

Evolution of fruit types and seed dispersal: A phylogenetic and ecological snapshot

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Abstract Success of flowering plants is greatly dependent on effective seed dispersal. Specific fruit types aid different mechanisms of seed dispersal. However, little is known about what evolutionary forces have driven the diversification of fruit types and whether there were phylogenetic constraints on fruit evolution among angiosperm lineages. To address these questions, we first surveyed the orders and families of angiosperms for fruit types and found no clear association between fruit types and major angiosperm lineages, suggesting there was little phylogenetic constraint on fruit evolution at this level. We then surveyed fruit types found in two contrasting habitats: an open habitat including the Indian desert and North American plains and prairies, and a closed forest habitat of Australian tropical forest. The majority of genera in the survey of tropical forests in Australia were fleshy fruit trees, whereas the majority of genera in the survey of prairies and plains in central North America were herbs with capsules and achenes. Both capsules and achenes are frequently dispersed by wind in the open, arid habitat, whereas fleshy fruits are generally dispersed by animals. Since desert and plains tend to provide continuous wind to aid dispersal and there are more abundant mammal and bird dispersers in the closed forest, this survey suggests that fruit evolution was driven at least in part by dispersal agents abundant in particular habitats.

Key words adaptation, angiosperm, animal dispersal, fruit development, wind dispersal.

Seed dispersal is essential for the success of plant reproduction and adaptation. Germination and growth away from the mother plant allows opportunities to find advantageous areas to inhabit, in addition to avoiding unfavorable conditions around the mother plant such as inbreeding and sibling competition (Willson & Traveset, 2000). The origin of fruits of angiosperms was a major evolutionary innovation that greatly enhanced seed dispersal efficiency and triggered rapid diversification of flowering plants. However, little is known about the evolutionary force that drove rapid diversification of fruit types.

Fossil records since the Cretaceous show a diversity of dispersal mechanisms present in both gymnosperms and angiosperms. Abiotic seed dispersal (mostly wind dispersal) was most prominent during the Cretaceous period, but a small portion of possible animal-dispersed seeds may have existed in both gymnosperms and angiosperms (Eriksson et al., 2000a). Although animal dispersal existed in gymnosperms and angiosperms before the Tertiary, dinosaurs were not frugivores and closed forest systems were not present, therefore providing little selection pressure on earlier production of fleshy fruits (Tiffney, 2004). At the beginning of the Tertiary period, several

events might have had substantial impact on fruit evolution, especially the marked increase in the abundance and diversity of fleshy fruits (Eriksson et al., 2000a, b; Tiffney, 2004).

One event was climatic change, featured by global temperature cooling down and an increase in moisture. The other was the extinction of dinosaurs and subsequent radiation of birds and mammals. Both events allowed the development of closed forest systems in the early Tertiary and the radiation of fleshy fruits, which was coupled with animal diversification in the forest habitats (Bolmgren & Eriksson, 2005).

The development of closed forests had several consequences. First, little wind travels through closed systems, making wind dispersal, especially for understory plants, more difficult. Second, the lack of light in closed forest communities favored larger seeds whose seedlings could have better chances to establish under the shaded conditions. The large seeds were more effectively dispersed by animals than by wind. Additionally, animals tended to deposit seeds in canopy gaps where there was adequate light to facilitate seedling establishment (Bolmgren & Eriksson, 2005). Finally, the closed forest systems increased the chance of interaction between plants and birds and mammals. The interaction was mutually beneficial, with plants providing nutritious fleshy fruits to

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animals and animals serving as effective agents for seed dispersal (Herrera, 1989; Clark et al., 2001). These factors greatly facilitated the co-radiation of fleshy fruits of angiosperms and the species of birds and mammals in the early Tertiary.

To better understand the evolution of fruit types during angiosperm diversification, we took two snapshots of the problem from phylogenetic and ecological perspectives. At first, we surveyed fruit types of all angiosperm orders and mapped them onto the angiosperm phylogeny. In this survey, we aimed to test the hypothesis that there were major shifts in fruit types during angiosperm diversification. If this was true, we should be able to observe shifts in fruit types associated with branches of the angiosperm phylogeny.

We surveyed 59 orders and 391 families for available fruit types (Table 1) from numerous websites and books (e.g., Angiosperm Phylogeny Website <http://www.mobot.org/MOBOT/Research/APweb/welcome.html>; The Families of Flowering Plants <http://delta-intkey.com/angio/>; Heywood, 1993; Kubitzki et al., 1993; Judd et al., 2002). We grouped various fruit types into three major categories: fleshy, dry dehiscent, and dry indehiscent. Fleshy fruits included berries, drupes, and pomes. Dry dehiscent fruits consisted of follicles and capsules (including siliques). Dry indehiscent fruits included samaras, schizocarps, nuts, and achenes (including utricles and caryopsis). The fruit types were mapped onto the phylogenetic tree from the Angiosperm Phylogeny Website. The visual inspection did not detect any association between fruit types and major clades (Fig. 1). Multiple fruit types are scattered across the angiosperm phylogeny. This indicates that there was little phylogenetic constraint on fruit evolution at least in this evolutionary scale. Fruit types may have evolved repeatedly within orders under natural selection.

