. 1994. Comparative analysis of ecological characteristics of British Angiosperms. *Biol. Rev.* 69: 95–115.
- Pignatti, S. 1982. Flora d'Italia, 3 vol. Edagricole, Bologna.
- Pignatti, S. 1994. *Ecologia del Paesaggio*. Torino: U.T.E.T., pp. 24–25.
- Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford.
- Renner, S. S. & Ricklefs, R. E. 1995. Dioecy and its correlates in the flowering plants. *Am. J. Bot.* 82: 596–606.
- Ricklefs, R. E. & Renner, S. S. 1994. Species richness within families of flowering plants. *Evolution* 48: 1619–1636.
- Richards, A. J. 1986. *Plant Breeding Systems*. George Allen & Unwin, London.
- Ridley, H. N. 1930. The dispersal of plants throughout the world. Ashford, Reeve, L. & Co., Kent.
- Sokal, R. R. & F. J. Rohlf 1979. *Biometria*. Editorial Blume, Madrid.
- Sorensen, A. E. 1986. Seed dispersal by adhesion. *Ann. Rev. Ecol. Syst.* 17: 443–463.
- Stamp, N. E. & Lucas, J. R. 1993. Ecological correlates of explosive seed dispersal. *Oecologia* 59: 272–278.
- Tiffney, B. H. & S. J. Mazer 1995. Angiosperm growth habitat, dispersal and diversification reconsidered. *Evol. Ecol.* 9: 93–117.

- Van der Pijl, L. 1982. Principles of dispersal in higher plants. 3rd ed. Springer-Verlag, Berlin.
- Willson, M. F. 1979. Sexual selection in plants. *Am. Nat.* 113: 779–790.
- Willson, M. F., Rice, B. L. & Westoby, M. 1990. Seed dispersal spectra: a comparison of temperate plant communities. *J. Veg. Sci.* 1: 547–563.
- Zar, J. H. 1996. Biostatistical analysis. Third Edition. Prentice Hall International Editions, London.