

SOME COMMENTS ON STILES' PAPER ON TEMPERATE  
BIRD-DISSEMINATED FRUITS

Stiles (1980) presented an interesting overview of the patterns of presentation and dispersal of bird-disseminated fruits of woody plants in the eastern deciduous forest of North America. Based mainly on literature records, he found that bird-disseminated fruits fall naturally into four major types, depending on characteristics of nutrient content, seed size, and persistence on the plant after ripening. He interpreted the existence of these distinct fruit types as the evolutionary outcome of the combined selective pressures posed on plants by seed dispersal agents and fruit-damaging organisms. I believe some of his conclusions are not adequately supported by the data used in the analyses. My objections fall into three categories: (1) inconsistencies in the classification of fruits into the four types, namely summer small-seeded (SS), summer large-seeded (SL), fall low-quality (FL), and fall high-quality (FH); (2) serious sampling deficiencies; and (3) inadequacy of the figures used to characterize the nutritive quality of fruits.

Table 1 in Stiles' paper shows some internal inconsistencies with regard to the classification of species into fruit types. No explicit statement is provided on the procedures followed to categorize species, and some puzzling assignments occur. *Cornus alterniflora*, *C. amomum*, *Sassafras albidum*, and *Rhamnus alnifolius*, all fruiting in summer (July-September) and rapidly dispersed, are placed in the FH class, whereas many other species with fruits available in the same period are included in either SS or SL categories (e.g., *Lonicera glaucescens*, *Prunus pennsylvanica*, *P. serotina*, *P. virginiana*, *Rubus allegheniensis*, *Rubus odoratus*, *Vaccinium* spp.). The five *Lonicera* species are presented as SS, despite the fact that data on seed size are provided for only a single species. In contrast, many species with complete data on fruiting dates and seed size are assigned to neither fruit type and question marks are presented instead (e.g., *Aralia hispida*, *A. spinosa*, *Bumelia lanuginosa*, *C. canadensis*, *Euonymus americanus*, *P. pumilia*, *Sambucus glauca*, *Sambucus pubens*, *Shepherdia canadensis*, and the three *Nyssa* species).

Among fall-fruiting species the only consistent difference between FH and FL types is apparently lipid content (summary at the bottom of table 1). *Rhus glabra* (22.4% lipids), *Rhus copallina* (26.1%), and *Myrica cerifera* (23.2%) are classed among FL species, while for instance *C. florida* (16.7%) is in the FH class. Stiles argued that the irregular classification of the former three species was because of their thin pericarps. Nevertheless, the arils of *Euonymus* seeds are also very thin, yet some of the species in this genus are included in the FH group even in absence of actual data on lipid content (*E. atropurpurens*, *E. obovatus*). *Cornus florida* and *C. racemosa*, with data on lipid content available, are placed in the FH class. No data on lipid values are given for the remaining six species in the genus, but they

were equitably partitioned among the FH, FL, and “question mark” groups (two species each).

The above inconsistencies reveal that the formal criteria used by Stiles to separate fruit types were, at best, extremely loose, and that replication of his classification would hardly be feasible. Using a conservative estimate of 15 species inconsistently assigned to fruit type, and adding this figure to the number of species in the question mark class, makes a total of 51 species. Hence at least 42% of all species in table 1 do not neatly belong to any fruit class. This raises further doubts on the actual existence of the suggested distinct fruit categories.

Actual data on lipid content of fruits are presented for only 29 species out of a total of 128 listed in his table 1. Information on seed size is available for 107 species, and complete data on the period of fruit availability are presented for 102 species. Information on sugar content of fruits is absent from table 1, yet sugar content (as measured by sweetness to human taste) is taken as one of the four criteria characterizing fruit types. In fact, the full set of data characterizing fruit types (fruiting season, lipid value, and seed size) is provided for only 23 species. Nevertheless, as many as 92 species were assigned to one of the four fruit classes in the summary at the bottom of the table. Data on nutrient (lipid) quality are available for only 3 of the 27 SS species, 1 of the 5 SL species, 3 of the 9 FH species, and 16 of the 51 FL species. Since nutrient quality is the single feature consistently separating FH and FL types, the reader cannot tell how as many as 91 species were assigned to one or other of these groups without having actual data on nutrient quality, unless hidden assumptions are involved in the procedure.