This led us ask the question of whether fruit evolution has been driven by dispersal mechanisms. If the answer is positive, fruit types favored by dispersal mechanisms prevalent in certain habitats should be more abundant than other fruit types. To test this hypothesis, we conducted a second survey looking at fruit types present in different types of habitats. We predicted that fleshy fruits would be abundant in dense forest habitats that inhabit many vertebrates and birds, whereas open habitats with more available wind would have a higher proportion of dry fruits frequently dispersed by wind.

In addition to habitats, we considered that growth form was also important because different growth

forms have advantages for seed dispersal in certain habitats more than others. Willson and Traveset (2000) suggested that wind dispersed plants were tall relative to other plants in the habitat. Taller trees in the forests have better access to wind currents and therefore the seeds are more likely to be dispersed by wind. In contrast, understory plants in closed forest systems tend to not have access to enough wind for efficient dispersal, and may consequently favor other dispersal mechanisms.

We surveyed two contrasting habitats, with Australian tropical forests representing the closed forest system and both Central North American plains and Indian desert representing open habitats. The total of 786, 922, and 247 genera were surveyed for the Australian tropical forests (Cooper, 2004), Central North American plains (Rydberg, 1932), and Indian desert (Bhandari, 1978), respectively (The data sets are available from the authors upon request). We compared animal-dispersed fleshy fruits and fruits favored by wind dispersal including samara, capsule, and achene (Pijl, 1982). Follicles and nuts were treated as a separate category because dispersal mechanism varies between abiotic and biotic in these two fruit types. Growth forms were grouped into trees, shrubs to small trees, herbs, and vines or mistletoes. Several genera had more than one fruit type and/or growth form, and in some cases a variant fruit type matched up with a specific variant growth form. To account for these variations we made an additional value for a unique variation in a genus. For instance, when a genus had only one growth form and two different fruit types, 2 values were used to separate the fruit types. Some genera had two growth forms and two fruit types, in which case two separate values were assigned, but the specific fruit type and growth form it corresponded to were coupled.

The results of the survey are presented as percent of genera that had particular fruit types in the given habitat. Figures 2A, C, and E display values for fruit types of each growth form and Figures 2B, D, and F help visualize the relative abundance of fruit types in each habitat. The fruit types are categorized according to the most frequent dispersal mechanism in the habitats, including fleshy fruits primarily dispersal by animals, dry fruits (capsule, samara, achene) often dispersed by wind, and other dry fruits (follicle and nut) with uncertain frequency of biotic and abiotic dispersal.

Australian tropical forests had the most diverse fruit types and growth forms (Fig. 2: A, B). The majority of genera were fleshy fruit trees. The following

Table 1 Fruit types surveyed in families of angiosperms. Families were grouped into orders corresponding to the phylogenetic tree from the Anigospem Phylogeny Website

