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Floral and Extrafloral Nectars of Costa Rican *Inga* trees: A Comparison of their Constituents and Composition¹

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ABSTRACT

Two types of nectaries occur in the neotropical genus *Inga* (Fabaceae: Mimosoideae). Floral nectar is ingested by visitors to flowers and foliar nectar is utilized by a variety of insects. Although their flowers are similar in appearance and morphology, different *Inga* species exhibit different floral behaviors and have different primary pollinators. The floral nectars of the eight species analyzed are, however, similar in proportions of various sugars. Freshly secreted floral nectars are sucrose-dominant, though over time the sucrose is hydrolyzed and nectars become hexose-rich. In some species, this change corresponds to a shift in the pollinator fauna. Amino acid constituents of floral nectars differ among *Inga* spp., but are constant within a species.

Extrafloral nectars are hexose-dominant and have substantially greater sugar concentrations than floral nectars. Extrafloral nectars of different species differ in array of amino acids present, but amino acids in floral and extrafloral nectar of a given species are similar, but not identical. Differences in composition of the two types of nectar produced by a given *Inga* species may result from natural selection by mutualists utilizing the nectar as well as non-evolutionary influences of the abiotic and biotic environment.

RESUMEN

Se encuentran dos tipos de nectarios en el género neotropical *Inga* (Fabaceae: Mimosoideae). El nectar de las flores es ingerido por los animales que visitan las flores, y el nectar foliar es a su vez utilizado por una gran variedad de insectos.

Aunque las flores de *Inga* tiene una apariencia y morfología similar, diferentes especies de este género muestran un comportamiento floral diverso y tienen plonizadores primarios diferentes. Los nectares florales de las 8 especies que se analizaron, tienen proporciones similares de varios azúcares en la solución del nectar. La sucrosa es dominante en las secreciones frescas de los nectares florales, y al pasar el tiempo, la sucrosa se hidroliza y los nectares se vuelven ricos en hexosa. En algunas especies este cambio corresponde a el cambio de la fauna polinizante. Los aminoácidos de los nectares florales difieren entre *Inga* spp., pero son constantes en cada de las especies.

La hexosa es dominante en los nectares extraflorales y estos tienen una concentración mas grande de azúcares que los nectares florales. Los nectares extraflorales de diferentes especies difieren en el orden de los aminoácidos presentes, y los aminoácidos en los nectares florales y extraflorales de algunas especies son similares, pero no son idénticos. Las diferencias de la composición de las dos clases de nectar producidos por una especie determinada del género *Inga* pueden resultar a partir de una selección natural de mutualistas los cuales utilizan el nectar, o pueden resultar a partir de influencias no evolucionarias del medio ambiente biótico y no biótico.

Key words: amino acids; composition; concentrations; extrafloral; floral; function; nectar; pollination; protection; sugars.

NECTARIES ARE PLANT SECRETORY STRUCTURES of diverse morphology, anatomy, and function (Bentley & Elias 1983). Nectaries mediate two major mutualistic interactions between plants and animals: pollination and protection. The nectar produced by floral nectaries is a reward for floral visitors, and is the primary physiological cost paid by the plant in nectar-based pollination systems. The animals that take floral nectar inadvertently transfer pollen, but

visit flowers for the purpose of meeting their own energetic and nutritional needs. Extrafloral nectaries are visited by ants, parasitoid wasps and flies, and other predators for the energy and nutritional considerations mentioned above; their associated effects on the plants are mostly beneficial, including protecting the plants directly and indirectly against herbivores (Bentley 1977, Keeler 1989, Koptur 1992).

Costa Rican *Inga* (Fabaceae: Mimosoideae) species have both floral and extrafloral nectaries (Koptur 1982, 1983a). Ecological interactions based on these nectaries have been studied in a number of species: lowland *Inga vera* ssp. *spuria* (Willd.) J.

