

Characteristics of the vertebrate-dispersed fruits of sixteen Northern Territory monsoon forest tree species

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ABSTRACT

The monsoon forests of the Top End of the Northern Territory contain an unusually high proportion of tree species with vertebrate-dispersed fruits, but the corresponding fauna is disproportionately species-poor. We document and compare the morphology, moisture content, nutrient content and crop size of sixteen common fleshy- or arillate-fruited tree species from the region. Arils were much richer in lipids and lower in carbohydrates than fleshy fruits. A gradient of flesh nutrient contents from high levels of carbohydrates to high levels of nutrients that are more costly for the plant to produce was identified. However, this gradient was not related to other fruit characters, providing only weak support for the generalist-specialist paradigm in the evolution of vertebrate-dispersed fruits. Evidence was obtained of a trade-off between the size and number of fruits. Compared to other tropical regions, the flesh of the species sampled was high in carbohydrates and low in costly nutrients.

KEYWORDS: Top End, rainforest, dispersal, frugivory, nutrients, moisture content, fruit morphology, crop size, fleshy fruits, arillate fruits, birds, flying-fox.

INTRODUCTION

Fleshy fruits attract animals – particularly vertebrates but also ants and some other invertebrates – in order to disperse their seeds (van der Pijl 1982). Fruits vary in colour, size, structure, nutritional content and abundance, thus attracting different animal species, or the same species in different proportions and frequencies (Snow 1971; Willson and Whelan 1990; Wheelwright 1993; Schaefer *et al.* 2003; Bollen *et al.* 2004; Lord 2004). The consequences of this variation for dispersal, reproductive success and the evolution of fruit characters has received much observational, experimental and theoretical attention (e.g. McKey 1975; Stapanian 1982; Fleming *et al.* 1993; Jordano 1995; Levey *et al.* 2002).

Fleshy fruits evolved with the development of environments in which germination sites are shady and spatially unpredictable – in short, the tropical rainforest – where they are strongly associated with the diversification of woody plants (Bolmgren and Eriksson 2005). Within tropical forests, the proportion of trees that are vertebrate-dispersed is positively correlated with mean annual rainfall (Hartshorn 1983; Willson *et al.* 1989; Bullock 1995). It is perhaps surprising then, that 84% of 166 tree species in the mostly semi-deciduous monsoon rainforests (hereafter,

monsoon forests) of the Top End of the Northern Territory have fleshy, arillate or other vertebrate-dispersed fruits (Table 1). This percentage is at the high end of the range for all tropical forests (Howe and Smallwood 1982), similar to that reported for the evergreen rainforests of north Queensland (Webb and Tracey 1981), and much higher than the comparable rate of 51% in a seasonally dry tropical forest in Costa Rica (Frankie *et al.* 1974).

This anomaly may be the product of processes that favour vagility (Russell-Smith and Dunlop 1987). Monsoon forest patches in the Top End are small (Russell-Smith 1991), such that tree populations may lack viability unless genetic diversity is maintained by dispersal among patches (Russell-Smith and Lee 1992; Shapcott 1998, 1999). Furthermore, the region's monsoon forest estate has expanded from Pleistocene refugia (Shapcott 2000), and many patches are on recent (Holocene) landforms (Russell-Smith and Dunlop 1987), a process demanding effective long-distance dispersal.

However, this richness amongst trees has no parallel amongst the frugivores able to provide dispersal services to them. There are at most eight obligate, non-destructive frugivores in Top End monsoon forests, all of which are birds, and an additional six opportunistically but

Table 1. Fruit types of the flowering plants of Top End monsoon forests and their assumed dispersal agents, summarised from Russell-Smith and Dunlop (1987). Presented fruits are dry, brightly coloured or glistening, and exposed when ripe so as to attract vertebrates; it corresponds to the mimetic endozoochore class of bird-dispersed plants as described by van der Pijl (1982).

| Fruit type (dispersal agents) | % of species | | |
|--------------------------------------|-----------------------|------------------------------|-----------------------|
| | Trees n = 166 spp. | Other plants n = 161 spp. | Total n = 327 spp. |
| Fleshy (vertebrates) | 65 | 48 | 57 |
| Arillate or funiculate (vertebrates) | 5 | 1 | 3 |
| Presented (vertebrates) | 14 | 3 | 9 |
| Other (abiotic or non-vertebrate) | 16 | 48 | 32 |

extensively frugivorous species (Table 2), a fauna that is depauperate compared to that in the tropical rainforests of north Queensland (Crome 1975) and Papua New Guinea (Brown and Hopkins 2002). The resultant ratio of one frugivore species for every ten tree species (14:140) is markedly less than the 1:3 ratio demonstrated for Neotropical forests (Fleming 2005).

