INFRASPECIFIC VARIATION IN *LATHYRUS NISSOLIA* L.

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ABSTRACT

The varieties described for *Lathyrus nissolia* by Continental authors are reviewed and their findings are clarified with the aid of cultural experiments and statistical techniques. Two well-marked varieties are recognized and their distributions are plotted on a map. Only one variety appears to occur naturally in the British Isles. Some preliminary observations are made on the breeding biology of the species and problems demanding further field study are indicated.

As *Lathyrus nissolia* is a very distinct species which is clearly separated from the rest of the genus by its grass-like phyllodes (hereafter referred to as leaves), its circumscription has been understood from early times and its taxonomy is free from troubles at the specific level. When, however, its infraspecific variation is examined a great confusion of taxa is found. This is due in part to the rather subtle nature of the characters involved and partly to the consideration by some of the early authors of too little material, both in the herbarium and in the field. My own interest in the subject was aroused by the fact that although the major Continental Floras all recognized varieties of this species, very little notice had been taken in British botany of their conclusions. Lousley writing in the Botanical Exchange Club Report for 1934 was almost alone in drawing attention to the Continental work and his note does not seem to have received the attention it deserved. The reason for this lack of interest by British botanists is now clear, since as a result of this study it will be seen that only one infraspecific taxon is represented in this country and the absence of interest was therefore probably occasioned by frustration rather than neglect.

HISTORICAL

A. Kerner was the first to draw attention to the variation within the species when he described *Lathyrus gramineus* in 1863. This he believed to be a related species which differed from *L. nissolia* by 'petiolis angustioribus concavis et leguminibus germinibusque glaberrimis'. Thus, by implication, Kerner suggested that *L. nissolia* (*sensu stricto*) has broader leaves and a hairy pod. As will be shown later, this was an error which was perpetuated by later authors till the present time. *L. gramineus* A. Kerner is a later homonym of *L. gramineus* Gray, which is itself a nomenclatural synonym of *L. nissolia* L. Uechtritz, writing a letter to the editor of the *Oesterr. Bot. Zeitschr.* in 1864, pointed out that *Orobus* (*Lathyrus*) *nissolia* was quite a variable plant, especially with regard to leaf width. He suggested that Kerner's *L. gramineus* was a variant of this species and went on to point out that the glabrous-podded forms are of frequent occurrence throughout the range of the species, to an extent that some authors of Floras have described it as having glabrous pods. He then made a short reference to a form which he referred to as *O. nissolia genuinus* which had a short fine pubescence. In making these observations, Uechtritz showed that he had an appreciation of the variability of this species unequalled by any of the older authors. Subsequent authors have considered that this letter includes a valid publication of the name *O. nissolia genuinus* and have presumed the trinomial to be of varietal rank. It seems clear to me, however, that he only used *genuinus* meaning 'in the strict sense' and did not visualize it as a formal nomenclatural unit. Freyn (1878) in a paper on the flora of Southern Istria provided a varietal epithet for the forms represented by Kerner's *L. gramineus*. He noted that his var. *glabrescens* had a narrow leaf and a glabrous or almost glabrous pod. In doing this he undermined the excellent observations about variation in leaf width made earlier

by Uechtritz and paved the way for later authors to further confuse the situation. In 1885 Uechtritz also provided a varietal epithet (var. *liocarpus*) for the glabrous-podded forms, citing *L. gramineus* A. Kerner as a synonym.

In his Flora of Lower Austria (1893) G. Beck recognized two varieties: *α pubescens* G. Beck which he described as being hairy-podded and *β gramineus* G. Beck which has a glabrous or somewhat rough pod. He cited var. *glabrescens* Freyn as a synonym of the latter. In the addendum to the Flora, Beck provided an additional name (var. *puberulus*) for var. *pubescens*. Since he gave no reason for this action, we must regard this as the publication of a later superfluous nomenclatural synonym.

Rouy, in *Flore de France* (1899) provided two further varietal epithets with the following descriptions:

lanceolatus Pétioles lancéolés-linéaires (4–10 mm de large); plante plutôt robuste.

linearis (*L. gramineus* Kern.) Pétioles étroitement linéaires (2–3 mm de large); plante plutôt grêle.