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TABLE 1. Sugars in *Inga* nectars. Multiple analyses are represented on separate lines. S = sucrose, G = glucose, F = fructose, malt = maltose, melez. = melezitose; fn = floral nectar, efn = extrafloral nectar. *Inga* species abbreviated by first three letters of specific epithet.

	BRE		DEN		LON		MOR		OER		PUN		QUA		VER	
	fn	efn	fn	efn	fn	efn	fn	efn	fn	efn	fn	efn	fn	efn	fn	efn
S	.48	.12	.36	.38	.44	.38	.58	ND	.66	.22	.39	.50	.32	ND	.40	.40
	.20	.20	.38	.61	.51	.38	.51	ND	.59	.27	.25	.45	.63	.17	.32	.32
	.27	.17	.42	.36	.41	.48	.42	.36	.32	.28	.48				.35	.35
	.52	.53	.42	.48					.27						.41	.41
	.25	.53	.32	.23	.21	.23	.22	.37	.18	.50	.32	.22	.29	.32	.34	.30
G	.42	.54	.28	.14	.09	.14	.29	.45	.24	.45	.28	.29	.13	.35	.41	.41
	.51	.43	.21	.28	.26	.28	.51	.28	.39	.39	.21	.23	.39	.37	.37	.37
	.19		.26	.31					.43	.43			.38	.68	.33	.33
	.27	.33	.39	.39	.35	.28	.20	.63	.16	.26	.28	.28	.24	.48	.26	.26
	.32	.26	.34	.25	.40	.25	.18	.55	.15	.26	.47	.26	.24		.23	.23
F	.20	.40	.37	.37	.32	.37	.32		.30	.30	.51	.29			.27	.27
	.29		.32	.19		.19			.31	.31					.25	.25
															.02	.02
Malt																
Melez.																
	.03		.05						.01	.01						
	.01	.02						.03	.03							
S		.14	.60	.60	.79	.60	1.4	.11	1.9	.28	.63	.99	.48	.1	.66	.65
G+F	.25	.25	.61	1.6	1.03	1.6	1.1	.06	1.5	.38	.34	.82	1.7	.20	.5	.5
	.39	.21	.71	.54	.71	.54			.46	.46	.39	.93		.55	.55	
Mean	1.09	.20	.74	.96	.84	.96	1.2	.09	1.7	.37	.45	.91	1.09	.15	.61	.65
Conc.	.66	.20	.67	.93	.84	.93	1.2	.09	1.7	.37	.45	.91	1.09	.15	.61	.65
$\bar{x}\%$ (wt/wt)	18.3	29	17	22.5	17.5	22.5	14	21	34.2	41	15.2	26	22	28	17.9	39
Low value	16	14	11	10	7	10	8	9	25	25	13	12	19	16	17	24
High value	20	45	22	37	28	37	22	43	40	64	17	42	26	40	19	53

Leon (Salas 1974); and seven species in montane forests in and around Monteverde (Feinsinger 1976, 1978; Koptur 1983b, 1984a, b, 1985). The genus offers an opportunity to test the hypothesis that nectar composition varies with function.

All nectars are aqueous solutions of sugars, amino acids, and other organic compounds (Baker & Baker 1975, 1983 a; Baker 1977). The sugar composition of freshly secreted floral nectar is characteristic of a species and correlates with the primary pollinator-type (Baker & Baker 1975, 1983b; Freeman et al. 1985; Elisens & Freeman 1988; Erhardt 1993; Galetto *et al.* 1993; Stiles & Freeman 1993). Sugar composition of extrafloral nectars is more variable within a species. Amino acid complements are also characteristic of plant species (Baker & Baker 1977, 1983a) but are not necessarily the same in floral and extrafloral nectar of the same species (Baker *et al.* 1978, Bernardello *et al.* 1991, Galetto & Bernardello 1992).