With a depauperate frugivore fauna that is thus likely to contain fewer specialists, evolutionary generalisation of frugivore-fruit relationships and thus of fruit characters, in Top End monsoon forests might be anticipated. McKey (1975) proposed that a typical generalised fruit is produced in abundance, synchronously within individuals and populations, is small and/or has small and often multiple seeds, and is cheap to produce – having high levels of moisture and carbohydrates and low levels of expensive nutrients such as lipids and protein. Willson *et al.* (1989) noted that bird-dispersed fruits in the Australasian region are predominantly red or black but sometimes blue or yellow, whereas mammal-dispersed fruits are frequently brown, green, orange or yellow. It is also possible that the range of evolutionary options for variation in fruit traits is constrained by soil moisture and/or canopy type (Bullock 1995; Franklin and Bach 2006). There has, however, been no attempt to systematically describe the traits of vertebrate-dispersed fruits in Top End monsoon forests beyond the characterisation of Russell-Smith and Dunlop (1987) summarised here in Table 1.

In this study, we describe the morphology, moisture and nutrient contents of the fruit of sixteen common vertebrate-dispersed (zoochorous) trees from the monsoon forests of the Top End of the Northern Territory. The observed traits are then evaluated for evidence of gradients and associations which might correspond to generalised and specialised dispersal syndromes *sensu* McKey (1975). Some implications of our results for frugivory in the monsoon forests of the Northern Territory are briefly discussed.

Table 2. Vertebrates that are obligate frugivores or extensively frugivorous and occur in Top End monsoon forests. The Top End occurrence of species marked with an asterisk is primarily in monsoon forests; others, such as the mistletoebird (Woinarski *et al.* 1988), may be more abundant in nearby savannas. The non-volant species have limited home ranges and thus are most unlikely to provide inter-patch dispersal services. Many other vertebrates consume and may disperse fruits but are not specialists. Some monsoon forest rodents consume fleshy fruits but also consume the seeds and are thus seed predators rather than dispersal agents (Begg and Dunlop 1985; Firth *et al.* 2005). Additional sources: Morton and Brennan (1991), Woinarski (1993), Bowman and Woinarski (1994), Higgins (1999), Palmer *et al.* (2000), Price (2004).

| Species | Family |
|--|-------------------|
| <i>More or less obligately frugivorous, volant</i> | |
| * Emerald dove <i>Chalcophaps indica</i> | Columbidae |
| * Banded fruit-dove <i>Ptilinopus cinctus</i> | Columbidae |
| * Rose-crowned fruit-dove <i>P. regina</i> | Columbidae |
| * Pied imperial-pigeon <i>Ducula bicolor</i> | Columbidae |
| * Common koel <i>Eudynamys scolopacea</i> | Cuculidae |
| * Channel-billed cuckoo <i>Scythrops novaehollandiae</i> | Cuculidae |
| * Figbird <i>Sphecotheres viridis</i> | Oriolidae |
| Mistletoebird <i>Dicaeum hirundinaceum</i> | Dicaeidae |
| <i>Opportunistically but extensively frugivorous, volant</i> | |
| * Yellow oriole <i>Oriolus flavocinctus</i> | Oriolidae |
| * Varied triller <i>Lalage leucomela</i> | Campephagidae |
| Great bowerbird <i>Chlamydera nuchalis</i> | Ptilonorhynchidae |
| Black flying-fox <i>Pteropus alecto</i> | Pteropodidae |
| <i>Opportunistically but extensively frugivorous, non-volant</i> | |
| * Black-footed tree-rat <i>Mesembriomys gouldi</i> | Muridae |
| Common brush-tailed possum | Phalangeridae |
| <i>Trichosurus vulpecula</i> | |

METHODS

Study area and species. Fruit samples and crop size data were collected from monsoon forests on Gunn Point Peninsula (12°24'S, 131°02'E), 40 km north-east of Darwin, Northern Territory. Mean annual rainfall is *c.* 1700 mm, with 97% falling in the wet season months of October to April. Temperatures are warm to hot throughout the year, with diurnal variation mostly less than 12°C and night-time temperatures rarely if ever dropping below 10°C.

On Gunn Point Peninsula as elsewhere in the Top End of the Northern Territory, monsoon forests occur as isolated and mostly tiny patches embedded within a dominant savanna matrix (Russell-Smith 1991). In the study area, they occur in two discrete landscape settings, on clay-loams around springs at the edge of floodplains, and on seasonally dry coastal cheniers (coral sands or sandy-loams). In the former setting, most trees are evergreen; in the latter, deciduousness is prominent (Bach 2002). Whilst there is some floristic overlap between settings, the contrast corresponds with the primary floristic

division within Top End monsoon forests (Russell-Smith 1991), with spring-fed sites belonging to Russell-Smith's Group 2 and the coastal chenier sites to Group 9.