These descriptions are important as they draw attention for the first time to a possible slight difference in leaf shape. Unfortunately Rouy was influenced by Kerner's early remarks on the narrowness of the leaves of the glabrous-podded forms and introduced the size restrictions shown above. In his general description Rouy refers to the pods being 'pubescents ou presque velus'. It is strange that he made no reference to the pods of the varieties. Ascherson & Graebner also writing in 1899 proposed a forma *gramineus* Aschers. & Graebn. and referred to its glabrous pods without mentioning the leaves. Hegi (1924) recognized two varieties, using the epithet *genuinus* Uechtr. ('pod hairy, leaves moderately broad') and *glabrescens* Freyn ('pod glabrous or somewhat rough, leaves smaller about 3 mm broad').

Finally Fiori in his Flora of Italy of 1925 proposed a var. *typicus*, with linear-lanceolate leaves 4–10 mm broad and with hairy pods, and a var. *gramineus* with linear leaves 2–3 mm broad and with glabrous pods. He cited var. *glabrescens* Freyn and var. *linearis* Rouy as synonyms of the latter and derived its epithet from Gray and Kerner. As we have already seen, *L. gramineus* Gray is a direct nomenclatural synonym of *L. nissolia* L.

My own studies in this field originated in an attempt to apply this maze of observations to the British material. Much time was spent looking for hairs on the pods of the broader-leaved forms, but it eventually became apparent that this kind of plant was not represented in the British flora (except by one specimen at the British Museum (Isle of Wight 1916) which, must, I think, be considered to be of adventive origin or a curatorial error). In considering the interpretation of the glabrous-podded variety, I was for a long time misled by the insistence of some Continental authors that narrow leaves went with glabrous pods. The situation seemed especially difficult as the British material included some conspicuous plants with exceptionally broad leaves of up to 1 cm in width. Early attempts to apply the var. *glabrescens* concept to British plants suggested that there might be two glabrous-podded varieties, but eventually it became clear that a continuous range of variation existed both in this country and on the Continent.

Some consideration was then given to finding additional reliable features to support the pod-pubescence character. At this stage Uechtritz's excellent remarks of 1864 were unknown to me, but inspection of the material at the British Museum and Kew suggested that a slight but constant difference in leaf *shape* was associated with the pod character. The plants with hairy pods had narrow-lanceolate leaves, while those with glabrous pods had linear-lanceolate leaves. As already noticed this was suggested by Rouy but he confused the issue by also suggesting an absolute difference in leaf width. In order to express this difference statistically a ratio was devised whereby the leaf length was divided into six equal parts and the width at one sixth from the apex (W_1) was divided by the width at one third from the apex (W_2). This is referred to hereafter as the *leaf ratio*. Fig. 1 shows a simple plastic scale which was made to facilitate the division of the leaves into six equal parts. By aligning the mid-rib of the leaf parallel to one of the horizontal lines of the scale, so that

its tip and base touched outermost sloping lines, the one-sixth and one-third points could quickly be found with an accuracy adequate for the present purpose.

As a pilot experiment fifty leaves each were measured from glabrous and hairy-podded specimens in the British Museum herbarium and average ratios worked out for them. The hairy-podded plants had a ratio of about 0·5, while the ratio of the glabrous-podded forms was about 0·7. At this point it became essential to clarify the nomenclatural position in

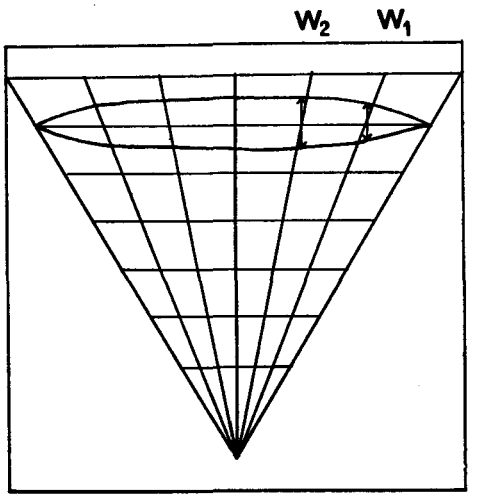

Fig. 1. Diagram showing the use of a simple transparent plastic scale for finding the positions for the measurement of the leaf-widths used in the *leaf ratio* determinations.

respect of these two varieties. Continental authors have always referred to the hairy-podded variety as being typical *L. nissolia* but when the Linnaean type was examined (Herb. Linn. no. 905/2) it was found to fit very exactly into the glabrous-podded group; the correct name for these plants is therefore var. *nissolia*. *L. nissolia* var. *pubescens* G. Beck (1893) is the correct name for the hairy-podded variety.

