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SHORT COMMUNICATION

DISTRIBUTION OF CANAVANINE IN THE PLANT KINGDOM

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Abstract—The seeds of seventy species of legumes belonging to the subfamily Papilionoideae were examined for the free amino acid canavanine. These data along with those from previously published surveys have been presented in table form. Altogether approximately 540 species of legumes belonging to the 150 genera have been examined; of these 60 per cent of the species and 35 per cent of the genera have been positive for the compound. To date, canavanine has been reported only from the subfamily Papilionoideae, in spite of extensive surveys for the compound among other plant taxa. Significant findings from our survey include strong positive tests from five of eighteen genera of the Podalyrieae, a tribe previously thought to be negative for the compound. It is suggested that the genetic factors giving rise to canavanine arose relatively early in the evolution of the Papilionoideae and have subsequently been selected for in at least a few genera of each of the several tribal groups which arose out of this ancestral complex.

INTRODUCTION

BELL,[1] Tschiersch[2] and Birdsong, Alston and Turner[3] were among the first to make taxonomic surveys for the free amino acid, canavanine, among plant groups. In spite of broad samplings among angiosperms generally, they found this compound in only the family Leguminosae, subfamily Papilionoideae. These authors examined 219 species of legumes distributed among 109 genera; canavanine was found in only sixty-eight species belonging to thirty-two genera. Subsequently, Tschiersch[4] and Nakatu *et al.*,[5] made similar surveys for canavanine among ninety-seven families, reporting canavanine only in the Leguminosae, confirming the results of earlier workers.

In this paper (Table 1) we summarize all of the above data plus original tests for approximately seventy additional species. Altogether approximately 540 species distributed among 150 genera of legumes have now been examined.

TABLE 1†. TAXA OF LEGUMINOSAE EXAMINED FOR CANAVANINE

I.	MIMOSOIDEAE 6 tribes, 7 genera, 10 species—all negative
II.	CAESALPINIOIDEAE 7 tribes, 17 genera, 26 species—all negative

[1] E. A. BELL, *Biochem. J.* **70**, 617 (1958).
[2] B. TSCHIERSCH, *Flora* **147**, 405 (1959).
[3] B. A. BIRDSONG, R. ALSTON and B. L. TURNER, *Can. J. Botany* **38**, 499 (1960).
[4] B. TSCHIERSCH, *Flora* **150**, 87 (1961).
[5] S. NAKATU, Z. MATUGAKI, H. SIMADA, T. KASIDA, T. MOTOMURA, M. OSIMA and N. SAKI, *Seikagaku* **34**, 253 (1962).

