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Seedling handedness in Fabaceae

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Abstract. Seedling handedness has been studied in 76 genera and 137 species of of the Fabaceae out of which 35 genera and 78 species exhibit handedness. Its presence is more common or sporadic in some tribes and completely absent in other tribes. The taxonomic implications of this character is discussed. The possible causes for the existence of seedling handedness are discussed.

Keywords. Handedness; Fabaceae; isomerism; bioisomerism; geomagnetic force.

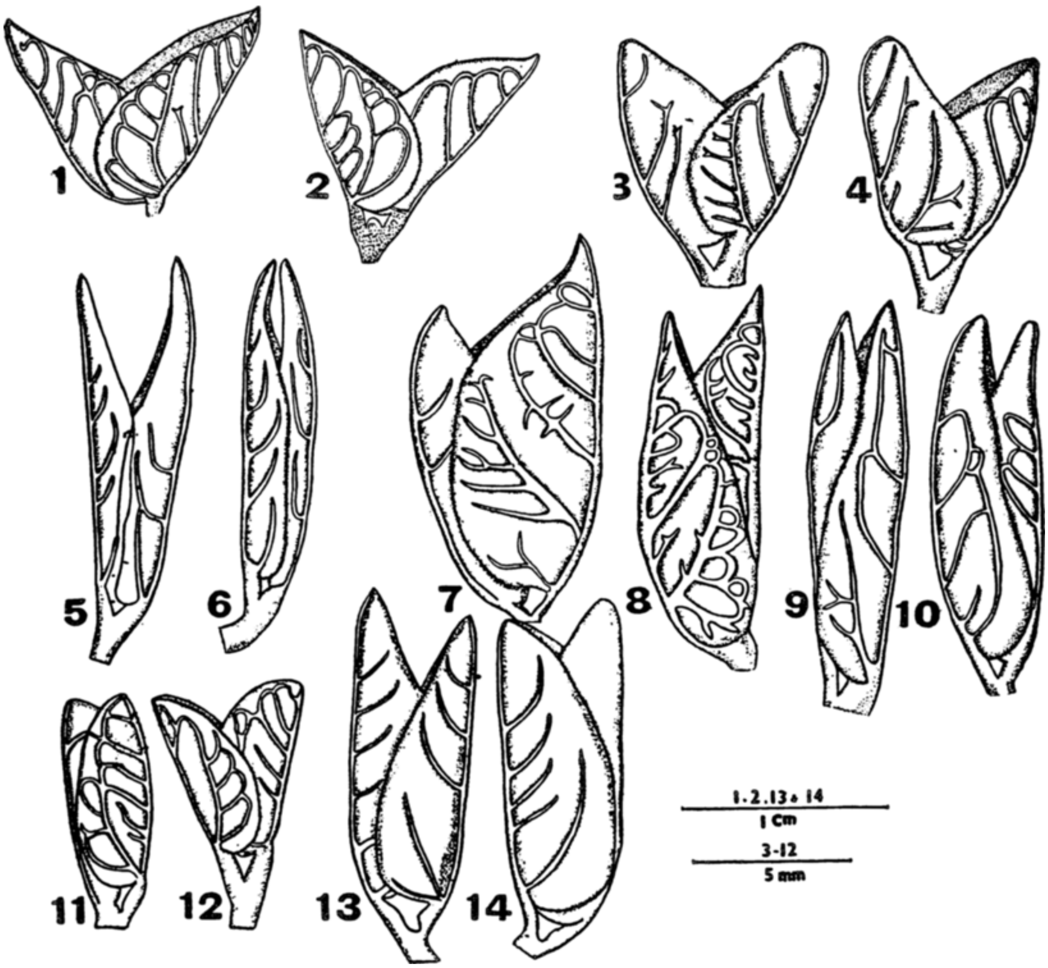
1. Introduction

The presence of a number of morphologically well-defined organs together with the complexity attained to exploit the maximum existing environment make phylogenetic studies of angiosperms more difficult. Plant taxonomy is largely based on floral character but not much emphasis is given to the morphological characters which also can serve in delimiting taxa. Seedling characters in general have received scant attention. Despite the studies of Arber (1961) on seedlings of various monocots and the application of seedling characters for taxonomic purposes (Burger 1972; Muller 1978) and genetic studies (Crow 1973). Studies relating to seedling handedness and its application in taxonomy have not been studied in detail. Recently, Cunnell (1978) studied 2000 species of angiosperms for their ptyxis but has failed to focus his attention on seedling handedness. Muller (1978) also studied several species but could not detect seedling handedness similar to the one comparable to that described by Compton (1912) in cereals. Bahadur *et al* (1980) reported for the first time seedling handedness in *Vigna mungo*. Recently seedling handedness was reported by Rao *et al* (1980) in *Phaseolus vulgaris* and in *Cajanus cajan* (Rao and Bahadur 1980).