Sixteen tree species were selected for study (Table 3), eight from the spring-fed patches and eight from seasonally dry sites, though species associated with one forest type may occur in the other type elsewhere. They were selected on the basis that: *a*, they were common in their respective forest type in the study area; *b*, their fruits are an important food resource for frugivorous birds and flying-foxes (Price 1998, Palmer *et al.* 2000); and *c*, no two species were from the same family, thus providing phylogenetic independence of fruit traits.

Analysis has been conducted using the units dispersed by vertebrates. In most species, this corresponds to the fruit. In *Cupaniopsis anacardioides* and *Myristica insipida*, the fruit is woody, splitting to reveal the arillate seed(s), and the dispersal unit is taken to be the seed plus its associated aril. *Cupaniopsis anacardioides* has three small seeds per fruit and thus three dispersal units per fruit, whereas *M. insipida* fruits contain a single large seed. The other exception is *Strychnos lucida*, in which the seeds are embedded in a semi-liquid pulp (mesocarp) which is surrounded by a thin but firm shell (exocarp). Observations indicate that birds normally break the shell and consume the contents, and damaged empty shells commonly remain on the tree. For *S. lucida*, the dimensions (length, width) are for the entire fruit, but mass, moisture content and nutrient analyses are for the contents only.

Fruit abundance. In the course of phenological studies (Bach 2002; Franklin and Bach 2006), fruit abundance was estimated monthly over 30 months for each of between eight and sixteen marked, mature individuals

of each species (females in dioecious species). Estimates were visual, aided with binoculars where necessary, and categoric, estimates being in classes of 0, 1–10, 11–50, 51–100, 101–500, 501–1000, ... 1000001–5000000. No distinction is made between unripe and ripe fruit because ripe fruit were rarely seen in the majority of species.

Fruit collection. Fresh, ripe fruit showing no sign of damage or desiccation were collected directly from three to five plants of each species (74 plants in total). In the case of the tall tree *Gmelina schlechteri*, fruit were collected from the ground. Collected fruits were kept cool until returned to the laboratory.

Morphological and nutrient analyses. In the laboratory, the samples were divided into two subsets: *a*, a random sample of 60 dispersal units per species for determination of morphological characters and moisture content; and *b*, a set of 6 to 10 dispersal units per species, two per tree, for nutrient analysis of the flesh. In the case of *Ficus virens*, the seeds are numerous and minute, and could not be separated from the flesh, so they were included in the nutrient analysis.

For each dispersal unit in subset *a*, length, width, number of seeds (*F. virens* excepted) and fresh mass of seeds and flesh were determined. *Per capita* dry mass and water content of flesh and seed were determined after freeze-drying. Length and width were measured to 0.01 cm. Where the fruit was the dispersal unit, the length was taken as the distance from the pedicel junction to the apex, and the width as the widest point perpendicular to the length; thus, in some cases width may be longer than length. Mass was determined on an electronic balance with a precision of 0.001 g.

Table 3. Classification and *a priori* characteristics of 16 species of monsoon forest trees from northern Australia. Canopy types are from Franklin and Bach (2006).

| Species | Family | Fruit type | Fruit colour | Canopy type |
|---|----------------|------------|---------------|------------------|
| <i>Canarium australianum</i> F.Muell. | Burseraceae | drupe | blue-purple | deciduous |
| <i>Carallia brachiata</i> (Lour.) Merr. | Rhizophoraceae | berry | red | evergreen |
| <i>Carpentaria acuminata</i> (H.Wendl. and Drude) Becc. | Arecaceae | berry | red | evergreen |
| <i>Cupaniopsis anacardioides</i> (A.Rich) Radlk. | Sapindaceae | arillate | orange-red | evergreen |
| <i>Diospyros compacta</i> (R.Br.) Kosterm. | Ebenaceae | berry | red | evergreen |
| <i>Drypetes deplanchei</i> (Brongn. and Griseb.) Merr. | Euphorbiaceae | drupe | orange-red | evergreen |
| <i>Elaeocarpus arnhemicus</i> F.Muell. | Elaeocarpaceae | drupe | blue | partly deciduous |
| <i>Ficus virens</i> Aiton | Moraceae | fig | white-purple | partly deciduous |
| <i>Gmelina schlechteri</i> H.J.Lam | Verbenaceae | drupe | red-purple | partly deciduous |
| <i>Maranthes corymbosa</i> Blume | | drupe | purple | evergreen |
| <i>Miliusa brahei</i> (F. Muell.) Jessup | Annonaceae | berry | purple-black | deciduous |
| <i>Mimusops elengi</i> L. | Sapotaceae | berry | orange-red | evergreen |
| <i>Myristica insipida</i> R.Br. | Myristicaceae | arillate | red | evergreen |
| <i>Strychnos lucida</i> R.Br. | Loganiaceae | berry | yellow-orange | partly deciduous |
| <i>Syzygium nervosum</i> DC. | Myrtaceae | berry | purple-black | evergreen |
| <i>Terminalia microcarpa</i> Decne. | Combretaceae | drupe | blue-purple | partly deciduous |