Order	Family	Fruit type	Order	Family	Fruit type
Amborellales	Amborellaceae	drupe		Luzuriagaceae	capsule, berry
Nymphaeaceae	Cabombaceae	follicle, achene		Alstroemeriaceae	capsule, berry
	Nymphaeaceae	berry, nut		Rhipogonaceae	berry
Austrobaileyales	Austrobaileyaceae	berrylet		Philesiaceae	berry
	Illiciaceae	Follicle		Smilacaceae	berry
	Trimeniaceae	berry		Liliaceae	capsule, berry
Chloranthales	Chloranthaceae	drupaceous	Asparagales	Orchidaceae	capsule
Magnoliales	Myristicaceae	follicle (aril)		Blandfordiaceae	capsule
	Magnoliaceae	follicle (aril), samara		Lanariaceae	capsule
	Degeneriaceae	follicle		Asteliaceae	berry, capsule
	Himantandraceae	drupe		Hypoxidaceae	berry, capsule
	Annonaceae	berry		Ixioliriaceae	capsule
Laurales	Calycanthaceae	achene, drupe		Tecophilaeaceae	capsule
	Gomortegaceae	drupe		Doryanthaceae	capsule
	Atherospermataceae	achene		Iridaceae	capsule
	Monimiaceae	drupe, achene		Xanthorrhoeaceae	capsule
	Hernandiaceae	samara, nut		Hemerocallidaceae	capsule, berry, nut
	Lauraceae	drupe, berry		Asphodelaceae	capsule
Canellales	Winteraceae	berry, follicle		Alliaceae	capsule
	Canellaceae	berry		Amaryllidaceae	capsule, berry
Piperales	Aristolochiaceae	capsule, berry, follicle		Aphyllanthaceae	capsule
	Piperaceae	drupe		Hyacinthaceae	capsule
	Saururaceae	capsule, or dry indehiscent		Agavaceae	capsule
Acorales	Acoraceae	berry		Asparagaceae	berry
Alismatales	Araceae	berry, capsule		Ruscaceae	berry
	Hydrocharitaceae	berry, capsule	Unplaced	Dasypogonaceae	capsule
	Alismataceae	achene	Arecales	Arecaceae	berry, drupe
	Limnocharitaceae	follicle	Poales	Rapateaceae	capsule
	Scheuchzeriaceae	follicle		Sparganiaceae	drupe, nut
	Aponogetonaceae	follicle		Typhaceae	drupe, achene like follicle
	Juncaginaceae	achene, follicle		Bromeliaceae	capsule, berry
	Posidoniaceae	spongy pericarp, dehiscent		Thurniaceae	capsule
	Ruppiceae	drupelet		Juncaceae	capsule
	Cymodoceaceae	achene, drupelet		Cyperaceae	achene
	Zosteraceae	achene		Mayacaceae	capsule
	Potamogetonaceae	achene, drupe		Eriocaulaceae	capsule
Petrosaviales	Petrosaviaceae	follicle		Xyridaceae	capsule
Dioscoreales	Nartheceaceae	capsule		Anarthriaceae	nut
	Taccaceae	berry, capsule		Centrolepidaceae	follicle
	Thismiaceae	capsule		Restionaceae	capsule, achene, nut
	Burmanniaceae	capsule		Flagellariaceae	drupe
	Dioscoreaceae	capsule, berry, samara		Joinvilleaceae	drupe
Pandanales	Velloziaceae	capsule		Ecdeiocoleaceae	achene, capsule
	Triuridaceae	achene		Poaceae	achene
	Stemonaceae	capsule (indehiscent of dehiscent)	Commelinales	Commelinaceae	capsule
	Pandanaceae	drupe, berry		Hanguanaceae	drupe
	Cyclanthaceae	berry		Philydraceae	capsule
Liliales	Corsiaceae	capsule		Haemodoraceae	capsule
	Campynemataceae	capsule		Pontederiaceae	capsule, nut
	Melanthiaceae	capsule	Zingiberales	Musaceae	berry
	Petermanniaceae	berry		Heliconiaceae	drupe, schizocarp
	Colchicaceae	capsule		Strelitziaceae	capsule (with aril)

Table 1 (continued)

Order	Family	Fruit type	Order	Family	Fruit type
	Lowiaceae	capsule		Cactaceae	berry
	Cannaceae	capsule	Santalales	Erythralaceae	drupe
	Marantaceae	capsule, berry		Olaceae	drupe, nut
	Zingiberaceae	capsule, berry		Misodendraceae	achene, nut
	Costaceae	capsule, nut, achene		Loranthaceae	berry, samara, drupe, nut
Ranunculales	Eupteleaceae	samara		Opiliaceae	drupe
	Lardizabalaceae	follicle, berry		Balanophoraceae	drupe, nut
	Circaeasteraceae	achene		Santalaceae	drupe, nut
	Menispermaceae	drupe		Viscaceae	berry
	Berberidaceae	berry	Saxifragales	Cercidiphyllaceae	capsule, follicle
	Ranunculaceae	follicle, achene, berry		Peridiscaceae	drupe, capsule
	Papaveraceae	capsule		Daphniphyllaceae	drupe
Sabiales	Sabiaceae	drupe		Hamamelidaceae	capsule
Proteales	Nelumbonaceae	nut		Altingiaceae	capsule
	Platanaceae	achene		Paeoniaceae	follicle
	Proteaceae	follicle, nut, achene, drupe		Crassulaceae	follicle
Trochodendrales	Trochodendraceae	follicle		Tetracarpaeaceae	follicle
Buxales	Didymelaceae	drupelet		Penthoraceae	follicle
	Buxaceae	capsule, drupe		Haloragaceae	drupe, nut
Gunnerales	Gunneraceae	drupe, nut		Cynomoriaceae	nut
	Myrothamnaceae	follicle		Iteaceae	capsule
Berberidopsidales	Aextoxicaceae	drupe (dry)		Pterostemonaceae	capsule
	Berberidopsidaceae	berry		Grossulariaceae	berry
Dilleniales	Dilleniaceae	follicle, achene		Saxifragaceae	capsule
Caryophyllales	Rhabdodendraceae	drupelet	Vitales	Vitaceae	berry
	Droseraceae	capsule	Zygophyllales	Krameriaceae	achene
	Nepenthaceae	capsule		Zygophyllaceae	capsule
	Drosophyllaceae	capsule	Celastrales	Celastraceae	capsule, drupe
	Ancistrocladaceae	nut		Lepidobotryaceae	capsule
	Dioncophyllaceae	capsule		Parnassiaceae	capsule
	Frankeniaceae	capsule		Pottingeriaceae	capsule
	Tamaricaceae	capsule	Oxalidales	Connaraceae	follicle, drupe
	Plumbaginaceae	capsule		Oxalidaceae	capsule, berry
	Polygonaceae	nut, achene		Cunoniaceae	follicle, drupe, nut, capsule
	Simmondsiaceae	capsule		Brunelliaceae	follicle
	Asteropeiaceae	capsule		Cephalotaceae	follicle
	Physenaceae	capsule		Elaeocarpaceae	capsule, drupe, berry
	Caryophyllaceae	capsule, nut	Malpighiales	Achariaceae	berry
	Achatocarpaceae	berry (with aril)		Violaceae	capsule, berry
	Amaranthaceae	achene, capsule		Salicaceae	capsule, berry, drupe
	Stegnospermataceae	capsule		Lacistemataceae	capsule
	Limeaceae	capsule		Turneraceae	capsule
	Lophiocarpaceae	achene, capsule		Malesherbiaceae	capsule
	Barbeuiaceae	capsule		Passifloraceae	berry, capsule
	Aizoaceae	capsule, berry, nut		Goupiaceae	drupe
	Phytolaccaceae	berry		Putranjivaceae	drupe
	Nyctaginaceae	achene, nut		Lophopyxidaceae	samara
	Molluginaceae	capsule		Clusiaceae	capsule, berry, drupe
	Halophytaceae	nutlet		Bonnetiaceae	capsule
	Basellaceae	utricle		Hypericaceae	berry, drupe
	Montiaceae	capsule		Malpighiaceae	samara, drupe, berry, nut
	Didiereaceae	capsule		Elatinaceae	capsule
	Portulacaceae	capsule		Ochnaceae	drupe, berry

