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Nectar Sugar Composition in *Erica*

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Abstract—The nectar sugar compositions of 50 species of *Erica* have been analysed by HPLC. A marked dichotomy in nectar sugars was evident within the genus. Of the ornithophilous species analysed, 29 had sucrose-dominant nectars and eight had hexose-dominant nectars. Both nectar types occurred within the artificial sections into which the genus is currently divided. Our results contradict the idea that flowers pollinated by passerine birds produce hexose-dominant nectars.

Introduction

The Cape Floristic Region has a plant species richness which exceeds those of all other temperate and many tropical floras (Bond and Goldblatt, 1984; Cowling *et al.*, 1992). An outstanding example of species diversity is the genus *Erica*, with 543 species occurring in the Cape Floristic Region (Baker and Oliver, 1967; Schumann and Kirsten, 1992).

Little is known about the pollination biology of this important genus. Using flower shape and field observations of pollinators, Rebelo *et al.* (1985) assigned 426 *Erica* species to pollination categories. They found 5% of the species to be wind pollinated, 15% to be bird pollinated, and the remaining 80% to be insect pollinated. Rebelo and Siegfried (1985) also examined flower colour and corolla length in relation to these pollination syndromes: ornithophilous species showed a higher incidence of colour polymorphism. The bird pollinators of *Erica* in the Cape Floristic Region are sunbirds (Nectariniidae). The sunbird most closely associated with *Erica* is the orange-breasted sunbird, *Nectarinia famosa*, and the curved tubular corollas of many ornithophilous *Erica* species match the curve and length of its beak (Rebelo *et al.*, 1985). Nothing is known of nectar rewards in *Erica* (Rebelo and Siegfried, 1985).

Studies on nectar composition have led to the suggestion that there are coevolutionary relationships between the sugar proportions in a flower's nectar and its type of pollinator. Flowers pollinated by passerine birds, such as sunbirds, are thought to produce nectars dominated by the monosaccharides glucose and fructose, whereas flowers pollinated by hummingbirds produce sucrose-dominant nectars (Baker and Baker, 1983, 1990). In view of the association between sunbirds and *Erica*, we have examined nectar sugar composition in 50 *Erica* species, with emphasis on those species exhibiting the ornithophilous pollination syndrome.

Materials and Methods

Nectar samples were collected between May and September 1993, mainly from cultivated plants in Kirstenbosch National Botanical Gardens, but occasionally from plants in their natural habitat. Species were identified using herbarium specimens and photographic records (Schumann and Kirsten, 1992).

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Nectar was sampled as spots (5–15 mm diameter) on filter paper (Whatman No. 1). The samples were air-dried and stored at −18°C before analysis. Nectar was recovered from the filter paper by rinsing with distilled water. Sugars were analysed by isocratic HPLC operating at 2.5 ml min^{-1} with a Waters Sugarpack column, acetonitrile–water (87 : 13) as eluent and detection by refractive index. Fructose, glucose and sucrose were determined as percentages of total sugars, using 8 mg ml^{-1} of each sugar as external standard.

Results

The sugar composition of 61 nectar samples from 50 species of *Erica* is shown in Table 1. Nomenclature and numbering of the species follows Schumann and Kirsten (1992). Proposed pollinators are taken from Rebelo *et al.* (1985), except for nine species not included in their list: these have been assigned pollinator types (given in parentheses) on the basis of flower shape. Rhinomyiophilous species (pollinated by long proboscid flies; Rebelo *et al.*, 1985) have been included with other entomophilous species: only *E. ampullacea* and *E. fastigiata* were sampled from this category. Of the species listed in Table 1, 13 are thus classified as entomophilous and 37 as ornithophilous. All five taxonomic sections of ornithophilous *Erica* species were included and the sampling represents about 40% of all ornithophilous *Erica* species in the Cape Floristic Region (Rebelo, 1987).

For the purposes of comparing nectar sugar ratios in floral nectars, Baker and Baker (1979, 1983, 1990) used a terminology which recognises four classes of nectar. These are: "sucrose-dominant", when the sucrose/glucose + fructose ratio is greater than 0.999; "sucrose-rich", with ratios between 0.5 and 0.999; "hexose-rich", with ratios between 0.1 and 0.499; and "hexose-dominant," with ratios less than 0.1.

