

Nectar Sugar Composition in Southern African Papilionoideae (Fabaceae)

BEN-ERIK VAN WYK

Department of Botany, Rand Afrikaans University, P.O. Box 524, Auckland Park, Johannesburg, 2006, South Africa

Key Word Index—Crotalariaeae; Lipariaeae; Podalyrieae; Papilionoideae; Fabaceae; nectar sugars; chemo-taxonomy.

Abstract—The nectar sugar composition of several genera of the subfamily Papilionoideae (Fabaceae) have been analysed, including many southern African endemic genera of the tribes Crotalariaeae, Podalyrieae and Lipariaeae. Nectar sugars were found to be conservative characters with limited taxonomic value. Most of the samples contained high concentrations of sucrose, reaching nearly 100% in species of *Virgilia* and *Cyclopia* of the tribe Podalyrieae. Fructose and glucose are present in more or less equal amounts, and are the dominant sugars in the nectar of *Erythrina* and *Sutherlandia* (both bird-pollinated) but also in *Pearsonia* and some species of *Lotononis* (both bee-pollinated). The conservative nature of nectar sugars is clearly seen in the two species of *Liparia* (tribe Lipariaeae) where there are morphological adaptations to bird pollination in *L. splendens* but no corresponding difference in the sugar composition of the nectar.

Introduction

The temperate parts of southern Africa have a relatively high degree of endemism in papilionoid legumes. All of the nine genera and approximately 100 species of the tribes Podalyrieae and Lipariaeae are endemic to the Cape Province. Of the 15 genera and 1223 species of the tribe Crotalariaeae, 13 genera and 642 species form part of the southern African flora (Polhill, 1976, 1981; Van Wyk, 1991). In a continuing study of evolutionary relationships within these three tribes, we have examined the taxonomic value of nectar sugars. Our main interest was to see if the patterns are conservative (as was found in the family Asphodelaceae) or whether nectar sugar composition is related to flower size and pollinator type.

Available information does not allow any meaningful comparison of nectar sugar compositions within the Fabaceae. Most of the 33 species studied by Percival (1961) had sucrose-rich nectar but her results were unfortunately semi-quantitative (subjective assessment by paper chromatography) and only a few tribes were represented. Studies of several species of *Erythrina* by Baker and Baker (1979, 1983a) [and their data cited in Cruden and Toledo (1977)] showed that hummingbird-pollinated species can be distinguished from those pollinated by perching birds—nectar of the former was sucrose-rich, while nectar of the latter was found to be hexose-rich. Interesting diurnal and nocturnal patterns were found in *Inga* (Mimosoideae) (Baker and Baker, 1983a). The pollination ecologies of *Erythrina* and *Inga* are highly specialized and are obviously uninformative about general patterns within the Fabaceae.

Materials and Methods

Nectar samples were mostly taken from plants in their natural habitat. Most of the species are from the tribes Podalyrieae, Lipariaeae and Crotalariaeae, but a few samples from other tribes were included for comparison. Voucher specimens are listed in Table 1. Over 100 samples were analysed, representing 71 species from 28 genera.

Procedures. Nectar was sampled as spots on Whatman no. 1 filter paper, air-dried and stored at -18°C . The nectar was eluted with distilled water ($3 \times 50 \mu\text{l}$), using a centrifuge. HPLC was performed isocratically at a flow rate of 2.5 ml min^{-1} on a "Waters Sugarpak" column, with acetonitrile–water (87:13) as eluent. The use of a

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refractive index detector allowed us to accurately calculate the sugar composition of each sample, using peak height and 8 mg ml⁻¹ of fructose, glucose and sucrose as external standards.