Table 1 (continued)

Order	Family	Fruit type	Order	Family	Fruit type
	Medusagynaceae	capsule, follicle		Sapindaceae	capsule, drupe, berry
	Quiinaceae	berry, follicle		Nitrariaceae	capsule, nut
	Phyllanthaceae	drupe	Huerteales	Dipentodontaceae	capsule
	Picrodendraceae	drupe		Gerrardinaceae	berry
	Balanopaceae	drupe		Tapisciaceae	drupe, berry
	Trigoniaceae	capsule, samara	Malvales	Neuradaceae	capsule, follicle
	Dichapetalaceae	drupe		Thymelaeaceae	berry, drupe, achene-like
	Chrysobalanaceae	drupe		Sphaerosepalaceae	capsule
	Euphroniaceae	capsule		Bixaceae	capsule
	Caryocaraceae	drupe		Cistaceae	capsule
	Centroplacaceae	capsule		Sarcolaenaceae	achene, nut, capsule
	Ctenolophonaceae	nut		Dipterocarpaceae	nut
	Erythroxylaceae	drupe		Muntingiaceae	berry
	Humiriaceae	drupe	Brassicales	Malvaceae	capsule, nut, follicle
	Irvingiaceae	drupe, samara		Akaniaceae	capsule
	Ixonanthaceae	capsule		Tropaeolaceae	samara, nut, drupe
	Linaceae	capsule, drupe, nut		Moringaceae	capsule
	Pandaceae	drupe, capsule		Caricaceae	berry
	Rafflesiaceae	berry, capsule		Setchellanthaceae	capsule, silique
	Rhizophoraceae	capsule, berry		Limnanthaceae	nut
Cucurbitales	Anisophylleaceae	drupe, samara, capsule		Koerberliniaceae	berry
	Corynocarpaceae	drupe		Bataceae	drupe
	Coriariaceae	achene, nut		Salvadoraceae	berry, drupe
	Cucurbitaceae	berry, capsule		Pentadiplandraceae	berry
	Tetramelaceae	capsule		Resedaceae	berry, capsule, follicle
	Datisceae	capsule		Gyrostemonaceae	achene
	Begoniaceae	capsule, berry		Tovariaceae	berry
Fagales	Fagaceae	capsule, nut		Capparidaceae	berry
	Myricaceae	drupe, achene		Cleomaceae	silique
	Juglandaceae	nut, drupe, nutlet		Brassicaceae	berry, capsule, silique
	Rhoipteleaceae	samara	Cornales	Loasaceae	capsule
	Ticodendraceae	drupe		Hydrangeaceae	drupe, samara
	Betulaceae	achene, samara, nut		Nyssaceae	drupe
	Casuarinaceae	samara		Cornaceae	drupe
Fabales	Polygalaceae	capsule, samara, drupe, berry, nut		Curtisiaceae	drupe, achene-like
	Surianaceae	berry, drupe, nut		Grubbiaceae	capsule
	Fabaceae	samara, follicle, achene, drupe, berry		Hydrostachyaceae	capsule, drupe
Rosales	Barbeyaceae	nut	Ericales	Balsaminaceae	capsule
	Cannabaceae	achene, drupe		Marcgraviaceae	berry
	Dirachmaceae	follicle		Tetrameristaceae	capsule
	Elaeagnaceae	achene (drupe-like)		Polemoniaceae	capsule
	Moraceae	drupe, achene		Fouquieriaceae	capsule
	Rhamnaceae	drupe, samara		Sladeniaceae	capsule
	Rosaceae	achene, drupe, follicle, pome		Pentaphylacaceae	berry
	Ulmaceae	nut, samara		Sapotaceae	berry
	Urticaceae	drupe, achene		Ebenaceae	drupe
	Celtidaceae	drupe		Maesaceae	berry, drupe
Sapindales	Kirkiaceae	achene, nut		Theophrastaceae	capsule
	Rutaceae	drupe, berry, samara, follicle, capsule		Primulaceae	drupe
	Meliaceae	samara, drupe		Myrsinaceae	berry, capsule
	Simaroubaceae	drupe		Mitrastemonaceae	capsule
	Anacardiaceae	drupe, dehiscent drupe		Theaceae	drupe, berry
	Burseraceae	capsule, berry, drupe, samara		Symplocaceae	capsule, drupe, samara