A synonymy of varietal names is given below:

LATHYRUS NISSOLIA L. VAR. NISSOLIA

Lathyrus gramineus A. Kerner, Oesterr. Bot. Zeitschr. **13**, 188 (1863) non Gray (1821).
L. nissolia var. *glabrescens* Freyn, Verh. K. K. Zool-bot. Ges. Wien **27**, 325 (1878).
L. nissolia var. *liocarpus* Uechtritz, Jahres-Bericht. Schlesischen **62**, 310 (1885).
L. nissolia var. *gramineus* G. Beck, Fl. Nied-Oesterr., 882 (1892).
L. nissolia var. *linearis* Rouy in Rouy & Fouc., Fl. France **5**, 253 (1899).
L. nissolia forma *gramineus* Aschers. & Graebn., Fl. Nordost. Flachl., 99 (1899).

Fig. 2. Graph showing the relation of mean leaf ratio and mean pod vein number for eleven populations. The lines represent twice the standard error of the means. ▲ = Linnean type specimen.

Fig. 3. Graph showing the relation of mean leaf ratio and mean pod diameter for eleven populations. The lines represent twice the standard error of the means. ▲ = Linnean type specimen.

Fig. 4. Graph showing the relation between mean pod vein number and mean pod diameter for eleven populations. The lines represent twice the standard error of the means. ▲ = Linnean type specimen.