In the present paper a survey of seedling handedness in Fabaceae is reported and its taxonomic implications are discussed. The causal factors for the handedness in plant organs are discussed.

2. Materials and methods

A total of 76 genera and 137 species spread over 9 tribes of Fabaceae have been investigated. Seeds of most of these were obtained through the courtesy of different research institutions, researchers and locally available species have also been tested. Seeds were sown in earthern flats as well as in petri dishes and their germination stages were carefully observed. The seedlings emerged on the third day of sowing, although several species took even 5 to 7 days. The seedlings have been classified as left, right and two types of neutrals following the procedure of Bahadur *et al* (1980). Handedness or bioisomerism in plants is based on the twisting (viewed from above) of plant organs which forms mirror images. A seedling is regarded as the right-handed when the folding of the first seedling leaves is in the counter-clockwise direction and in the left-handed seedlings the direction of the folding will be in clockwise direction (figures 1–14). A seedling that lacks overlapping is regarded as neutral. In some selected genera the left and right-handed seedlings have been scored and were statistically analysed by Chi-square test. The neutrals have been omitted in table 2, due to their negligable number.



Figures 1–14. Camera lucida drawings of left and right handed seedling leaves of *Vigna* and *Phaseolus* spp. **1, 2.** *V. angularis*. **3, 4.** *P. atropurpurius*. **5, 6.** *V. radiata*. **7, 8.** *P. lunatus*. **9, 10.** *P. aconitifolius*. **11, 12.** *V. trilobata*. **13, 14.** *V. catjang*.

Table 1. Break-up of the tribe-wise distribution of seedling-handedness in Fabaceae.

Tribe	Number of Genera	Number of Species
Genisteae	1	1
Trifoleae	1	1
Galegeae	..	..
Hedysareae	9	9
Vicieae	..	..
Phaseoleae	21	64
Dalbergieae	3	3
Sophoreae	..	..
Loteae	..	..
	35	78

Table 2. The distribution of left and right-handed seedlings in some Fabaceae.

Species	Twist of the first pair of leaves		L+R	L−R	LH/RH	LH%	X^2	P-value
	Left	Right						
Phaseolus vulgaris	339	349	688	−10	0·986	49·27	0·03	>0·5
P. multiflorus	98	74	172	+24	0·755	43·58	2·41	>0·1
P. atropurpurius	282	326	594	−44	1·15	56·85	11·25	<0·1
P. calcaratus	108	124	232	−26	0·871	43·14	2·96	<0·1
P. lunatus	94	114	208	−20	0·825	45·19	1·92	>0·1
P. aconitifolius	85	97	124	−10	0·823	47·71	1·03	>0·1
P. acutifolius	86	88	174	−2	0·977	49·23	0·023	>0·5
Vigna mungo	2755	4448	7203	−1693	0·619	38·80	39·80	<0·1
V. radiata	3356	4865	8221	−1509	0·681	40·88	27·36	<0·1
V. angularis	83	125	208	−42	0·664	39·72	8·48	<0·1
V. sublobata	128	166	294	−38	0·771	43·54	4·912	<0·1
V. trilobata	190	224	414	−34	0·850	45·89	2·79	<0·1
V. catijang	286	331	617	−45	0·864	46·34	3·28	<0·1
Glycine max	302	338	640	−36	0·892	47·27	3·17	<0·1
Dolichos lablab	124	152	276	−28	0·815	44·90	3·20	<0·1
D. biflorus	452	520	972	−68	0·801	46·40	4·70	<0·1
Psophocarpus tetragonolobus	102	91	193	−11	1·12	52·82	0·63	<0·5
Cajanus cajan	2380	2645	5025	−265	0·899	47·06	13·97	<0·1
Atylosia lineata	38	47	85	−9	0·828	44·79	0·95	<0·5
Erythrina stricta	15	10	25	+5	1·15	60·00	1·00	..

3. Results and discussion

A perusal of the data presented in table 1, shows that the occurrence of seedling handedness varies from tribe to tribe and out of 137 species examined only 78 species exhibit seedling handedness since its presence is either common or sporadic in some tribes while it is completely absent in others. In the tribe Phaseoleae, a majority of the genera examined show seedling handedness where as in Hedysareae nine genera and in Dalbergeae three genera show this character. In the tribes Genisteae and Trifoleae only one species in each of the genera examined show seedling handedness. On the contrary none of the genera examined in tribes Galegeae, Viceae, Sophoreae and Loteae show seedling handedness. It was noted that for a species to show seedling handedness, the first pair of leaves should be simple and opposite. However, in *Robinia*, where the first seedling leaves are simple yet overlapping of the margins was found to be absent because these leaves were found to be in two different levels and this prevents over lapping. Further, the seedling handedness seems to be associated with a particular seed shape. In general kidney-shaped seeds show twisting of the first pair of leaves, with the exception of *Sesbania* and *Tephrosia*, which are not characterised by kidney-shaped seeds. On the other hand in *Cajanus* and *Glycine* the shape is broadly oval but still exhibit seedling handedness.