Results

The nectar sugar composition in 111 samples from 71 species and 28 genera of the Fabaceae is shown in Table 1. Most of the samples from the tribes Podalyrieae, Liparieae and Crotalarieae had a high proportion of sucrose and relatively low proportions of fructose and glucose. No other sugars were detected in any of the samples. In contrast with the general pattern, hexose-rich nectar was found in species of *Lotononis* and *Pearsonia* (tribe Crotalarieae) and also in *Erythrina* (tribe Phaseoleae) and *Sutherlandia* (tribe Galegeae). The two hexose sugars occur in more or less equal proportions, but often with slightly more fructose than glucose. The number of samples from the Podalyrieae, Liparieae and Crotalarieae seems adequate to allow a comparison of mean values for the percentage sucrose. These are 86.5 in the Podalyrieae (x = 44), 68.6 in the Liparieae (x = 12) and 50.2 in the Crotalarieae (x = 34). A visual summary of the results is given in Fig. 1.



FIG. 1. NECTAR SUGAR COMPOSITIONS IN VARIOUS GENERA AND SPECIES FROM THREE TRIBES OF SOUTHERN AFRICAN FABACEAE: FROM LEFT TO RIGHT: CROTALARIEAE, LIPARIEAE AND PODALYRIEAE, RESPECTIVELY. (Samples and species are numbered as in Table 1.)

TABLE 1. SUGAR COMPOSITION IN 111 NECTAR SAMPLES FROM 71 SPECIES AND 28 GENERA OF THE FABACEAE, MAINLY FROM THE SOUTHERN AFRICAN TRIBES CROTALARIEAE, PODALYRIEAE AND LIPARIEAE

Sample number (see also Fig. 1)	Genera and species	Locality or voucher specimen*	Nectar composition			
			(%) Fructose	(%) Glucose	(%) Sucrose	
Papilionoideae						
Tribe Crotalarieae						
1.	<i>Aspalathus carnosus</i> Berg.	ALS 430	15	14	71	
2.	<i>A. nivea</i> Thunb.	BVW 2937	21	18	61	
	<i>A. sceptorum-aureum</i> Dahlgr.	ALS 650	21	9	70	
4.	<i>A. setacea</i> Eckl. & Zeyh.	BVW 2939	16	12	72	
5.	<i>A. sp.</i>	BVW 2941	19	14	67	
1a.	<i>Crotalaria agatiflora</i> Schweinf.	sample 1	17	9	74	
		sample 2	Fourie 1b	24	11	65
		sample 3	Fourie 1c	24	17	59
2.	<i>C. capensis</i> Jacq.	BVW 3041	13	7	80	
3.	<i>D. doidgeae</i> Verdoorn	sample 1	BVW 3042	12	8	80
		sample 2	BVW 3043	14	11	75