This paper compares the compositions of floral and extrafloral nectars within and among Costa Rican *Inga* species. Since the two types of nectaries are visited by very different kinds of organisms, the hypothesis to be tested is: floral nectars of different species will be more similar to one another than floral and extrafloral nectars of the same species; *i.e.*, function is more important than taxonomy in determining nectar composition.

Inga flowers are borne in inflorescences, and have reduced perianth parts, with the showy display provided by the many white stamens. The main reward for *Inga* floral visitors is nectar, contained within the tube formed by the connate staminal filaments. Larger flowered species had more nectar than smaller flowered species, and tended to attract larger visitors. All *Inga* species studied in and around Monteverde received a substantial amount of pollinator service from hawkmoths, and many also had hummingbirds as major pollinators (of secondary importance are smaller Lepidoptera). Differences in flower size, as well as differences in flower opening times and floral fragrance result in a large number of sympatric *Inga* species having different pollinators (Koptur 1983b).

All Costa Rican *Inga* species have extrafloral nectaries, located between opposite leaflets on the compound leaves. These foliar nectaries are secreting nectar on young and developing leaves (Koptur 1984a). Nectary morphology ranges from cupular (*e.g.*, *I. densiflora*) to pit-and-mound (where nectar fills a cavity and oozes out a pore; as in *I. punctata*). Foliar nectar is secreted continuously day and night,

and is visited by a variety of ants day and night that provide protection against a wide range of insect herbivores (Koptur 1984a). At higher elevations, where nectar-drinking ants are rare or absent, the nectaries are visited by other predators (such as vespid wasps) and parasitoids (such as braconid and ichneumonid wasps and tachinid flies) that provide alternative antiherbivore defense (Koptur 1985, 1989a, 1991).

METHODS

Nectar samples for chemical analysis were collected from fresh flowers that had been isolated and opened inside heavy paper bags (Pollen-Tector bags, Carpenter Paper Company, Iowa). For each species, nectar from three or four individuals from the same population was collected and analyzed separately. Extrafloral nectar was collected from bagged leaves from which insects were excluded for 24 hours. Samples were spotted onto filter paper and dried for later analysis, using methods developed by Herbert and Irene Baker (Baker & Baker 1973, 1975, 1976a, b, 1983a, b), as follows. Samples were eluted in a known volume of distilled water, and the solution spotted on large filter paper and run against sugar standards in descending paper chromatography. Sugars were then quantified fluorometrically. A part of each sample was dansylated and amino acids were separated using two-dimensional thin-layer chromatography, detecting and identifying individual amino acids by position and fluorescence under UV light. Overall amino acid concentration was measured by comparison with the histidine scale (Baker & Baker 1973, 1975), where a score of 1 = .49 μM and each scale step indicates a doubling of concentration (*e.g.*, 2 = .98 μM ; 9 = 12.5 mM). Overall nectar sugar concentrations were measured in the field using a pocket refractometer (measuring % sugar on a wt/wt scale; Bolten *et al.* 1979) or from nectar spots on paper (Baker 1979). Lipids were detected using an osmic acid spot test and quantified against a soy oil scale.

Voucher specimens for all species except *Inga vera* were collected at Monteverde, Puntarenas Province, Costa Rica (*I. vera* was collected from Guanacaste Province) and are in CR, MO, and UC. Species included in this study (with taxonomic authorities) are *Inga brenesii* Standley, *I. densiflora* Benth., *I. longispica* Standley, *I. mortoniana* J. Leon, *I. oerstediana* Benth. ex Seemann, *I. punctata* Willd., *I. quaternata* Poeppig, and *I. vera* ssp. *spuria* (Willd.) J. Leon.

TABLE 2. Amino acids (A.A.) in *Inga nectars*. Amino acids indicated by three-letter abbreviations. +/— indicates presence/absence (++) = strong, (+++) = very strong) tr = trace, ? = possibly present, nd = not detected. *Inga* species abbreviated by first three letters of specific epithet.

