

Nutritional Value of the Aril of *Trichilia cuneata*, a Bird-Dispersed Fruit

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ABSTRACT

Fruits of *Trichilia cuneata* (Meliaceae), a common tree in drier forests of Central America, are eaten by a number of birds. The fruits are 10 to 12 mm in diameter, covered by a yellowish-brown, capsular exocarp, and contain three to six seeds distributed among three locules. Each seed is covered by an orangish-red aril that averages 59.7 percent lipid and 15.1 percent protein, which makes this species one of the most nutritious known. The fleshy tissue of only 15 of 59 other species for which we found data contained at least 10 percent protein (dry wt.). Only nine species of 57 had fleshy tissue containing more than 40 percent lipid (dry wt.). Between 1971 and 1972, weights of whole fruits decreased by 36 percent, perhaps in response to a severe drought in the area. The decrease was not equally distributed among component tissues of the fruit. Exocarp decreased by 36 percent, aril by 4 percent, and seeds by 62 percent. However, the reduction in weight per seed was not so dramatic, for two reasons. First, the number of seeds per fruit decreased by 26 percent. Secondly, many seeds did not develop. Thus, the decrease in weight per normally developed seed was only 18 percent. The fruit of *Trichilia cuneata* was attractive to both specialized (4 species) and opportunistic (11 species) frugivorous birds and is intermediate ("a generalist") in several dispersal-related characteristics.

RESUMEN

Varias especies de aves comen las frutas de *Trichilia cuneata* (Meliaceae), un árbol común de los bosques secos de América Central. Las frutas miden de 10 a 12 mm de diámetro, tienen el exocarpo capsular pardo-amarillento, y contienen tres hasta seis semillas distribuidas entre los tres loculos. Se cubre cada semilla por un arilo rojo-anaranjado comprendido de un promedio de 59.7% lípidos y 15.1% proteína. Una reducción en peso total de una fruta y en peso de semilla, y una disminución en el número de semillas maduras por fruta en 1972 correlacionaban con una sequía rigurosa. Las frutas de *Trichilia cuneata* atraían aves especialistas en fruta (4 especies) como éstos que la comen oportunísticamente (11 especies). Este especie de árbol es "generalista" en que muestra varios característicos intermedios de dispersión.

THE INTERACTION BETWEEN FRUIT TREES and their animal seed dispersers is complex and influenced by variable characteristics of both groups of organisms. One important variable is the nutrient content of the aril or pericarp, *i.e.*, that part of the fruit normally digested by birds, which includes not only an energy source, but also specific substances such as protein. The extractable nutrient content must be great enough to make the fruit a worthwhile food resource for the disperser. At the same time, nutrient content of a single fruit cannot be so great as to interfere with the production of sufficient fruits for seed dispersal. The number of seeds dispersed must be adequate to ensure production of a viable offspring during the tree's reproductive life span. What constitutes an adequate nutrient content varies according to the needs of the dispersers, which, in turn, will depend upon whether they are omnivorous or totally frugivorous (McKey 1975), whether the fruit is used to feed growing young or just adults (Foster 1978), the reproductive condition of the disperser (Crome 1975a, b), etc. By the same token, the tree may adjust the nutrient content of its fruit in times of stress, it may maintain some minimum nutrient content but reduce the numbers of fruits produced, or it may do both (*e.g.*, see McDiarmid *et al.* 1977).

Despite the importance of nutrient content of those parts of the fruit normally exploited by dispersers, the composition of very few non-domesticated fruit species is known (Snow 1981), and the majority of these are Australian (Crome 1975a). Thus, although we may talk about a particular tree species and its relationships with its dispersers, attempts to theorize about general plant characteristics that promote dispersal, about differences among dispersers in the way fruit is used, and about the evolution of diet compositions, are severely hampered, particularly with regard to neotropical species. This situation will persist until we have a much larger data base. Thus, it is useful to report information of this type whenever data are available.

