

VERTEBRATE-DISPERSED PLANTS OF THE IBERIAN PENINSULA: A STUDY OF FRUIT CHARACTERISTICS¹

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Abstract. This study examines the characteristics of ripe fruits of 111 species (35 families, 62 genera) of vertebrate-dispersed plants (with fleshy fruits) native to the Iberian Peninsula. The sample included 58% of the species, 87% of the genera, and 95% of the families of fleshy-fruit-producing plants occurring in the area. Species were characterized by 23 variables related to the design of the fruit (size, mass of seeds and pulp, number of seeds, seed size) and the organic and inorganic chemical constituents of pulp (water, lipids, protein, fiber, non-structural carbohydrate, ash, Ca, Na, Mg, K, P, Fe, Cu, Zn, Mn). Qualitative variables related to geographical distribution at two different scales (northern temperate vs. southern mediterranean; mediterranean lowlands vs. highlands), growth form, fruit color, and display type of the infructescence, were used to categorize species and perform comparisons of fruit characteristics. Factor analysis (FA) was used to examine trait covariation and identify major independent trends of variation in fruit structure and pulp composition. Factor scores of species were used to examine patterns related to taxonomic affiliation and ecological characteristics of species.

With increasing fruit size, pulp mass increased more slowly than seed mass, and thus the pulp/seed mass ratio decreased. The ratio of pulp to seed was greatest in small-seeded fruits. Trees tended to produce the greatest amount of pulp per seed, and herbs the smallest amount. In the species with the smallest seeds the biomass of the pulp exceeded that of the seeds. Major trends of interspecific variation in fruit design included: (1) fruit size (54.5% of variance); (2) inverse relationship between number of seeds/fruit with mass of single seeds and mass of pulp allocated to each seed (23.1%); (3) variation in pulp/seed mass ratio (16.6%). Fruit size, seed size, and pulp/seed mass ratio tended to vary independently of each other. There was significant heterogeneity in factor scores of species differing in geographical distribution, growth form, fruit color, and display type. Interspecific patterns in fruit design were strongly influenced by phylogeny, although no predictable relationship existed between fruit structure and taxonomic affiliation.

Water was the dominant constituent of fresh pulp (range = 19.3–91.1%, mean = 70.8%). On a dry mass basis, nonstructural carbohydrate (NSC) represented 25.8–93.5% (mean = 67.0%), fiber 2.6–52.0% (16.3%), lipids 0.2–58.8% (6.9%), and protein 0.9–27.7% (5.0%). Based on factor analysis, there was a strong negative correlation between NSC and lipids (Factor 1, 46.5% of variance), and a complementary variation of NSC and fiber (Factor 2, 25.5%). Factors 3 (14.8%) and 4 (11.5%) corresponded to variation in protein and water, respectively. No significant heterogeneity in factor scores existed among groups of species based on geographical distribution or type of display. Heterogeneity did exist with regard to fruit color and plant growth form. No predictable relationship existed between phylogeny and pulp organic composition, although taxonomic diversity had some influence on interspecific variability.

With the single exception of the joint occurrence of Ca and Mg, the concentration of any mineral element in the pulp of a species was not predictably associated with the amounts of other elements in the pulp. Composition of the inorganic fraction was not significantly related to either geographical distribution of the species or type of fruit display. Species groups based on fruit color or growth form differed significantly in total mineral content. No phylogenetic correlates were apparent in the constitution of the inorganic fraction of fruit pulp.

The broadest patterns revealed by this study were of a “null type.” The few “positive” ones have rather restricted implications as to the overall constitution of fruits, and only one-third of these seem attributable to the selective action of frugivores on fruit traits. The study failed to reveal any overwhelming influence of the disperser/dispersal environment on the characteristics of Iberian fruits taken as a whole, particularly with reference to interspecific variation. Phylogeny, architectural constraints, and species-specific energy and nutrient allocation patterns, seemed most important in explaining observed variation in fruit constitution.

Key words: bicolored displays; carbohydrates; fiber; fleshy fruits; frugivory; fruit color; fruit structure; Iberian Peninsula; lipids; mineral elements; phylogeny; protein; pulp chemical composition; seed dispersal; vertebrate-dispersed plants.

INTRODUCTION

Many higher plants have their seeds dispersed by frugivorous animals with which they maintain a food-mediated mutualistic relationship (Ridley 1930, van

der Pijl 1982, Janzen 1983). Plants provide food to dispersal agents in the form of nutritious accessory structures closely associated with the seeds. Earlier formulations of the ecological and evolutionary interactions between plants and mutualistic vertebrate dispersers conferred great significance on the nutritional value of the food reward produced by the plants (Snow

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1971, Morton 1973, McKey 1975, Howe and Estabrook 1977).

Investigations that have examined the chemical and nutritional configuration of vertebrate-disseminated, fleshy diaspores ("fruits" hereafter) of wild plants fall into two major categories: (1) those aimed at determining the "food value" of fruits to wildlife, or other commercial or applied purposes (e.g., Wainio and Forbes 1941, Kuusi 1969, Short and Epps 1976, 1977, Halls 1977, Everitt and Alaniz 1981, Ingold and Craycraft 1983). The vast majority of these studies analyzed whole fruits (seeds plus nutritious tissues all together), and the information they provide is virtually useless for studies of plant-disperser interactions (Herrera 1982a); and (2) the numerous studies that in recent years have considered the nutritional properties of the reward alone (i.e., the tissues actually digested by dispersal agents) because they were directly or indirectly concerned with the ecological or evolutionary aspects of the mutualistic relationship. Most of these studies report on nutritional characteristics of the fruits of one or a few species (e.g., Foster 1977, McDiarmid et al. 1977, Snow 1977, 1979, Pulliainen 1978, Howe 1980, Howe and Vande Kerckhove 1980, Graber and Powers 1981, Herrera and Jordano 1981, Poddar and Lederer 1982, Williams 1982, Foster and McDiarmid 1983, Godschalk 1983, Jordano 1983, Estrada et al. 1984, Herrera 1984c). Only a few workers elucidated interspecific patterns of fruit reward characteristics in broad multispecies plant assemblages (Frost 1980, Stiles 1980, Herrera 1981a, b, 1984a, Viljoen 1983, Wheelwright et al. 1984, Johnson et al. 1985). The present study analyzes the fruit characteristics (structural and nutritional) of 111 species of vertebrate-dispersed plants from a large geographical area. Information on fruit design and organic and inorganic (macroelements and trace elements) constituents of fruit pulp are considered simultaneously.

Justification, objectives, and approach

Reciprocal selective pressures between fruit-producing plants and their vertebrate dispersal agents may lead to coevolution (Snow 1971, McKey 1975, Janzen 1983). In the few documented instances where this process seems to have occurred, it seems to be of a diffuse nature, involving large sets of plant and disperser species (Herrera 1982b, 1984a, 1985a, Howe and Smallwood 1982, Janzen 1983). Accordingly, the elucidation of patterns in naturally occurring species assemblages is probably the most reliable procedure to judge the occurrence of this plant-animal evolutionary interaction (see, e.g., Janson 1983, Herrera 1984b, Wheelwright 1985a, b, Wheelwright and Janson 1985). To obtain meaningful results, however, it seems necessary: (1) to deal with as complete a species set as possible, to reduce or eliminate biases resulting from small sample sizes (in the case of analyses of fruit char-

acteristics, biases would likely result from considerable differences between species in ease of fruit collection and pulp sample preparation, and fruit abundance); and (2) to estimate the amount and identify the nature of interspecific heterogeneity that is missed due to incomplete sampling of local or regional species assemblages (see Herrera 1981a, Wheelwright et al. 1984 for further discussion).

The present study was specifically designed to search for interspecific patterns indicative of (diffuse) evolutionary interactions between plants and their dispersal agents. I deliberately avoided a priori formulation of specific hypotheses to be tested. This seemingly unorthodox procedure stemmed from the objectives of this paper, namely (1) to find out whether, and with what frequency, distinct patterns of interspecific variation in fruit features are actually discernible in a large species assemblage; and (2) where some pattern exists, to examine if it may reasonably be attributed to a selective action of seed dispersers. This approach provides justification for the analytical procedure chosen (see Methods: Data Analysis). First, I searched for trends of variation in fruit features rather than assuming a priori (on coevolutionary grounds) that these patterns actually exist (and generating ad hoc hypotheses to be tested). Second, I tested if the major trends of interspecific variation were correlated significantly with several variables indicative of a species' disperser/dispersal environment. And third, I examined the relationship between interspecific variation and phylogeny. Step 1 represents an exploratory, hypothesis-free (in relation to seed dispersal ecology) search for interspecific patterns; step 2 tests the hypothesis that fruit features of a species bear some relationship to its disperser/dispersal environment; and step 3 examines an alternative hypothesis to explain interspecific fruit variation, namely phylogenetic constraints. This three-step procedure was aimed at testing the more general hypothesis that the *major* trends of interspecific variability in fruit characteristics are attributable to differential disperser/dispersal environments. It is a logically valid procedure, as (1) all the variables in the exploratory analyses are potentially relevant to the plant-disperser interaction; and (2) hypothesis testing in steps 2 and 3 relies on externally derived, objectively defined trends of interspecific variation.

STUDY AREA

Samples of ripe fruits were collected at four widely separated areas in the Iberian Peninsula (Fig. 1), generally at several nearby localities in each area: (A) Cantabrian Mountains. León, Asturias, and Cantabria provinces, northwestern Spain (collection period: October 1980). Deciduous forests (dominated by *Fagus sylvatica*) and associated successional scrub in gaps, forest edges, and river banks. (B) Central Pyrenees. Navarra and Huesca provinces, northeastern Spain

(September 1981). Extensive mixed forests dominated by *Abies alba*. (C) Sierra de Cazorla. Jaén province, southeastern Spain (1978–1983). Montane mediterranean sclerophyllous scrub and pine (*Pinus nigra*) forests (Herrera 1984a, Obeso 1985). (D) Lowlands in the lowermost Guadalquivir River valley. Sevilla, Huelva, and Cádiz provinces, southwestern Spain (1978–1983). Diverse formations of mediterranean scrub on fertile alluvial and coastal sandy soils (Herrera 1984a, Jordano 1984).

The four areas fall into one of two contrasting phytogeographical and bioclimatic regions of the Iberian Peninsula (Rivas-Martínez et al. 1977, Bellot 1978, Rivas-Martínez 1981). The two southern areas experience a mediterranean climate, while the two northern ones have a typical cool temperate climate (Linés Escardó 1970). The mesophytic flora and vegetation of the Pyrenees and Cantabrian Mountains have close affinities with those found in Atlantic western Europe, while those of the two southern areas are typically representative of those in the Mediterranean Basin, with a prevalence of sclerophyllous, evergreen taxa (Rivas-Martínez et al. 1977, Bellot 1978).

THE SPECIES SAMPLE

This study examined the fruit characteristics of 111 plant species (in 35 families and 62 genera) native to the Iberian Peninsula (Appendix 1). Over half of the species were in the Rosaceae, Liliaceae, Caprifoliaceae, and Rhamnaceae families. Each of the remaining 31 families contributed only 0.9–4.5% of the species (21 families were represented by single species). The sample was dominated by shrubs (52.3% of the species). Trees represented 25.2%, herbs 15.3%, and woody vines 7.2%, of the species. Deciduous plants (including perennial herbs) accounted for 60.4% of the species.

The sample included 94.6% of the families, 87.3% of the genera, and an estimated 57.5% of the species with fleshy fruits that occur on the Iberian Peninsula (total number of taxa present based on information in Tutin et al. 1964–1980). Variability in fruit features increased with increasing level in the taxonomic hierarchy. The proportion of total variability in fruit characteristics of the whole flora that was represented in my sample was, therefore, much closer to the percents of families and genera that were examined than to the percent of species. Most taxa not included in the analyses, for which I was unable to collect samples, were either narrow endemics or belonged to species complexes, including the microspecies in *Rosa* and *Rubus*, which accounted for 55% of the 82 "missing" species.

The geographical provenance of the fruit samples is shown in Fig. 1. The proportions of species collected from each area do not reflect accurately, however, their distributional pattern in the Iberian Peninsula (sampling effort differed greatly between areas, and many

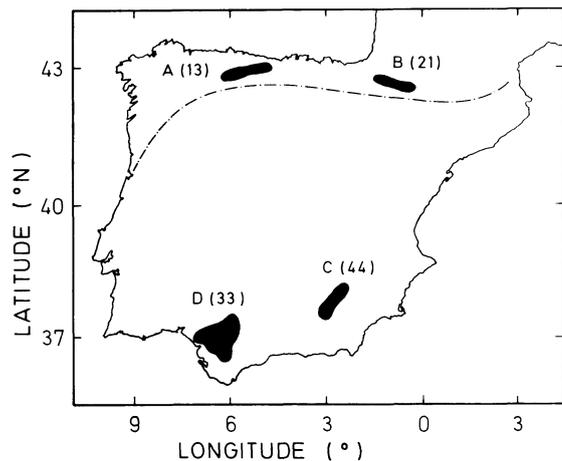


FIG. 1. Collecting areas (shaded) in the Iberian Peninsula of fruit samples used for this study (see Study Area for general descriptions). In parentheses, number of fruit species collected in each area. Dotted line schematically depicts the major division between northern temperate and southern mediterranean phytogeographical and climatic regions (based on Rivas-Martínez 1981).

species occurred in several areas). Relative to the major bioclimatic and phytogeographical distinction outlined above, 41.5% of the species in the sample had broad distributions encompassing both mediterranean and northern regions. The remaining species were restricted to either northern (25.2%) or southern (33.3%) regions. Within the mediterranean region, 32.5% of the 83 species occurred in both lowland and highland areas, 47.0% were restricted to lowlands, and 20.5% to the highlands. Categories of species based on differential geographical occurrence will be used in the analyses.

METHODS

Qualitative variables

Species were categorized according to each of the following attributes (frequencies in the sample are indicated if not mentioned earlier): (1) growth form (herb, shrub, woody vine, tree); (2) distribution pattern in the Iberian Peninsula (northern and/or mediterranean regions); (3) distribution pattern in the mediterranean region ("Andalusia" hereafter) (lowlands and/or highlands); (4) color of ripe fruit (black, 26.1%; red-to-orange, 38.7%; "others," including white, blue, brown, yellow, pink, and green, 35.2%; see Appendix 1); (5) type of display (bicolored, 22.5%, or not, 77.5%). A species was considered to possess a bicolored display if "... the ripe fruit contrasts markedly with either the preripe fruit . . . or some accessory structures (e.g., capsule, pedicel, stem), which have conspicuous, non-green color themselves" (Willson and Thompson 1982). In the case of variables 4 and 5, assignment of species to classes was made on the basis of personal experience with all the species in the field, and later corroborated

by presenting color slides of fruits and fruiting displays to other people.

The relation between time of fruit maturation and some structural and nutritional fruit characteristics has been examined in detail elsewhere (Herrera 1982*b*) for a large set of southern Spanish species, thus this aspect does not receive further consideration here.

