

Nectar types in Indian plants

BIR BAHADUR, ARTHI CHATURVEDI and N RAMA SWAMY

Department of Botany, Kakatiya University, Warangal 506 009, India

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Abstract. Nectar composition (sugars and amino acids) of 100 species representing 83 genera from 34 families of angiosperms have been studied. The distribution of the 3 common sugars viz., sucrose, fructose and glucose in nectars of the species studied can be broadly divided into 6 types, based on the presence or absence of any one of the sugars viz sucrose-glucose-fructose, sucrose-glucose, sucrose-fructose, glucose-fructose, glucose and sucrose types with some variations. α -Amino acids were processed in 85 species. Distribution of amino acids was studied in some species and was found to be useful in detecting flower visitors.

Keywords. Nectar composition; sugars; amino acids.

1. Introduction

Pollination is successful in many plant species as a consequence of pollinators seeking nectar, whose function is to attract the pollinators and its nutritional properties are important to most pollinators, especially those who do not obtain nourishment in any other form viz bees, bumble bees and butterflies (Harborne 1982). The extent of pollen flow affects important processes in the fertilisation of entomophilous plants e.g., optimal nectar secretion (Hartling 1979; Hartling and Plowright 1979). Heinrich (1979) suggested that the 'correct' amount of nectar secreted by a flower will be a balance between plant frugality on the one hand and the necessity to obtain pollinator visits on the other.

Nectar composition with regard to sugars in several species was earlier studied by Fahn (1949), Wykes (1952), Percival (1961) and Southwick *et al* (1981), while Baker and Baker (1979) have first detected the presence of amino acids in 260 species of flowering plants and Harborne (1982) in several species of *Rhododendron*. A similar study on Indian plants is lacking. Therefore the study has been carried out on the nectar composition not only with regard to sugars and α -amino acids but also essential amino acids in some selected species.

2. Material and methods

For qualitative analysis the nectar was taken from freshly opened flowers (protected by bags) by means of fine glass capillaries or plastipak syringes. The nectar composition of 100 species (table 1) with regard to sugars and amino acids have been studied following the technique of Buchan and Savage (1952) and Ranjan *et al* (1955), respectively. Chromatographic separation of sugars and amino acids of freshly secreted nectar was done by solvent (*n*-butanol 4:acetic acid 1:water 5); run approximately for 6–8 hr depending on the concentration of the sample and sprayed by aniline-di-phenyl amine reagent (for sugars) and 0.2% ninhydrin in acetone (for amino acids) and developed in

Table 1. Species and types of nectar in Angiosperms.