Trichilia cuneata Rdlk. (Meliaceae) is a particularly important species in this context because its fruits are heavily exploited by birds (Leck 1969). The fruits are covered by a capsular exocarp that dehisces to expose shiny orangish-red aril (Fig. 1) containing a variable number of seeds. Birds pluck and swallow the seeds and aril, digesting the latter and either regurgitating the seeds or passing them through the gut undigested. We analyzed the nutrient content of the aril of fruits of *T. cuneata*, and herein report the results of the analyses. We also



FIGURE 1. Fruits of *Trichilia cuneata* from Guanacaste Province, Costa Rica. Fruit on right has part of the exocarp removed to expose the shiny, orangish-red aril.

provide observations on the phenology of the tree and comment on the characteristics of its fruit relative to the dispersers it attracts.

METHODS

Trichilia cuneata is a common component of forests and second-growth woodlands from Guatemala to Panama (Standley 1937). Trees of this dioecious species grow to heights of 10–12 m but may begin flowering and fruiting when only 3–4 m tall with a DBH of *ca* 7 cm. Individual trees do not necessarily flower or fruit every year. The fruits are 10–12 mm in diameter and covered by a yellowish-brown capsular exocarp (Fig. 1). The ovary is usually 3-loculed, with one to two ovules (seeds) per cell.

We studied this species in the bottomland forest along the Rio Higuera, *ca* 2 km SE Estación Experimental Enrique Jiménez Nuñez, Guanacaste Province, Costa Rica, the same site at which Leck (1969) worked. The area,

classified as Tropical Dry Forest (Tosi 1969), is described by Sawyer and Lindsey (1971) and by Janzen (1973). Rainfall is seasonal. Usually, the wet season extends from May to October with a 2- to 4-week dry period in July or August. Average annual rainfall from 1971–1976 was 1612 mm (range = 1290–2106 mm). We studied the species in 1971 and 1972. In 1972, the area experienced a severe drought with a total rainfall of only 1290 mm; total rainfall in 1971 was 1922 mm.

We gathered 25 fruits from each of six trees on 28 July 1971, and 10 fruits from each of six trees (not necessarily the same ones as in 1971) on 10–11 August 1972. Total wet weights of the fruit components were taken and divided by 25 and 10, respectively, and the seeds were counted. The arils of the fruits from 1972 were dried and returned to the laboratory where they were vacuum desiccated over concentrated sulphuric acid, homogenized, and analyzed for nutrient content. Ash, lipid, protein, and trichloroacetic acid (TCA)-soluble carbohydrate contents were determined according to methods outlined in Lowry *et al.* (1951), Dubois *et al.* (1956), Freeman *et al.* (1957), and McDiarmid *et al.* (1977). Structural carbohydrates were determined by subtraction (Merrill and Watt 1973). Energy content was determined using the conversion factors of 9.5 kcal/g lipid, 5.65 kcal/g protein, and 4.1 kcal/g carbohydrate (Paine 1971). Irene Baker of the Department of Botany, University of California, Berkeley, determined the amino acid content of acid hydrolyzed material using methods reported in Baker and Baker (1976). Presence of tryptophan was determined spectrophotometrically (Spies and Chambers 1949) from unhydrolyzed material.

RESULTS AND DISCUSSION

At Estación Jiménez, flowering occurs in March and the first half of April. Ripe fruits may appear as early as mid-May in some years. They reach peak abundance in June

TABLE 1. Wet weights (grams) of whole fruits and fruit parts of *Trichilia cuneata* from Estación Jiménez, Costa Rica.

	Whole fruit	Exocarp	Aril	Seeds ^a
		1971		
Mean ^b	.7284	.2023	.2308	.2953
Range	.616–.878	.181–.244	.159–.286	.237–.348
Coefficient of Variation	12.39	11.47	19.84	13.95
% whole fruit	—	27.77	31.69	40.54
		1972		
Mean ^b	.4638	.1287	.2218	.1133
Range	.424–.542	.107–.161	.187–.265	.105–.126
Coefficient of Variation	9.64	17.40	11.95	5.56
% whole fruit	—	27.75	47.82	24.43

^a Includes normal and undeveloped seeds.

^b N = 6 trees.