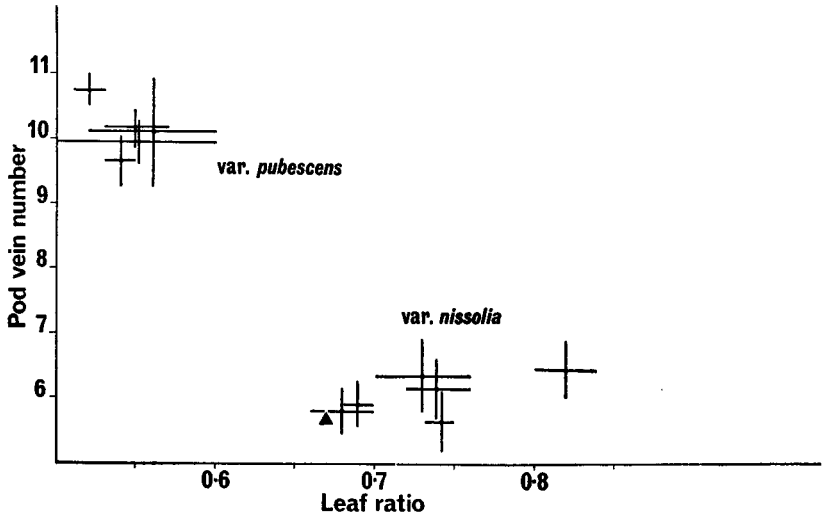

Fig. 2

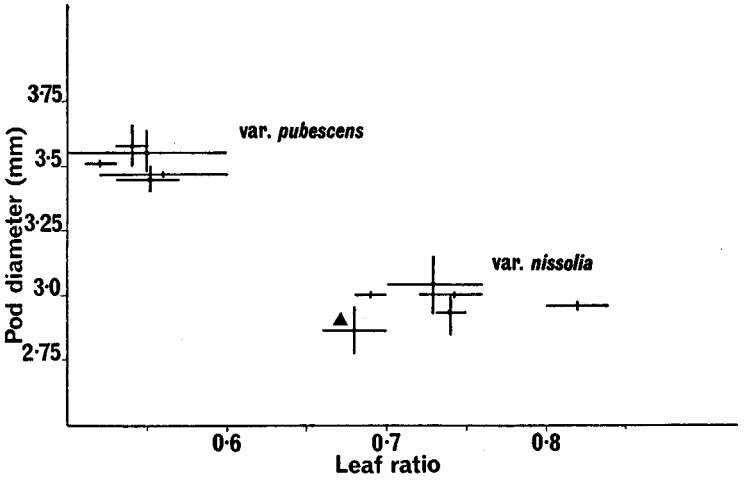

Fig. 3

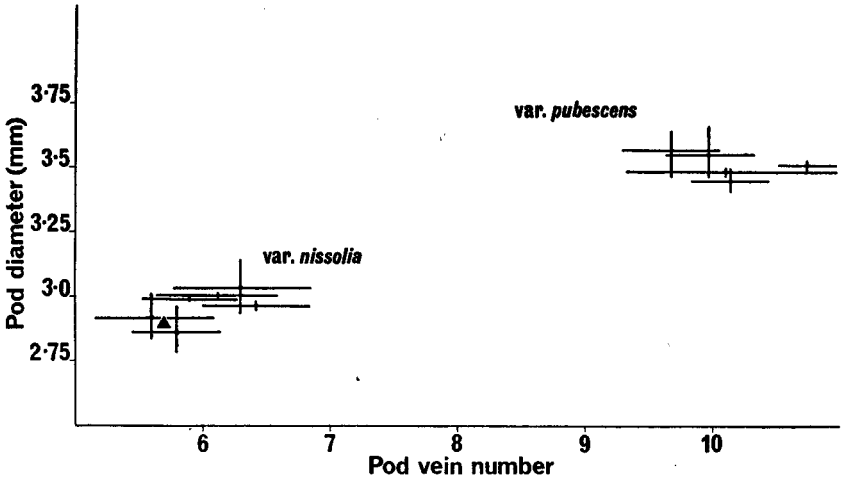

Fig. 4

L. nissolia subsp. *amanus* Rechinger. Ark. för Bot. **5**, 268 (1960).
(See discussion later in this paper.)

LATHYRUS NISSOLIA VAR. PUBESCENS G. Beck, op. cit., 882 (1892).
Lathyrus nissolia var. *puberulus* G. Beck, op. cit., 1329 (1893). Illegitimate substitute name.
L. nissolia var. *lanceolatus* Rouy in Rouy & Fouc., Fl. France **5**, 253 (1899).
L. nissolia var. *typicus* Fiori, Nuova Fl. Anal. Ital. **1**, 909 (1925).

EXPERIMENTAL TAXONOMY

Having reached these conclusions by more or less traditional methods, it seemed clear that cultural methods with statistical investigation would provide the best means of further clarifying the separation of these varieties. Through the courtesy of the directors of several botanic gardens and by direct collection in the field, seeds of ten strains of *L. nissolia* were obtained for culture the following season. The seeds were sown directly in the ground in patches so that clumps would be formed by the growing plants. Previous experience had shown that germination is very slow and irregular unless the testa is filed before the seeds are sown. The following characters were observed in the living plants. The foliage of var. *nissolia* is rather yellowish-green compared to that of var. *pubescens* which is relatively glaucous bluish-green. I have not been able to detect this colour difference in herbarium material. The colour difference is most noticeable when the plants are massed in clumps, under these conditions the plants can be separated by this character at a distance of several yards. In my experience plants of var. *nissolia* are in full flower 4 months plus after planting, while plants of var. *pubescens* sown on the same day come into flower 3 months plus after planting. The generally quicker growth rate of var. *pubescens* is noticeable at all stages when the plants are grown side by side.

Var. *nissolia* is very variable in height, from 10 cm dwarfs to 100 cm giants. Its stem is often nearly simple, sometimes with a second main branch from near the base. Var. *pubescens* on the other hand is rather uniform in stature, varying between about 25–35 cm. It frequently has a rather bushy growth habit with up to six or seven stems of equal magnitude rising from the base. In addition to the leaf ratio character already described, two other characters were tested statistically on the cultured populations. These were (1) The number of major veins on a pod valve at a position half way along its length (*Pod vein number*) and (2) the diameter of the pod measured at the same position. For each culture 50 leaves and 50 pods were collected, only one of each being taken from each plant. Only lower leaves from fully developed plants were used and likewise only fully grown but unripened pods were selected. The results of the analysis are shown graphically in Figs. 2, 3 and 4. In each case the mean value for the 50 samples is plotted together with lines representing twice the standard error of the mean which is used as an indication of the variability within each population. Some measurements were also made of the Linnean type specimen and figures representing this plant are included on the graphs. In each case its clear association with the glabrous-podded variety can be seen.