Taxon	Sugars				α -Amino acids
	Sucrose	Glucose	Fructose	Unknown	
<i>Brassica nigra</i> (Brassicaceae)	+	+	-	-	+
* <i>Hybanthes ennaespermus</i> (Violaceae)	++	+	+	-	++
<i>Tribulus terrestris</i> (Zygophyllaceae)	+	+	-	-	+
<i>Impatiens balsamina</i> (Balsaminaceae)	+	+	+	-	+
<i>I. sultanii</i> (Balsaminaceae)	+	+	-	-	+
<i>Murayya koenigii</i> (Rutaceae)	+	+	+	1	++
<i>Moringa oleifera</i> (Moringaceae)	++	+	+	-	+
<i>Hibiscus rosasinensis</i> (Malvaceae)	++	+	+	-	+
<i>H. schizopetalous</i> (Malvaceae)	++	+	-	1	++
<i>H. micranthus</i> (Malvaceae)	++	+	+	-	+
<i>H. cannabinus</i> (Malvaceae)	+	+	+	-	+
<i>Sida acuta</i> (Malvaceae)	+	+	-	-	+
<i>Abelmoschus esculentum</i> (Malvaceae)	++	++	+	-	++
<i>Pavonia zeylanica</i> (Malvaceae)	++	+	+	-	+
<i>Malva viscus arboreus</i> (Malvaceae)	++	++	-	-	+
<i>Althaea rosea</i> (Malvaceae)	++	+	+	-	+
<i>Zizyphus jujuba</i> (Rhamnaceae)	+	+	+	-	+
<i>Phaseolus atropurpureus</i> (Papilionaceae)	+	+	+	-	+
<i>Psophocarpus tetragonolobus</i> (Papilionaceae)	++	+	-	-	+
<i>Crotalaria juncea</i> (Papilionaceae)	+	+	+	-	+
<i>Delonix regia</i> (Caesalpineaceae)	+	+	+	-	+
<i>Peltophorum ferrugianum</i> (Caesalpineaceae)	++	+	-	2	-
<i>Caesalpineia pulcherrima</i> (Caesalpineaceae)	++	+	+	-	+
<i>Kalanchoe</i> sp. (Crassulaceae)	+	+	+	-	+
<i>K. pinnata</i> (Crassulaceae)	+	+	+	-	+
<i>K. verticillata</i> (Crassulaceae)	+	+	+	-	+
<i>K. bhidei</i> (Crassulaceae)	+	+	-	-	+
<i>Punica granatum</i> (Punicaceae)	++	++	++	-	-
<i>Momordica charantia</i> (male) (Cucurbitaceae)	+	+	+	-	++
<i>Lagenaria vulgaris</i> (male) (Cucurbitaceae)	+	+	+	-	++
<i>Coccinea indica</i> (male) (Cucurbitaceae)	+	+	-	-	++
(female)	++	+	-	--	+
<i>Luffa acutangula</i> (male) (Cucurbitaceae)	++	+	-	-	+
Sepal (female)	+	+	-	-	+
<i>Cucurbita maxima</i> (male) (Cucurbitaceae)	+	+	+	-	+
<i>Cucumis sativus</i> (male) (Cucurbitaceae)	+	+	+	1	+
<i>Passiflora foetida</i> (Passifloraceae)	++	++	++	-	-
* <i>Turnera subulata</i> (pin) (Turneraceae)	+	++	++	(Mannitol)	+
<i>T. subulata</i> (Thrum) (Turneraceae)	++	++	++	(Mannitol)	+
<i>T. ulmifolia</i> (Homo.) (Turneraceae)	++	++	++	(Mannitol)	+
<i>Opuntia dillenii</i> (Cactaceae)	+	-	+	-	-
<i>Ixora coccinea</i> (Rubiaceae)	+	+	+	-	+
<i>Hamelia patens</i> (Rubiaceae)	+	+	+	-	++
<i>Oldenlandia umbellata</i> pin (Rubiaceae)	+	+	+	-	+
<i>Mussaenda frondosa</i> (Rubiaceae)	++	+	+	-	+
<i>Borreria hispida</i> (Rubiaceae)	-	+	+	-	+
<i>Gaillardia pulchella</i> (Compositae)	-	+	-	-	+
<i>Zinnia elegans</i> (Compositae)	-	+	+	(Compositae)	++
<i>Jasminum officinale</i> (Oleaceae)	+	+	-	-	+
<i>Thevetia nerifolia</i> (Apocynaceae)	++	+	+	1	-

Table 1. (continued).