TABLE 2. Number and wet weights (grams) of seeds and wet weight of aril per seed (grams) from fruits of *Trichilia cuneata* sampled at Estación Jiménez, Costa Rica.

	Total seeds per fruit	Weight per seed	Devel. seeds per fruit	Weight per devel. seed	Undevelop. seeds per fruit	Weight ^a of aril per seed
			1971			
Mean ^b	5.37	.0550	4.28	(.0543) ^c	1.09	.0429
Range	4.8–5.6	.042–.065	3.7–5.0	—	0.36–1.76	.033–.054
Coefficient of Variation	6.10	14.91	11.79	—	45.28	18.29
% whole fruit	—	7.55	—	(7.45)	—	—
			1972			
Mean ^b	3.96	.0290	2.03	.0447	1.93	.0565
Range	3.2–4.9	.024–.033	1.8–2.2	.041–.047	1.4–2.7	.049–.073
Coefficient of Variation	14.16	11.03	8.05	4.92	22.39	14.71
% whole fruit	—	6.25	—	9.64	—	—

^a Calculated using total number of seeds.

^b N = 6 trees.

^c Calculated assuming proportional weights comparable to those in 1972.

and July when fruits on moderate- and large-sized trees number in the thousands. Fruits persist in greatly reduced numbers through the end of August. The fruits are heavily used by both frugivorous and omnivorous species of birds; however, in any given year many drop to the ground unused or dry or rot on the tree. Leck (1969) reported 13 species of birds feeding on *Trichilia* fruits. In addition, we observed feeding by Turquoise-browed Marmots (*Eumomota superciliosa*) and Keel-billed Toucans (*Ramphastos sulfuratus*), two species he did not record.

FRUIT WEIGHTS.—The weights of whole fruits varied considerably more between years than within years between trees (Table 1). Fruits sampled in 1972 averaged only about two-thirds the weight of those sampled in 1971. Interestingly, the absolute amounts of tissue comprising the exocarp and seeds changed appreciably, while the amount of aril remained approximately the same (Table 1). In terms of percent composition by tissue, about 28 percent of the fruit was devoted to exocarp in both years. However, *ca* 16 percent less of the total fruit weight was devoted to seeds in 1972, while there was an increase of that same amount in aril weight. This is reflected in the *ca* 32 percent increase in average amount of aril (gms wet wt.) per seed between 1971 and 1972 (Table 2).

Despite the 62 percent decrease in the amount of tissue devoted to all seeds from 1971 to 1972 (Table 1), the reduction in weight per seed (47%) was not so extreme for two reasons. First, although two seeds may develop in each of the three locules of a *Trichilia* fruit (*i.e.*, 6 per fruit), they rarely do (Table 2). In 1971, the average number of seeds per fruit was 5.37; in 1972, it was only 3.96. Secondly, some of the seeds commonly remain tiny and undeveloped. In 1971, an average of

1.09 (20%) of the seeds in each fruit was of this type. In 1972, this figure increased to 1.93 (49%). In 1971, therefore, the average number of fully developed seeds per fruit was 4.28, while in 1972, it was only 2.03. As a result, the decrease in total tissue devoted to seed production in 1972 in large part reflected the 53 percent decrease in the number of full-sized seeds produced rather than a decrease in the weight of each fully-developed seed, though this was also a factor (Table 2). In 1972, a developed seed averaged 0.0447 g, whereas the undeveloped ones averaged only 0.0127 g. In 1971, the two categories of seeds were not weighed separately. However, if their proportional weights were comparable to those in 1972, then the average wet weight of a normal (developed) seed would have been 0.0543 g in 1971 or about 21 percent heavier than normal seeds of 1972. This represents a decrease in average weight of normal seeds of only 18 percent from 1971 to 1972 though total tissue per fruit devoted to seeds decreased by 62 percent.