LATHYRUS NISSOLIA SUBSP. AMANUS RECHINGER

In 1952 Dr. K. Rechinger kindly drew my attention to his then unpublished subsp. *amanus* from the Amanus range in northern Syria. This is founded on Haradjian nos. 222, 266 and 275 in the Delessert Herbarium at Geneva. Rechinger's description reads 'Differt a planta typica pedunculo folium fulcrantum aequante vel eo longiore'. I later had the opportunity of examining the type material and was unable to find any additional features by which it could be separated from var. *nissolia*. While I have not seen another specimen with such relatively long peduncles, I have seen plants ranging widely between the var. *amanus* condition and the more normal state. For these reasons I prefer to regard the Amanus material as a highly localized population of the type variety. Judging from the

material that has reached the major European herbaria from Asia Minor, *Lathyrus nissolia* is a rare and scattered plant in this region. I would therefore suppose that this long-peduncled population has developed in the seclusion of the Amanus mountains and the character has become established in the population through the habitual self-pollination which I believe is normal in this species.

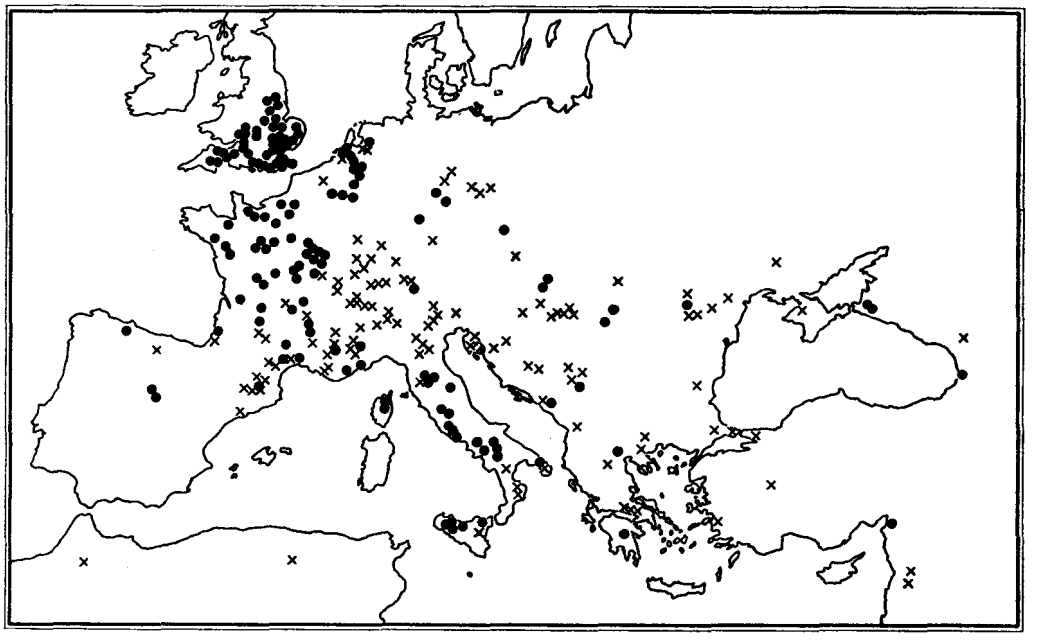

Fig. 5. Map showing the distribution of the varieties of *Lathyrus nissolia.* ● = var. *nissolia*, × = var. *pubescens.*

Distribution

The accompanying map (Fig. 5) shows the distribution of the two varieties throughout the known range of the species. The British range is adapted from the map in the *Atlas of the British Flora* while the remainder has been plotted from the records provided by specimens which I have examined myself. It will be noted that while the distribution is sympatric over the greater part of the range, the British Isles only has var. *nissolia* with the exception of one record of var. *pubescens* from the Isle of Wight. A specimen in the British Museum Herbarium forms the basis for this record. The label provides no additional information other than the date 1916. In view of the lack of any other records and absence of var. *pubscens* from the north-west part of France, I am disposed to regard the Isle of Wight record as either an adventive stray or else the result of some curatorial error involving a mixing of labels. Apart from a broadly Continental trend in the distribution of var. *pubescens*, compared with the exploitation of more oceanic conditions by var. *nissolia*, no obvious distributional patterns can be seen from the map.