4.	<i>C. humilis</i> Eckl. & Zeyh.	BVW 3108	28	18	54	
1.	<i>Lebeckia ambigua</i> E. Mey	BVW 3120	25	15	60	
2.	<i>L. cytisoides</i> Thunb.	BVW 3117	25	17	58	
3.	<i>L. macrantha</i> Harv.	BVW 3055	28	26	46	
4.	<i>L. pauciflora</i> Eckl. & Zeyh.	BVW 3134	28	25	47	
5.	<i>L. pungens</i> Thunb.	BVW 3252	42	40	18	
5a.	<i>L. sericeae</i> Thunb.	sample 1	ALS 392	22	17	61
5b.		sample 2	BVW 3078	24	17	59
6.	<i>L. simsiana</i> Eckl. & Zeyh.	BVW 3123	23	19	58	
1.	<i>Lotononis calycina</i> (E. Mey.) Benth.	BVW 2621	50	46	4	
2.	<i>L. foliosa</i> H. Bol.	BVW 2607	51	41	8	
3.	<i>L. galpinii</i> Duemmer	ALS 574	49	39	12	
4.	<i>L. oxyptera</i> (E. Mey.) Benth	BVW 3131	31	30	39	
5.	<i>L. sericophylla</i> Benth.	ALS 572	44	41	15	
6.	<i>L. umbellata</i> (L.) Benth.	BVW 3234	50	47	3	
1.	<i>Pearsonia sessilifolia</i> (Harv.) Duemmer					
	subsp. <i>marginata</i> (Schinz) Polhill	BVW 2924	50	44	6	
2.	<i>P. uniflora</i> (Kensit) Polhill	BVW 3033	47	44	9	
	<i>Polhillia canescens</i> Stirton	BVW 2092	29	20	51	
1.	<i>Rafnia cuneifolia</i> Thunb.	BVW 3153	14	10	76	
2.	<i>Rafnia ovata</i> E. Mey.	BVW 3135	27	25	48	
3.	<i>Rafnia perfoliata</i> E. Mey.	BVW 3125	9	6	85	
	<i>Wiborgia obcordata</i> (Berg.) Thunb.	BVW 3126	18	16	66	
Tribe Liparieae						
	<i>Amphithalea ericifolia</i> (L.) Eckl. & Zeyh. ssp. <i>ericifolia</i>	ALS 599	23	26	51	
1a.	<i>Liparia parva</i> Vogel ex Walp.	sample 1	BVW 3243a	35	32	33
1b.		sample 2	BVW 3243b	29	24	47
1c.		sample 3	BVW 3243c	31	24	45
2.	<i>L. splendens</i> (Burm. f.) Bos & de Wit					
2a		sample 1	NBG	16	12	72
2b.		sample 2	NBG	16	13	71
	<i>Priestleya hirsuta</i> (Thunb.) DC.					
		sample 1	ALS 640a	17	13	70
		sample 2	ALS 640b	10	8	82
		sample 3	ALS 640c	4	2	94
1.	<i>Xiphotheca canescens</i> (Thunb.) Schutte & Van Wyk <i>ined.</i>	ALS 595	6	7	87	
2.	<i>X. tecta</i> (Thunb.) Schutte & Van Wyk <i>ined.</i>	ALS 597	13	11	76	
3.	<i>X. lanata</i> (Thunb.) Schutte & Van Wyk <i>ined.</i>	ALS 673	4	1	95	
Tribe Podalyrieae						
1.	<i>Cyclopia falcata</i> (Harv.) Kies					
1a.	var. <i>falcata</i>	sample 1	ALS 598a	3	1	96
1b.		sample 2	ALS 598b	7	5	88
2.	var. <i>ovata</i> Kies		ALS 602	8	4	88