RESULTS

Flesh from the second subset was removed and pooled into replicate samples (trees), freeze-dried, ground and stored in sealed vials at -80°C prior to analysis. Ash content was determined gravimetrically after heating weighed samples (approximately 1 g) at 500°C in a muffle furnace overnight. To determine soluble carbohydrate content, samples of *c.* 0.006 g were analysed spectrophotometrically using the phenol-sulphuric acid method of Dubois *et al.* (1956). Total lipid content was determined gravimetrically after extraction from samples of *c.* 0.1 g with chloroform-methanol (2:1) (Bligh and Dyer 1959). Total Kjeldahl Nitrogen content was determined using samples of *c.* 0.1 g digested in sulphuric acid. Since high lipid contents can interfere with the nitrogen analysis (Oomah and Bushuk 1983), samples were defatted before analysing for nitrogen (residues of the lipid extraction stored on filter paper). The digested samples were then analysed using a flow injection analyser (Lachat Instruments QuikChem method 13-107-06-2-D).

To assess the efficiency of each method, trials were conducted in which known amounts of glucose (a soluble carbohydrate), stearic acid (a lipid) and glycine (a protein) were processed as for the flesh samples. Recovery rates (mean \pm s.d.) were: glucose – $99.2 \pm 7.5\%$ ($n = 14$); stearic acid – $102.91 \pm 3.31\%$ ($n = 12$); and glycine – $100.032 \pm 4.319\%$ ($n = 10$). As these rates were considered sufficiently accurate, no adjustment was made to the analytical results.

Data analysis. Our index of maximum crop size for each species is the median of the maximum fruit abundance recorded for individuals of that species over the thirty months of recording. As crop size varied hugely among species (our index ranges over 2.5 orders of magnitude, Table 4), this method was considered to be of sufficient accuracy for correlative purposes.

Flesh/dispersal unit mass was estimated using fresh weights. Crude protein content was estimated by multiplying Total Kjeldahl Nitrogen content by 6.25.

For the 14 non-arillate species, the correlation matrix for eight fruit characters (dispersal unit mass, flesh/dispersal unit mass, flesh moisture content, % dry mass of ash, soluble CHO, lipids and protein, and maximum crop size) were examined using Principal Components Analysis (PCA) implemented in Statistica (StatSoft 1984–2004). As maximum crop size was not normally distributed, data were converted to an index based on the observation classes (see Methods) in which the smallest observed median maximum crop size class (51–100) was scored as one, the next possible class as two and so on, the largest observed class (10,001–50,000) receiving a score of eight. For *F. virens*, flesh was taken to comprise 100% of the dispersal unit mass.

The fruits of seven species (44%) were berries, six (38%) were drupes, two (13%) were arillate and one was a fig (Table 3). The ripe fruits of eight species (50%) including the arils of the two arillate species were red, orange-red or yellow-orange and six (38%) were blue, purple, blue-purple or purple-black, the remaining two species being white-purple and red-purple (Table 3). Dispersal units ranged in mass (size) from the 0.29 g (0.7 x 0.8 cm) berry of *Carallia brachiata* to the 4.46 g (2.7 x 1.6 cm) drupe of *Maranthes corymbosa* (Table 4). Most dispersal units were single-seeded, with a maximum of 3.1 seeds per unit in the berry of *Diospyros compacta* (Table 4).

The arils of *Cupaniopsis anacardioides* and *Myristica insipida* had lower moisture and carbohydrate content, and higher lipid and protein content, than the flesh of any non-arillate species (Table 4). This was markedly so for lipid content, which was 4.2 and 6.1 times higher respectively than the most lipid-rich non-arillate species (*Canarium australianum*). Amongst non-arillate species, flesh varied from 53–81% of dispersal unit (fresh) mass and flesh moisture content from 60–96% by mass (Table 4). The nutrient content (dry mass) of the flesh of non-arillate species varied from 27–70% soluble carbohydrate, 3–9% ash, 2–12% lipids and 2–7% protein (Table 4).

Principal Components Analysis of non-arillate species demonstrated an association of high levels of protein, lipids and ash with low levels of soluble carbohydrates (CHO) (Fig. 1; gradient approx. parallel to Factor 1). A second association existed between larger dispersal unit mass and smaller crop size. In the first two factors of the PCA, the moisture content of flesh was unrelated to any other fruit character.