Quantitative variables

Species were characterized by a set of quantitative variables related to the design of the ripe fruit and the organic and inorganic constituents of the pulp. As the emphasis of this study is placed on patterns of interspecific variation, a single set of values was used per species coming from a sample of fruits collected at a single locality. When more than one set of data was available for a species, that coming from the region or area where the species was more abundant or widespread was used.

Design of the fruit.—Average values for length, diameter, wet and dry mass of whole fruit, dry mass of seeds and pulp, number of seeds, and mass of single seeds, were obtained for samples of 20–40 fruits of each species. Linear measurements were taken to the nearest 0.1 mm, and masses to the nearest 0.1 mg (see Herrera 1982*b*, 1984*a*, for further details on methods). Some ratios and linear combinations of these variables used in the analyses are described in Fruit Morphology and Constitution: Pulp/Seed Allocation, below.

Organic and inorganic pulp constituents.—Fruits were dried to a constant mass (usually for 2–4 d) in a forced-air oven (set at 40°C and maximum airflow) and then separated into pulp and seeds. Drying at low temperature kept to a minimum the loss of volatile compounds present in the pulp of some species. I never observed any sign of fungal damage to fruits while drying. The number of constituents determined was a function of the amount of dry pulp available. In the best possible case, the following constituents were determined: crude protein (estimated as total N \times 6.25; 4.4 may be a more accurate conversion factor [Milton and Dintzis 1981], but the absolute value of this factor is largely irrelevant in the present comparative context), crude lipids, acid-detergent fiber, nonstructural carbohydrate (obtained by difference), ash, macroelements (Ca, Na, K, Mg, and P), and trace elements (Fe, Cu, Zn, and Mn). Total N was determined by the Kjeldahl method. Lipids were determined gravimetrically after extraction with diethyl ether in a Soxhlet apparatus. Ash content was determined by incineration in a muffle furnace at 600° for at least 12 h. Acid-detergent fiber (“fiber” hereafter) was determined following the procedures outlined by Goering and Van Soest (1970). Minerals were determined by atomic absorption spectrophotometry on acid extracts of ashed samples.

Water content of fresh pulp was also determined. To avoid significant water loss during manipulation, fresh fruits were deep-frozen (–20°), pulp and seeds sepa-

rated and weighed while frozen, and subsequently dried at 40° to constant mass in a forced-air oven and reweighed.

Patterns of missing data

Data on the 23 quantitative variables described above were not available for every species in the sample. On the whole, 82.6% of the maximum possible number of data entries ($2553 = 111 \times 23$) were considered in the analyses. Data on fruit design were available for 99%, on ash and organic constituents for 83%, and on mineral elements for 66%, of the 111 species in the sample. Sixty-nine species had complete data sets.

To investigate possible departures from randomness of the missing data, which could bias the analyses, Mahalanobis (1936) generalized distances (D^2 ; see e.g., Sneath and Sokal 1973) from individual species to the group centroid were computed in the 23-dimension space defined by the quantitative variables. Only variables with available values (nonmissing) were used in the computations. As the absolute values of distances depend on the number of dimensions entering the computations, and these varied among species, an “average” distance was obtained for every species by dividing the resulting figures by the number of nonmissing variables. The mean (\pm SD) of average distances of species with nonmissing ash and organic constituents data (1.1 ± 1.15 , $N = 92$) significantly exceeded ($t = 2.22$, $P = .028$) the mean for species with missing data (0.51 ± 0.45 , $N = 19$). The mean of average distances of species with nonmissing mineral element data (1.07 ± 0.96 , $N = 73$) did not differ significantly ($t = 0.89$, $P = .37$) from the mean of species with missing data (0.88 ± 1.29). Given that squared multiple correlations of each variable with all the other variables ranged between 0.602–0.996 (mostly >0.850 ; $P < .0001$ or better), thus demonstrating strong multicollinearity in the 23-variable set, these results indicate that (1) no bias existed in the case of mineral element missing data; and (2) a significant bias existed in the data set examined for ash and organic constituents. For these variables, the available data tended to overestimate interspecific variance in these parameters, thus enhancing the possibilities of detecting underlying trends through increase in the levels of interspecific variability.

Data analysis

Separate analyses were conducted on the sets of variables related to fruit design, water and organic fraction of pulp, and mineral fraction of pulp. With minor departures, the same analytical sequence was applied to each of these groups of variables.

To identify the major independent trends of fruit- or pulp-trait variation between species, factor analysis (Cooley and Lohnes 1971) was applied, using BMDP4M program with Varimax rotation and Kaiser’s normalization (Cuadras 1981, Frane et al. 1981). Factor load-

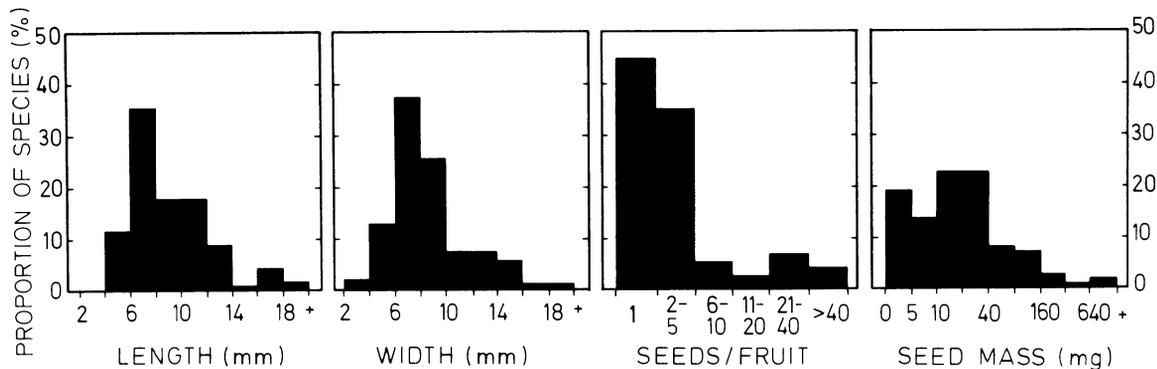


FIG. 2. Frequency distributions of fruit length and transverse diameter ("width"), average number of seeds per fruit, and average mass of individual seeds for 111 vertebrate-dispersed, fleshy-fruit-producing plant species from the Iberian Peninsula. Note geometric scale on the horizontal axis for the seed mass distribution.

ings of original variables were used to assess covariation of fruit or pulp traits. Using factor scores of species as a simplified, reduced expression of original data on fruit or pulp characteristics, interspecific patterns were investigated. Separate one-way analyses of variance, each having one of the qualitative variables as the categorizing factor, were conducted on species factor scores. The latter were normally or near normally distributed, standardized (mean = 0, SD = 1) parameters, thus could properly be used as input in ANOVA. Factor scores were also used to assess phylogenetic correlates of fruit traits.

After completing the above procedure for the three sets of variables (fruit design, water-organic fraction, mineral fraction), factor scores of species resulting from the three analyses were treated simultaneously. The full complement of factor scores for individual species was taken as a reduced overall description of its fruit attributes based on the most significant (in terms of percent variance accounted for) trends of interspecific variation.

FRUIT MORPHOLOGY AND CONSTITUTION

General

Ninety-two out of the 111 species examined (82%) produced berries or drupes (true fruits in the botanical sense). The remaining species produced arillate seeds (three species); pseudocarps (six species); polydrupes (two species); aggregations of modified, fleshy bracts (gymnosperms, seven species); or syconia (*Ficus*, one species). Although these fruits differed with regard to their anatomy and origin, all were functionally equivalent for seed dispersal.

Frequency distributions of fruit size were skewed to the right (Fig. 2), with a few extreme species having fruits longer and wider than 18 mm. The modal class of fruit length and width was 6–8 mm, and most species had fruits 6–12 mm long and 6–10 mm wide. Fruits of most species were few-seeded (80% of species had, on average, ≤ 5 seeds per fruit), while a few species had

well in excess of 100 seeds per fruit (Fig. 2). The mean size of individual seeds varied over three orders of magnitude (range 0.2–698 mg), but most species fell between 10 and 40 mg. There was a weak bimodality in the distribution of seed sizes, with peaks at < 5 and 10–40 mg.

Pulp/seed allocation

Dry mass of pulp per fruit (DMP , in grams) was positively associated with dry mass of seeds per fruit (DMS , in grams). The relation is best described by the power function $DMP = 0.58 DMS^{0.75}$ ($r^2 = 0.408$, $N = 108$, $P < 10^{-9}$). The essence of this nonlinear relationship was that, among species, fruits with small seed masses had more pulp per seed mass unit, and that fruits with larger seed masses had much less pulp per seed mass unit. The (biomass) investment in dispersal (disperser reward) per mass unit of propagule was thus lowest among species having the highest seed masses per fruit.

The amount of pulp per seed ($DMP/NS = PS$, in grams) was strongly correlated with the average dry mass of an individual seed ($DMS/NS = DM1S$, in milligrams). The relation is described by the fitted function $PS = 0.0021 DM1S^{0.82}$ ($r^2 = 0.601$, $N = 108$, $P < 10^{-9}$). As seed size increased (among species), the amount of pulp per seed also increased, but, as pulp per seed increased more slowly than seed mass, the smallest seeds had proportionally more pulp. In small-seeded species pulp mass exceeded seed mass, and was less than seed mass in large-seeded species (Fig. 3).

The shape of the relation between pulp per seed and seed mass was different for species with different growth forms (Fig. 3). Covariance analysis of linearized regressions (obtained by logarithmic transformation of data) revealed a significant heterogeneity between growth forms ($F = 10.51$, $df = 3, 104$, $P < 10^{-5}$). If seed mass was held constant, over most of the seed-size range trees produced more pulp per seed than herbs (smallest amount), vines, or shrubs (Fig. 3). The slope of the curve for trees (0.53) was smaller than those for the

other growth forms, which were fairly similar (0.78–0.81).

Trends of variation

Results of factor analysis (FA) of fruit design variables are presented in Table 1. Three variables were added to the eight original variables: *PS*; *RY* = dry mass of pulp/fresh mass of the whole fruit; and *PTS* = dry mass of pulp/total dry mass of seeds in a fruit (see Herrera 1981a, 1982b for rationale for considering these variables). All variables were logarithmically transformed prior to the analysis.

The major interspecific trend emerging from FA involved variation in absolute fruit size (F1, 54.5% of variance; Table 1). All linear and mass measures of the whole fruit (and component parts) had high positive loads on F1. The second interspecific gradient (F2, 23.1%) illustrated the inverse relationship between number of seed/fruit with mass of single seeds and *PS* (mass of pulp per seed); there was a decrease in the size of single seeds, and the mass of pulp allocated to each, as seed number increased. The third factor (F3, 16.6%) was mainly related to variation in the pulp/seed mass ratio.

Since the factors represent independent (uncorrelated) gradients of variation, these results suggest that, among species, fruit size, seed size, and pulp/seed mass ratio, tended to vary independently of each other. Independent variation is subject, however, to some obvious architectural constraints. For any given fruit size, the upper limit to individual seed size was roughly linearly related to fruit size (after logarithmic transformation of both variables), as illustrated by the plot of species on the plane defined by F1 and F2 (Fig. 4).

Interspecific patterns

Ecological patterns.—Results of one-way analyses of variance testing for interspecific heterogeneity in factor scores between groups of species (defined on the basis of growth form, distribution, fruit color, and display type) are summarized in Table 2. With the single exception of fruit color, all classification criteria yielded some statistically significant results.

Species scores on F1 and F2 varied significantly with growth form. On average, trees were characterized by large fruits with medium-to-large seeds; herbs by medium-sized fruits with small seeds; and shrubs and vines by medium-to-small fruits with medium-to-large seeds, although there was extensive overlap between growth forms in F1 and F2 ranges. The average (\pm SD) F1 score for species with monochrome fruit displays (0.15 ± 1.04 , $N = 81$) exceeded the corresponding figure for species with bicolored displays (-0.43 ± 0.74 , $N = 25$). Bicolored displays were thus predominantly found among species with small fruits.

Species scores on F1 were not significantly related to the geographical distribution of species (Table 2).

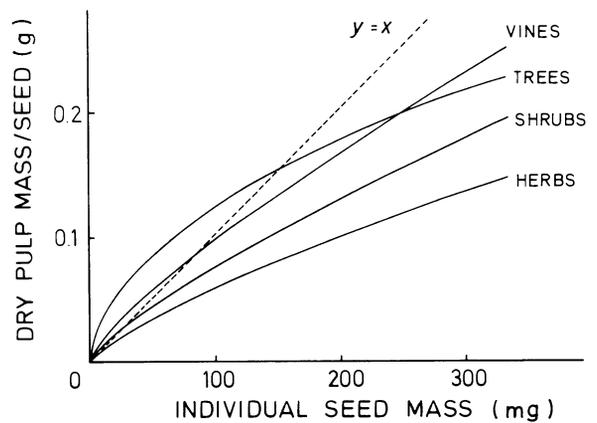


FIG. 3. Interspecific variation in the ratio of pulp mass to seed number with individual seed mass. Shown are fitted equations (solid lines) for vines ($y = 10^{-2.6}x^{0.81}$), trees ($y = 10^{-2.0}x^{0.53}$), shrubs ($y = 10^{-2.7}x^{0.80}$), and herbs ($y = 10^{-2.8}x^{0.78}$), and the $y = x$ line for reference (dashed line). There is significant heterogeneity among regressions.

There was significant variation in F2 scores related to species' distribution. Species confined to Andalusia had the largest values (0.41 ± 0.72 , $N = 46$), those confined to the northern region the smallest values (-0.50 ± 0.96 , $N = 25$), and species shared were intermediate (-0.11 ± 1.07 , $N = 35$). A broad-scale geographical pattern therefore existed, with northern species tending to produce fruits with more numerous and smaller seeds than mediterranean species. Species scores on F3 (a factor directly related to the pulp/seed mass ratio, Table 1) were significantly related to the distribution of species within Andalusia (Table 2). Species confined to the lowlands had the smallest values (-0.54 ± 0.67 , $N = 17$), those confined to the highlands the largest

TABLE 1. Factor analysis of the correlation matrix of (log-transformed) fruit design variables. Only loadings >0.25 are shown.

Variables	Factor loadings		
	F1	F2	F3
Length	0.941
Diameter	0.976
Mass (fresh)	0.991
Mass (dry)	0.953
Pulp mass (dry)	0.900
Seed mass (dry)	0.789	...	-0.589
Number of seeds	0.416	-0.906	...
Mass of 1 seed (dry)	...	0.893	-0.383
<i>PS</i> *	0.402	0.823	...
<i>PTS</i> *	0.864
<i>RY</i> *
Cumulative proportion of variance (%)	54.5	77.6	94.2

* Measures of pulp and seed mass proportions: *PS* = pulp dry mass per seed; *RY* = (dry mass of pulp)/(fresh mass of the whole fruit); *PTS* = (dry mass of pulp)/(total dry mass of seeds in the fruit).

values (0.16 ± 1.01 , $N = 37$), and species shared were intermediate (-0.06 ± 0.74 , $N = 27$).