TABLE 1—CONTINUED

Sample number (see also Fig. 1)	Genera and species	Locality or voucher specimen*	Nectar composition		
			(%) Fructose	(%) Glucose	(%) Sucrose
3a.	<i>C. genistoides</i> (L.) R. Br.	sample 1 ALS 614a	6	2	92
3b.		sample 2 ALS 614b	6	2	92
3c.		sample 3 ALS 624	10	8	82
3d.		sample 4 ALS 625	3	2	95
3e.		sample 5 ALS 626	1	—	99
4a.	<i>C. intermedia</i> E. Mey	sample 1 ALS 645	1	—	99
4b.		sample 2 ALS 646	3	3	94
4c.		sample 3 ALS 658a	7	4	89
4d.		sample 4 ALS 658b	2	1	97
5a.	<i>C. maculata</i> (Andr.) Kies	sample 1 ALS 635	3	2	95
5b.		sample 2 ALS 611	10	5	85
6.	<i>C. pubescens</i> Eckl. & Zypf.	ALS 685	4	1	95
7a.	<i>C. subternata</i> Vogel	sample 1 ALS 639a	1	1	98
7b.		sample 2 ALS 639b	—	1	99
7c.		sample 3 ALS 639c	3	1	96
7d.		sample 4 ALS 639d	1	1	98
8.	<i>C. galioides</i> (Berg.) DC.	ALS 787	10	8	82
1.	<i>Podalyria biflora</i> (Retz.) Lam.	BVW 3157	4	1	95
2.	<i>P. buxifolia</i> Willd.	BVW 3168	25	26	49
3a.	<i>P. calyptata</i> Willd.	sample 1 BVW 3136	8	5	87
3b.		sample 2 BVW 3141	12	10	78
4a.	<i>P. cuneifolia</i> Vent.	sample 1 BVW 3171	17	18	65
4b.		sample 2 BVW 3158b	13	13	74
5.	<i>P. glauca</i> DC.	BVW 2956	19	17	64
6.	<i>P. leipoldtii</i> L. Bol.	ALS 596	18	15	67
7a.	<i>P. tayloriana</i> L. Bol.	sample 1 BVW 3169a	14	13	73
7b.		sample 2 BVW 3169b	11	7	82
7c.		sample 3 BVW 3169c	13	12	75
1a.	<i>Virgilia divaricata</i> Adamson	sample 1 BVW 2605	6	5	89
1b.		sample 2 ex cult.	12	4	84
1c.		sample 3 ex cult.	13	2	85
1d.		sample 4 ex cult.	10	4	86
1e.		sample 5 BVW 2647a	7	3	90
1f.		sample 6 BVW 2647b	4	2	94
1g.		sample 7 BVW 2647c	1	0	99
2.	<i>V. oroboides</i> (Berg.) Salter				
2a.	ssp. <i>oroboides</i>	ALS 534	32	25	43
2b.	ssp. <i>ferruginea</i> Van Wyk	sample 1 BVW 2644a	6	3	91
2c.		sample 2 BVW 2644b	6	2	92
2d.		sample 3 BVW 2643a	5	3	92
2e.		sample 4 BVW 2643b	5	1	94
2f.		sample 5 BVW 2643c	1	—	99
Other tribes of Papilionoideae					
Tribe Sophoreae					
	<i>Bolusanthus speciosus</i> (H. Bol.) Harms	PRE	6	4	90
	<i>Calpurnia aurea</i> (Ait.) Benth.	PRE	5	3	92
	<i>Sophora japonica</i> L.	JHB	6	4	90
Tribe Tephrosieae					
1.	<i>Tephrosia grandiflora</i> Pers.	BVW 2942	10	9	81
2.	<i>T. longipes</i> Meisn.	BVW 1776	9	4	87
3.	<i>T. sp.</i>	BVW 3156	11	11	78
Tribe Phaseoleae					
1.	<i>Erythrina caffra</i> Thunb.	NBG	52	48	—
2.	<i>E. humeana</i> Spreng.	NBG	49	51	—
	<i>Dipogon lignosus</i> (L.) Verdc.	ALS 660	6	3	91
	<i>Rhynchosia arida</i> Stirton	BVW 3029	26	22	52
	<i>Vigna vexillata</i> (L.) Benth.	ALS 566	6	4	90

TABLE 1—CONTINUED

Sample number (see also Fig. 1) Genera and species	Locality or voucher specimen*	Nectar composition		
		(%) Fructose	(%) Glucose	(%) Sucrose
Tribe Psoraleeae				
<i>Psoralea pinnata</i> L.	BVW 2746	16	11	73
Tribe Aeschynomeneae				
<i>Ormocarpum kirkii</i> S. Moore	BVW 2932	20	15	65
Tribe Galegeae				
1. <i>Sutherlandia frutescens</i> (L. R. Br.				
1a. var. <i>incana</i> E. Mey.	sample 1 BVW 3162a	46	51	3
1b.	sample 2 BVW 3162b	47	49	4
2. var. <i>frutescens</i>				
3. <i>S. speciosa</i> Schltr.				
4. <i>S. microphylla</i> Burch. ex DC.				
	sample 1 JHB	46	49	5
	sample 2 BVW 3191	47	46	7
Caesalpinioideae				
<i>Bauhinia galpinii</i> N.E. Br.				
1. <i>Schotia afra</i> (L.) Thunb.	PRE	2	—	98
1a. var. <i>afra</i>	KBG	55	45	—
1b. var. <i>longifolia</i> (E. Mey.) Harv.	ex Gamsberg 51	48	1	—

*All voucher specimens are in the Rand Afrikaans University Herbarium (JRAU); collection of B.-E. Van Wyk and A. L. Schutte abbreviated as BVW and ALS. Locality abbreviations: JHB, Johannesburg Botanic Garden; KBG, Karoo Botanic Garden, Worcester; NBG, Kirstenbosch Botanic Garden, Cape Town; PRE, Pretoria Botanic Garden.