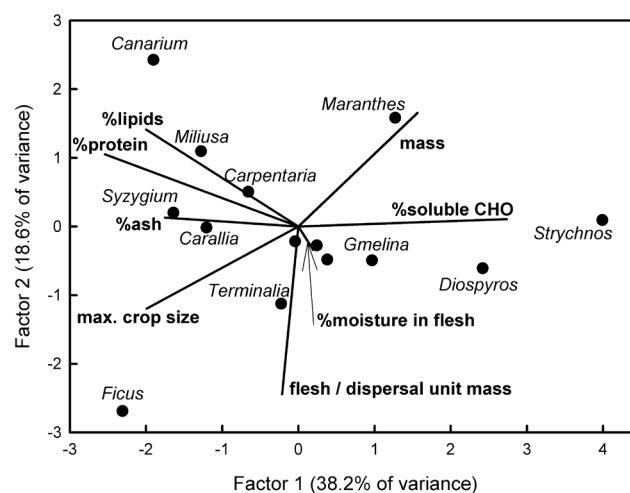


Fig. 1. The first two factors of a Principal Components Analysis of fruit characters of 14 non-arillate monsoon forest tree species. Fruit characters (lines, labelled in bold) are as in Table 4; their factor scores have been multiplied by three for clarity. Not all tree species are labelled; species are spelt out in full in Table 3.

DISCUSSION

Associations and gradients amongst fruit traits.

Our demonstration of a nutrient gradient in the flesh of fruits from high concentrations of proteins, lipids and ash to high concentrations of soluble carbohydrates is similar to the primary gradient identified by Herrera (1987) in an analysis of 111 temperate-zone plants. Although excluded from our gradient analysis, the arillate species serve to reinforce this primacy, both arillate species having exceptionally high levels of lipids and protein and low levels of soluble carbohydrates. In that lipids, protein and ash are expensive nutrients whereas soluble carbohydrates are cheap to produce, this gradient represents a spectrum of dispersal syndromes ranging from specialised to generalised (McKey 1975).

However, other traits thought to represent extremes of adaptive specialisation and generalisation in dispersal syndromes (McKey 1975) were not consistently associated with the primary gradient we identified. We found evidence of a trade-off between crop size (measured as the number of fruits) and individual fruit mass, but this was not related to the nutrient gradient. There was no relationship between the primary gradient and relative commitment to flesh or seed. Multiple seeds, a feature associated with generalised dispersal syndromes, were a feature of two species with high content of soluble carbohydrates (*Diospyros compacta*, *Strychnos lucida*) but also of two species towards the other end of the primary gradient (*Ficus virens*, *Miliusa brahei*). Franklin and Bach (2006) identified *Carpentaria acuminata* and *F. virens* as fruiting asynchronously among individuals, a feature associated with dispersal specialisation, and both species had 'specialised' fruit nutrients, i.e. low to moderate levels of soluble CHO and high concentrations of one or more of ash, lipids or protein. However, the **generalist-specialist** paradigm predicts that asynchronous fruiting will be associated with small maximum crop sizes, whereas *F. virens* had the largest crop size and *C. acuminata* the equal second largest crop size in this study. In Herrera's (1987) study, protein and ash contents were positively correlated but protein and lipid content were not. Furthermore, and in converse to predictions arising from the generalised-specialised paradigm, Herrera (1987) found that fruit size was negatively correlated with lipid content (and thus was positively correlated with soluble carbohydrate content), whilst flesh / dispersal unit mass was negatively correlated with protein content.

Exceptionally high levels of lipids and protein and correspondingly low levels of moisture and soluble carbohydrates may be a general feature of the arils of vertebrate-dispersed fruit (Howe and Vande Kerckhove 1981; Foster and McDiarmid 1983; Pizo and Oliveira 2001). The arillate *Myristica insipida* of this study exhibits additional traits which may be regarded as specialised (cf McKey 1975). These include small crop size, a fairly

large dispersal unit with a particularly large seed, and fruiting phenology. Though flowering by female plants (the species is dioecious) is seasonal (Armstrong and Irvine 1989, Franklin and Bach 2006), *M. insipida* fruits throughout the year (Franklin and Bach 2006) with progressive ripening of a few fruit at a time (C.S. Bach pers. obs.). Furthermore, and notwithstanding small crop sizes, energetic allocation to fruit production in *M. insipida* far outweighs commitment to flowering (Armstrong and Irvine 1989).