A thorough survey of literature shows that twisting of the plant part has been used effectively in delimiting orders, families and even species. Engler and Prantl (1915) kept the order Contortae under Sympetalae which is characterised by corolla usually with twisted aestivation. Hutchinson (1964) employed effectively twisting of the keel petals and styles for taxonomic purposes in the family Papilionaceae. Rao *et al* (1979a, b) also proposed a tentative classification of Papilionaceae based on the contortion of the vexillum and wing petals, where the corolla handedness was found to be specific and associated with some tribes and absent in others. Hence seedling handedness presently studied may also be used as a taxonomic pointer in delimiting taxa in a large family like Fabaceae. Further the seedling handedness in Fabaceae appears to have evolved in a uniform pattern as shown by its presence in some tribes and *vice versa* in others.

The data in table 2, show that in the majority of the species the right-handed seedlings were found to be higher than the left-handed seedlings. Further, if only *Phaseolus* and *Vigna* species are considered, the American species (*Phaseolus multiflorus* and *P. lunatus*) gave a higher number of the L seedlings and in the Asian species (*Vigna mungo* and *V. radiata*) showed the reverse condition. The results also show that in other species the distribution of L and R seedlings vary. For instance, in *Psophocarpus tetragonalobus* and *Erythrina stricta* the L seedlings were found to be more, though statistically not significant. On the other hand, the number of the R seedlings was found to be more in *Glycine max*, *Dolichos lablab*, *D. biflorus* and *Cajanus cajan*. Such difference in the distribution of the L and R seedlings was also observed in a number of cereals (Compton 1912). However, what makes the differences in the distribution of the L and R seedlings is presently unknown (table 2). Smartt (1976) observed that in American species of *Phaseolus* the style twists towards the right and in the Asian species it twists to the left. Davis (1974) observed that *Mikania scandens* (Compositae) twists towards the right in the Southern Hemisphere and the reverse occurs in the Northern Hemisphere.

The seedling handedness observed in Fabaceae is a clear case of isomerism as both the L and R seedlings represent stereoisomeric forms that have been variously designated in the literature as isomeric and bioisomeric (Bahadur 1974; Bahadur *et al* 1977; Meyen 1973), enantiomorphic (Davis 1974) and bio-enantiomorphic objects (Dubrov 1978). The causal factors for the existence of isomeric forms of seedlings are so far unknown. Bahadur *et al* (1977) and Rao (1980) have reviewed the possible reasons for the existence of handedness in plant organs. Bahadur and Venkateshwarlu (1976) first hypothesised that handedness may be due to the presence of optically active substances, i.e. Levo and Dextro compounds in the plant metabolism. Thus, according to them, molecular chirality is expressed in biological chirality. However, the views of Bahadur and Reddy (1975) seem to be more appropriate and knowledgeable todate and according to them the left and right-handedness in plants and plant parts may be due to stereoisomerism of hormone molecules present in the plant systems.

However, Dubrov (1978) believes that the geomagnetic force determines the biosymmetric status of living objects and this probably may occur at the time of untwisting of the chromosomes and replication of DNA. Davis (1974) on the other hand opines that handedness is influenced by geophysical forces. Sulima (ex. Dubrov 1978 p. 134) established empirically that the left-handedness prevailed in even year 1960, 1962, 1964 and 1968 when the north-polar geomagnetic conditions predominated while right-handedness dominated in the odd years 1961, 1963, 1965, 1967 and 1969 during the manifestation of south-polar geomagnetic conditions.

Hence the causal factors for the existence of the L and R forms of seedlings are to be sought and it is hoped that it might open up a new area in the study of plants to which we propose the term stereo-botany.

According to Rao (1980) plants developing from the left-handed seedlings were found to be metabolically superior with regard to quantity of chlorophyll/g tissue, size and density of stomata coupled with transpiration rates and number of root characters. This possibly is responsible for the higher yield in contrast to the plants developing from the right-handed seedlings. Such differences in the left and right-handed plants was not only observed with regard to seedlings but also with regard to ovule position (either to the left or right) (Horovitz *et al* 1976) and according to them, left/right ovule position influences the seed set and out crossing rates in flowers of *Medicago sativa* (Fabaceae). Kihara (1972) points out the use of R/L characters will enable us to achieve clear theoretical and practical results and consequently fuller understanding of the vital process. He further says "As there is a possible relationship between the foliar arrangement and yield of crop plants, it is necessary to examine the differences between the R and L strains in their utilization of solar energy."

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