Taxon		Sugars				α -Amino acids
		Sucrose	Glucose	Fructose	Unknown	
<i>Vinca rosea</i>	(Apocynaceae)	++	+	+	1	+
<i>Allamanda cathartica</i>	(Apocynaceae)	+	+	+	-	++
<i>Datura alba</i>	(Solanaceae)	+	+	-	-	+
<i>Cestrum fasciculatum</i>	(Solanaceae)	++	++	+	-	+
<i>Physalis peruvianum</i>	(Solanaceae)	++	+	-	-	+
Flower fruit		++	++	-	-	+
<i>Physalis minima</i>	(Solanaceae)	+	+	+	-	+
<i>Petunia hybrida</i>	(Solanaceae)	++	+	+	-	-
<i>Ipomoea palmata</i>	(Convolvulaceae)	++	+	+	1	+
<i>I. aquatica</i>	(Convolvulaceae)	++	+	+	-	-
<i>I. terrestris</i>	(Convolvulaceae)	++	+	+	-	-
<i>Quamoclit pinnata</i>	(Convolvulaceae)	+	+	+	1	+
<i>Argyreia speciosa</i>	(Convolvulaceae)	++	+	-	1	+
<i>Russelia equisetiformis</i>	(Scrophulariaceae)	++	+	++	1	-
<i>Sophubia delphinifolium</i>	(Scrophulariaceae)	-	+	+	-	+
<i>Sesamum indicum</i>	(Pedaliaceae)	+	-	-	-	+
<i>Pedaliium murex</i>	(Pedaliaceae)	+	+	-	-	+
<i>Martynia diandra</i>	(Martyniaceae)	+	+	-	1	+
<i>Tecomaria capensis</i>	(Bignoniaceae)	++	-	+	-	+
* <i>Spathodea campanulata</i>	(Bignoniaceae)	++	++	++	-	+
<i>Bignonia speciosa</i>	(Bignoniaceae)	+	++	++	-	-
<i>Tecoma grandiflora</i>	(Bignoniaceae)	+	+	+	-	++
<i>Thunbergia grandiflora</i>	(Acanthaceae)	++	++	++	-	+
<i>Crossandra infundibuliformis</i>	(Acanthaceae)	-	+	+	-	+
<i>Crossandra undulaefolia</i>	(Acanthaceae)	+	++	-	1	+
<i>Ecbolium linneanum</i>	(Acanthaceae)	++	++	+	1	-
<i>Rungia repens</i>	(Acanthaceae)	-	+	+	-	+
<i>Eranthemum variegatum</i>	(Acanthaceae)	++	++	+	-	++
<i>Exanthemum roseum</i>	(Acanthaceae)	+	+	-	-	+
<i>Andrographis paniculata</i>	(Acanthaceae)	+	+	-	-	+
<i>Ruellia tuberosa</i>	(Acanthaceae)	+	+	-	-	+
<i>Gmelina hystrix</i>	(Verbenaceae)	++	++	+	-	++
<i>Duranta plumieri</i>	(Verbenaceae)	-	+	+	-	+
<i>Verbena bipinnatifida</i>	(Verbenaceae)	+	+	-	-	+
<i>Stachytarpheta indica</i>	(Verbenaceae)	+	+	+	-	+
<i>Clerodendron inerme</i>	(Verbenaceae)	+	++	-	1	+
<i>Vitex negundo</i>	(Verbenaceae)	+	+	-	-	+
<i>Lantana camara</i>						
Pink flowers	(Verbenaceae)	+	+	+	-	+
Yellow flowers	(Verbenaceae)	++	+	+	1	+
<i>Holmskioldia sanguinea</i>	(Verbenaceae)	++	++	-	-	-
<i>Salvia plebeia</i>	(Labiatae)	+	+	-	-	+
<i>Ocimum sanctum</i>	(Labiatae)	+	+	+	-	+
<i>Leucas aspera</i>	(Labiatae)	+	+	+	-	+
<i>Antigonon leptopus</i>	(Polygonaceae)	+	+	+	-	-
<i>Jatropha pandurifolia</i>						
(male)	(Euphorbiaceae)	+	+	+	-	+
(female)	(Euphorbiaceae)	+	+	+	-	+
<i>J. glandulifera</i> (male)	(Euphorbiaceae)	-	+	+	-	+
<i>J. podagrica</i> (male)	(Euphorbiaceae)	+	++	-	-	+
<i>Euphorbia heterophylla</i>	(Euphorbiaceae)	+	-	+	-	++

Table 1. (continued).

Taxon		Sugars				α-Amino acids
		Sucrose	Glucose	Fructose	Unknown	
<i>E. geniculata</i>	(Euphorbiaceae)	+	+	-	-	++
<i>E. milli</i>	(Euphorbiaceae)	++	++	+	-	+
<i>Spathodea plicata</i>	(Orchidaceae)	-	+	+	-	+
<i>Canna indica</i>	(Cannaceae)	++	++	+	1	-
<i>Pancreatium longiflorum</i>	(Amaryllidaceae)	+	+	-	-	++
<i>C. asiaticum</i>	(Amaryllidaceae)	+	+	-	1	+
<i>Zephyranthes citrina</i>	(Amaryllidaceae)	++	+	-	-	+

+, Present; ++, more; -, absent; 1, 2, No. of unknown sugars present.
Amino acid composition studied for the species marked with asterisk.

Table 2. Sugar combinations in nectar of some Indian plants.

No. of species studied	SGF		SG			SF	GF	G	S
	SGF	SGF + 1 unknown	SG	SG	+ 1 or 2 unknown				
Polypetalae (38)	22	4	9	2		1	-	-	-
Gamopetalae (50)	19	7	11	4		1	6	1	1
Monochlamydae (7)	3	-	2	-		1	1	-	-
Monocotyledons (5)	-	1	2	1		-	1	-	-

an electric oven at 60°C and 110°C for aminoacids and sugars, respectively. Presence of α-amino acids was detected by treating the dried nectar spots on Whatman No. 1 chromatographic paper with 0.2% ninhydrin in acetone following the technique of Baker and Baker (1973a).