It is possible, therefore, to identify species that are particularly consistent with the **generalist-specialist** paradigm for the evolution of fruit characters, but also many that are not. This paradigm currently receives at most only highly qualified acceptance (Howe 1993; Levey *et al.* 2002). Exceptions may arise, or the paradigm fail completely, for a variety of reasons including that selection on fruit characteristics for dispersal is limited by phylogenetic and abiotic constraints (Herrera 1992, 1998; Hampe 2003), that dispersal success may often be irrelevant to plant demographics (Howe and Miriti 2004), that the relationship between fruit and frugivores may be in disequilibrium (Levey and Benkman 1999) or strongly asymmetric (Bascombe *et al.* 2006), or that attraction of a variety of dispersal agents may lead to differing and even opposing selection pressures (Russo 2003). Furthermore, the examination of co-evolution in plants and their vertebrate dispersers is confounded by often complex scale-dependence (Russo 2003; Burns 2004; Garcia and Ortiz-Pulido 2004). Rather than reject the paradigm, we prefer the interpretation that it is but one of many effects influencing a complex mutualistic system, many of which do not directly relate to the behaviour of vertebrate dispersal agents. In his much more extensive study, Herrera (1987) drew similar conclusions, noting in particular the roles of phylogeny, constraints to fruit architecture, and species-specific energy and nutrient allocation patterns in influencing fruit traits.

Some implications for frugivory. We sampled only a small proportion of tree species in Top End monsoon forests – c. 14% of fleshy-fruited species and 25% of arillate species – and in selecting common species our study may be biased towards generalists. Thus it is not possible for us to appraise the hypothesis that Top End monsoon forests have been filtered to favour generalised dispersal syndromes, or that species have evolved in that direction. The species we selected were, compared to a range of tropical environments as summarised by French (1991; Table 6), of typical mass (1.64 cf 1.76 g), flesh / dispersal unit wet mass (60.5 cf 57.4%) and % moisture in flesh (76 cf 72%) (data are means of species means). However, mean levels of soluble CHO were higher (42 cf 31%), and levels of lipids (12 cf 21%) and protein (5.3 cf 8.8%, estimated using the same conversion from % nitrogen as applied to our data) lower than in other regions, suggesting either that our sample, or Top End monsoon

Table 4. Dimensions, moisture content and nutrient content of the dispersal units of 16 species of monsoon forest trees from northern Australia. Data are means \pm standard error. For dimensions and moisture content, n = 60 for each species. For nutrient analyses, n = 10 per species (2 per tree x 5 trees) except *E. arnhemicus*, *C. acuminata* and *S. nervosum*, for which n = 6 per species (2 per tree x 3 trees). Maximum crop size is the median of the maximum observed for each individual of the species. Flesh (% mass) is flesh / dispersal unit (fresh) mass x 100. Bracketed measurements for *F. virens* are for the flesh combined with the numerous tiny seeds. Bracketed means indicate that *Ficus virens* has been excluded.