Using this terminology, the 37 ornithophilous species in Table 1 fall into two distinct groups: 29 sucrose-dominant species (in which sucrose was at least 77% of total sugar) and eight hexose-dominant species (in which sucrose was 8% or less of total sugar). It is striking that there were no intermediate types which could be classified as sucrose-rich or as hexose-rich. This is clearly visible in Fig. 1 for the species from

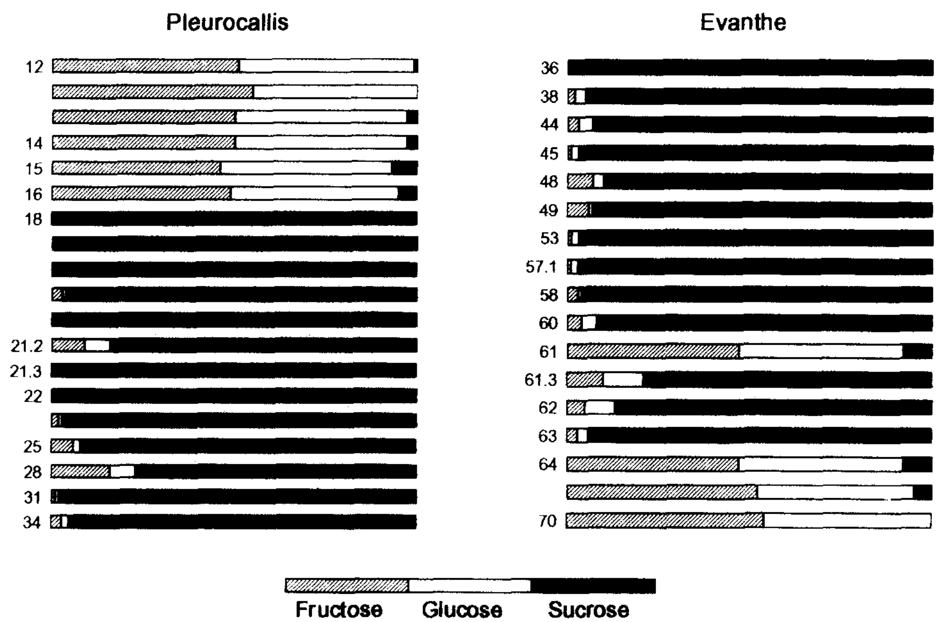

FIG. 1. NECTAR SUGAR COMPOSITIONS IN *ERICA* SPECIES BELONGING TO THE SECTIONS PLEUROCALLIS AND EVANTHE. Species are numbered as in Table 1

TABLE 1. NECTAR SUGAR COMPOSITIONS IN 61 SAMPLES FROM 50 SPECIES AND 12 SECTIONS OF THE GENUS *ERICA*

No.	Section	Species	Proposed pollinator	Nectar composition Fructose (%)	Glucose (%)	Sucrose (%)
1	Gigandra	*coccinea* L.	bird	tr*	tr	100
5		*plukenetii* L.	bird	1	tr	99
		plukenetii L.	bird	0	0	100
6	Didymanthera	*monadelpha* Andr.	bird	1	tr	99
7		*banksia* Andr.	bird	3	1	96
9		*viridiflora* Andr.	(bird)	3	1	96
12	Pleurocallis	*mammosa* L.	bird	51	48	1
		mammosa L.	bird	55	45	0
		mammosa L.	bird	50	47	3
14		*bauera* Andr.	(bird)	50	47	3
15		*gilva* Wendl.	(bird)	46	47	7
16		*sessiliflora* L.	bird	49	46	5
18		*grandiflora* L.	bird	tr	tr	100
		grandiflora L.	bird	tr	tr	100
		grandiflora L.	bird	tr	tr	100
		grandiflora L.	bird	3	1	96
		grandiflora L.	bird	tr	tr	100
21.2		*thomae* L. Bol.	bird	9	7	84
21.3		*porteri* Compton	bird	0	0	100
22		*phylicifolia* Salisb.	bird	tr	tr	100
		phylicifolia Salisb.	bird	2	1	97
25		*pinea* Thunb.	bird	6	2	92
28		*regia* Bartl.	bird	16	7	77
31		*vestita* Thunb.	bird	1	1	98
34		*longifolia* Ait.	bird	3	2	95
36	Evanthe	*patersonia* Andr.	bird	tr	tr	100
38		*foliacea* Andr.	bird	2	3	95
44		*bibax* Salisb.	bird	3	4	93
45		*curviflora* L.	bird	1	2	97
48		*conspicua* Soland.	bird	7	3	90
49		*densifolia* Willd.	(bird)	6	1	93
53		*discolor* Andr.	bird	1	2	97
57.1		*leucotrachela* H. A. Bak.	bird	1	2	97
58		*versicolor* Andr.	bird	3	1	96
60		*diaphana* Spreng.	(bird)	4	4	92
61		*glandulosa* Thunb.	(bird)	47	45	8
61.3		*fourcadei* L. Bol.	(bird)	10	11	79
62		*perspicua* Wendl.	bird	5	8	87
63		*colorans* Andr.	bird	3	3	94
64		*verticillata* Berg.	bird	47	45	8
		verticillata Berg.	bird	52	43	5
70		*brachialis* Salisb.	bird	54	46	0
75	Dasyanthes	*tumida* Ker-Gawl.	bird	50	50	tr
77		*cerinthoides* L.	bird	8	6	86
		cerinthoides L.	bird	5	1	94
79	Bactridium	*fascicularis* L.	bird	3	7	90
80		*massonii* L.	bird	1	1	98
89	Euryloma	*ampullacea* Curtis	insect	3	22	75
96	Ceramus	*incarnata* Thunb.	(insect)	51	49	0
103	Callista	*cylindrica* Thunb.	insect	24	24	52
104		*fastigiata* L.	insect	tr	13	87
145	Ephebus	*haematocodon* Salter	insect	50	34	16
163		*perlata* Sincl.	insect	51	46	3
173		*sphaeroidea* Dulfer	insect	49	44	7
244	Orophanes	*sitiens* Klotzsch	insect	37	32	31
245		*blandfordia* Andr.	insect	2	2	96
247		*verecunda* Salisb.	insect	53	47	0
278	Pachysa	*formosa* Thunb.	(insect)	50	46	4
281		*glomiflora* Salisb.	insect	46	43	11
		glomiflora Salisb.	insect	49	48	3
283		*urna-viridis* H. Bol.	insect	tr	tr	100