Table 1 (continued)

Order	Family	Fruit type	Order	Family	Fruit type
	Styracaceae	capsule		Verbenaceae	capsule
	Diapensiaceae	capsule, berry		Boraginaceae	drupe, samara
	Actinidiaceae	capsule	Solanales	Montiniaceae	capsule
	Roridulaceae	capsule		Sphenocleaceae	capsule
	Sarraceniaceae	capsule		Hydroleaceae	capsule
	Clethraceae	drupe, samara		Convolvulaceae	berry, capsule
	Cyrtillaceae	capsule, berry, drupe		Solanaceae	capsule, drupe, nut
unplaced	Ericaceae	capsule	Aquifoliales	Cardiopteridaceae	drupe
	Oncothecaceae	drupe		Stemonuraceae	berry
	Icacinaceae	samara		Phyllonomaceae	drupe
Garryales	Eucommiaceae	berry		Helwingiaceae	drupe
	Garryaceae	nut, drupe		Aquifoliaceae	drupe
unplaced	Boraginaceae	capsule, drupe, berry	unplaced	Polyosmaceae	capsule, berry
Gentianales	Rubiaceae	capsule		Escalloniaceae	follicle, capsule
	Gentianaceae	capsule, drupe, berry, follicle		Paracryphiaceae	capsule
	Loganiaceae	capsule		Sphenostemonaceae	drupe
	Gelsemiaceae	follicle, drupe, berry	Asterales	Rousseaceae	capsule, berry
	Apocynaceae	capsule		Campanulaceae	berry
Lamiales	Plocospermataceae	capsule, samara, drupe, berry		Pentaphragmataceae	berry
	Oleaceae	nut		Alseuosmiaceae	drupe
	Tetrachondraceae	capsule		Phellinaceae	capsule, drupe
	Calceolariaceae	capsule, berry		Argophyllaceae	capsule
	Gesneriaceae	capsule		Stylidiaceae	capsule, berry
	Acanthaceae	capsule, berry		Menyanthaceae	capsule, drupe, nut
	Bignoniaceae	capsule		Goodeniaceae	achene-like
	Byblidaceae	capsule		Calyceraceae	achene
	Cyclocheilaceae	drupe, nutlet		Asteraceae	drupe
	Lamiaceae	capsule	Dipsacales	Diervillaceae	drupe, berry, capsule, achene
	Lentibulariaceae	capsule		Caprifoliaceae	berry, drupe
	Martyniaceae	schizo (drupelet), drupe		Linnaeaceae	achene-like
	Myoporaceae	capsule		Morinaceae	achene-like
	Paulowniaceae	schizo (nut), capsule		Dipsacaceae	samara, achene
	Phrymaceae	capsule	Apiales	Torricelliaceae	berry
	Plantaginaceae	berry		Griselinaceae	drupe, berry
	Schlegeliaceae	capsule, achene		Araliaceae	capsule, berry
	Scrophulariaceae	capsule		Pittosporaceae	samara
	Stilbaceae	drupe, nutlet		Myodocarpaceae	drupe

most abundant plants were vines and shrubs/small trees with fleshy fruits, and trees and shrubs/small trees with capsules. It should be noted that about one fifth of genera with capsules surveyed in this habitat had arils, and the majority of them were trees. This is worthy of attention since fruits with arils are commonly bird dispersed. Genera with samaras or achenes were less abundant.

Most angiosperm genera surveyed in the Prairies and Plains of Central North America were shrubs and herbs (Fig. 2: C, D). A high proportion of genera were herbs with capsules, followed by herbs with achenes. These two fruit types are generally dispersed by wind

in this habitat. The very few fleshy genera had various growth forms. Similarly, the majority of genera in the survey of the Indian desert are herbs with capsules and achenes (Fig. 2: E, F). Shrubs/small trees had the highest proportion of fleshy fruits relative to other growth forms in the Indian desert, with about an equal ratio of fleshy to wind dispersed fruits. Desert trees produced a higher ratio of wind dispersed fruits.