Although we cannot account directly for the between-year differences in weights of fruit components and seed numbers, we suggest that they relate to differences in rainfall between the two years. The stress of the 1972 drought may have influenced seed production and fruit quality, as was suggested for *Stemmadenia donnell-smithii* by McDiarmid *et al.* (1977). For *S. donnell-smithii*, the fruiting phenology is such that the drought of 1972 affected the fruit crop of 1973. Thus, the equivalent comparison is between fruits of 1972 and 1973 rather than between 1971 and 1972 as in *Trichilia*. The mean weight of *Stemmadenia* fruits decreased by 14.8 percent between the two years. In contrast to *Trichilia*, however, the decrease was more uniform over all tissues. Percent compositions in 1972 (N = 9 fruits) and 1973 (N = 4) were,

TABLE 3. Nutrient composition of arils from fruits of *Trichilia cuneata* sampled at Estación Jiménez, Costa Rica, in August 1972.

Tree ^a	Water ^b %	Ash %	Lipid %	Protein %	Carbohydrate %	
					TCA-sol.	Structural ^c
A	54.66	3.52 (2) ^d	54.99 (2)	15.30 (2)	18.47 (3)	7.72
B	54.21	2.96 (2)	58.10 (2)	13.98 (2)	23.17 (2)	1.79
C	52.54	3.85 (2)	64.66 (2)	14.46 (2)	27.29 (4)	—
D	53.55	3.09 (2)	60.02 (2)	13.90 (2)	20.91 (2)	2.08
E	56.16	3.34 (2)	59.23 (2)	16.31 (2)	21.63 (4)	—
F	50.96	2.71 (2)	61.07 (2)	16.70 (2)	22.60 (3)	—
Mean	53.68	3.245	59.68	15.11	22.345	—
Coef. var.	3.34	12.65	5.38	7.92	13.09	—

^a For each tree, arils of 10 fruits were combined for analysis.

^b Water content expressed as percent wet weight of tissue. All other values expressed as percent dry weight of tissue.

^c Determined by subtraction from 100%.

^d Numbers in parentheses indicate number of subsamples analyzed.

respectively, husk: 82.79 and 84.56 percent, aril: 8.79 and 7.07 percent, and seeds: 8.41 and 8.37 percent. Also of interest is the general decrease in variability of the various tissue weights (except exocarp in *Trichilia*) and seed numbers between years in *T. cuneata* (see coefficients of variation, Tables 1 and 2) and *S. donnell-smithii* (McDiarmid and Foster, unpubl. data). This may reflect a decreased flexibility in allocation to seed and aril components when the total nutrients devoted to each fruit are reduced.

NUTRIENT CONTENT.—The ash, lipid, protein, and carbohydrate compositions of the arils of fruits collected in 1972 are presented in Table 3; the values are remarkably uniform. The amounts of structural carbohydrate and ash are quite low as has been demonstrated for the arils of certain other tropical species (e.g., Foster 1977, McDiarmid *et al.* 1977, Snow 1981). The protein content (\bar{x} % dry wt. = 15.11), however, is exceptionally high when compared to the fleshy parts (i.e., aril, pericarp, or equivalent normally digested by frugivorous birds) of other tropical, bird-dispersed fruits. Fruits of only eight of 59 (13.6%) other species for which data are available had a percent protein composition (dry wt.) equal to 75 percent or more of the average percentage in *T. cuneata* (i.e., $\geq 11.33\%$ dry wt.). However, 15 species contained at least 10 percent protein. The species with these percentages are: *Bactris cusea*—13 (Palmae); *Ficus leptoclada*—20.56 (Moraceae); *Ocotea wachenheimii*—14; *Ocotea* sp.—10.8; *Endiandra hypotephra*—11.49; *E. muelleri*—10.73; *Litsea leafeana*—10.1; unidentified sp. 1—10.87; unidentified sp. 2—10 (Lauraceae); *Dacryodes* sp.—11 (Burseraceae); *Cissus sterculiifolia*—10.71 (Vitaceae); *Didymopanax morototoni*—11.88 (Araliaceae); *Planchonella obovoidea*—14.73 (Sapotaceae); *Stemmadenia donnell-smithii*—10.95 (Apocynaceae); *Solanum toruam*—11.18; *S. viride*—19.86 (Solanaceae); [values derived

from Snow 1962, 1971, 1981; Crome 1975a and pers. comm.; McDiarmid *et al.* 1977]. Frost (1980) reported values greater than 10 percent for four subtropical species studied in Natal, Africa. One of these, *Ekebergia capensis* (21.6%) is a member of the Meliaceae, as is *Trichilia*.