Taxonomic patterns.—Distribution of species in the F2–F3 plane was plotted separately for the major orders and superorders represented in the sample (Fig. 5). These two axes were chosen to emphasize fruit structural features, as F1 was mostly related to fruit size (Table 1). There were no significant differences between gymnosperms and angiosperms (F2: $F = 0.09$, $P = .76$; F3: $F = 0.03$, $P = .86$); angiosperm superorders (F2: $F = 2.08$, $P = .11$; F3: $F = 1.51$, $P = .22$); and dicots and monocots (F2: $F = 1.84$, $P = .18$; F3: $F = 3.21$, $P = .08$). Within superorders, no heterogeneity existed in Rosidae (F2: $F = 1.01$, $P = .40$; F3: $F = 1.02$, $P = .40$). Significant heterogeneity did occur among orders of Asteridae (F2: $F = 34.13$, $P < .0001$; F3: $F = 5.82$, $P = .01$), although neither F2 (seed size-ness) nor F3 (pulp/seed mass ratio) scores varied consistently with evolutionary advancement (according to criteria in Stebbins 1974). It may therefore be concluded that, in general, no predictable relationship existed between phylogeny and fruit structure in the sample of species examined here. In some cases, however, interspecific variation in fruit structure was significantly related to variation in taxonomic affiliation (orders within Asteridae).

WATER CONTENT AND ORGANIC FRACTION OF PULP

General

Data on protein, nonstructural carbohydrate, lipids, and fiber content of dry pulp were available for 91 species (53 genera, 33 families). Water content of fresh pulp (WCP) was available for only 46 species (38 genera, 24 families). Even with the method used, this magnitude was difficult to determine accurately because of

TABLE 2. Summary of one-way analyses of variance testing for interspecific heterogeneity in factor scores (from factor analysis of fruit design variables, Table 1) among groups of species, based on qualitative variables.

Qualitative variable	F values		
	F1	F2	F3
Growth form	6.42***	3.39*	NS
Geographical distribution			
over the Iberian Peninsula	NS	8.74***	NS
over Andalusia	NS	NS	3.86*
Fruit color	NS	NS	NS
Display type	6.74**	NS	NS

* $P < .05$; ** $P < .01$; *** $P < .001$; NS = nonsignificant.

the watery nature of most fruit pulps. Average WCP was 70.8% (range 19.3–91.1%; Fig. 6). There were only three species with relatively dry fruits ($15\% < WCP < 50\%$). WCP was strongly related to water content of the whole fresh fruit (WCF; $r = 0.843$, $N = 46$, $P < 10^{-9}$). WCF was readily determined, and data were available for 109 species. These figures were used as indirect estimates of WCP in some of the analyses below. This procedure may have introduced a slight error component in the data, but it had the advantage of increasing considerably the sample size for this variable. Examination of residuals from the WCP-WCF regression (Sokal and Rohlf 1981) did not detect either outliers or systematic departures from linear regression in the sample.

The dominant component of the dry pulp of most of the species studied was carbohydrate (Fig. 6). Structural carbohydrates (fiber) represented $< 20\%$ pulp dry mass in most species (74% of sample). Nonstructural carbohydrate (NSC) accounted for 60–90% of pulp dry mass in 73% of the species. Protein and lipids were minor constituents of fruit pulp. More than 70% (lipids) or 60% (protein) of species had $< 5\%$ dry mass of either of these constituents. Extremely high lipid content was exhibited by *Pistacia lentiscus* (58.8%), *P. terebinthus* (55.6%, Anacardiaceae), *Laurus nobilis* (54.3%, Lauraceae), *Olea europaea* (41.9%, Oleaceae), and *Rhus coriaria* (36.9%, Anacardiaceae). Extreme values for protein were shown by *Bryonia dioica* (27.7%, Cucurbitaceae), *Mandragora autumnalis* (19.8%, Solanaceae), *Sambucus nigra* (18.8%), and *S. racemosa* (12.8%, Caprifoliaceae). Figures for the first two species must be taken with caution, since the correction factor used to obtain protein content from total N may be inappropriate in these cases. Both species are known to contain nonprotein N in the pulp of ripe fruits (R. C. Soriguer, *personal communication*), which may have raised protein content artificially (Milton and Dintzis 1981). Fruits of other species known to have high alkaloid concentrations in fruit pulp (e.g., *Atropa* spp.) did not yield abnormally high protein content with the procedure used.

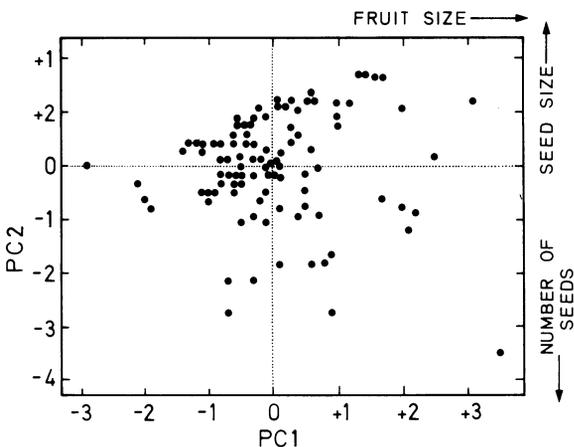


FIG. 4. Distribution of plant species over the plane defined by the first two factors (Table 1) resulting from the correlation matrix for fruit design variables ($N = 109$ species). Directions of increase of variables associated with each gradient are shown by arrows at margins of the graph.

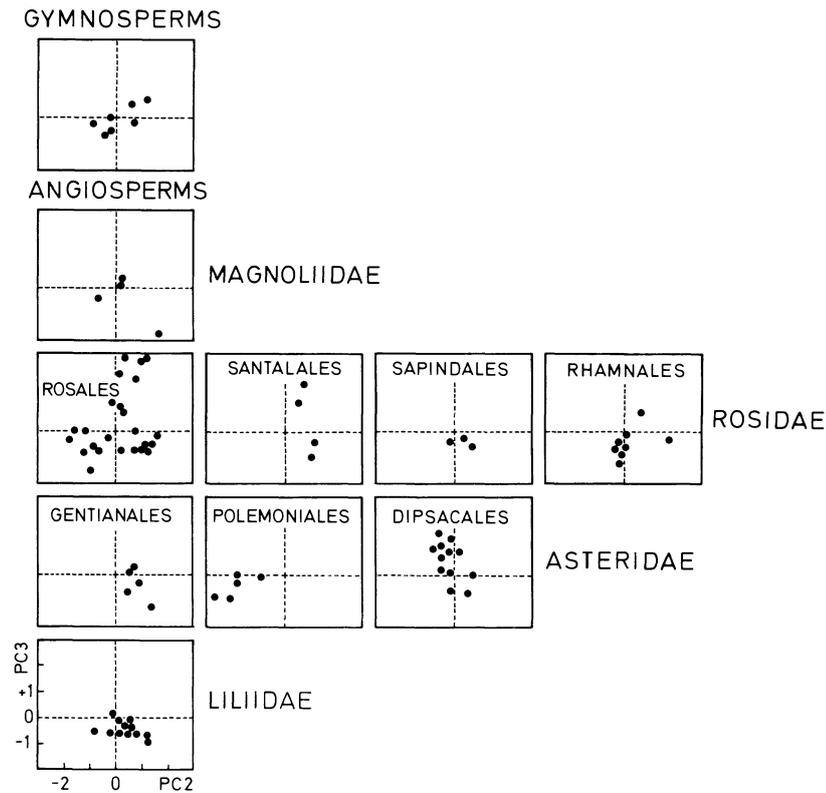


FIG. 5. Distribution of plant species over the plane defined by the second and third factors resulting from the correlation matrix for fruit structural variables (Table 1), plotted separately for the major orders and superorders present in the sample (classification based on Stebbins 1974). Evolutionary advancement increases from top to bottom and, within rows, from left to right. For angiosperms, only orders and superorders with at least three species in the sample are shown.

Trends of variation

In this and the following sections WCF is used as an indirect estimate of WCP. Lipid content data were log-transformed for the analyses.

The five constituents considered were significantly interrelated (Table 3). The negative correlation between NSC and lipids was the strongest of the six significant pairwise associations. The complementary variation of these two constituents actually represented an independent trend of interspecific variation, and corresponded to the first factor emerging from FA (Table 4). F1 accounted for 46.5% of variance. A complementary relation between NSC and fiber is implicit in the second factor (F2, 25.5% of variance). F3 and F4, accounting for 14.8 and 11.5% of variance, respectively, corresponded to the variation of protein and water, respectively. These results indicate that non-nitrogenous organic constituents of fruit pulp (fiber, NSC, and lipids) were responsible for the principal trends of variation, and explained the largest proportion of interspecific variance (72%) in the set of species examined. Variation in water and protein content had little significance in terms of variance accounted for and took place independently of each other and of the non-nitrogenous organic fraction. To summarize, there

were two major independent gradients in pulp composition, both included the non-nitrogenous fraction, and involved complementary relationships between lipids, NSC, and fiber.

The distribution of species over the plane defined by these two gradients revealed the existence of three distinct "lines" of fruit pulp composition (Fig. 7). The extremes of these lines included fruit pulps that were either (1) low in lipids and fiber, and high in NSC (lower left, Fig. 7); (2) low to intermediate in lipids, high in fiber, and intermediate in NSC (upper central); or (3) high in lipids, and low in fiber and NSC (lower right). However, there were many species with intermediate characteristics (i.e., those around the origin).

Interspecific patterns

Ecological patterns.—One-way analyses of variance of species scores on F1, F2, and F3 did not reveal any significant heterogeneity between groups of species defined on the basis of geographical distribution. Species restricted to Andalusia, restricted to the north, and shared by the two regions, were statistically indistinguishable with regard to scores on the first three factors. Likewise, no differences were found between the areas of Andalusia.

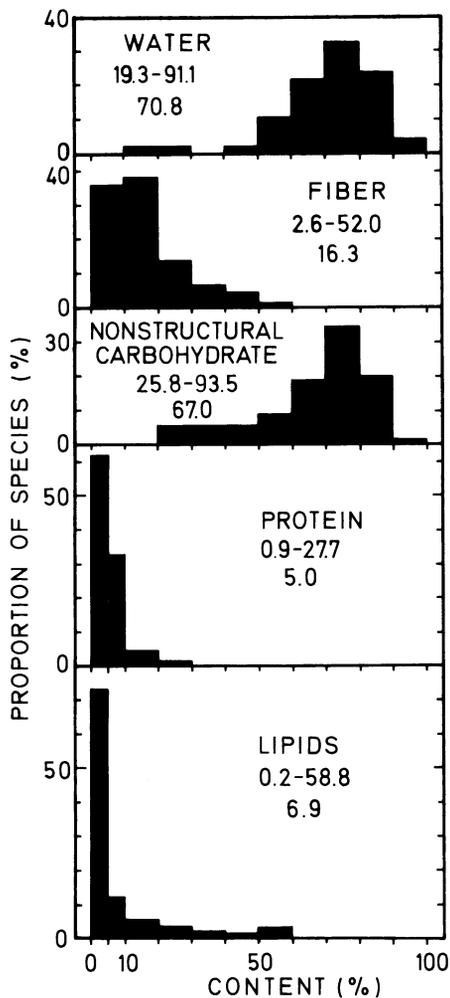


FIG. 6. Frequency distributions of contents of water (as percent of fresh pulp mass) and organic constituents (as percent of dry pulp mass). $N = 46$ species for water, 91 species for organic components. Ranges and means are shown for each constituent.

Species with and without bicolored displays did not differ significantly in their scores for any of the first three factors. Comparisons based on fruit color and growth form did yield significant results for F2 and F3, respectively ($F = 9.11$, $df = 2,88$, $P = .0003$ for F2 and color; $F = 6.65$, $df = 3,87$, $P = .0004$ for F3 and growth form). Species with black fruits tended to have the lowest F2 scores, those with red-to-orange fruits were intermediate, and species with other colors had the highest scores. Fiber content thus increased, and NSC decreased, in the direction black, red-to-orange, and others. There was a steady increase in F3 scores (related to protein content) in the direction trees-shrubs-vines-herbs. It is remarkable that F1 scores, representing the most important trend of variation, did not vary significantly with any of the characteristics considered.

Taxonomic patterns.—Distribution of species over the F1–F2 plane is plotted in Fig. 8 separately for orders and superorders represented by at least three species. Gymnosperms and angiosperms were similar in F1 scores ($F = 0.002$, $P = .96$), but differed significantly in F2 scores ($F = 14.15$, $P = .0003$). Angiosperm fruits tended to have lower fiber, and higher nonstructural carbohydrate content than gymnosperm fruits. There were no significant differences between angiosperm superorders (F1: $F = 1.63$, $P = .19$; F2: $F = 0.37$, $P = .78$) or between dicots and monocots (F1: $F = 0.97$, $P = .33$; F2: $F = 0.07$, $P = .79$). Significant heterogeneity in both F1 ($F = 18.34$, $P < .0001$) and F2 ($F = 6.61$, $P = .001$) scores existed between orders of Rosidae. There was a consistent relationship between evolutionary advancement (according to criteria in Stebbins 1974) and reduction in F2 scores (reduced fiber content, increased nonstructural carbohydrate) in this superorder. The relationship of F1 scores with evolutionary advancement was an inconsistent one. No significant differences between orders were found within Asteridae (F1: $F = 1.63$, $P = .22$; F2: $F = 0.05$, $P = .95$).

Phylogeny is thus clearly involved in the composition of the organic fraction of fruit pulp, but the relationship is a weak one. Species in different superorders, or even in separate classes, may sometimes have quite similar F1 and F2 values (compare, e.g., the clusters of species near the origin in Rhamnales, Dipsacales, and Liliidae). Furthermore, the two major gradients of pulp composition (as described by F1 and F2) were generated by differences among certain higher taxonomic categories. Variation within these categories tended to be much less important.

MINERAL FRACTION OF PULP

General

Data on total mineral content of pulp (ash) were available for 94 species (55 genera, 33 families). Values fell in the range 0.5–13.3% dry mass, but frequency distribution was skewed to the right and most species

TABLE 3. Product-moment correlation matrix for water and organic constituents of fruit pulp, $N = 91$ species (lipid content data log-transformed).

	WCF†	Fiber	NSC‡	Protein
Fiber	-0.357***			
NSC	0.392***	-0.612***		
Protein	NS	NS	-0.360***	
Lipids	-0.210*	NS	-0.722***	NS

* $P < .05$; *** $P < .001$; NS = nonsignificant.

† WCF = water content of the fresh whole fruit (see Water Content and Organic Fraction of Pulp: General for justification of using this variable as an indirect estimate of water content of pulp WCP.)