Chromosome number

The chromosome number of this species has been reported as being $2n = 14$ on several occasions including Simonet (1932) and Senn (1938). The vast majority of *Lathyrus* species have been found to be diploids with the base number 7; only four species have been recorded as polyploids. One of the most interesting of these was reported by Marks in 1950. He found that a tetraploid form of *Lathyrus pratensis* was common in this country. A detailed cytological investigation or *L. nissolia* would very probably prove rewarding.

General summary and conclusions

One of the most important observations resulting from this study is that individual plants can always be placed with comparatively little difficulty into one or other of the two varieties. Plants with markedly intermediate characters do not seem to occur and I have not detected any hybrids among the very large number of sheets that I have examined. Attempts to produce artificial hybrids under cultural conditions were not successful. My observations suggest that this species is habitually self-pollinated—despite the apparent adaptation of its flowers towards entomophily. Buds enclosed in bags to prevent the access

Table 1

Character	var. *nissolia*	var. *pubescens*
1. Pods	Glabrous or somewhat scabrous	With short bristly hairs
2. Leaf shape	Linear lanceolate (leaf ratio about 0·7)	Narrowly lanceolate (leaf ratio about 0·5)
3. Mean pod diameter	About 3·0 mm	About 3·5 mm
4. Mean pod vein number	About 6	About 10
5. Colour of living plant	Relatively yellowish-green	Relatively blue-green
6. Growth rate	In full flower four months plus after planting	In full flower three months plus after planting
7. Habit	Very variable in height, stem often simple	Relatively uniform in height and frequently with a rather bushy habit with several stems of equal size

of insects always set seed perfectly normally, while emasculated flowers were never found to set any seed, although unprotected by bags. I have never observed the flowers being visited by any insects, in the wild or in cultivation. These observations are confirmed by Kirchner who says '. . . the flowers frequently do not open at all but nevertheless set healthy fruits, being cleistogamously fertilized'. Knuth does not record any insect visitors to these flowers in his *Handbook of Flower Pollination*. This habitual self-pollination presumably provides an explanation of why hybrids apparently do not occur and also why the varieties remain distinct despite the very large overlap in their ranges. The question remains as to what status in the taxonomic hierarchy should be accorded to these taxa. Since interbreeding does not seem to occur and since the individuals can always be assigned to a variety without undue difficulty, it would seem that they might well be regarded as distinct species or at least sub-species. But since the evidence from genetics and cytology remains to be clarified, I prefer for the present to retain the existing varietal status, for which validly published names are available, rather than to further burden the literature with additional names at a new status which may prove undesirable after further studies have been executed. I am content for the present to draw attention to the interesting infraspecific variation of this plant, with the hope that other workers will make observations on its biology in the field, especially in those areas where both varieties are known to occur. It would be interesting to know if the difference in flowering times encountered under cultural conditions holds good when the varieties are growing in the same area in the wild and if natural hybrids ever occur in regions where both varieties are present. The characters which separate the two varieties are summarized in Table I.

Acknowledgments

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References

KIRCHNER, E. O. O. (1888). *Flora von Stuttgart:* 515.

KNUTH, P. (1908). *Handbook of Flower Pollination.* Trans. Ainsworth Davies **2**, 337.

LOUSLEY, J. E. (1935), in Distributor's Report for 1934. *Rep. Bot. Exch. Club.* **10**, 964.

MARKS, G. E. (1950). Referred to in *Rep. John Innes Hort. Inst.*, 1949, 7.

PERRING, F. H. & WALTERS, S. M. (1962). *Atlas of the British Flora.* London. p. 116.

SENN, H. A. (1938). Contribution for a Revision of the Genus *Lathyrus. Amer. Journ. Bot.* **25**, 73.

SIMONET, M. (1932). Numérations Chromosomiques dans les Genres *Baptisia, Thermopsis* et *Lathyrus. Comptes Rendus Acad. Sci. Paris* **195**, 739.