A.A.	Inga species (abbreviated)																							
	BRE			DEN			LON			MOR			OER			PUN			QUA			VER		
	fn	efn	+	fn	efn	+	fn	efn	+	fn	efn	+	fn	efn	+	fn	efn	+	fn	efn	+	fn	efn	+
ala	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
arg	+	+	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
asn	+	+	nd	?	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
asp	+	+	?	tr	tr	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
cys	+	+	?	?	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	tr	tr	tr	
glu	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
gln	+	+	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
gly	++	+	+	tr	tr	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
his	nd	+	nd	tr	tr	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	nd	
ile	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
leu	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
lys	nd	+	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	
met	+	tr	nd	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
phe	+	+	+	+	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	++	
pro	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
ser	+	+	nd	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
thr	+	+	nd	?	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
trp	+	+	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	tr	
tyr	+	+	+	+	++	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	++	
val	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
g-NH4	+	+	+	+	nd	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	nd	
Unkn.	4	3	nd	+	nd	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	nd	
Total Amino acid concentration (histidine scale—low = 1; high = 10)																								
23		5	5	5	9	9	6	6	6	5	4	4	4	6	2	2	6	3	8	4	4	4	4	
Total Amino acids present in each sample (:s not included)																								
23		24	11	17	17	17	18	18	18	19	15	15	15	11	16	16	16	16	22	18	18	18	18	

RESULTS

The detailed results of sugar analyses of floral and extrafloral nectars are given in Table 1. Floral nectar sugar concentrations ranged from 14 to 34 percent, with most species averaging less than 20 percent sugar. These are lower mean concentrations than extrafloral nectars, which, with one exception, range from 21 to 41 percent. Extrafloral nectar samples from *I. longispica* were very dilute (1–11%), and it was not possible to detect sugars and amino acids in the samples I collected; this suggests that the samples were probably mostly water, diluted by the continual misty surroundings of the cloud forest.

A useful method of comparing sugar composition is to use sucrose-hexose ratios (Baker & Baker 1983b). If a nectar has equal concentrations of all 3 sugars (sucrose and the two hexoses: fructose and glucose), the ratio is .5; greater than or equal to .5 is designated sucrose-dominated, and greater than or equal to 1.0 is sucrose-rich. Nectars with ratios from .1 to .499 are hexose-dominated, and less than .1, hexose-rich. The *Inga* floral nectars are all sucrose-dominated and sucrose-rich (Table 1: S/(G + F)). Many of the extrafloral nectars exhibit lower ratios than their floral counterparts (being hexose-rich, hexose-dominated, sucrose-dominated, and sucrose-rich). This difference in sucrose-hexose ratio is significant using a paired samples *t*-test on nectar type vs average ratio ($t = 3.549$, $df = 14$, $P = .003$).

The presence and absence of individual protein amino acids and various nonprotein amino acids is indicated in Table 2. Overall concentrations of amino acids ranged from a low of .98 μM in extrafloral nectar of *I. punctata* to a high of 12.5 mM in *I. densiflora* extrafloral nectar. In several species it was not possible to detect any amino acids in the extrafloral nectar (*I. longispica*, *I. mortioniana*, and *I. quaternata*), but all floral nectars had a complement of amino acids.

The amino acid arrays of the nectars were examined with cluster analysis (SYSTAT 1992) and McClade (Maddison & Maddison 1992). Cluster analysis is most appropriate for categorical data (James & McCulloch 1990), in this case, the presence and absence of the individual amino acids. Data from Table 2 were entered, with presence for scores of "tr" and any number of "+", and absence for all other table entries. In the SYSTAT package I chose Cluster-Join, and used percentage distance metrics and single-linkage methods (which use the distance between the two closest members of clusters to calculate distance between clusters). I then ex-