All of the presumed essential amino acids for birds (arginine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, tryptophan, valine, and threonine) are found in *T. cuneata* aril (Foster 1978). Whether these occur in optimum relative amounts is not known. In addition, the following non-essential amino acids are present: alanine, aspartic acid, cysteine, glutamic acid, proline, serine, tyrosine, and the non-protein amino acid, γ -amino butyric acid.

The lipid content (\bar{x} % dry wt. = 59.68) of *T. cuneata* aril also is extremely high. Fleshy parts of fruits of only six of 57 other bird-dispersed tropical species had a percent lipid content (dry wt.) equivalent to 75 percent or more of the average percentage in *T. cuneata* (i.e., $\geq 44.76\%$). Fleshy parts of only nine species contained at least 40 percent lipid (dry wt.). The species with these percentages are: *Hibbertia scandens*—55.06 (Dilleniaceae); *Cinnamomum elongatum*—44 (Lauraceae); *Virola sebifera*—54 (digestible fat), *Virola surinamensis*—63.1, *Virola* sp.—59.47, *Myristica muelleri*—43.6 (Myristicaceae); *Stemmadenia donnell-smithii*—63.9 (Apocynaceae); *Dysoxylum* sp. aff. *D. klanderi*—87.74 (Meliaceae); *Breynia stipitata*—44.39 (Euphorbiaceae) [values derived from Crome 1975a and pers. comm., McDiarmid *et al.* 1977, Howe and Vande Kerckhove 1980, Howe 1981, Snow 1962, Foster and McDiarmid, unpubl. data]. Frost (1980) also reported three subtropical species with more than 40 percent lipid, one of these being *Trichilia emetica*.

The high lipid content of *T. cuneata* aril is reflected in its caloric content per ash-free gram dry wt. (Table 4) which showed little variation between trees (C.V. =

1.463). Considerably more variation is seen when caloric content of individual fruits is considered (C.V. = 9.704). This is more indicative, however, of variation in the weight of the aril than in its nutrient content.

Although conclusions regarding nutrient characteristics of different plant families remain tentative because fruits of so few (often only one) tropical species from each family have been analyzed, suggestions of patterns emerge. Arils of the four species of Myristicaceae for which we reviewed data are high in lipid. Likewise, the fleshy parts of the fruits of six of the 12 species of Lauraceae for which we found data are high in protein. *Stemmadenia donnell-smithii* is also high in lipid and protein; however, it is the only species of Apocynaceae for which we had information. We have some data for three other tropical species of Meliaceae, the family that includes *Trichilia*. Arils of these species average only 5.18 percent protein (range = 3.24–6.18%). *Dysoxylum* sp. was high in lipid, as noted above. A third species, *Melia azederach*, contained 4.61 percent (dry wt.) lipid (Crome, pers. comm.). Percentages for two subtropical species in the family Meliaceae are even lower; *Ekebergia capensis* and *Trichilia emetica* contained 21.6 (dry wt.) and 8.5 percent protein, and 8.6 and 46.9 percent lipid, respectively (Frost 1980). Meliaceae appears to be an important group in terms of fruits with high nutrient content. These conclusions are similar to those of Snow (1980) who included the Meliaceae, Myristicaceae, and Lauraceae among the six families he categorized as having highly nutritious fruits important for specialized frugivorous birds.

It is interesting that *Trichilia cuneata* and *Stemmadenia donnell-smithii* are the only species we found that were high in both lipid and protein. These species are relatively common in the forest along the Rio Higuérón, have complementary fruiting seasons, and share many avian dispersers. Of the nine species reported by McDiarmid *et al.* (1977: Table 6) to feed most commonly on *S. donnell-smithii*, five also are regular users of *T. cuneata* (Leck 1969). Three of the other four are northern migrants not present in Costa Rica during the *Trichilia* fruiting season. Leck (1969) reported multiple observations of seven species feeding on *Trichilia*. All but two of these also feed on *Stemmadenia* (McDiarmid *et al.* 1977).