Discussion

It has been suggested that there are coevolutionary relationships between the sugar ratios of nectar and the types of pollinators that are attracted (Baker and Baker, 1975, 1979, 1982, 1983a,b; Freeman and Worthington, 1985; Freeman *et al.*, 1983, 1984, 1985; Lammers and Freeman, 1986; Spira 1981; Stiles 1976). To explain those cases where nectar sugars and pollinators are not correlated, it has been suggested that some plant taxa have a "phylogenetic constraint" and therefore do not develop distinct pollination syndromes (Baker and Baker, 1982, 1983a). Our results for the tribes Podalyrieae, Liparieae and Crotalariaeae support the latter view. Perhaps the most significant example is that of the genus *Liparia*, where one of the two species (*L. splendens*) shows definite adaptations to bird-pollination and is generally accepted as bird-pollinated (Marloth, 1925; Skead, 1967; Rebelo, 1987). Instead of high hexose levels as in other species from bird-pollinated genera (see results for *Erythrina* and *Sutherlandia* in Table 1), the nectar of *L. splendens* has a high level of sucrose (more than 70%). *Liparia parva*, which lacks the bird syndrome, has roughly equal proportions of fructose, glucose and sucrose. If nectar sugar composition is related to pollinators, one would also not expect a similar "balanced" nectar in *Amphithalea ericifolia*. This species is pollinated by small bees and has minute flowers quite unlike those of *Liparia*.

Sucrose-rich nectars are associated with pollination by hummingbirds, hawkmoths, butterflies and long-tongued bees, while hexose-rich nectars are likely to be utilized by passerine birds, bats, flies and short-tongued bees (Baker and Baker, 1983a). Waller (1972) and Bachman and Waller (1977) showed, through feeding experiments, that honeybees have a preference for sucrose-rich solutions of sugars. Schaffer and Schaffer (1977) found that species of *Agave* with sucrose-rich nectar are pollinated by carpenter bees (*Xylocopa* spp.) and bumblebees (*Bombus* spp.). The high levels of sucrose in the tribe Podalyrieae seem to support the notion of a "long-tongued bee syndrome". Species of *Podalyria*, *Cyclopia* and *Virgilia* are pollinated almost exclusively

by large xylocopid bees, particularly *Xylocopa capensis*, *X. flavorufa*, *X. caffra* and *X. watmoughii* (Van Wyk, 1983; Nicolson, 1990). Field observations over many years have shown that the large size and firm texture of these flowers prevent access by small bees. In view of the variation within some of the genera however, the dominance of sucrose in the tribe Podalyrieae (and the lower levels in the other two tribes) appear to be little more than general trends. According to Polhill (1976, 1981) the Podalyrieae, Liparieae and Crotalareae are closely related to the Sophoreae. The latter or parts thereof is an obvious choice as outgroup for the other three tribes. The Sophoreae is represented in Table 1 by samples from *Bolusanthus*, *Calpurnia* and *Sophora*, all showing more than 90% sucrose. At the tribal level, it therefore seems reasonable to interpret high sucrose concentrations as unspecialized. Even if the flight energetics of *Xylocopa* demand high sucrose levels (Louw and Nicolson, 1983), the correlation (and implied coevolution) is not entirely convincing. Referring specifically to the apparent relationship between nectar types and short- or long-tongued bees, Baker and Baker (1983b) acknowledge the difficulty of distinguishing between cause and effect.

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