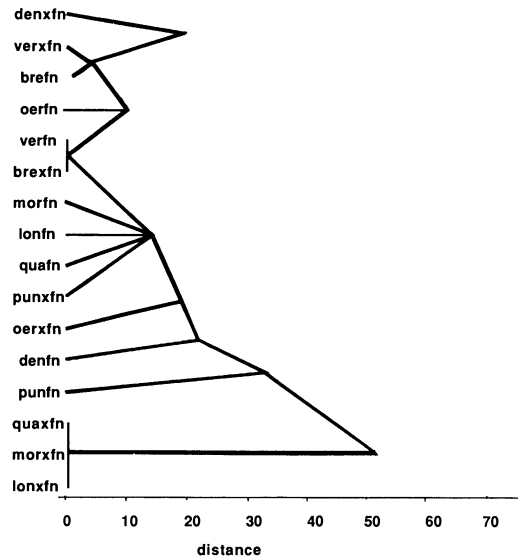


FIGURE 1. Dendrogram from cluster analysis of amino acids in *Inga* nectars. Each nectar is identified by species (first three letters of specific epithet) and type (fn = floral, xfn = extrafloral). Distance metric is normalized percent disagreement single linkage method (nearest neighbor).

amined the data using McClade, an interactive graphic program for analyzing phylogenies and studying character evolution, to find the trees with the shortest lengths in order to better resolve the clusters.

When both floral and extrafloral nectars are considered together (Fig. 1), the nectars cluster more in accordance with taxonomy than function. The floral nectar of *Inga vera* and the extrafloral nectar of *I. brenesii* both have all the amino acids present, and cluster together (distance = 0); the floral nectar of *brenesii* and extrafloral nectar of *vera* are a cluster (distance 4.7); and *oerstediana* floral nectar clusters close to all of the above (distance = 9.5). The floral nectars of *mortioniana*, *longispica*, and *quaternata* cluster with the extrafloral nectar of *punctata* (distance 14.3); *oerstediana* extrafloral nectar, *densiflora* floral nectar, and *punctata* floral nectars have fewer amino acids and join this cluster more distantly ($d = 19.0, 23.8, \text{ and } 33.3$, respectively). The extrafloral nectar of *I. densiflora* is missing other amino acids and is a distance of 19 from the *vera*/*brenesii* cluster. The most distant cluster ($d = 52.4$) is that formed by the three extrafloral nectars with no detectable amino acids.

If we look only at the floral nectars (Fig. 2) we can see influence of both taxonomy and function. The larger-flowered species (*brenesii*, *oerstediana*,

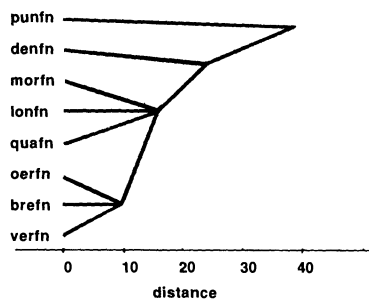


FIGURE 2. Dendrogram from cluster analysis of amino acids in *Inga* floral nectars. Explanation as in Figure 1.

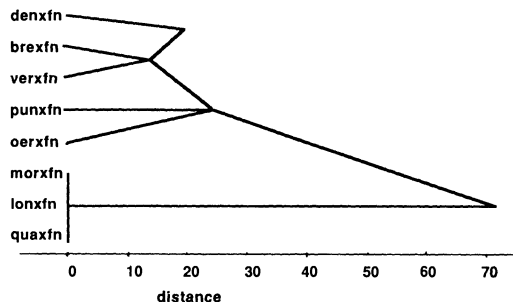


FIGURE 3. Dendrogram from cluster analysis of amino acids in *Inga* extrafloral nectars. Explanation as in Figure 1.