3. Results and discussion

3.1 Sugars of nectar

The nectars of the majority of the species examined consists of three common sugars of plant metabolism viz sucrose (S), glucose (G) and fructose (F) (table 2). In a survey of the distribution of the 3 common sugars in nectars of 100 species studied, the nectars are broadly divided into 6 groups as shown in table 2 based on the presence or absence of sugars.

Perusal of the data in table 1 shows that the most common type of sugar combination of the angiosperms nectar is SGF type occurring in 56 of the 100 species studied, out of which the nectar of 12 species also possess an unidentified sugar. SGF type of sugar combination in nectar is followed by the SG type (31 species), out of which the nectar of 7 species possess 1 or 2 unidentified sugars. A total of 38 species of polypetalae studied showed the presence of SGF, SG and SF (*Opuntia dellenii*-Cactaceae) type only but among the gamopetalous species studied, *Tecomaria capensis* (Bignoniaceae) possess SF sugar combination; 6 species studied possess GF combination and the nectar of

Gaillardia pulchella (Compositae) was found to be only of G type and *Sesamum indicum* (Pedaliaceae) has S type nectar while in the rest of the species SGF or SG type occur. The presence of 4 sugars viz G, S, F and mannitol in varying concentrations has been recorded in the nectar of pin and thrum form of distylous *Turnera subulata* (Bahadur *et al* 1985). The nectar of *Spathodea campanulata* (Bignoniaceae) consists of S, G and F but S occurs in traces.

The nectar of the 7 species of monoclamydae studied show the following sugar combinations viz SGF, SG, SF and GF. The nectar of 5 monocotyledonous species shows SGF + 1 unknown (*Canna indica*), SG (*Zephyranthes citrina* and *Pancreatium longiflorum*), SG + 1 unknown (*Crinum asiaticum*) and GF (*Spathoglottis plicata*) types of sugar combinations.

The long tubed flowers with deep seated nectary is characterised by sucrose dominating nectar while open flowers with unprotected nectar is dominated by F and G (Percival 1961); more S in the former and less S in the latter (Southwick *et al* 1981) and further Baker and Baker (1975) also suggested high amino acid contents in the long tubed flowers with deep seated nectary than the nectar of open flowers with unprotected nectar and exposed nectary. Loper *et al* (1976) and Corbet *et al* (1979) suggested that low sucrose in the open flowers results from more rapid breakdown to hexoses immediately after the nectar is secreted.

According to Harborne (1982) the angiospermous nectars exhibit an evolutionary trend i.e., nectar with mainly S to those with mainly G and F. He argues that this confers advantage to the pollinator as the latter is the only assimilable form of sugars in the nectar.

The present study though limited supports the earlier findings, although some variations were observed i.e., in flowers with deep seated nectar (*S. campanulata* and *Bignonia speciosa*) or open nectar flowers (*Euphorbia milli*) (see table 1). These trends are interpreted to reflect a higher degree of specialisation of concealed nectar flowers to their pollinators.

Apart from the major variants described minor variations also exist. The 3 sugars of the angiosperms nectar varies not only in number but in their concentration as well, which forms the essential constituent of the feed of the specific pollinators visiting the flowers constituting the rewarding mechanisms and in turn with pollinators energetics.

The chemical composition of nectar varies enormously among the species and in some cases it varies with floral age, sex, season and location (Percival 1961; Shuel 1975; Baker 1978).

3.2 Amino acids of nectar

The presence of amino acids in plant nectars remained undetected until recently. Apart from Ziegler (1956; 3 species), Luttge (1961, 1962; 5 species) and Percival (1961) made a ninhydrin test on nectars of some unidentified species obtaining a positive colour reaction but apparently interpreted it as indicating the presence of enzymes, while Baker and Baker (1973a, b) reported the amino acids as regular constituents in 260 of 266 plant nectars surveyed by them.

In the present study 85 out of 100 species examined showed the presence of α -amino acids (see table 1). The amino acids present in most nectars occur as traces but are sufficient to provide the required nitrogen supply to the insect visitors (see Harborne 1982). Detailed amino acid distribution was studied in 3 species and it was found that 7

amino acids occur in *Hybanthus ennaespermus* and thrum flower form of distylous *T. subulata* while the pin form has only 5 amino acids (see table 3). It is strange that the copious nectar of *S. campanulata* contains two amino acids only viz alanine and isoleucine (see table 3).