‡ NSC = nonstructural carbohydrate.

TABLE 4. Factor analysis of the correlation matrix of water and organic constituents of fruit pulp (Table 3). Only loadings >0.25 are shown.

	Factor loadings			
	F1	F2	F3	F4
Lipids	0.991
NSC*	-0.645	-0.500	-0.293	...
Fiber	...	0.979
Protein	0.987	...
WCF†	0.969
Cumulative proportion of variance (%)	46.5	71.9	86.8	98.2

* NSC = nonstructural carbohydrate.

† WCF = water content of the fresh whole fruit (used as an indirect estimate of WCP).

(65%) had between 2 and 6% (Fig. 9; geometric mean = 4.00%).

The amounts of five macroelements (Na, Mg, P, Ca, K) and four trace elements (Fe, Zn, Cu, Mn) in the pulp were determined for 73 species (46 genera, 29 families). K tended to be the most abundant macroelement (geometric mean = 14.0 mg/g dry mass), followed in decreasing order of importance by Ca (2.0 mg/g), P (0.7 mg/g), Mg (0.4 mg/g), and Na (0.2 mg/g) (Fig. 10). The concentration of each element was extremely variable between species. Extreme values for Ca, the most variable macroelement, were 0.2–14.0 mg/g. The Ca/P ratio was generally biased towards the first of these elements. It was >1 in 87.7% of species (geometric mean = 2.7, range = 0.4–64.4).

Fe tended to be the most abundant trace element (geometric mean = 31.4 mg/kg), followed by Zn (8.5 mg/kg), Cu (3.6 mg/kg), and Mn (2.2 mg/kg) (Fig. 10). Certain species exhibited remarkable concentrations of some trace elements, as illustrated by the upper extremes of observed ranges (Fig. 10).

Trends of variation

FA was performed on the data for ash and the nine individual elements from 71 species. Original data were log-transformed to normalize distributions. The first factor (F1, 38.3% of variance) involved variation in ash and K content (Table 5). As K was the dominant element in the mineral fraction (Fig. 10), variation in F1 mainly related to variation in the total mineral content of fruit pulp. F2 (18.8% of variance) described a parallel variation in Ca and Mg. The remaining factors (F3 through F8), accounting all together for 39.9% of the variance, were each related to variation in a single element (Table 5). All factor loadings were positive, and were either very high (>0.8) or very low (<0.25), with intermediates virtually absent. The highest loadings of the various mineral constituents consistently occurred on separate factors. These results lead to the conclusion that, with the single exception of the Ca-Mg pair, relative concentrations of the var-

ious elements in fruit pulp vary independently of each other in the 71-species sample considered. No complementary relationship existed between any pair of elements (no significant negative pairwise correlation in the original correlation matrix), and Ca-Mg represented the only example of joint occurrence. In other words, the concentration of any given element in the fruit pulp of a species was not predictably associated with the configuration of other elements in the same pulp (excepting Ca-Mg).

The distribution of species over the F1–F2 plane did not depart significantly from a normal bivariate distribution. Neither distinct groups of species nor trends of interspecific variation were discernible.

Interspecific patterns

Ecological patterns.—There was no significant geographical pattern to the constitution of the mineral fraction of fruit pulp. Likewise, species with and without bicolored displays did not differ significantly in their scores on any of the first three factors.

Species groups based on color of fruit or growth habit differed significantly in F1 scores ($F = 3.53$, $df = 2,67$, $P = .035$; $F = 6.91$, $df = 3,66$, $P = .0004$; color and growth habit, respectively), but not in either F2 or F3. There was a steady increase in F1 in the direction trees-shrubs-vines-herbs (Fig. 11). This trend indicates that mineral content of fruit pulp varies with growth form. Species with black fruits tended to have the highest mineral content, those with red-to-orange fruits were intermediate, and species with other colors had the smallest mineral contents. Although fruit color and growth form were unrelated in the 111-species set ($G = 3.44$, $df = 6$, $P = .75$), there was a marginal association between color and growth form in the 71-species sub-

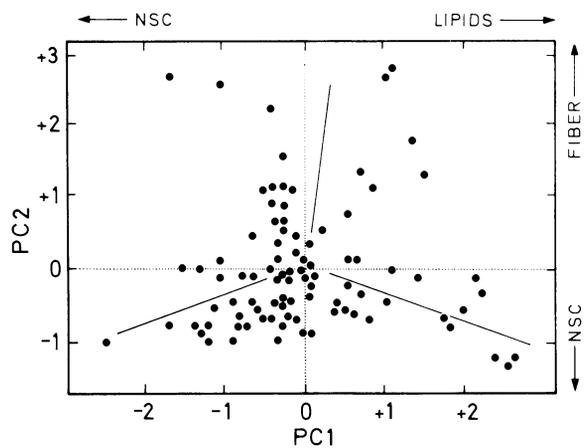


FIG. 7. Distribution of plant species over the plane defined by the first two factors (Table 4) resulting from the correlation matrix for water and organic constituents of fruit pulp ($N = 91$ species). Directions of increase of variables associated with each gradient are shown by arrows at margins of the graph (NSC = nonstructural carbohydrate). The three diverging lines refer to the main trends in fruit pulp constitution.

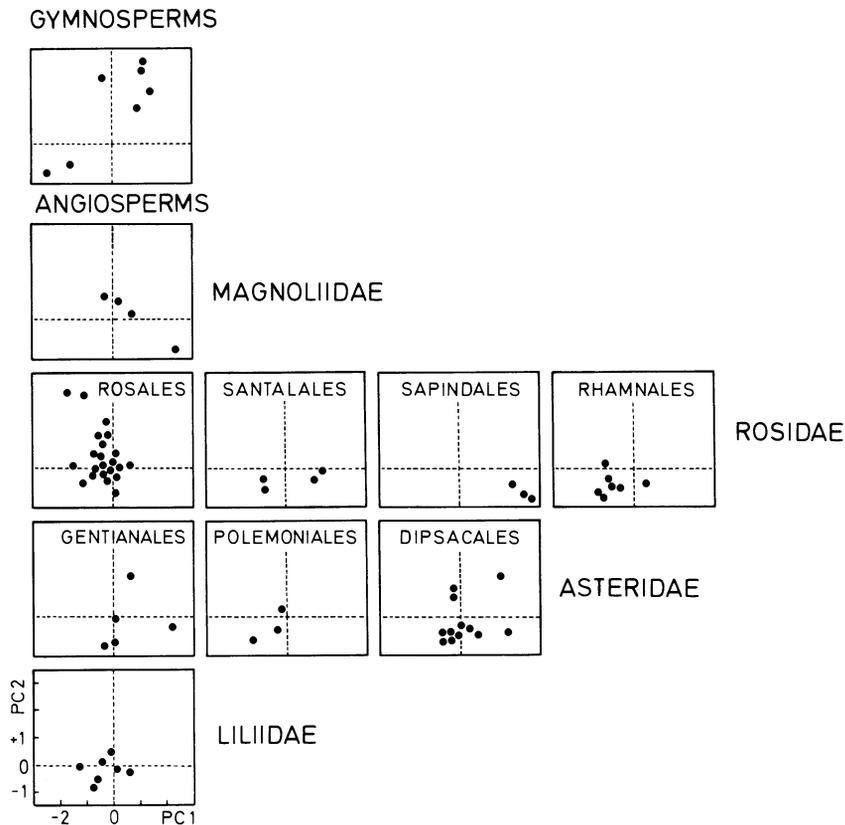


FIG. 8. Distribution of plant species over the plane defined by the first two factors resulting from the correlation matrix for water and organic pulp constituents (Table 4), plotted separately for various higher taxonomic categories (classification based on Stebbins 1974). Evolutionary advancement increases from top to bottom and, within rows, from left to right. For angiosperms, only orders and superorders with at least three species in the sample are shown.

sample used in the analyses of the mineral fraction ($G = 8.1$, $df = 6$, $P = .20$). When growth form was held constant, variation of F1 scores with fruit color was no longer significant within any of the four growth forms. Thus growth form was the only significant source of interspecific variation in mineral content of fruit pulp.

Taxonomic patterns.—A comparative analysis of factor scores for higher taxonomic categories failed to disclose any relevant pattern. As an alternative, a classification analysis was performed. A matrix of Euclidean distances between species was computed after standardization (mean = 0, $SD = 1$) of raw mineral content data (ash plus nine elements). Based on this matrix, a classification of species was produced using a single linkage amalgamation procedure (Engelman 1981). Taken as a whole, the classification bore no resemblance to the one expected from taxonomic affinities between species (Fig. 12). The simple inspection of the dendrogram reveals that species belonging to the same genus, or genera in the same family, were not consistently associated (e.g., in Rosaceae and Caprifoliaceae), and phylogenetically distant groups (gymnosperms, dicotyledons, monocotyledons) were intermixed. These

results suggest that variation in the inorganic fraction of fruit pulp is largely independent of phylogeny.

THE WHOLE FRUIT: DESIGN PLUS PULP CONSTITUENTS

The preceding analyses provided partial views of fruit constitution. This section presents a synthesis based on the simultaneous consideration of the sets of factor scores resulting from the separate analyses of fruit design (FDe's hereafter) and organic (FOr's) and inorganic (FIn's) pulp constituents.

One-third of the 27 possible (linear) correlations (among species) between factor scores belonging to different factor sets were statistically significant (Table 6). Fruit size (FDe1) was negatively correlated with lipids (FOr1) and positively correlated with fiber-NSC (FOr2). Lipid and NSC thus tended to decrease, and fiber content to increase, with increasing fruit size. Seed size-seediness (FDe2) was negatively correlated with Ca-Mg (FIn2). This denotes an increase in Ca-Mg of the pulp with increasing mass of individual seeds: Pulp/seed mass ratio (FDe3) was correlated positively with fiber (FOr2) and negatively with protein (FOr3) and

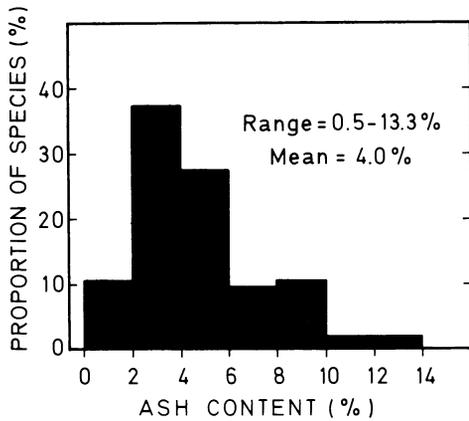


FIG. 9. Frequency distribution of ash content of fruit pulp in a sample of 94 Iberian plant species. Mean = geometric mean.

K-ash (FIn1). Across species, fiber content increased, and protein, K, and ash content decreased with increasing pulp/seed mass ratio. In addition to the correlations with FDe1 and FDe3 mentioned earlier, fiber (FOr2) was also positively correlated with Ca-Mg (FIn2), indicating a parallel variation in fiber and Ca-

Mg. Protein (FOr3) was positively correlated with both K-ash (FIn1) and P (FIn3).

Reduction of these elemental pairwise relationships into some major trend(s) of overall covariation between factors was attempted by performing FA of their correlation matrix. Not a single pair of variables (factor scores) loaded significantly on the same factor, i.e., all the original factors were independent of one another. Therefore, although there were some significant pairwise correlations, fruit design, organic, and inorganic constituents did not covary.

DISCUSSION

Interspecific variability in fruit attributes

Vertebrate-dispersed plants of the Iberian Peninsula are very heterogeneous in terms of taxonomical affiliation (35 families, 3.2 species/family on average). Substantial interspecific variability in fruit characteristics is to be expected from phylogenetic effects alone. Interspecific variability of Iberian fruits in external fruit dimensions is, however, relatively small. Fruiting plants of a Costa Rican montane forest with a similar level of relative taxonomic diversity (3.2 species/family) display much greater variance in fruit size, as a consequence of the contribution of large-fruited species

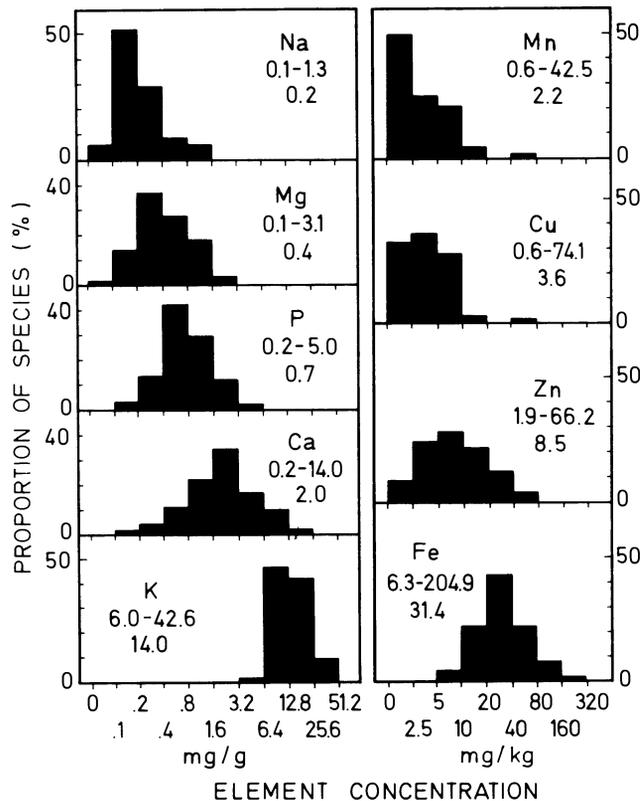


FIG. 10. Frequency distributions of macroelement and trace element concentration in fruit pulp ($N = 73$ species in all cases). Range and geometric mean are shown beneath element symbols.

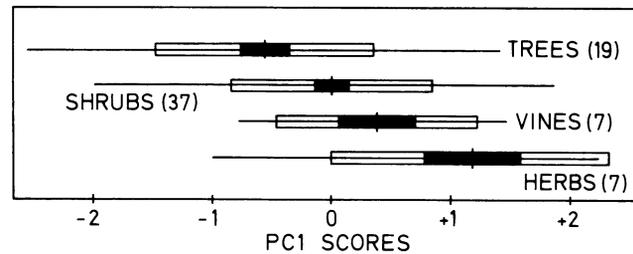


FIG. 11. Variation with growth form of F1 scores resulting from factor analysis of the mineral fraction data (Table 5). Short vertical lines indicate means, filled boxes are standard errors, open boxes are standard deviations, and horizontal lines are ranges. Number of species in each category is shown in parentheses.