TABLE 1—*continued*

III. PAPILIONOIDEAE	
1. SOPHOREAE	
Ammodendron (1)	–
Bolusanthus (1)	–
Calpurnia (1)	–
Cladrastis (1)	–
**Ormosia* (2)	–
**Pickeringia* (1)	–
**Sophora* (3)	–
Virgilea (1)	–
2A. PODALYRIEAE (N. Hemisphere)	
**Anagyris foetida*	
**Baptisia* (8)	–
Piptanthus (1)	–
**Thermopsis* (4)	–
2B. PODALYRIEAE (S. Hemisphere)	
**Brachysema praemorsum*	–
**Burtonia scabra*	–
**Chorizema dicksonii*	–
**Cyclopia subternata*	–
**Daviesia acicularis*	–
**Daviesia corymbosa*	–
**Daviesia genistifolia*	–
**Dillwynia ericifolia*	+
**Dillwynia juniperina*	+
**Dillwynia sericea*	+
**Gompholobium marginatum*	+
**Gompholobium tomentosum*	+
**Jacksonia scoparia*	–
**Mirabelia oxyloboides*	+
**Mirabelia pungens*	–
**Oxylobium lanceolatum*	+
**Oxylobium robustum*	+
**Podalyria calptrate*	–
**Podalyria cuneifolia*	–
**Pultenaea microphylla*	+
**Pultenaea stipularia*	+
**Viminaria denudata*	–
3. GENISTEAE	
3a. Lipariinae (o)	
3b. Bossiaeinae	
**Bossiaea foliosa*	+
**Bossiaea pulchella*	+
**Hovea elliptica*	–
**Templetonia egena*	–
**Templetonia retusa*	–
3c. Crotalariinae	
**Aspalathus* (1)	–
**Crotalaria* (7)	–
**Lebeckia* (1)	–
**Lotononis bainsii*	–
3d. Spartiinae	
Adenocarpus (2)	–
**Argyrolobium* (1)	–
Calycotome (1)	–
Laburnum (2)	–
3. GENISTEAE—*continued*	
3d. Spartiinae—continued	
Lupinus (8)	–
Petteria (1)	–
Spartium (1)	–
3e. Cytisinae	
**Cytisus* (7)	–
**Genista* (5)	–
**Hypocalyptus obcordatus*	+
Ulex (1)	–
4. TRIFOLIEAE	
Medicago (7)	+
Melilotus (3)	+
**Ononis* (4)	+
Trifolium (8)	+
Trigonella (3)	+
5. LOTEAE	
Anthyllis (2)	+
Dorycnium (4)	+
Hymenocarpus (1)	+
Lotus (5)	+
**Securigera* (1)	+
Tetragonolobus (1)	+
6. GALEGEAE	
6a. Indigoferinae	
Indigofera (7)	–
6b. Psoraliinae	
Amorpha (4)	–
Dalea (2)	–
Petalostemum (2)	–
Psoralea (4)	–
6c. Brongniartiinae	
Harpalyce (1)	–
6d. Tephrosiinae	
Galega (1)	+
Milletia (3)	+
Mundulea (1)	+
Tephrosia (4)	–
Wistaria (3)	+
6e. Robiniinae	
Coursetia (1)	+
Gliricidia (1)	+
Olneya (1)	+
Robinia (4)	+
Sesbania (8)	+
6f. Coluteinae	
**Clianthus* (2)	+
Colutia (6)	+
Smirnowia (1)	+
Sutherlandia (1)	+
Swainsonia (3)	–
6g. Astragalinae	
Astragalus (*ca.* 120 spp.)	+
Astragalus (*ca.* 15 spp.)	–
Calophaca (1)	+

TABLE 1—*continued*

6. GALEGEAE—*continued*	
6g. Astragalinae—continued	
Caragana (6)	+
Glycyrrhiza (2)	+
Halimodendron (1)	+
**Oxytropis campestris*	−
**Oxytropis montanus*	+
7. HEDYSAREAE	
7a. Coronoillinae	
Coronilla (3)	+
**Hippocrepis balearica*	−
Hippocrepis comosa	+
Hippocrepis comosa	−
Hippocrepis unisiliquosa	−
Ornithopis (3)	+
Scorpiurus (1)	+
7b. Euhedysarinae	
Alhagi (1)	−
Ebenus (1)	−
Hedysarum (7)	+
Onobrychis (1)	−
7c. Aeschynomeninae	
**Aeschynomene* (3)	−
Chaetocalyx (1)	−
Cyclocarpa (1)	−
Nissolia (1)	−
7d. Patagoniinae	
Adesmia (3)	−
7e. Stylosanthinae	
Arachis (1)	−
Stylosanthes (1)	−
Zornia (1)	−
7f. Desmodiinae	
Desmodium (5)	+
Lespedeza (8)	−
Lespedeza tomentosa	−
Lespedeza tomentosa	+
**Uraria picta*	+
8. DALBERGIEAE	
8a. Pterocarpinae	
Dalbergia (2)	−
Pterocarpus (1)	−
8. DALBERGIEAE—*continued*	
8b. Lonchocarpinae	
Lonchocarpus (2)	+
8c. Geoffraeinae (0)	
8d. Anomalae (0)	
9. VICIEAE	
Abrus (1)	−
Cicer (1)	−
Lathyrus (3)	−
Lens (1)	−
Vicia (17)	+
Vicia (30)	−
10. PHASEOLEAE	
10a. Glycininae	
Centrosema (2)	−
Cologania (3)	−
Glycine sinensis	+
Glycine hispida	−
**Glycine soja* (8 cultivars)	−
**Hardenbergia monophylla* (1)	+
Kennedya (4)	+
Erythrinae	
10b. Apios (2)	−
Erythrina (3)	−
Mucuna (3)	−
Mucuna sp.	+
Stizolobium (1)	−
10c. Galactinae	
Galactia (1)	+
10d. Diocleinae	
Canavalia (5)	+
Pueraria (1)	−
10e. Cajaninae	
Cajanus (1)	−
Eriosema (1)	−
Rhynchosia (4)	−
10f. Phaseolinae	
Dolichus (6)	−
Phaseolus (8)	−
Strophostyles (1)	−
Vigna (5)	−