Overall, the majority of genera in the survey of tropical forests in Australia were fleshy fruit trees, while the majority of genera in the survey of prairies and plains in central North America were herbs with capsules and achenes. Both capsules and achenes are

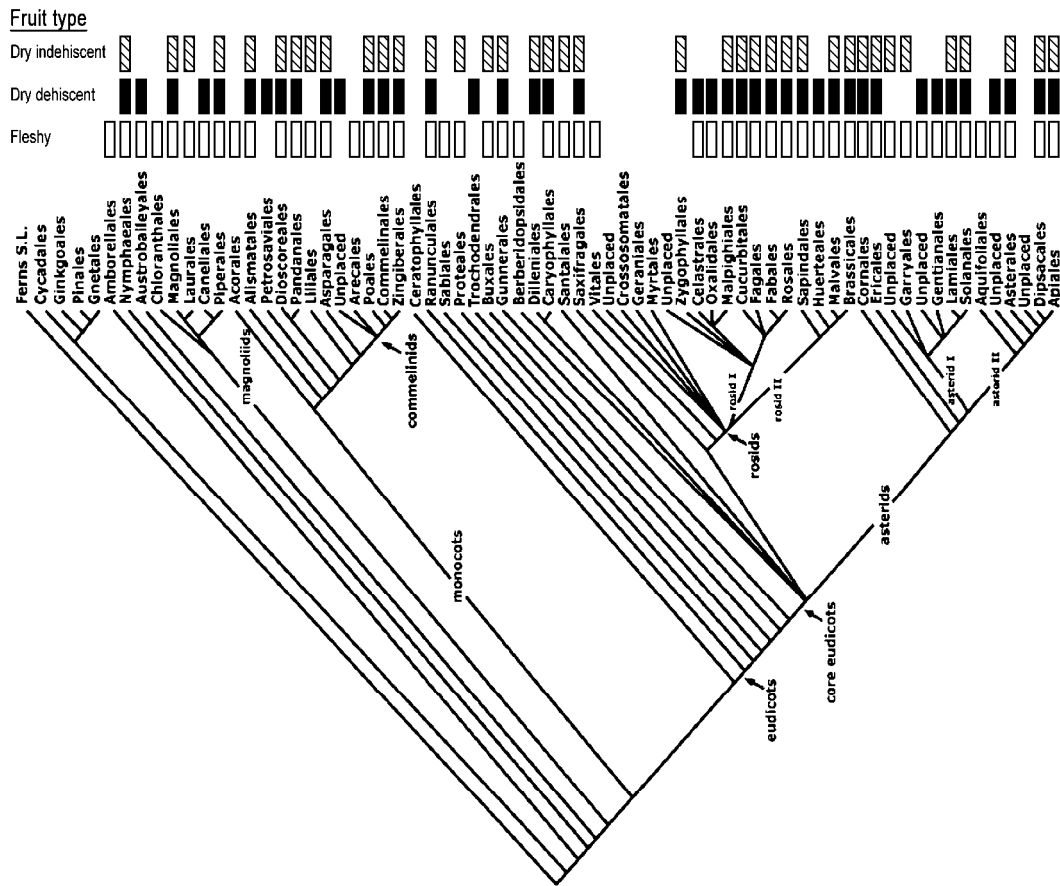


Fig. 1. Fruit types mapped on the phylogeny of angiosperm orders. Categories of fruit types include fleshy fruits (white bars), dry dehiscent fruits (back bars), and dry indehiscent fruits (hatched bars).

frequently dispersed by wind in these open and arid habitats, while fleshy fruits are generally dispersed by animals. Since desert and plains tended to provide continuous wind to aid dispersal, there may not be selective pressures for producing fleshy fruits that are developmentally more costly. However, the high abundance of fleshy fruits in the survey of Australian tropical forests may indicate a possible clue to selection pressures on angiosperms for fleshy fruits due to the high proportion of available mammal and bird dispersers relative to the open habitats. Moreover, trees, shrubs, and vines that have the positional advantage to attract birds have a higher proportion of fleshy fruits than herbs. Therefore, the survey supports the hypothesis that fruit evolution was driven at least in part by dispersal agents abundant in particular habitats.

This study perhaps raises more questions than it answers. While we showed that there lacked a phylogenetic constraint on fruit type evolution across

major lineages of angiosperms, one could easily ask how far down the phylogenetic hierarchy this holds true. There have been at least several molecular phylogenetic studies showing that the same fruit type evolved independently within an angiosperm family (Morgan et al., 1994; Smith, 2000; Knapp, 2002; Zjhra et al., 2004; Motley et al., 2005), suggesting that the phylogenetic constraint remains weak for families with variable fruit types. Many more investigations are needed at the familial and lower levels before any generalization can be made.