(Wheelwright et al. 1984). Fruit size distributions strongly skewed to the right are apparently characteristic of tropical fruiting plant assemblages (see also Beehler 1983, Janson 1983, Pratt 1983, Prevost 1983) but not of midlatitude ones, if Iberian plants are representative (see also Johnson et al. 1985). The vast majority of Iberian species produce small berries or drupes. Large fruits (>14 mm) are extremely infrequent, as are nonberrylike fruits, such as husk-covered arillated seeds, which are common in tropical and subtropical floras (Skutch 1980, Knight and Siegfried 1982, Beehler 1983, Janson 1983). This narrow range of variation in fruit size and type contrasts with the broad interspecific variation in structure (e.g., seed size, seediness, pulp/seed mass ratio) and pulp composition. Although interspecific differences in fruit internal structure or pulp composition were not consistently related to systematic affinities, the taxonomic diversity represented in my species sample explained much of the observed interspecific variability in these features (Figs. 5 and 8). Thus, fruits of most species tended to be equivalent in size and type, did not reflect taxonomic differences, and differed broadly in internal structure and chemical composition of pulp, which was consistent with phylogenetic diversity.

Levels of interspecific variability differed for the various pulp constituents. Protein and lipids were the most

predictable constituents among Iberian plants. More than 90% (protein) or 80% (lipids) of the species had less than 10% pulp dry mass of either constituent. This contrasts with the greater variation in water, fiber, NSC, and ash content (Figs. 6 and 9). Frequency distributions were all significantly skewed. Lipid ($g_i \pm SE = 3.00 \pm 0.26$) and protein (3.47 ± 0.26) distributions were strongly, and fiber (1.42 ± 0.25) and ash (1.06 ± 0.25) moderately, skewed to the right, whereas water (-1.47 ± 0.36) and NSC (-0.93 ± 0.26) were moderately skewed to the left. This suggests a strong trend towards reduced lipid and, particularly, protein content, a moderate one towards reduced fiber and ash, and a further moderate trend towards increased water and NSC content.

The concentration of individual mineral elements in the pulp is the least predictable compositional feature of Iberian fruits. Individual macroelements and trace elements exhibit broad ranges of variation, and extreme values generally differ by one or more orders of magnitude. There are not, on the other hand, apparent phylogenetic correlates in the differential composition of the mineral fraction, and taxonomically related species are often more dissimilar than unrelated species. The possibility exists that composition of the mineral fraction is a labile character dependent more on environmental (e.g., soil nutrients) than genetic proper-

TABLE 5. Factor analysis of the correlation matrix of fruit pulp mineral constituents in a set of 71 plant species. Only loadings >0.25 are shown.

	Factor loadings							
	F1	F2	F3	F4	F5	F6	F7	F8
Ash	0.932
K	0.833
Ca	...	0.941
Mg	0.286	0.674	0.266
P	0.958
Na	0.952
Fe	0.970
Cu	0.256	...	0.885	0.285	...
Zn	0.275	0.892	...
Mn	...	0.294	0.895
Cumulative proportion of variance (%)	38.3	57.1	69.0	77.2	83.6	89.1	93.6	97.0

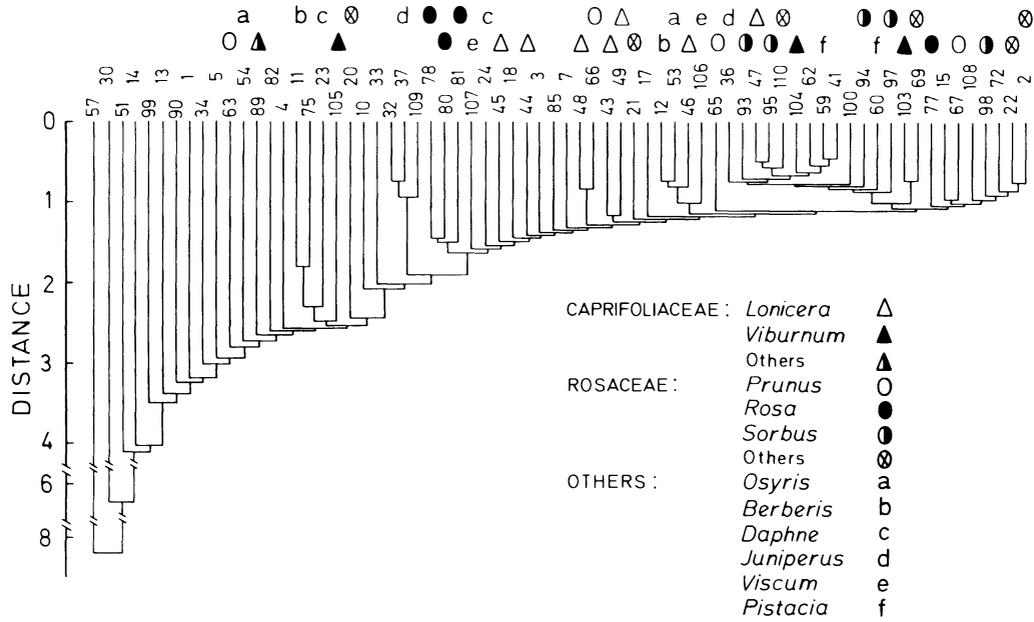


FIG. 12. Classification of plant species according to the composition of the mineral fraction of fruit pulp (based on a matrix of Euclidean distances; see Mineral Fraction of Pulp: Interspecific patterns: Taxonomic patterns). Genera having at least two species in the sample, and all species in Rosaceae and Caprifoliaceae (the most numerous families), have been coded according to the key shown. Numbers identifying species are those listed in Appendix 1.

ties. Two lines of evidence, however, are inconsistent with this possibility. First, some species growing side by side yielded contrasting mineral configurations (in Appendix 2 see [1] *Prunus mahaleb*, *P. spinosa*, *Lonicera etrusca*, *L. splendida*, and *Berberis hispanica* on one side, or [2] *Osyris quadripartita*, *Phillyrea angustifolia*, *Myrtus communis*, *Smilax aspera*, and *Chamaerops humilis*, on the other; in each set, samples come from the same locality and year). Second, in other species for which I have appropriate data, the relative contribution of different elements to the mineral fraction is fairly constant for samples collected at sites with contrasting soil characteristic (C. M. Herrera, *personal observation*).

The relative distribution of species in the three character spaces defined by design, pulp-organic, and pulp-inorganic variables illustrates different levels of interspecific variability among sets of attributes. The character spaces are defined by the first three factors

for each set of variables. All possible pairwise Euclidean distances between species were computed in each space, and statistics were obtained for the resulting frequency distributions (Table 7). Average packing of species was closest in the space corresponding to pulp organic constituents, loosest in the mineral constituents space, and intermediate in the space of design variables. Skewness followed an opposite trend, increasing from mineral constituents through design to organic constituents. The potential influence of phylogenetic diversity on variability was the same for the three sets of variables, thus these results demonstrate that the trends to reduce interspecific variation in fruit constitution differed among sets of variables and decreased in the direction organic-design-inorganic.

Fruit structure

The analysis of pulp/seed allocation showed that, among species, (1) pulp mass increased more slowly

TABLE 6. Product-moment correlation coefficients between species factor scores. FDe's (fruit design attributes), FOR's (organic pulp constituents), and FIn's (inorganic pulp constituents) were obtained in separate analyses (see Table 1, 4, 5). Correlations were computed only for species having complete data sets ($N = 69$). Factor scores of the same set are uncorrelated.

	FOR1	FOR2	FOR3	FIn1	FIn2	FIn3
FDe1	-0.396**	0.355**	NS	NS	NS	NS
FDe2	NS	NS	NS	NS	-0.403***	NS
FDe3	NS	0.266*	-0.266*	-0.377**	NS	NS
FOR1				NS	NS	NS
FOR2				NS	0.315**	NS
FOR3				0.304**	NS	0.539***

* $P < .05$; ** $P < .01$; *** $P < .001$; NS = nonsignificant.

than seed mass, hence the amount of pulp accompanying a mass unit of seed is greatest for the smallest fruits (see Willson and Schemske 1980, Herrera 1981*b*, for similar results in intraspecific contexts); (2) with increasing individual seed size, the amount of pulp per seed decreased; (3) in the smallest seeded species, pulp biomass exceeded seed biomass; and (4) holding individual seed size constant, trees tended to produce the greatest amount of pulp per seed, herbs the smallest, and shrubs and vines were intermediate.

Since pulp (chemical) quality was not consistently related to either seed or pulp mass per fruit (Table 6), results 1–3 negate a general selective action of seed dispersers on fruit design in the direction of favoring an increase in reward (pulp) with increasing ballast (seeds). In fact, species with the smallest individual seeds and seed masses per fruit are those offering the greatest relative amounts of pulp to frugivores. These results are best explained as a consequence of selection against large fruit size coupled with architectural constraints on fruit design (see Herrera 1981*a*). These constraints are also apparent in the results of factor analysis for design variables. For any given fruit size, there is an upper limit to the size of individual seeds it can enclose, but individual seed size may fall anywhere below this limit. Result 4 is presumably a consequence of differences between growth forms in average relative resource allocation to propagules and ancillary structures (Salisbury 1942, Abrahamson and Gadgil 1973, Gaines et al. 1974, Abrahamson 1979).

Interspecific patterns in fruit structure were not discernible among the species examined. Disregarding the architectural constraints noted above, FA revealed that fruit size, seed size, and pulp/seed mass ratio tended to vary independently of each other among species.

Chemical composition of pulp

Factor analysis of the correlation matrix for water and organic constituents of fruit pulp revealed two independent trends, related to complementary variation of lipids and NSC on one hand, and fiber and NSC on the other. The first trend approaches the earlier view of a dichotomy of fruits into high- and low-reward types (e.g., Snow 1971, McKey 1975, Howe and Estabrook 1977), while the second has not been suggested before. In the plane defined by the first two factors, however, species did not segregate into distinct clusters, but they formed a dense clump at intermediate values, with three relatively ill-defined departing lines. This indicates that (1) most possible combinations of NSC, lipids, and fiber were represented; (2) distinct pulp composition "types" were not apparent; and (3) rather than the lipid- vs. NSC-rich continuum suggested by some authors, there are three pulp composition types, whose extremes are: high lipid–low NSC–low fiber; low lipid–high NSC–low fiber; and medium lipid–medium NSC–high fiber. Few species, however, can be unequivocally placed in one of these "fruit types."

TABLE 7. Relevant statistics (\pm SE) of frequency distributions of all possible pairwise Euclidean distances between species, in each of the character spaces defined by the first three factors for fruit design and organic and inorganic pulp constituents.

Fruit attributes	N*	Median	δ_1
Design	5565	1.879 \pm 0.020	0.911 \pm 0.033
Organic pulp constituents	4095	1.701 \pm 0.025	1.230 \pm 0.038
Inorganic pulp constituents	2415	2.149 \pm 0.025	0.648 \pm 0.050

* N = number of elemental distances in each set.

Further, protein and water varied independently and each was independent of the three pulp types. In other words, a particular configuration of NSC, lipids, and fiber may have associated any protein and water content value. Thus energy (NSC, lipids), nitrogen, and water varied independently among species. Complementarity of the two energy-yielding components (NSC and lipids) was the only predictable relation found. These results differ from earlier work (e.g., Snow 1971, McKey 1975, Howe and Estabrook 1977, Stiles 1980, Stiles and White 1982), particularly with regard to the independent occurrence of protein and lipids, and water and NSC.

Multivariate methods have been used to elucidate the structure of interelement correlation matrices in vegetation or plant parts (Garten et al. 1977, Golley and Richardson 1977, Garten 1978). In spite of some problems inherent in this approach (Pinder and Giesy 1981), these studies have demonstrated, with few exceptions, the generality of correlations between concentrations of elements and the existence of an underlying "factorial structure" (see Garten 1978). This structure is probably a consequence of similarity of elements in physiological function or nutrient uptake and accumulation, and factors may be interpreted on the basis of biochemical functions of elements in cells (Garten et al. 1977, Garten 1978). Results of the factor analysis of the interelement correlation matrix for fruit pulp departed noticeably from that general pattern. With the exception of the Ca-Mg association, elements tended to vary across species independently of each other, with no underlying factorial pattern. The association Ca-Mg has been found often in analyses of other plant parts, and corresponds to a structural component (Garten et al. 1977, Garten 1978). The significant correlation found here between Ca-Mg and fiber (Table 6) was consistent with this fact. The virtually random assortment of the other elements seems a unique characteristic of fruits (see also Golley and Richardson 1977: Table 7). I suggest that, since ripe fruits generally are physiologically isolated from the parent plant, and the pulp performs little or no metabolic activity, the constraints imposed on mineral configuration by the requirements of a functional enzymatic machinery are

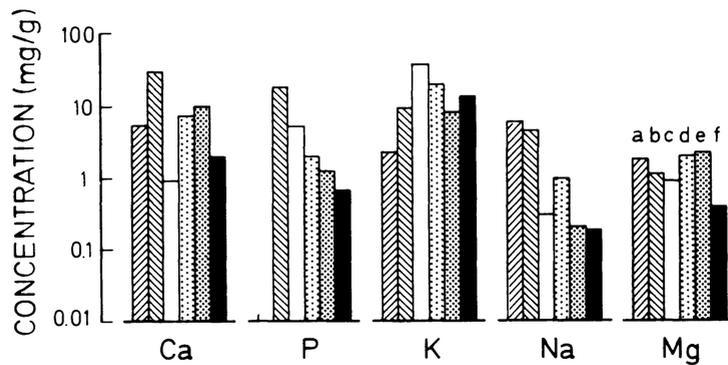


FIG. 13. Average concentration of mineral elements (on a dry mass basis) in the pulp of Iberian fruits and other biological materials (note logarithmic vertical scale): (a) invertebrates (computed from data in Werner 1983); (b) vertebrates (birds and mammals: Robbins 1983); (c) macrofungal fruit bodies (Grönwall and Pehrson 1984); (d) herbs (Garten 1978, Auclair 1979, Whittaker et al. 1979, Boring et al. 1981, Nordstrom 1984); (e) shrub and tree foliage (Woodwell et al. 1975, Lossaint and Rapp 1978, Whittaker et al. 1979, Boring et al. 1981); (f) Iberian fruits (this study).

relaxed to a large extent. This is consistent with the Ca-Mg association, since the structural component it reflects (cell walls: Garten 1978) occurs regardless of metabolic activity.

Fruit composition in relation to other biological materials

Differences in availability and nutritional value between fleshy fruits and other vertebrate foods (particularly insects) seem essential to understand ecological, physiological, and behavioral differences between frugivores and other groups (Snow 1971, Morton 1973, White 1975, Foster 1978, Milton 1981, Thomas 1984). Nevertheless, no previous study has placed fruit pulp in the context of other biological materials considering many fruit species and a variety of nutritional components, particularly mineral elements. I perform such a comparison in this section. It must be emphasized that considering nutritional traits alone ignores important aspects such as resource abundance, ease of foraging, digestibility, and spatio-temporal patterning. Accordingly, the comparisons that follow only indicate differences in resource-specific, inherent nutritional value, and are not intended to bear on differential net food value of the resources compared.