† This table brings together the data of several groups of workers[1–5]; data for *Lathyrus* and *Vica* are from Bell and Fowden (*Taxonomic Biochemistry and Serology* (Edited by A. LEONE). Ronald Press, London (1964)). Taxa marked with an asterisk (*) were examined in the present study; numerals in parenthesis refer to the number of species examined for the genera concerned; plus (+) refers to the presence of canavanine; minus (−) indicates that canavanine was not detected. Data for the genus *Astragalus* are mostly those of L. Fowden and P. M. Dunnill (Personal communication).

METHODS AND MATERIALS

The methods described by Bell[1] were used in the present survey, for extracting and identifying canavanine in the legume seeds. In all species reported here as positive, the compounds reacting positively with the pentacyanoammonioferrate reagent (PCAF) had the same mobility on paper chromatograms as canavanine itself.

Seeds for the present study were obtained from several sources. Species belonging to the Podalyrieae were

mostly provided by the Division of Plant Industry, C.S.I.R.O., Canberra, Australia (1963 Seed Exchange List). Some of the tests were made on seed flour obtained from Dr. R. N. Lester; voucher specimens for this material are the same as those used by him in a serological study of these taxa.[6] The remaining collections were obtained from miscellaneous sources, mostly botanical gardens, and we've had to accept the names which accompanied the seed packets.

The arrangement of tribes and subtribes for the taxa listed in Table 1 follows the system of Taubert.[7]

RESULTS AND DISCUSSION

Canavanine has been found only in the family Leguminosae, subfamily Papilionoideae, occurring in 60 per cent of the approximately 540 species examined and 35 per cent of the 150 genera (Table 1). Heretofore canavanine was thought to be absent from the tribes Sophoreae and Podalyrieae, but we have detected the compound in five of twelve genera from Southern Hemisphere taxa of the latter tribe. The Sophoreae, like the Podalyrieae, is a large, highly diversified tribe, therefore it is likely that additional sampling will reveal canavanine in that tribe also. Since canavanine is so widespread in the Papilionoideae, it appears that the ability of legume species to produce canavanine appeared at a very early time in the evolution of the subfamily, its present, somewhat erratic, occurrence in some of the tribes perhaps reflecting the channeling of relatively simple controlling factors (i.e. one or a few genes) among several to numerous ancestral taxa. That is to say, we prefer to think that canavanine arose very early in the evolution of the subfamily and that it has been maintained in several divergent stem lines arising out of this ancestral complex. This contrasts with an alternative hypothesis which would have canavanine arise independently in the several tribal and/or subtribal lines which possess the compound.

Birdsong, Alston and Turner[3] have discussed the systematic implications of the distribution of canavanine in the Leguminosae and, except for the demonstration of this compound in the Podalyrieae, we have added no new data that might demand different interpretations. However, it should be noted that because of the absence of canavanine in the Podalyrieae and Sophoreae, these authors were tempted to offer the hypothesis that "species with the proper genomes for the formation of canavanine did not arise until the Papilionoid line was well established". It now appears that such "genomes" were present in some of the earliest Papilionoid types and it may be that a more intensive search among the Caesalpinioideae, especially the more advanced tribes Swartzieae and Sclerolobieae,[8] will yet reveal the compound in that subfamily also.

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[6] R. N. LESTER, R. E. ALSTON and B. L. TURNER, *Am. J. Botany* **52**, 165 (1965).
[7] P. TAUBERT, *Naturlichen Pflanzenfamilien* III, 70 (1894).
[8] B. L. TURNER and O. S. FEARING, *Am. J. Botany*, **46**, 49 (1959).