SS and SL species are both characterized, according to Stiles, by having low lipid level. Nevertheless, this trend is only barely supported, as it is based on data from only 4 species out of a total of 32 in these two classes. The suggested pattern of lower lipid content among summer fruits disappears if one simply includes in this group species such as *Solanum dulcamara* (28.77% lipids), *Sambucus canadensis* (12.94/16.0%), and *Magnolia acuminata* (21.99%), all of which fruit in summer and have data on seed size and lipid content in table 1, but which are inexplicably left by Stiles without any assignment to fruit type. Furthermore, he missed the lipid content data for seven species in his table 1 which are in fact available in Short and Epps (1977), one of his two bibliographical sources for fruit quality (although an explicit statement regarding this is not found in the paper). Four of these missed species are presented in table 1 as FL, and the remaining three (*Aralia spinosa*, *M. grandiflora*, *M. virginiana*) are in the question mark class. These latter three species fruit in summer and their lipid values, according to Short and Epps (1977), are 16.9, 11.3, and 38.5%, respectively. If one compares these figures with those corresponding to SL and SS species in table 1 (4.45, 3.86, 7.58, and 3.80%), the conclusion emerges that the missing species are not a random subsample of summer-fruiting species with regard to lipid content. Had Stiles included lipid values of the former, it would have become evident that the suggestion of lower lipid levels among summer-fruiting species lacks any factual basis.

These sampling deficiencies cast serious doubts on both the actual occurrence of the four fruit types recognized by Stiles and the validity of the proposed

differences between them. Although his table 1 looks impressive at first glance, the four fruit types do not actually emerge from the analysis of a 128-species sample, but rather from an extremely reduced subset comprising less than 25% of total species. The summary at the bottom of the table is in fact little more than a gathering of tentative species assignments. On the other hand, irregularities in species assignments and the abundant use of the question mark class for species with complete data, all strongly suggest fuzzy limits between fruit categories.

The most serious criticism to Stiles' paper, however, relates to the figures used to describe nutrient quality of fruits. For 16 of the 29 species with lipid values in table 1 he explicitly indicated that the figures presented correspond to analyses of whole fruits (pericarp and seeds together). Nevertheless, after screening the original data sources used (Wainio and Forbes 1941; Short and Epps 1977) I found that the data for most of the remaining species also come from the analysis of whole fruits (see Short and Epps 1976, 1977). In fact, only for two species (*Lindera benzoin*, *P. virginiana*) is the actual lipid value of pericarp alone shown. Hence, the vast majority of Stiles' data on fruit quality refer to whole fruits.

Lipid content figures resulting from the analysis of whole fruits depend simultaneously on (1) pulp/seed dry weight ratio, (2) lipid content of seeds, and (3) lipid content of pericarp. 1 and 2 vary greatly among plant taxa (Levin 1974; White 1974; Herrera 1981a). Pericarp/seed dry weight ratios for five species in Stiles' list (*Ilex opaca*, *C. florida*, *Lindera benzoin*, *P. pennsylvanica*, *Sorbus americana*) range from 0.22 to 5.00 (computed from figures in White [1974]). Depending on the value of this ratio, lipid content of whole fruits will be closer to the lipid content of either seeds (<1) or pericarp (>1). Interspecific comparisons of the lipid content of whole fruits tell us almost nothing about the actual nutrient content of pericarp alone, unless appropriate information on 1 and 2 above is included. Since these latter two components presumably vary independently, no straightforward, predictable relationship is to be expected a priori between the lipid content of whole fruits and corresponding figures for the pericarp alone. Nutritive value of the pulp, along with the relative pericarp richness of the fruit, is what is of interest to seed dispersers (e.g., Snow 1971; McKey 1975; Howe and Vande Kerckhove 1980; Herrera 1981b), since this is the only fruit component useful to legitimate dispersers (which do not digest seeds). Consequently, Stiles' figures on fruit nutrient quality have an uncertain meaning in relation to the actual reward offered by the plants to dispersers.

To summarize, those conclusions in Stiles' paper which rely on the existence of four distinct fruit adaptive types must be seriously questioned for the following reasons. (1) The figures used to describe the nutritive quality of fruits to dispersers are, at best, only very indirectly related to their actual food value. (2) Even if these figures are consistently and linearly correlated with actual fruit profitability, the existence of a seasonal pattern in fruit quality is based on a very limited set of data and it disappears after correcting for some irregularities and omissions in the data. Distinctness of fruit types is further contradicted by irregularities in Stiles' own assignment of species to fruit categories. (3) Even if four fruit adaptive types actually exist in the forests studied by Stiles, his conclusions should be applicable only to the small, probably unrepresentative subset of species for which complete

data exist (11%–33% of total species in each category). Generalizations to the entire fruit-producing flora in the region, with which presumably the entire set of avian dispersers has interacted in ecological and evolutionary time, are not warranted by the data.

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