Iberian fruits do not depart substantially from those of other regions with respect to the gross nutritional configuration of the pulp (e.g., Crome 1975, White 1975, Coombe 1976, Frost 1980, Herrera 1981a, Stiles and White 1982, Viljoen 1983, Wheelwright et al. 1984, Johnson et al. 1985). Relative to other biological materials, fruit pulp strongly differs from invertebrates and vertebrates in average percent protein (5.0% in fruits; 65.3 and 62.8% in invertebrates and vertebrates, respectively), lipids (6.9 vs. 19.8 and 23.2%), ash content on a dry mass basis (4.0 vs. 7.3 and 13.9%), and water content on a fresh mass basis (70.8 vs. 61.7 and 57.9%) (averages for animals based on data in White

1975, Robbins 1983, Redford and Dorea 1984). The pulp of the average Iberian species is therefore inferior to average animal material not only in protein, as is often stressed in the literature for fruits in general, but also in mineral and lipid content; fruit pulp exceeds animal material only in water and NSC (67.0% dry mass). The dominant role of protein in animal material is taken over by nonstructural carbohydrate in fruits, in strikingly similar average proportions. Furthermore, average protein values of Iberian fruits fall below the lower limits of ranges reported by Mattson (1980) for a variety of living plant parts. The (dry) pulp of fruits represents, on average, one of the poorest protein sources found in nature.

The lower concentrations of most macroelements in fruit pulp with respect to other biological materials (Fig. 13) reflect the lower total mineral content noted above. Relative to animals, the pulp of Iberian fruits is, on average, lower in Ca, P, Na, and Mg, and higher in K. The difference is greatest for Na and P. The signs of these differences are in agreement with the general pattern of animal-plant contrast, with K overrepresented and Na and P underrepresented in plants relative to animals (Fig. 13). Among plant materials, fruit pulp is lowest in P, Na, and Mg, and next to lowest in Ca and K. These results indicate that, on average, fruits do not represent particularly good sources of any mineral element except K. Nevertheless, fruit pulp is not particularly rich in K relative to herbs, foliage, and macrofungal fruit bodies. This is inconsistent with suggestions of increased K demands to plants derived from the fleshy-fruit-producing habit (Milewski 1982). For four species with available data (*Arbutus unedo*, *Juniperus oxycedrus*, *Phillyrea angustifolia*, *Viburnum tinus*), the concentration of K in foliage (10.0 ± 3.4 mg/g dry mass) does not differ significantly from that in fruit pulp of the same species (11.2 ± 4.9 mg/g) (see also Bollard 1970: Table VII).

Ecological patterns

The five qualitative variables used to categorize species in the analyses of variance of factor scores were chosen to assess indirectly general associations between fruit characteristics and either type of dispersal agent (fruit color and display), composition of the disperser assemblage (geographical distribution), or ecological characteristics of the plant largely independent of dispersal (growth form). Fruits disseminated by birds and terrestrial mammals, the only dispersal agents known so far for fleshy-fruited Iberian plants (Guitián and Callejo 1983, Guitián 1984, Herrera 1984a, Jordano 1984), have been shown elsewhere to differ in coloration and type of display (Janson 1983, Knight and Siegfried 1983, Gautier-Hion et al. 1985). The assemblage of vertebrate frugivores found in northern and southern Iberia differ greatly in species composition, and similar differences exist between the Andalusian lowlands and highlands (Guitián 1984, Herrera 1984a, 1985b, *in press*, Jordano 1984, Obeso 1985). Finally, growth form may be used as a rough indication of plant architecture, size, and, in general terms, successional status.

Out of a total of 45 analyses of variance performed in this paper (3 types of fruit descriptive variables \times 3 factors \times 5 qualitative variables), only 9 (20%) yielded statistically significant results, i.e., revealed significant heterogeneity in species' factor scores among character states of the qualitative variables. The latter tend to differ, however, in the degree with which they co-vary with fruit attributes (factor scores). Growth forms differ significantly in aspects of design, organic and inorganic pulp constituents (four significant analyses out of nine). Geographical distribution (with its associated variation in vegetational formations, dispersal environments, and frugivore assemblages) yielded two, and fruit color and display type yielded three significant analyses. The proportion of significant heterogeneity tests for growth form (4/9) is (marginally) significantly higher ($P = .053$, Fisher test) than that for geographical distribution, color, and display combined (5/36). This suggests that fruit features tend to vary more frequently in relation to inherent attributes of the plants (combined under "growth form") than in relation to "indicators" of the disperser/dispersal environment.

The major finding emerging from these analyses is the overall lack of agreement between trends of interspecific variation in fruit characteristics and variation in qualitative variables that may reasonably be related to variation in the disperser/dispersal environment. Of particular notice is the finding that northern Iberian plants, mostly dispersed by thrush-sized birds and mammalian carnivores (Delibes 1978, Garzón and Palacios 1979, Guitián and Callejo 1983, Calviño, Canals et al. 1984, Calviño, Castro et al. 1984, Guitián 1984) differ significantly from southern Iberian species, most-

ly dispersed by warbler-sized birds (Jordano and Herrera 1981, Jordano 1982, 1984, Herrera 1984a, 1985b), only with respect to seed size–seed number. They are similar in every other respect.

General discussion

The objectives of this paper were (1) to find out whether distinct patterns of interspecific variation in fruit features were discernible (i.e., structural-compositional syndromes); and (2) if patterns existed, whether these were attributable to the selective action of frugivores. The preceding analyses revealed a variety of interspecific patterns. These include "null type" and "positive" patterns (see Table 8 for a summary). Null patterns should be considered as the combined outcome of phylogenetic constraints on fruits and of an "error term" (in its statistical sense) including ecological and evolutionary variables not accounted for as well as random effects. Positive patterns, in turn, may be classed into three groups depending on whether they are interpretable without reference to frugivores, require a consideration of the latter, or no obvious hypothesis may yet be advanced to account for it (Table 8).

Three patterns may be attributable to frugivores. First, bicolored displays tend to increase attraction to fruits (Morden-Moore and Willson 1982, Willson and Melampy 1983). The fact that they occur more often among small-sized fruits may be because increasing conspicuousness is most important among these fruits. Second, the smaller seeds of northern Iberian species, which are more often dispersed by mammalian carnivores, may reflect easier escape from grinding teeth. Third, predominantly small-sized fruits and low morphological diversity, as compared with other plant assemblages, may be a consequence of the relatively small size of the dominant frugivores and their reduced diversity (only mammalian carnivores and small to medium-sized birds; Herrera 1985b, Wheelwright 1985a).

Five patterns may be interpreted without reference to frugivores. The increase in N and total mineral content from trees through herbs is in accordance with general patterns of nutrient concentration in vegetative parts of the various growth forms (e.g., Woodwell et al. 1975, Adamandiadou et al. 1978, Whittaker et al. 1979, and other references in Fig. 13). The relationships between pulp/seed mass ratio, fruit size, and seed number, with growth form may be understood in relation to differential patterns of resource allocation to ancillary reproductive structures. Architectural constraints (see also Herrera 1981a) are probably responsible for the inverse relationship between seed size and pulp mass invested per seed. No hypotheses can be advanced at present to account for the relationships between fiber content and fruit color, and between pulp/seed mass ratio and elevation in Andalusia.

Some positive patterns are contrary to expectations

TABLE 8. Summary of major patterns revealed by this study.

Null patterns	Positive patterns: presumed origin		
	Frugivores	Other factors*	Unknown
Independent variation of fruit size, seed size, and pulp/seed mass ratio	Bicolored displays predominate among small fruits	Smallest seeds receive most pulp Pulp/seed mass ratio variation with growth form	Relation of fiber content with fruit color Variation of pulp/seed mass ratio with elevation in Andalusia
Independent variation of water, protein, and lipid content	Northern species have more, smaller seeds	Nitrogen content variation with growth form	
Almost random co-occurrence of mineral elements across species	Narrow range fruit sizes; predominantly small fruits	Fruit size and seediness variation with growth form	
No overall covariation of fruit design and organic and inorganic pulp constituents		Total mineral content variation with growth form	
Those underlying the 36 (80%) analyses of variance that failed to detect heterogeneity			

* Includes architectural constraints and growth form-specific resource and nutrient allocation patterns.

derived from coevolution-based views of plant-frugivore interaction. Prominent among these are the inverse relation between seed size and pulp mass per seed, and the extreme mismatch of mineral concentrations and the requirements of vertebrates (in particular Ca/P and Na/K ratios: Robbins 1983).

CONCLUSION

This study has attempted for the first time an objective assessment of the importance of the disperser/dispersal environment in accounting for observed interspecific variation in fruit features, relative to other factors such as phylogeny, architectural constraints, or species-specific energy and nutrient allocation patterns. In the case of Iberian fruits, these latter factors combined seem most important in explaining interspecific variability in fruit characteristics. The general hypothesis tested, namely that *major* trends of interspecific variability in fruit characteristics are attributable to differential disperser/dispersal environments, is not supported by the results. The broadest patterns revealed by this study fall in the null-type class (Table 8), and the few positive patterns found have in all cases rather restricted implications as to the overall constitution of fruits. Furthermore, only one-third of these seem attributable to the selective action of frugivores on fruit traits. No overwhelming influence of the disperser/dispersal environment on the characteristics of the fruits of Iberian plants taken as a whole has been detected. It must be noted that a large number of statistical tests, often involving the same data sets, have been performed in this study, with the consequent likelihood of committing Type I error. The weak evidence of correlation between traits was thus found in spite of a liberal statistical approach designed to detect patterns and neglecting potential Type I error effects. Accounting for these would imply a reduction in the levels of statistical significance, thus rendering some tests (and the implied relationships) nonsignificant.

As with any statistical analysis yielding negative re-

sults, the possibility also exists here of committing Type II error. The negative results of this study, therefore, do not strictly demonstrate that frugivores or the dispersal environment have been not influential on the evolution of Iberian fruits. These results, however, are predominantly negative only in relation to the particular hypothesis tested here. They actually provide positive evidence in favor of an alternative view of the evolutionary interaction between plants and their dispersal agents. This view considers that historical and phylogenetic constraints on plant distribution and morphology; weak selective pressures from dispersers; generally slower evolutionary rates of plants relative to animals; differential duration of plant and animal taxa; influence of nonmutualistic organisms; spatio-temporally inconsistent selective pressures on plants; and incongruency between the habitat ranges of animal and plant species, all combine to greatly decrease the adaptedness of plant fruiting traits to their current disperser/dispersal environments (Herrera 1982c, 1984a, c, 1985a, 1986, *in press* Howe, 1984, Wheelwright, *in press*). The results of this study are precisely those expected from this alternative view.

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APPENDIX 1

TABLE A1. Growth form, distributional status in the Iberian Peninsula, and fruit characteristics, of the 111 vertebrate-dispersed plant species examined in this study.