The ecological survey also needs to be expanded in habitat types and sample sizes so that the hypothesis can be statistically tested. Whenever possible, empirical observation should be conducted to conform the dispersal mechanisms, especially for fruits with unclear or multiple dispersal agents. For instance, in this survey capsules (not including capsules with arils) were considered to be generally wind dispersed. However, some plants with capsules have ballistic (or

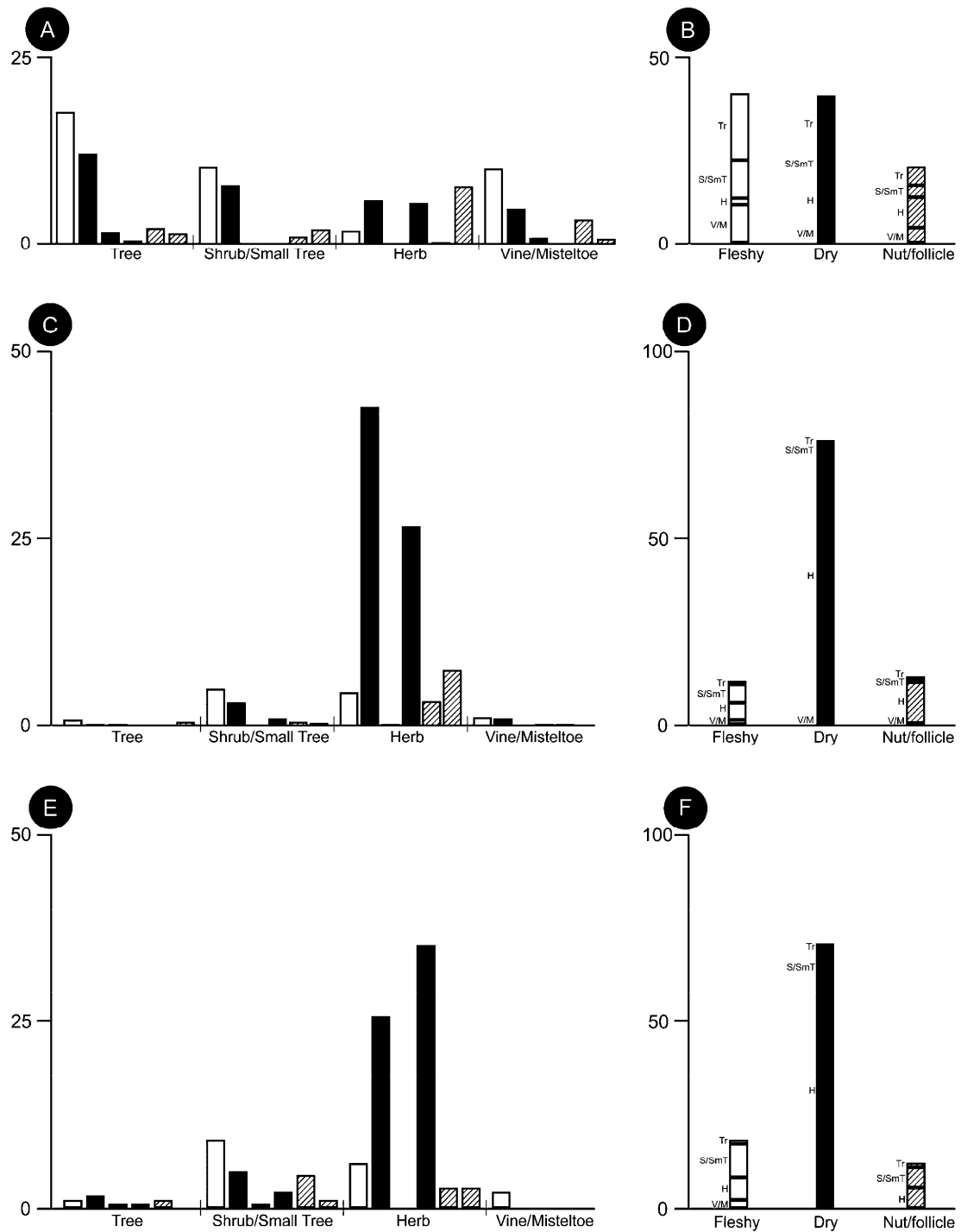


Fig. 2. Survey of fruit types in different habitats. **A, C, E,** Percent abundance of fruit types of specific growth forms in the Australian Tropical Forest, Prairies and Plains of Central North America, and Indian Desert, respectively. White bars: fleshy fruits; black bars: dry fruits from left to right, capsule, samara, and achene; hatched bars: dry fruits from left to right, follicle and nut. **B, D, F,** Percent abundance of growth forms for fleshy fruits, dry fruits often dispersed by wind (capsule, samara, and achene), and follicle and nut in the Australian Tropical Forest, Prairies and Plains of Central North America, and Indian Desert, respectively. Tr, tree; S/SmT, shrub and small tree; H, herb; V/M, vine and mistletoe.

explosive) dispersal methods that are successful in understory environments as well as open environments. This may in part explain the abundance of capsules in the closed tropical forests of Australia. In addition, many epiphytes have access to wind currents in tropical forests and can therefore rely on wind dispersal. Better knowledge of dispersal mechanisms would make surveys more accurate since it may serve as the source of selection pressure on fruit type and may reveal more information on the evolutionary patterns and significance of fruit types in various environments.