and *vera*) have the widest range of visitors and probable pollinators (Koptur 1983b), and also have the fullest complements of amino acids, clustering closely with each other. All three species are members of the same section (*Inga*) and series (*Inga*) of the genus *Inga* (Leon 1966). The two smaller-flowered species of the same section (but a different series) are the least like the other nectars, having the fewest amino acids, and cluster together. Both *densiflora* and *punctata* have small flowers that mostly open synchronously (*densiflora* at dawn; *punctata* at dusk) with another shift of flowers opening at the opposite time, and are pollinated by skippers, hummingbirds, and hawkmoths (Koptur 1983b); more specialization (relatively speaking) may have selected for fewer or particular amino acids in these floral nectars. The two medium-size flowered species (*mortoniana* and *quaternata*) cluster together; they are members of section *Leptinga*. Both these species have long-lived flowers active for more than one peak of activity (Koptur 1983b), and a wide variety of none-too-abundant floral visitors. They cluster with *longispica* (the only member of section *Bourgonia* included in this study) which has small flowers arranged in a spike for which only Lepidopteran floral visitors were recorded (Koptur 1983b).

Considering only the extrafloral nectars (Fig. 3) the three with no detectable amino acids cluster together, far ($d = 70$) from the others. The two closest are *brenesii* and *vera* ($d = 14.3$), not far from *densiflora* ($d = 19$) and the *punctata*-*oerstediana* cluster ($d = 24$). We therefore have two main groups: those with and those without amino acids. Of those with amino acids, the species do not cluster in the same way the floral nectars do. Taxonomy, after all, is based largely on reproductive structures! The extrafloral nectars of all these species are visited by ants, wasp and fly parasitoids, wasp

predators, and other insects; they are secreted continuously and in small quantities. There is much less differentiation among the *Inga* species in extrafloral nectar visitors compared with floral nectar visitors.

Lipids were detected only in the floral nectar of *Inga brenesii* and not in either floral or extrafloral nectars of the other species. This nectar contained from 2 to 5 mg per ml lipids.

DISCUSSION

Extrafloral nectars show a much wider range of solute concentrations than floral nectars, even when collected from inside bags (that presumably protect them from the ambient conditions). Extrafloral nectaries are exposed, and the nectar droplets are subject to drying and dilution from the environment; whereas, floral nectar is partially concealed in the floral tube, with only the top surface exposed to humidity and wind (Corbet *et al.* 1979). The average concentration of nectar is influenced by the weather conditions at the time it is produced: *Inga oerstediana*, with the highest average concentration, only occurred at the lowest elevation, which is the warmest and driest site (Koptur 1983b).

In the extensive surveys done by the Bakers, as well as in studies by other researchers, the great majority of flowers pollinated by hawkmoths and hummingbirds have nectars that are sucrose-rich or sucrose-dominated (ratio $>.5$ or $=.5$). Hummingbirds prefer sucrose over hexose mixture over glucose over fructose (Martinez del Rio 1990), and they are able to digest sucrose as their passerine floral-visiting counterparts cannot (Martinez del Rio *et al.* 1992). *Inga* floral nectars fit this pattern well; field studies have shown that primary pollinators are indeed hawkmoths and hummingbirds (Koptur 1983b). *Inga brenesii*, with flowers that open (an-

thesis) continuously day and night is occasionally visited by bats (Koptur 1983b); some nectar samples were hexose-dominated, appropriate to bat visitors (Baker & Baker 1983a). Sucrose-hexose ratios may change with flower age and exposure to microbes, e.g., in *Inga vera* ssp. *spuria* (Baker & Baker 1983b), accommodating different guilds of visitors.

Sucrose-hexose ratios in *Inga* extrafloral nectars were, in general, much lower than those of floral nectars. Except for *I. densiflora* and *I. punctata*, these ratios were less than .5 (hexose-rich to hexose-dominated). It is plausible that since extrafloral nectar is more exposed than floral nectar, quicker breakdown of the disaccharide sucrose to its hexose components commonly occurs. If the nectaries had not been bagged for some hours to allow accumulation of extrafloral nectar by excluding visitors, the ratios would have been considerably lower (S. Koptur, pers. obs.). It is unexpected that *I. densiflora* and *I. punctata* have maximum ratios higher than those found in their floral nectars. This may be due to the timing of extrafloral nectar secretion and collection; it could be that the high sucrose content was in very fresh nectar.