*tr = Trace.

sections Pleurocallis and Evanthe. There was no difference in corolla length (values taken from Schumann and Kirsten, 1992) between ornithophilous *Erica* species with the two nectar types: species with sucrose-dominant nectars had a corolla length of 20.6 ± 5.9 mm (mean ± SD), whereas species with hexose-dominant nectars had corollas of 19.3 ± 3.4 mm.

Among the entomophilous species, five (including the two rhinomyiophilous species, *E. ampullacea* and *E. fastigiata*) had sucrose-dominant nectars, five had hexose-dominant nectars, and three nectars can be classified as hexose-rich. Although the sample size is small, it can be seen that sections Orophanes and Pachysa include species with sucrose-dominant and hexose-dominant nectars.

Discussion

Erica nectars show a marked dichotomy in sugar composition, almost all of the species analysed in this study having nectars at the extremes of the sucrose–hexose continuum. Moreover, these extremes are seen within sections of the genus, Pleurocallis and Evanthe being good examples (Fig. 1). Such a sharp dichotomy between sucrose and hexose nectars is more likely to be found between genera than between species. It has recently been shown that nectar sugar compositions are generally conservative within genera (van Wyk, 1993; van Wyk *et al.*, 1993).

The genus *Erica* is currently divided into 41 artificial sections, based mainly on the shape of the corolla and the relative sizes of corolla and calyx (Schumann and Kirsten, 1992). As a result, the sections appear to be correlated with the principal pollination syndromes within the genus (Rebelo *et al.*, 1985; and see Table 1). The discontinuities observed here are more likely to be related to natural (taxonomic) affinities rather than to pollination syndromes because both sucrose-dominant and hexose-dominant nectars are found within ornithophilous and entomophilous categories. Relationships within *Erica* are poorly understood (E. G. H. Oliver, pers. comm.), so that nectar sugars may be a useful independent source of taxonomic information. Note, for example, the sharp discontinuity within the section Pleurocallis, suggesting that *E. mammosa* and related species (12–16 in Fig. 1) form a natural group within the section. The overall pattern suggests a repeated switch from high to low sucrose, or vice versa, within various unrelated groups.

Our results contradict the findings of Baker and Baker (1983, 1990) regarding the nectar composition of flowers pollinated by passerine birds. In 35 species pollinated by sunbirds, they found all but one of the nectars to be hexose-dominant or hexose-rich, whereas in 140 species pollinated by hummingbirds, the nectars were prevailingly sucrose-dominant or sucrose-rich (Baker and Baker, 1983). A particularly clear example was the genus *Erythrina*, in which 27 hummingbird pollinated species had a mean sugar ratio of 1.30, while 23 passerine bird pollinated species had a mean sugar ratio of 0.04 (Baker and Baker, 1990). This and similar findings have led to recent investigations of the sugar preferences of various passerine birds and the physiological basis of such preferences. A preference for sucrose appears to be correlated with intestinal activity of the enzyme sucrase (Martinez del Rio *et al.*, 1988; Martinez del Rio, 1990).

The results described in this paper show no relationship between hexose-rich nectars and passerine bird pollinators. Not only were 29 out of 37 ornithophilous *Erica* species found to have sucrose-dominant nectars, but these 29 species had a mean sucrose proportion of $93.8 \pm 6.2\%$ (mean ± SD). This is very high when compared to hummingbird pollinated species of *Erythrina*: the mean sugar ratio of 1.30 (Baker and Baker, 1990) corresponds to a nectar containing, if fructose and glucose concentrations were equal, 22% fructose, 22% glucose and only 56% sucrose. The sunbird-pollinated *Erica* species have much higher nectar sucrose concentrations than many hummingbird pollinated flowers. Obviously deserving of attention are the sugar preferences and digestive physiology of sunbirds, but our results do not support the simplistic idea that pollination syndromes can be deduced from nectar types.

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