McKey (1975) assigned seed-dispersing birds to two categories, the "specialized frugivores" that obtain all or most of their nutrients from fruits and are effective seed dispersers, and the "opportunistic frugivores" that use fruits primarily as a source of carbohydrates and water, but do not disperse many of the seeds from the trees whose fruits they exploit. Though he used these two extremes as a basis for his discussion, McKey noted that in reality they are not distinct but represent points on a continuum with regard to degree of dietary specialization on fruit. He associated with these categories particular

TABLE 4. Average weights and energy values of aril from fruits of *Trichilia cuneata* collected in 1972.

Tree ^a	Mean wt (gms)/fruit			Mean energy content of fruit (kcal) ^b	
	Wet	Dry	Ash-free dry	Per ash-free gram dry wt	Per fruit
A	0.2327	0.1055	0.1018	7.1621	0.7291
B	0.2651	0.1214	0.1178	7.3328	0.8638
C	0.2088	0.0991	0.0953	7.3264 ^c	0.7004
D	0.2181	0.1013	0.0982	7.4542	0.7320
E	0.2190	0.0960	0.0928	7.3976 ^c	0.6865
F	0.1870	0.0917	0.0892	7.4428 ^c	0.6639
Mean	0.2218	0.1025	0.0992	7.3527	0.7293

^a For each tree, arils from 10 fruits were combined for analysis.

^b To convert kcals to kilojoules, multiply by 4.184.

^c Percent nutrient composition from Table 3 adjusted proportionally to equal 100% for the calculation of these values.

types of fruits that birds in each category might be expected to use. Briefly summarized, those exploited by specialized frugivores should be large, have a relatively soft seed coat, be highly nutritious, and be produced in limited amounts over a long fruiting season. Those exploited opportunistically, in contrast, should be small, have a relatively hard seed coat, be low in protein and lipids yet high in carbohydrates, and be produced in large numbers over a short fruiting season. The rationale behind these predictions was given by McKey (1975) and is not repeated here. Overall, however, he suggested that those trees that attract specialized frugivores do so by producing a few high quality (and costly) fruits to attract a few high quality dispersers. Those trees evolved to attract opportunistic frugivores, on the other hand, produce large quantities of poorer quality (less costly) fruits to attract more, but poorer quality (*i.e.*, less efficient) dispersers.

Howe (1981) reviewed McKey's theoretical framework, primarily from the view of nutrient richness of the fruits and diversity of the avian disperser assemblage. He cited instances in which bird species expected to feed on fruit opportunistically specialized on certain small fruits produced in quantity and instances in which high quality fruits were exploited by large assemblages of birds, including several species of opportunists. Howe generally found McKey's framework useful, but insufficient, because of evidence that in some instances both opportunistic and specialized frugivores exploit fruit from trees of each category.

Trichilia cuneata presents a somewhat different problem. In Howe's (1981) examples, the dispersers and their behaviors did not conform to the expected, with birds normally considered as opportunistic frugivores regularly

exploiting high quality, energy-rich fruits. With *T. cuneata*, it is the tree species that does not fit the categories cited above. In part, the difficulty arises from the vagaries of trying to determine what is "small" or "large," "abundant" or "rare," etc. However, on the basis of our familiarity with a variety of tropical fruit trees, we suggest that *T. cuneata* produces small fruits with highly nutritious aril, and seeds with a coat of medium hardness (one can split a seed with a fingernail after applying moderate pressure). The crop size is moderately large and the fruiting season intermediate in length. Thus, *T. cuneata* shares or is intermediate between traits of both fruit tree categories outlined by McKey (1975). Not unexpectedly, it is visited by both specialized (4 species) and opportunistic (11 species) frugivores, which may explain its mixed array of characteristics, or vice versa. (It is likely that the characteristics of fruit trees and their dispersers are coevolved, and we do not wish to argue which came first in this

context.) Rather than being "specialized" for exploitation by either specialist frugivores or opportunistic ones, *T. cuneata* is a "generalist" permitting exploitation by both groups.

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