Species	(Family)	Growth form*	Fruit color†	Bi-colored fruit display	Geographical distribution‡				Fruit length (mm)	Fruit diameter (mm)	Fruit fresh mass (mg)
					N	A	AH	AL			
1 <i>Actaea spicata</i> (Ranunculaceae)	H	BLA	-	+	+	-	-	8.7	8.6	354.6	
2 <i>Amelanchier ovalis</i> (Rosaceae)	LS	BLU	+	+	+	+	-	7.0	7.3	195.2	
3 <i>Arbutus unedo</i> (Ericaceae)	T	R-O	+	-	-	+	+	14.9	17.1	3226.0	
4 <i>Arctostaphylos uva-ursi</i> (Ericaceae)	SS	R-O	-	+	-	-	+	7.6	8.6	273.0	
5 <i>Arum italicum</i> (Araceae)	H	R-O	-	+	+	+	+	11.1	9.2	387.4	
6 <i>Asparagus acutifolius</i> (Liliaceae)	SS	GRE	-	-	-	+	+	6.5	7.1	147.0	
7 <i>Asparagus albus</i> (Liliaceae)	SS	R-O	-	-	-	-	+	5.8	6.5	148.2	
8 <i>Asparagus aphyllus</i> (Liliaceae)	SS	GRE	-	-	-	-	+	6.5	7.4	225.3	
9 <i>Atropa baetica</i> (Solanaceae)	H	BLA	-	-	-	+	-	10.0	12.1	646.8	
10 <i>Atropa belladonna</i> (Solanaceae)	H	BLA	-	+	-	-	-	11.4	13.4	762.8	
11 <i>Berberis hispanica</i> (Berberidaceae)	SS	BLU	-	-	-	+	-	9.3	5.5	139.0	
12 <i>Berberis vulgaris</i> (Berberidaceae)	SS	PIN	-	+	+	-	-	10.4	5.5	148.3	
13 <i>Bryonia dioica</i> (Cucurbitaceae)	H	R-O	-	+	+	+	+	6.7	6.9	168.6	
14 <i>Celtis australis</i> (Ulmaceae)	T	BRO	-	-	-	+	+	10.1	8.9	508.7	
15 <i>Chamaerops humilis</i> (Palmae)	SS	BRO	-	-	-	-	+	14.5	13.9	1712.0	
16 <i>Convallaria majalis</i> (Liliaceae)	H	R-O	-	+	-	-	-	10.0	8.5	375.0	
17 <i>Corema album</i> (Empetraceae)	SS	WHI	-	-	-	-	+	6.2	6.6	158.0	
18 <i>Cornus sanguinea</i> (Cornaceae)	LS	BLA	+	+	+	+	-	6.4	6.8	173.3	
19 <i>Cotoneaster integerrimus</i> (Rosaceae)	LS	R-O	-	-	+	+	-	7.0	5.7	96.3	
20 <i>Cotoneaster granatensis</i> (Rosaceae)	LS	R-O	-	-	-	+	-	7.5	7.0	164.8	
21 <i>Crataegus laciniata</i> (Rosaceae)	T	R-O	-	-	-	+	-	11.9	11.8	869.1	
22 <i>Crataegus monogyna</i> (Rosaceae)	T	R-O	-	+	+	+	+	12.1	9.3	675.4	
23 <i>Daphne gnidium</i> (Thymaelaeaceae)	SS	R-O	-	-	-	+	+	6.2	5.0	102.1	
24 <i>Daphne laureola</i> (Thymaelaeaceae)	SS	BLA	-	+	-	+	-	9.4	6.4	204.5	
25 <i>Daphne oleoides</i> (Thymaelaeaceae)	SS	R-O	-	-	-	+	-	5.9	4.9	89.4	
26 <i>Ephedra fragilis</i> (Ephedraceae)	SS	R-O	-	-	-	+	+	8.0	6.2	176.7	
27 <i>Euonymus europaeus</i> (Celastraceae)	LS	YEL	+	+	+	-	-	7.5	5.1	87.3	
28 <i>Ficus carica</i> (Moraceae)	T	BLA	-	+	+	+	+	33.5	30.6	13 910.0	
29 <i>Fragaria vesca</i> (Rosaceae)	H	R-O	-	+	+	+	-	9.4	9.5	274.4	
30 <i>Frangula alnus</i> (Rhamnaceae)	T	BLA	+	+	+	+	+	6.2	6.9	185.3	
31 <i>Hedera helix</i> (Araliaceae)	WV	BLA	-	+	+	+	-	7.2	8.4	281.5	
32 <i>Hippophae rhamnoides</i> (Elaeagnaceae)	LS	YEL	-	+	-	-	-	5.8	5.0	72.0	
33 <i>Ilex aquifolium</i> (Aquifoliaceae)	T	R-O	-	+	+	+	-	8.5	7.9	289.0	
34 <i>Iris foetidissima</i> (Iridaceae)	H	R-O	+	-	+	-	+	7.5	7.1	192.2	
35 <i>Jasminum fruticans</i> (Oleaceae)	SS	BLA	-	-	+	+	+	7.3	6.9	237.3	
36 <i>Juniperus communis</i> (Cupressaceae)	LS	BLU	-	-	+	-	-	6.2	6.2	110.7	
37 <i>Juniperus oxycedrus</i> (Cupressaceae)	T	BRO	-	-	+	+	+	9.3	9.7	467.3	
38 <i>Juniperus phoenicea</i> (Cupressaceae)	T	BRO	-	-	+	+	+	7.9	8.3	224.8	
39 <i>Juniperus sabina</i> (Cupressaceae)	LS	BLU	-	-	+	-	-	6.3	7.4	165.0	
40 <i>Juniperus thurifera</i> (Cupressaceae)	T	BLU	-	-	+	-	-	9.0	9.2	277.7	
41 <i>Laurus nobilis</i> (Lauraceae)	T	BLA	-	-	+	-	+	14.8	12.2	1234.1	
42 <i>Ligustrum vulgare</i> (Oleaceae)	SS	BLA	-	+	+	+	-	7.1	6.1	162.9	
43 <i>Lonicera arborea</i> (Caprifoliaceae)	LS	WHI	-	-	-	+	-	7.6	8.0	286.8	
44 <i>Lonicera etrusca</i> (Caprifoliaceae)	WV	R-O	-	+	-	+	-	8.5	6.5	191.9	
45 <i>Lonicera implexa</i> (Caprifoliaceae)	WV	R-O	-	-	-	+	+	7.2	6.3	162.9	
46 <i>Lonicera periclymenum</i> (Caprifoliaceae)	WV	R-O	-	+	+	+	+	7.9	6.8	179.9	
47 <i>Lonicera pyrenaica</i> (Caprifoliaceae)	SS	R-O	-	+	-	-	-	8.1	8.6	358.0	
48 <i>Lonicera splendida</i> (Caprifoliaceae)	WV	YEL	-	-	-	+	-	11.8	7.9	384.5	
49 <i>Lonicera xylosteum</i> (Caprifoliaceae)	LS	R-O	-	+	-	-	-	7.8	9.3	415.0	
50 <i>Mandragora autumnalis</i> (Solanaceae)	H	YEL	-	-	-	-	+	22.0	16.2	3314.4	
51 <i>Myrtus communis</i> (Myrtaceae)	LS	BLU	+	-	-	-	+	11.5	8.5	388.5	
52 <i>Olea europaea</i> (Oleaceae)	T	BLA	-	-	-	-	+	11.8	8.8	619.5	
53 <i>Osyris alba</i> (Santalaceae)	SS	R-O	-	-	+	+	+	8.3	9.4	488.8	
54 <i>Osyris quadripartita</i> (Santalaceae)	LS	R-O	-	-	-	-	+	7.5	7.3	245.1	
55 <i>Paeonia broteroi</i> (Paeoniaceae)	H	BLA	+	-	-	+	-	9.3	6.9	257.1	
56 <i>Paris quadrifolia</i> (Liliaceae)	H	BLU	-	+	-	-	-	8.7	10.7	455.0	
57 <i>Phillyrea angustifolia</i> (Oleaceae)	LS	BLA	+	-	-	+	+	5.2	5.2	80.8	
58 <i>Phillyrea latifolia</i> (Oleaceae)	T	BLA	+	-	+	+	-	7.1	7.5	259.4	
59 <i>Pistacia lentiscus</i> (Anacardiaceae)	LS	BLA	+	-	-	+	+	5.2	5.3	102.4	
60 <i>Pistacia terebinthus</i> (Anacardiaceae)	T	BLU	+	-	+	+	-	6.4	5.8	181.9	
61 <i>Polygonatum odoratum</i> (Liliaceae)	H	GRE	-	+	-	+	-	9.1	9.2	347.7	
62 <i>Polygonatum verticillatum</i> (Liliaceae)	H	R-O	-	+	-	-	-	7.6	8.5	259.0	
63 <i>Prunus mahaleb</i> (Rosaceae)	T	BLA	+	+	-	+	-	8.0	8.3	378.0	

TABLE A1. Continued.

Fruit dry mass (mg)	Dry mass seeds (mg)	Dry mass pulp (mg)	Mean seed number	Mean 1-seed mass (mg)
77.9	52.8	25.1	8.1	6.5
90.7	22.1	68.6	7.3	3.0
1123.6	51.3	1072.3	12.9	4.0
115.3	57.8	57.5	5.0	11.6
135.1	83.5	51.6	2.2	38.0
90.8	44.1	46.7	1.1	40.1
57.3	28.4	28.9	1.1	25.8
98.9	58.7	40.1	1.5	39.1
156.2	59.2	97.0	35.2	1.7
178.2	105.5	72.7	119.6	0.9
50.7	21.4	29.3	1.5	14.3
45.9	20.3	25.6	1.6	12.7
57.9	36.1	21.8	3.3	10.9
386.4	134.0	222.4	1.0	134.0
1321.3	669.2	652.1	1.0	669.2
109.7	45.4	64.3	3.5	13.0
40.1	29.6	10.5	3.0	9.9
89.5	52.6	36.9	1.0	52.6
54.1	37.7	16.4	2.0	18.9
74.9	49.9	25.0	2.0	25.0
396.2	227.9	168.3	2.4	95.0
294.7	123.7	171.0	1.0	123.7
18.5	9.0	9.5	1.0	9.0
44.0	22.3	21.7	1.0	22.3
17.3	6.6	10.7	1.0	6.6
72.9	21.7	51.2	1.0	21.7
55.2	42.8	12.4	1.2	35.7
2603.8	1327.2	1276.6	1215.9	1.1
63.3	26.0	37.3	88.0	0.3
60.4	41.6	18.8	2.6	16.0
88.3	36.4	51.9	2.2	16.5
22.3	10.7	11.6	1.0	10.7
146.8	103.0	43.8	3.2	32.2
99.6	56.5	43.1	1.0	56.5
71.3	32.1	39.2	1.2	26.8
63.6	31.3	32.3	2.8	11.2
266.9	86.8	180.1	1.4	62.0
80.3	34.9	45.4	7.5	4.7
78.0	27.0	51.0	2.5	10.8
235.9	69.2	166.7	3.1	22.3
980.4	697.7	282.7	1.0	697.7
42.4	24.4	18.0	1.1	22.2
88.5	22.2	66.3	2.2	10.1
66.3	27.0	39.3	3.0	9.0
74.4	37.7	36.7	2.7	14.0
52.9	22.5	30.4	3.9	5.8
55.1	11.7	43.4	5.7	2.1
107.7	25.4	82.3	3.6	7.1
65.8	17.2	48.6	3.2	5.4
478.1	222.4	255.7	25.3	8.8
107.1	39.7	67.4	7.5	5.3
311.3	221.0	90.3	1.0	221.0
195.2	99.4	95.8	1.0	99.4
103.4	80.3	23.1	1.0	80.3
143.5	135.5	8.0	1.0	135.5
96.0	69.9	26.1	12.4	5.6
42.2	29.2	13.0	1.0	29.2
95.9	54.3	41.6	1.0	54.3
54.4	25.4	29.0	1.0	25.4
88.7	49.3	39.4	1.0	49.3
124.9	72.9	52.0	4.1	17.8
100.5	59.9	40.6	2.7	22.2
127.9	79.5	48.4	1.0	79.5

TABLE A1. Continued.

Species	(Family)	Growth form*	Fruit color†	Bi-colored fruit display	Geographical distribution‡				Fruit length (mm)	Fruit diameter (mm)	Fruit fresh mass (mg)
					N	A	AH	AL			
64 <i>Prunus padus</i> (Rosaceae)	T	BLA	+	-	+	-	-	7.9	7.9	306.8	
65 <i>Prunus prostrata</i> (Rosaceae)	SS	R-O	-	-	-	+	-	7.1	7.1	215.0	
66 <i>Prunus ramburii</i> (Rosaceae)	LS	BLU	-	-	-	+	-	9.7	8.1	437.2	
67 <i>Prunus spinosa</i> (Rosaceae)	LS	BLU	-	+	+	+	-	12.7	13.9	1631.0	
68 <i>Putoria calabrica</i> (Rubiaceae)	SS	R-O	-	-	-	+	-	5.4	3.7	33.1	
69 <i>Pyrus bourgaeana</i> (Rosaceae)	T	BRO	-	-	-	-	+	20.5	23.3	6754.2	
70 <i>Rhamnus alaternus</i> (Rhamnaceae)	T	BLA	+	-	+	-	+	5.9	6.0	137.4	
71 <i>Rhamnus alpinus</i> (Rhamnaceae)	LS	BLA	-	+	+	-	-	7.4	8.6	339.0	
72 <i>Rhamnus catharticus</i> (Rhamnaceae)	T	BLA	-	+	+	-	-	6.3	7.4	208.0	
73 <i>Rhamnus lycioides</i> (Rhamnaceae)	SS	BLA	+	-	-	+	+	5.7	6.1	131.9	
74 <i>Rhamnus myrtifolius</i> (Rhamnaceae)	SS	BLA	+	-	-	+	-	6.2	6.8	178.0	
75 <i>Rhus coriaria</i> (Anacardiaceae)	LS	BRO	-	-	-	-	+	5.2	4.8	21.1	
76 <i>Ribes alpinum</i> (Grossulariaceae)	SS	R-O	-	+	-	+	-	6.4	6.3	103.0	
77 <i>Rosa canina</i> (Rosaceae)	LS	R-O	-	+	+	+	+	15.0	9.2	652.0	
78 <i>Rosa</i> sp. 1 (Rosaceae)	SS	R-O	-	-	-	+	-	13.0	9.4	452.0	
79 <i>Rosa</i> sp. 2 (Rosaceae)	SS	BRO	-	-	+	-	-	10.3	10.4	554.7	
80 <i>Rosa</i> sp. 3 (Rosaceae)	LS	R-O	-	-	+	-	-	23.3	16.6	3220.5	
81 <i>Rosa</i> sp. 4 (Rosaceae)	LS	R-O	-	+	-	-	-	22.2	17.9	2860.0	
82 <i>Rubia peregrina</i> (Rubiaceae)	WV	BLA	+	-	-	+	+	5.8	6.1	101.3	
83 <i>Rubus idaeus</i> (Rosaceae)	SS	PIN	-	+	+	-	-	10.2	12.3	762.0	
84 <i>Rubus ulmifolius</i> (Rosaceae)	LS	BLA	+	+	+	+	+	13.1	14.6	729.5	
85 <i>Ruscus aculeatus</i> (Liliaceae)	SS	R-O	-	-	-	+	+	11.1	11.9	984.0	
86 <i>Ruscus hypophyllum</i> (Liliaceae)	SS	R-O	-	-	-	-	+	14.4	11.3	1048.9	
87 <i>Sambucus ebulus</i> (Caprifoliaceae)	H	BLA	+	+	+	+	+	5.4	6.2	139.7	
88 <i>Sambucus nigra</i> (Caprifoliaceae)	LS	BLA	+	+	+	+	-	5.3	4.0	43.4	
89 <i>Sambucus racemosa</i> (Caprifoliaceae)	LS	R-O	-	+	-	-	-	6.3	5.5	102.6	
90 <i>Smilax aspera</i> (Liliaceae)	WV	BLA	+	-	-	+	+	7.3	7.3	191.7	
91 <i>Solanum dulcamara</i> (Solanaceae)	H	R-O	-	+	+	-	+	11.0	7.7	372.8	
92 <i>Solanum nigrum</i> (Solanaceae)	H	GRE	-	-	-	-	+	6.7	7.2	214.1	
93 <i>Sorbus aria</i> (Rosaceae)	T	R-O	-	+	+	+	-	11.0	11.0	689.0	
94 <i>Sorbus aucuparia</i> (Rosaceae)	T	R-O	-	+	+	-	-	10.0	9.3	450.9	
95 <i>Sorbus domestica</i> (Rosaceae)	T	BRO	-	+	-	+	-	21.1	19.3	4150.0	
96 <i>Sorbus latifolia</i> (Rosaceae)	T	YEL	-	-	-	-	-	13.9	12.5	1235.0	
97 <i>Sorbus mougeotti</i> (Rosaceae)	T	R-O	-	+	-	-	-	10.7	9.7	479.0	
98 <i>Sorbus torminalis</i> (Rosaceae)	T	BRO	-	-	-	+	-	11.6	9.8	764.9	
99 <i>Tamus communis</i> (Dioscoreaceae)	H	R-O	-	+	+	+	+	11.8	10.8	712.5	
100 <i>Taxus baccata</i> (Taxaceae)	T	R-O	+	+	+	+	-	10.9	10.3	764.0	
101 <i>Vaccinium myrtillus</i> (Ericaceae)	SS	BLU	-	+	+	-	-	6.4	6.7	192.0	
102 <i>Vaccinium uliginosum</i> (Ericaceae)	SS	BLU	-	+	-	-	-	7.3	6.7	180.0	
103 <i>Viburnum lantana</i> (Caprifoliaceae)	LS	BLA	+	+	+	+	-	8.8	6.4	161.0	
104 <i>Viburnum opulus</i> (Caprifoliaceae)	LS	R-O	-	+	+	-	-	10.2	8.9	...	
105 <i>Viburnum tinus</i> (Caprifoliaceae)	LS	BLU	+	-	-	+	-	8.1	5.4	104.9	
106 <i>Viscum album</i> (Loranthaceae)	SS	WHI	-	+	-	+	-	8.3	7.5	294.0	
107 <i>Viscum cruciatum</i> (Loranthaceae)	SS	R-O	-	-	-	+	+	5.8	6.2	150.7	
108 <i>Vitis vinifera</i> (Vitaceae)	WV	BLU	-	-	-	+	-	10.1	9.8	639.7	
109 <i>Ziziphus lotus</i> (Rhamnaceae)	LS	BRO	-	-	-	-	+	17.3	15.4	1996.4	
110 <i>Malus sylvestris</i> (Rosaceae)	T	BRO	-	+	+	+	-	29.2	30.3	13 808.1	
111 <i>Prunus avium</i> (Rosaceae)	T	R-O	-	+	+	-	-	

* Growth form: H, herb; SS, small shrub; LS, large shrub; WV, woody vine; T, tree.

† Color of ripe fruit: BLA, black; BLU, blue; BRO, brown; GRE, green; PIN, pink; R-O, red-orange; WHI, white; YEL, yellow.