The fact that most nectars do not contain all the plant essential amino acids (all of which are contained in phloem sap) has been used as evidence for secretion vs excretion of nectar (Percival 1961, Baker & Baker 1983a). Nectaries selectively secrete substances that attract organisms to the plant; and over evolutionary time, natural selection by the important nectar drinkers has resulted in emphasis of certain components over others. The most specialized nectar in an array of nectars is therefore the one with the fewest essential amino acids, or that is the most different from phloem sap.

Inga vera floral nectar has all the essential amino acids, and is therefore the least different from phloem sap (and perhaps the least specialized, via the logic expressed above). Its flowers are visited by a variety of large pollinators, from hawkmoths to bats (Salas 1974). The extrafloral nectar of this species has all amino acids but histidine and lysine (Table 2). These results, and those for *I. oerstediana*, differ slightly from those reported by Baker *et al.* (1978). It may be that specimens collected in disparate locations are distinct taxa (taxonomic revision is continuing in this genus), or that there are population or habitat differences in nectar constituents. Also, insect visitors to flowers can add amino acids to nectar by direct contact or by dislodging pollen into the nectar (Willmer 1980), and perhaps their samples came from flowers that were not fresh, having been visited or damaged (Gottsberger *et al.* 1990).

In general, the larger-flowered *Inga* species have the widest range of amino acids in their floral nectar, and this may correspond to serving the widest array of floral visitors, from large bats, hummingbirds, and hawkmoths, to smaller moths, butterflies, wasps, and other insects. Species with smaller flowers and/or more restricted activity times have fewer amino acids in their nectars. The species cluster (with regard to amino acid complements) in accordance with the taxonomic divisions of the genus (Leon 1966).

Extrafloral nectars show less differentiation among those that have amino acids present; and there is not direct correspondence between the floral and extrafloral nectar of the same species, as found in a larger survey of amino acid complements by Baker *et al.* (1978). In extrafloral nectar of only five *Inga* species were amino acids detected and identified. In three species (*I. brenesii*, *I. densiflora*, *I. punctata*), extrafloral nectars had more amino acids than floral nectars, but in the other two (*I. vera*, *I. oerstediana*) the floral nectars had more than the extrafloral nectars. We cannot say, therefore, that one type of nectary is more specialized than the other. All *Inga* nectars analyzed so far contain six amino acids: alanine, glycine, isoleucine, proline, tyrosine, and valine. Two other amino acids, asparagine and glutamic acid, may also occur, but were questionably detected in two species. It is interesting to observe that cysteine, thought to be especially important to ants, is present in only three of the eight floral nectars but present in four of the five extrafloral nectars in which any amino acids were detected. Some ants have been found to prefer artificial nectars with amino acids present over comparable sugar-only artificial nectars, but other ants have not been found to discriminate (Koptur 1979, Lanza & Varga 1993).

Substantial amounts of lipids were detected in the floral nectar of *Inga brenesii*. None were detected in the extrafloral nectar of this or any other species. It may be that these lipids replenish the fat-body stores of long-lived hawkmoth pollinators, which feed only on nectar as adults, or supplement the dietary needs of hummingbirds.

Patterns like those described in this study present some hypotheses that can be tested with field and laboratory experiments. Do components of floral nectars increase longevity or fecundity of pollinators? Do ants and other visitors to extrafloral nectaries prefer certain amino acids over others? And are these amino acids more common in extrafloral nectaries? Recent evidence that plants can respond with greater volumes of extrafloral nectar when damaged (Koptur 1989b), or produce nectar of

different constitution (Smith *et al.* 1990), indicates that many interactions may be more dynamic than previously realized. The volume of floral nectar may increase with flower visitation, and the composition of floral nectar may be altered by visitors, affecting the quality of nectar experienced by subsequent visitors. Much could be learned from more work with more plant and animal species to elucidate the various roles of nectar constituents in plant/animal interactions.

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