The combined phylogenetic and ecological analyses will begin to address the functional question of whether the developmental constraint on fruit types is weak enough to allow quick evolution of new fruit types in response to natural selection. Obviously, this question can also be addressed from developmental genetic approaches, which has lagged much behind floral evolutionary developmental studies. Nevertheless, such studies could be readily launched and considerably accelerated with the availability of genome sequences, functional genomic tools, and growing knowledge of genes controlling fruit development in model organisms (Liljegren et al., 2004; Tanksley, 2004; Kellogg, 2006).

References

- Bhandari MM. 1978. Flora of the Indian desert. India: United Book Traders.
- Bolmgren K, Eriksson O. 2005. Fleshy fruits—origins, niche shifts, and diversification. *Oikos* 109: 255–272.
- Clark CJ, Poulsen JR, Parker VT. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* 33: 606–620.
- Cooper W. 2004. Fruits of the Australian tropical rainforest. Australia: Nokomis Editions.
- Herrera CM. 1989. Seed Dispersal by Animals: A role in angiosperm diversification? *The American Naturalist* 133: 309–322.
- Eriksson O, Friis EM, Lofgren P. 2000a. Seed size, fruit size, and dispersal systems in angiosperms from the early Cretaceous to the late Tertiary. *The American Naturalist* 156: 47–58.
- Eriksson O, Friis EM, Pedersen KR, Crane PR. 2000b. Seed size and dispersal systems of early Cretaceous angiosperms from Famalicão, Portugal. *Plant Science* 161: 319–329.
- Heywood, VH. 1993. Flowering plants of the world. Updated Edition. New York: Oxford University Press.
- Judd WS, Campbell CS, Kellogg EA, Stevens PE, Donoghue MJ. 2002. Plant systematics: A phylogenetic approach. Sunderland, MA: Sinauer Associates.
- Kellogg EA. 2006. Progress and challenges in studies of the evolution of development. *Journal of Experimental Botany* 57: 3505–3516.
- Knapp S. 2002. Tobacco to tomatoes: a phylogenetic perspective on fruit diversity in the Solanaceae. *Journal of Experimental Botany* 53: 2001–2022.
- Kubitzki K, Rohwer JG, Bittrich V. 1993. The families and genera of vascular plants. Heidelberg, Berlin: Springer-Verlag.
- Liljegren S, Roeder A, Kempin S, Gremski K, Ostergaard L, Guimil S, Reyes D, Yanofsky M. 2004. Control of fruit patterning in *Arabidopsis* by INDEHISCENT. *Cell* 116: 843–853.
- Morgan DR, Soltis DE, Robertson KR. 1994. Systematic and evolutionary implications of *rbcL* sequence variation in Rosaceae. *American Journal of Botany* 81: 890–903.
- Motley TJ, Wurdack KJ, Delprete PG. 2005. Molecular systematics of the Catesbaeae-Chiococceae complex (Rubiaceae): flower and fruit evolution and biogeographic implications. *American Journal of Botany* 92: 316–329.
- Rydberg PA. 1932. Flora of the Prairies and Plains of Central North America. New York: New York Botanical Garden.
- Smith JF. 2000. A phylogenetic analysis of tribes Beslerieae and Napeantheae (Gesneriaceae) and evolution of fruit types: Parsimony and maximum likelihood analyses of *ndhF* sequences. *Systematic Botany* 25: 72–81.
- Tanksley SD. 2004. The genetic, developmental, and molecular bases of fruit size and shape variation in tomato. *Plant Cell* 16: S181–189.
- Tiffney BH. 2004. Vertebrate dispersal of seed plants through time. *Annual Review of Ecology, Evolution and Systematics* 35: 1–29.
- van der Pijl L. 1982. Principles of dispersal in higher plants. New York: Springer-Verlag.
- Willson MF, Traveset A. 2000. The ecology of seed dispersal. In: Fenner M ed. *Seeds: The ecology of regeneration in plant communities*. 2nd ed. Wallingford: CAB International. 85–110.
- Zjhra ML, Sytsma KJ, Olmstead RG. 2004. Delimitation of Malagasy tribe Coleae and implications for fruit evolution in Bignoniaceae inferred from a chloroplast DNA phylogeny. *Plant Systematics and Evolution* 245: 55–67.