| Species | Length (cm) | Width (cm) | Mass (g) | Seeds per unit | Maximum crop size | Flesh (% mass) | Moisture (% mass) | | Nutrient content of flesh (% dry mass) | | | |
|----------------------------------|----------------|----------------|------------------|----------------|-------------------|-----------------|-------------------|-----------------|--|------------------|------------------|-------------------|
| | | | | | | | Flesh | Seed | Ash | Lipids | Protein | Soluble CHO |
| Arillate species | | | | | | | | | | | | |
| <i>Cupaniopsis anacardioides</i> | 1.2 \pm 0.02 | 0.7 \pm 0.01 | 0.38 \pm 0.010 | 1 \pm 0 | 300 | 29.6 \pm 0.61 | 52.3 \pm 0.80 | 19.9 \pm 0.90 | 3.6 \pm 0.16 | 51.6 \pm 2.64 | 9.3 \pm 0.55 | 23.1 \pm 1.71 |
| <i>Myristica insipida</i> | 2.0 \pm 0.02 | 1.2 \pm 0.01 | 1.77 \pm 0.035 | 1 \pm 0 | 75 | 18.1 \pm 0.60 | 35.1 \pm 0.49 | 46.5 \pm 1.65 | 1.2 \pm 0.09 | 75.2 \pm 0.60 | 5.7 \pm 0.18 | 9.2 \pm 0.59 |
| Non-arillate species | | | | | | | | | | | | |
| <i>Canarium australianum</i> | 2.2 \pm 0.04 | 1.3 \pm 0.01 | 2.62 \pm 0.078 | 1 \pm 0 | 750 | 56.3 \pm 0.28 | 62.5 \pm 0.27 | 17.6 \pm 0.19 | 5.6 \pm 0.17 | 12.4 \pm 1.13 | 7.2 \pm 0.35 | 35.5 \pm 1.25 |
| <i>Carallia brachiata</i> | 0.7 \pm 0.01 | 0.8 \pm 0.01 | 0.29 \pm 0.006 | 1 \pm 0 | 750 | 70.1 \pm 0.43 | 96.4 \pm 0.29 | 55.1 \pm 0.46 | 5.4 \pm 0.22 | 9.1 \pm 0.64 | 5.9 \pm 0.19 | 41.8 \pm 1.23 |
| <i>Carpentaria acuminata</i> | 1.7 \pm 0.01 | 1.7 \pm 0.02 | 3.28 \pm 0.078 | 1 \pm 0 | 3000 | 62.1 \pm 0.41 | 92.1 \pm 0.18 | 38.7 \pm 0.45 | 9.4 \pm 0.19 | 2.8 \pm 0.15 | 5.7 \pm 0.17 | 42.7 \pm 0.88 |
| <i>Diospyros compacta</i> | 1.1 \pm 0.01 | 1.3 \pm 0.01 | 1.49 \pm 0.040 | 3.1 \pm 0.17 | 300 | 67.6 \pm 1.22 | 76.2 \pm 0.38 | 37.9 \pm 0.86 | 3.2 \pm 0.18 | 1.6 \pm 0.19 | 2.4 \pm 0.06 | 57.8 \pm 0.84 |
| <i>Drypetes deplanchei</i> | 1.3 \pm 0.01 | 0.9 \pm 0.01 | 0.70 \pm 0.012 | 1 \pm 0 | 300 | 68.9 \pm 0.73 | 76.3 \pm 0.37 | 28.0 \pm 0.16 | 6.7 \pm 0.17 | 3.1 \pm 0.19 | 5.1 \pm 0.16 | 44.1 \pm 1.20 |
| <i>Elaeocarpus arnhemicus</i> | 1.4 \pm 0.01 | 1.0 \pm 0.01 | 0.95 \pm 0.014 | 1 \pm 0 | 3000 | 59.2 \pm 0.77 | 68.1 \pm 0.39 | 26.7 \pm 0.26 | 2.9 \pm 0.27 | 4.0 \pm 0.33 | 3.7 \pm 0.09 | 40.4 \pm 1.45 |
| <i>Ficus virens</i> | 1.0 \pm 0.01 | 1.0 \pm 0.02 | 0.54 \pm 0.025 | many | 30000 | | (77.2 \pm 0.45) | | (6.7 \pm 0.41) | (6.1 \pm 0.59) | (5.1 \pm 0.18) | (31.0 \pm 2.11) |
| <i>Gmelina schlechteri</i> | 1.9 \pm 0.03 | 1.4 \pm 0.01 | 2.32 \pm 0.063 | 1 \pm 0 | 300 | 81.0 \pm 0.26 | 89.7 \pm 0.25 | 30.9 \pm 0.34 | 4.2 \pm 0.24 | 2.2 \pm 0.14 | 5.6 \pm 0.12 | 50.5 \pm 1.04 |
| <i>Maranthes corymbosa</i> | 2.7 \pm 0.03 | 1.6 \pm 0.02 | 4.46 \pm 0.178 | 1 \pm 0 | 750 | 53.2 \pm 1.25 | 84.5 \pm 1.45 | 42.7 \pm 0.37 | 5.0 \pm 0.24 | 3.9 \pm 0.09 | 4.7 \pm 0.22 | 52.2 \pm 0.72 |
| <i>Milusa brahei</i> | 1.3 \pm 0.02 | 1.4 \pm 0.02 | 1.39 \pm 0.050 | 1.4 \pm 0.07 | 300 | 66.4 \pm 0.55 | 83.2 \pm 0.18 | 39.8 \pm 0.24 | 8.8 \pm 0.43 | 9.4 \pm 0.46 | 6.3 \pm 0.22 | 45.0 \pm 1.23 |
| <i>Mimusops elengi</i> | 1.3 \pm 0.01 | 1.2 \pm 0.01 | 1.00 \pm 0.020 | 1 \pm 0 | 300 | 75.4 \pm 0.45 | 60.4 \pm 0.27 | 35.6 \pm 0.25 | 5.0 \pm 0.14 | 2.1 \pm 0.13 | 5.1 \pm 0.14 | 44.9 \pm 1.73 |
| <i>Strychnos lucida</i> | 2.0 \pm 0.04 | 2.0 \pm 0.04 | 3.93 \pm 0.260 | 2.1 \pm 0.15 | 75 | 72.0 \pm 0.62 | 85.4 \pm 0.37 | 29.3 \pm 0.43 | 3.3 \pm 0.33 | 2.0 \pm 0.18 | 1.8 \pm 0.16 | 70.3 \pm 3.02 |
| <i>Syzygium nervosum</i> | 0.9 \pm 0.01 | 1.0 \pm 0.01 | 0.57 \pm 0.013 | 1 \pm 0 | 3000 | 55.8 \pm 1.01 | 83.6 \pm 0.21 | 51.1 \pm 0.61 | 5.4 \pm 0.10 | 4.9 \pm 0.19 | 5.9 \pm 0.17 | 27.2 \pm 0.49 |
| <i>Terminalia microcarpa</i> | 1.2 \pm 0.01 | 0.9 \pm 0.02 | 0.63 \pm 0.022 | 1 \pm 0 | 3000 | 71.6 \pm 0.49 | 92.3 \pm 0.20 | 33.3 \pm 0.54 | 8.1 \pm 0.50 | 2.5 \pm 0.39 | 4.7 \pm 0.18 | 52.5 \pm 1.19 |
| Mean of species means | | | | | | | | | | | | |
| Arillate species | 1.6 | 1.0 | 1.08 | 1 | | 23.9 | 43.7 | 33.2 | 2.4 | 63.4 | 7.5 | 16.2 |
| Non-arillate species | 1.5 | 1.3 | 1.73 | (1.3) | | 66.1 | (80.8) | (35.9) | 5.7 | 4.7 | 4.9 | 45.4 |
| All species | 1.5 | 1.2 | 1.64 | 1.2 | | (60.5) | (76.0) | (35.5) | 5.3 | 12.0 | 5.3 | 41.8 |