The nectar of *H. ennaespermus* (Violaceae) pollinated by lady bird beetle (*Coccinella septempunctata*) exhibit high amino acid content and possess 7 amino acids (table 3) out of which valine, leucine and glutamic acids are essential for insect nutrition (see Baker and Baker 1976); ornithophilous *S. campanulata* (Bignoniaceae) has only 2 amino acids viz alanine and isoleucine of which the latter being essential. Distylous *T. subulata* (Turneraceae) is pollinated by a wide variety of insects including bees and butterflies (Bahadur and Ramaswamy 1984), the nectar is characterised by 7 (thrum form) and 5 amino acids (pin form), (see table 3) (Bahadur *et al* 1985) out of which leucine, isoleucine, tryptophan and phenylalanine are essential for insect nutrition.

Baker *et al* (1978) studied the amino acid composition in the nectars of floral and extrafloral nectaries of *T. ulmifolia* and noted 7 amino acids in extrafloral nectar but 23 amino acids in the floral nectar. Further they did not detect any quantitative differences in amino acids in various geographical races of *T. ulmifolia*, eventhough pin and thrum forms of *T. subulata* show differences (Bahadur *et al* 1985). Apart from the presence of essential (insect nutrition) α -amino acids as mentioned earlier, the other amino acids noted were alanine, phosphoserine, proline, ethanolamine, amino-*n*-caproic acid, α -amino butyric acid and α -amino octanoic acid. Wilson (1983) reports that the nectar of flowers pollinated by specialised carrion flies and by beetles commonly have very high amino acids contents (although these flower corollas are not especially long) where as nectars from flowers pollinated by bats and birds (except the north American humming birds) have low average amino acids contents and often long corollas, as the present study on *S. campanulata* and *H. ennaespermus* confirms.

Opler and Keeler examined tropical plants in Costa Rica and their results show that in the Neo tropics 'humming bird flowers' often show little amino acid in the nectar. These results are understandable because hummingbirds as well as the 'old world flowers visiting birds' have a useful alternative source of protein making materials in the

Table 3. Composition of amino acids in nectar of 3 species studied.

Amino acids	<i>Hybanthus ennaespermus</i>	<i>Turnera subulata</i>		<i>Spathodea campanulata</i>
		Pin form	Thrum form	
Alanine	-	+	+	+
Phenyl alanine	-	-	+	-
Phosphoserine	+	-	-	-
Proline	++	-	-	-
Glutamic acid	++	-	-	-
Ethanolamine	+	-	-	-
Amino- <i>n</i> -Caproic acid	+	+	-	-
α -amino butyric acid	-	++	++	-
α -amino octanoic acid	-	+	+	-
Valine	+	-	-	-
Leucine	+	+	+	-
Tryptophan	-	-	+	-
Isoleucine	-	-	+	+

+, Present; ++, more; -, absent.

insects they prey (Baker and Baker 1973a) as the nectar study on *S. campanulata* confirms. Apart from this, the calyx water in *S. campanulata* is equally rich in amino acids and is easily available to any bird with pointed beak. Thus in a single visit, the pollinator derives the dual benefit of sugars and amino acids from the nectar and amino acids from calyx water (unpublished results).

Baker and Baker (1973a, b, 1975) correlated the increase in concentration of amino acids in the nectar with the evolution of specialisation in the pollination systems. They suggested that although amino acids are present in the nectar of plants species belonging to families generally considered as primitive, higher concentrations occur more consistently in those considered as more advanced.

Apart from sugars and amino acids in the nectar, proteins, lipids and antioxidants (such as vitamin 'C') other vitamins and even toxins occur (Baker and Baker 1975; Baker 1978; Rhoades and Bergdahl 1981; Stephenson 1981). The biological significance of intraspecific variations in nectar composition to pollinator energetics is unexplored.

It is concluded that the nectar is utilised by the pollinators primarily as a source of sugars which provides energy to them. However, other components of the nectar and in particular the role of amino acids and fluctuation in sugar concentration in attracting the pollinators is not well understood, although Corbet (1978) noted marked differences in nectar volume in *Echium vulgare* and sugar concentration and interpreted the change in terms of loss or gainup sugar or water secretion by the plant, removal by bee and other physical factors.

Thus, the nectar offers great potential for further work and Corbet (1978) rightly pointed out that 'the dynamic complexity of nectar can be seen as just another technical obstacle to the assessment of the caloric rewards available for flower visitors; or it can be seen as a phenomenon worth studying in its own right, as a rich source of unanswered questions for zoologists and micrometeorologists as well as for botanists and beekeepers'.