‡ N, Northern Iberian Peninsula; A, Andalusia; AH, Andalusian highlands; AL, Andalusian lowlands. Entries without "+" or "-" indicate that appropriate distributional information is lacking.

TABLE A1. Continued.

Fruit dry mass (mg)	Dry mass seeds (mg)	Dry mass pulp (mg)	Mean seed number	Mean 1-seed mass (mg)
142.4	69.8	72.6	1.0	69.8
58.3	35.1	23.2	1.0	35.1
215.7	110.1	105.6	1.0	110.1
502.7	241.9	260.8	1.0	241.9
8.6	5.6	3.0	2.0	2.8
2873.0	233.9	2639.1	7.9	29.6
58.8	35.9	22.9	3.0	12.0
100.0	48.7	51.3	3.0	16.2
88.1	69.4	18.7	3.5	19.8
61.7	30.9	30.8	2.5	12.4
62.8	47.7	15.1	3.0	15.9
19.3	8.8	10.5	1.0	8.8
30.0	11.2	18.8	3.3	3.4
292.4	103.3	189.1	11.0	9.4
223.0	100.8	122.2	8.6	11.7
237.0	80.7	156.3	5.9	13.7
1351.7	661.2	690.5	31.7	20.9
1113.3	454.3	659.0	38.5	11.8
23.4	11.1	12.3	1.2	9.3
150.4	79.9	70.5	39.3	2.0
186.4	55.2	131.2	28.8	1.9
385.7	243.4	142.3	1.4	173.9
294.9	240.1	54.8	1.6	150.1
32.2	9.3	22.9	3.0	3.1
8.0	3.5	4.5	2.6	1.3
17.2	8.9	8.3	3.0	3.0
63.7	38.6	25.1	1.5	25.7
84.0	40.9	43.1	27.6	1.5
48.4	39.3	9.1	40.2	1.0
285.7	30.4	255.3	3.8	8.0
114.0	2.3	111.7	1.4	1.6
1990.0	54.2	1935.8	1.8	30.1
417.6	38.5	379.1	1.6	24.1
147.3	9.7	137.6	2.7	3.6
344.7	51.7	293.0	2.5	20.7
144.9	87.0	57.9	4.5	19.3
228.2	69.9	158.7	1.0	69.9
41.3	11.9	29.4	50.0	0.2
31.1	9.3	21.9	22.4	0.4
59.0	32.1	26.9	1.0	32.1
...	1.0	...
74.0	37.6	36.4	1.0	37.6
69.4	11.4	58.0	1.0	11.4
43.0	11.2	31.8	1.0	11.2
182.4	49.6	132.8	1.8	27.6
963.1	351.8	611.3	1.0	351.8
2665.6	104.5	2561.1	3.3	31.7
...	1.0	...

APPENDIX 2

TABLE A2. Pulp constituents of the fruits of vertebrate-dispersed Iberian plants examined in this study. Species are coded by their numbers in Appendix 1. All constituents expressed in relation to dry mass of pulp except for WCF.

Species	Lip-ids (%)	Pro-tein (%)	Fi-ber (%)	NSC* (%)	WCF† (%)	Ash (%)	Ca (g/kg)	Mg (g/kg)	P (g/kg)	K (g/kg)	Na (g/kg)	Fe (mg/kg)	Mn (mg/kg)	Zn (mg/kg)	Cu (mg/kg)
1	2.6	9.6	22.7	51.8	77.9	13.3	14.0	2.0	1.8	36.0	0.2	38	5	23	7
2	2.5	1.9	11.4	80.9	59.6	3.8	3.3	0.7	0.4	9.4	0.2	34	2	9	3
3	2.9	3.7	28.1	67.0	65.2	1.1	2.8	0.2	0.6	6.5	0.3	53	1	15	2
4	5.8	2.8	26.1	62.7	60.0	2.5	1.4	0.3	0.6	9.5	0.6	63	1	66	7
5	2.2	6.6	7.9	76.7	65.1	6.7	8.3	0.8	2.1	17.3	0.8	41	4	35	4
6	56.2	6.0
7	1.5	4.0	7.3	80.8	61.3	6.4	0.2	0.1	0.5	27.6	0.3	43	1	4	1
8	56.1
9	0.8	6.5	4.2	85.4	75.4	3.0	1.6
10	2.5	7.3	8.9	69.5	78.1	11.9	1.4	0.5	1.6	19.0	0.3	25	1	13	11
11	4.3	5.1	22.1	66.9	63.5	2.9	1.9	0.4	1.1	18.5	0.2	138	4	16	4
12	6.3	4.8	16.8	68.8	69.0	3.3	1.8	0.3	1.1	11.0	0.1	29	6	10	6
13	4.9	27.7	21.6	37.1	65.7	9.3	2.5	0.9	5.0	30.0	0.2	60	3	8	3
14	0.9	3.7	10.6	81.5	24.1	4.9	2.9	3.1	1.1	12.5	0.2	20	1	2	2
15	1.3	3.2	18.3	77.3	23.9	3.6	0.8	0.3	0.4	17.0	0.2	19	3	4	4
16	70.5
17	5.8	2.2	11.2	77.1	74.6	3.7	0.6	0.2	0.4	9.0	0.4	35	4	10	6
18	24.9	6.4	10.3	53.8	48.4	4.7	2.1	1.0	1.3	19.0	0.2	38	1	7	3
19	50.4
20	2.8	6.8	17.8	64.2	54.6	8.4	9.8	1.6	1.0	26.5	0.2	43	11	16	5
21	1.8	3.8	21.0	74.2	54.4	4.9	4.8	0.6	0.9	16.3	0.1	30	1	11	7
22	2.3	2.5	20.5	72.4	56.4	4.3	4.4	0.6	0.5	12.5	0.3	28	3	6	4
23	2.6	7.8	5.6	80.5	81.9	3.5	1.1	0.5	1.2	13.8	0.6	109	3	10	8
24	1.5	5.2	8.8	78.7	78.8	6.1	0.7	0.2	1.1	24.0	0.1	64	3	15	2
25	5.1	9.0	7.5	73.4	81.0
26	0.6	4.9	6.2	83.3	58.7	5.1	0.6
27	37.7
28	2.3	3.5	5.8	87.4	81.3	1.9
29	76.9
30	1.4	4.4	8.1	74.3	67.4	11.8	5.1	1.4	0.4	24.0	0.4	44	43	9	9
31	31.9	5.0	16.1	47.4	70.0	0.5
32	2.4	5.6	11.9	52.5	69.0	2.4	2.2	0.3	0.6	8.5	0.4	19	6	39	6
33	3.0	4.8	15.9	72.5	49.8	4.7	2.6	1.4	0.9	17.5	0.2	23	8	18	8
34	6.9	4.8	15.6	64.4	45.0	8.4	1.1	0.6	2.3	25.0	1.1	38	5	7	7
35	7.4	4.8	31.3	53.9	69.9	3.9
36	16.4	4.1	38.5	39.8	51.5	2.3	2.0	0.2	0.5	11.0	0.3	20	2	6	3
37	10.4	2.5	33.8	51.9	29.0	3.0	2.8	0.5	0.4	8.5	0.4	19	6	44	7
38	14.6	4.9	52.0	28.3	36.4	2.6
39	12.9	6.6	49.3	28.8	53.6	2.4
40	3.4	3.7	46.8	42.3	15.1	3.7
41	54.3	6.2	10.6	26.2	20.6	2.6	0.3	0.1	0.5	10.0	0.2	30	1	2	1
42	3.3	5.9	13.7	73.8	74.0	4.7	3.2	0.9	1.8	20.0	0.4	53	5	29	8
43	2.7	2.7	7.4	79.8	69.1	7.4	3.0	0.4	0.5	12.5	0.1	18	1	5	2
44	2.3	3.5	6.7	78.2	69.2	9.3	2.9	0.4	1.0	15.0	0.1	50	1	9	3
45	1.9	3.3	8.5	81.6	54.3	5.5	2.4	0.2	0.3	14.0	0.1	73	1	5	2
46	6.8	4.7	7.6	77.3	70.6	3.5	3.2	0.3	1.4	13.0	0.1	28	5	10	5
47	2.3	3.3	5.4	86.1	83.5	2.9	1.8	0.3	0.7	10.0	0.1	25	1	3	4
48	1.7	3.3	7.3	78.0	70.4	9.6	1.8	0.1	0.2	9.5	0.1	23	1	4	1
49	3.0	2.1	9.2	79.7	84.5	6.1	4.0	0.5	0.6	11.5	0.2	6	1	14	5
50	3.8	19.8	15.2	56.1	85.7	6.0
51	2.0	3.7	26.8	70.2	72.4	5.2	8.5	1.4	0.4	9.5	1.3	55	4	6	3
52	41.9	7.9	15.9	33.3	49.7	1.6	0.5
53	1.5	5.4	6.4	85.6	60.0	3.2	1.4	0.5	1.1	13.0	0.1	23	6	15	2
54	1.5	6.3	11.3	73.8	57.8	8.2	1.8	0.5	1.4	30.5	0.6	24	8	23	5
55	44.2
56	78.9	7.3
57	2.3	2.9	5.6	88.4	47.8	1.1	0.9	0.4	0.5	12.1	1.3	54	1	51	74
58	3.1	2.3	5.6	86.9	63.0	2.2
59	58.8	5.5	7.7	25.8	46.8	2.5	0.5	0.1	0.4	9.5	0.1	25	1	5	3
60	55.6	7.6	6.1	28.7	51.2	2.5	0.4	0.2	1.0	10.8	0.1	39	1	5	4
61	63.8	8.2
62	1.7	2.5	9.0	84.2	61.2	2.6	0.9	0.2	0.4	8.0	0.1	25	3	8	2
63	3.2	2.8	5.7	83.4	63.8	6.3	1.0	0.3	0.4	15.7	0.3	205	1	3	1
64	0.8	5.2	16.4	72.4	53.9	5.3	1.6
65	3.5	5.2	15.7	75.8	67.2	4.8	0.6	0.1	0.4	21.6	0.2	33	1	8	1

TABLE A2. Continued.

Species	Lip-ids (%)	Pro-tein (%)	Fi-ber (%)	NSC* (%)	WCF† (%)	Ash (%)	Ca (g/kg)	Mg (g/kg)	P (g/kg)	K (g/kg)	Na (g/kg)	Fe (mg/kg)	Mn (mg/kg)	Zn (mg/kg)	Cu (mg/kg)
66	1.1	3.2	10.2	75.8	50.7	9.8	0.7	0.2	0.4	12.0	0.1	44	1	3	1
67	2.2	4.1	27.9	60.8	68.9	5.0	1.3	0.3	0.9	17.5	0.2	29	1	4	2
68	73.9
69	0.7	3.6	46.0	47.7	57.5	2.0	1.8	0.3	0.7	10.0	0.2	18	1	17	5
70	0.9	6.8	5.6	81.7	55.8	5.1
71	1.2	3.2	4.4	69.7	70.5	...	1.0	0.1	0.1	8.5	0.1	13	1	2	2
72	5.4	3.8	9.9	76.6	57.6	4.2	3.7	0.3	0.6	13.5	0.2	19	3	6	3
73	0.9	5.1	4.6	88.2	53.2	1.2
74	64.7
75	36.9	4.8	17.6	37.4	8.5	1.8	2.4	0.6	1.7	10.0	0.2	125	7	20	9
76	2.9	3.5	14.0	75.0	74.4	4.7
77	2.8	4.3	15.3	72.5	55.2	5.1	5.2	0.3	0.3	11.0	0.1	13	5	3	1
78	1.7	4.1	15.6	72.6	50.7	5.9	6.8	1.1	0.7	17.3	0.2	18	8	5	3
79	57.3	2.6
80	1.6	5.4	15.3	71.7	57.4	6.0	6.2	0.6	1.4	14.5	0.1	15	7	4	2
81	3.6	4.0	13.2	73.2	61.1	6.0	6.7	0.6	0.9	15.0	0.2	25	8	19	4
82	9.9	5.2	14.8	64.5	76.9	5.9	10.3	0.9	1.6	18.0	0.3	93	6	21	5
83	80.3
84	74.4	2.1
85	0.9	5.5	14.9	73.8	61.2	5.3	2.0	0.3	0.5	18.0	0.1	44	5	15	3
86	3.0	6.0	20.6	60.8	71.9	9.7
87	77.0
88	3.3	18.0	20.5	52.7	81.6	5.5
89	22.8	12.8	8.2	49.1	83.2	7.1	3.4	1.0	3.1	21.5	0.1	38	7	18	10
90	2.1	5.3	15.7	68.5	66.8	8.7	5.3	0.6	1.2	37.6	0.3	120	11	25	9
91	77.5
92	78.9
93	2.8	3.0	30.1	61.6	53.2	2.4	2.2	0.4	1.1	10.4	0.2	15	1	6	4
94	3.1	3.2	15.9	76.1	76.6	1.7	1.6	0.4	1.3	9.0	0.2	29	1	3	6
95	1.3	2.8	46.4	47.3	52.0	2.2	1.9	0.2	0.6	8.5	0.2	15	1	4	4
96	2.2	2.4	25.6	66.2	66.2	3.6	0.5
97	3.5	2.5	19.6	72.2	69.3	2.2	1.3	0.3	0.6	7.5	0.4	6	1	3	5
98	2.9	1.9	35.0	56.1	54.8	4.1	2.5	0.3	0.2	13.0	0.1	13	1	4	3
99	3.2	4.1	12.9	67.0	79.8	13.1	10.3	1.0	0.2	42.6	0.2	70	5	9	4
100	0.2	2.3	2.6	93.5	66.3	1.4	0.2	0.1	0.4	6.0	0.2	25	1	5	1
101	78.5
102	82.7
103	2.6	1.7	26.0	66.9	62.7	2.8	1.1	0.3	0.6	11.5	0.2	25	1	14	9
104	4.2	1.0	8.4	82.9	77.6	3.6	1.1	0.2	0.5	11.0	0.2	38	1	3	4
105	21.6	3.7	37.0	34.0	29.5	4.3	5.3	0.9	0.8	17.6	0.4	122	12	24	5
106	8.6	4.1	9.5	73.9	76.9	3.9	1.3	0.5	1.4	15.0	0.1	38	3	10	2
107	14.3	5.9	15.1	60.2	71.4	4.6	2.5	0.6	1.6	20.5	0.2	30	3	12	14
108	1.7	2.4	6.5	86.8	71.4	2.5	2.2	0.7	0.4	12.5	0.2	23	1	4	2
109	1.2	2.4	17.6	76.8	49.8	2.0	1.3	0.3	0.7	8.0	0.3	6	3	39	6
110	5.4	2.4	15.4	74.3	80.7	2.5	0.7	0.3	0.7	8.5	0.1	13	2	2	3
111	1.6	11.8	11.6	0.7	0.3	0.7	20.0	0.2	26	5	4	1

* NSC = nonstructural carbohydrate.

† WCF = water content of the whole fruit (seeds plus pulp).