forests in general, feature nutritionally cheap fruits. Based on colour, the species we selected are all consistent with a bird-dispersal syndrome (see particularly Willson *et al.* 1989) and, while there is some colour overlap with other dispersal syndromes, notably mammals, no colours specifically associated with a mammal dispersal syndrome – green and brown – were documented. This does not mean that no species was adapted to dispersal by mammals, but could mean that some species were adapted to dispersal by both birds and mammals.

There are no obligately frugivorous mammals in the Top End of the Northern Territory, and the extensively frugivorous mammal that is also flighted and thus offers potential for dispersal among isolated patches (Palmer and Woinarski 1999) is the black flying-fox, *Pteropus alecto* (Table 2). There is no quantitative data on the diet of the black flying-fox in the Top End, but Palmer *et al.* (2000) provided a list of 14 species of fruit consumed which includes seven of the species included in this study. All seven are also consumed by birds (Price 1998) (as are all the remaining species with the possible exception of *D. compacta*). Van der Pijl (1982) noted a range of characters associated with dispersal by bats, including exposed position such as cauliflory (fruits on the trunk), nocturnal and often musty, sour or rancid odour, drab colour and large size. Other than colour and size, these are not characters assessed here. We note that several monsoon forest tree species in the region are cauliflorous including palms (by structural definition) and several figs (*Ficus hispida*, *F. racemosa*). Fruit of the rotten cheese-fruit, *Morinda citrifolia*, a widespread species of coastal and sub-coastal monsoon forests in the Top End (Liddle *et al.* 1994) are large, odorous and greenish-white, and may thus be particularly adapted to dispersal by bats.

The apparently specialised dispersal syndrome of arillate fruits demonstrated here and in other studies is consistent with a number of studies suggesting that arillate fruits attract a relatively narrow and specialised suite of vertebrates (Howe and Vande Kerckhove 1981; Foster and McDiarmid 1983; Brown and Hopkins 2002). Seventy-six percent of 70 feeding observations at *M. insipida* fruits in the Top End of the Northern Territory were of a single species, the obligately frugivorous rose-crowned fruit-dove, *Ptilinopus regina* (Price 1998). In Papua New Guinea, Brown and Hopkins (2002) found a positive association between birds of paradise and arillate fruits.

An alternate perspective on plant dispersal strategies is that fruit flesh could provide an attractive dry-season moisture resource for frugivores (Herrera 1982; Prinzing and Schleucher 1998). This hypothesis leads to the prediction that species that fruit in the dry season, and especially species from dry monsoon forests where free water may be scarce at that time, should contain high moisture levels. Of the two species in this study whose fruit ripen in the dry season (Franklin and Bach 2006), one – *Mimusops elengi* – had exceptionally low moisture

levels. However, the second – *S. lucida* – features a semi-liquid pulp encased in an impervious shell which could well function as a source of moisture for frugivores.

In the Top End of the Northern Territory, the diet of only two vertebrate frugivores has been studied (Healey 1992; Palmer *et al.* 2000), and studies of avian frugivory are notably scant. Price *et al.* (1999), Price (2004) and Bach and Price (2005) provided alternative perspectives on the relationship between frugivores and their food resources. However, studies conducted from a plant ecological perspective, including patterns of fruit consumption, are needed to shed light on the adaptive and evolutionary processes at work on the Top End flora including the impact of a depauperate fauna on the rich assemblage of vertebrate-dispersed trees. No such autecological studies currently exist.

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