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References

- Bahadur B and Ramaswamy N 1984 Pollination biology of heterostylous *Turnera subulata* J. E. Smith; *J. Palynol.* **20** 198-209
- Bahadur B, Rama Swamy N, Chaturvedi A and Farooqui S M 1985 Floral nectaries in two species of *Turnera* L. (Turneraceae); *New Bot.* **12** 117-127
- Baker H G and Baker I 1973a Amino acids in nectar and their evolutionary significance; *Nature (London)* **241** 543-545
- Baker H G and Baker I 1973b Some anthecological aspects of evolution of nectar producing flowers, particularly amino acid production in nectar; in *Plant Taxonomy and Ecology* (ed.) V H Heywood, (London: Academic Press) pp 243-264
- Baker H G and Baker I 1975 Studies of nectar constitution and pollinator plant coevolution; in *Coevolution of Animals and Plants*; (eds.) L E Gilbert and P H Raven (Austin: University of Texas Press)
- Baker H G and Baker I 1976 Analysis of amino acids in flower nectars of hybrids and their parents with phylogenetic implications; *New Phytol.* **76** 87-98

- Baker H G, Oplar P A and Baker I 1978 A comparison of the amino acid complements of floral and extra floral nectars; *Bot. Gaz.* **139** 322–332
- Baker H G 1978 Chemical aspects of the pollination biology of woody plants in the tropics; in *Tropical Trees as Living systems*; (eds.) P B Tomlinson and M H Zimmerman (Cambridge: Cambridge University Press)
- Buchan J L and Savage R I 1952 Paper chromatography of some starch conversion products; *Analyst* **77** 401
- Corbet S A 1978 Bees and the nectar of *Echium vulgare*; in *The pollination of flowers by insects*; (ed.) A J Richards (London: Academic Press) pp. 1–30
- Corbet S A, Willmer P G, Beament J W L, Unwin D M and Prys-Jones O E 1979 Post-secretory determinants of sugar concentration in nectar; *Plant Cell Environ.* **2** 293–308
- Fahn A 1949 Studies in the ecology of nectar secretions; *Pales. J. Bot. Jerusalem* **4** 207–224
- Harborne J B 1982 *Introduction to Ecological Biochemistry*; (London: Academic Press)
- *Hartling L K 1979 *An investigation of the relationship between bumble bee foraging behaviour and the pollination of red clover: a component analysis approach*; M.Sc. thesis, University of Toronto, Canada
- Hartling L K and Plowright R L 1979 An investigation of inter- and intra-inflorescence visitation rates by bumble bees on red clover with special reference to seed set; *Proc. IVth Int. Symp. on Pollination, Md. Agric. Exp. Sta. Spec. Misc. Publ.* **1** 457–460
- Heinrich B 1979 *Bumble bee economics*; (Massachusetts: Harvard University Press)
- Loper G M, Waller G D and Berdel R L 1979 Effect of flower age on sucrose content in nectar of *Citrus*; *Hortic. Sci.* **11** 416–417
- Luttge U 1961 Über die Zusammensetzung des Nektars und den Mechanismus Seiner Sekretion I; *Planta* **56** 189–212
- Luttge U 1962 Über die Zusammensetzung des Nektars und den Mechanismus Seiner Sekretion II; *Planta* **59** 108–114
- Percival M 1961 Types of nectar in angiosperms; *New Phytol.* **60** 235–281
- Ranjan S, Govind Jee and Laloraya M M 1955 Chromatographic analysis on the amino acid metabolism of healthy and diseased leaves of *Croton sparciflorus*; *Proc. Natl. Inst. Sci. India* **21** 41–47
- Rhoades D F and Bergdahl J C 1981 Adaptive significance of toxic nectar; *Am. Nat.* **117** 798–803
- Shuel R W 1975 The production of nectar; in *The hive and the honey bee* (Hamilton, Illinois: Dadant and Sons) pp 265–282
- Shouthwick E E, Loper G M and Sadwick S E 1981 Nectar production, composition, energetics and pollinator attractiveness in spring flowers of western New York; *Am. J. Bot.* **68** 994–1002
- Stephenson A G 1981 Toxic nectar deters nectar thieves of *Catalpa speciosa*; *Am. Midl. Nat.* **105** 381–383
- Willson M J 1983 *Plant Reproductive Ecology* (New York: John Wiley and Sons)
- Wykes G R 1952 An investigation of the sugars present in the nectar of flowers of various species; *New Phytol.* **51** 210–215
- Ziegler H 1956 Untersuchungen über die Leitung and Sekretion der Assimilate; *Planta* **47** 447–500

*Original not referred.