

Morphological variation in the *Vicia sativa* L. aggregate

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ABSTRACT

Wild and cultivated strains of *Vicia sativa* L. agg. (incl. *V. angustifolia* L. and *V. segetalis* Thuill.) and *V. lathyroides* L. have been examined for 50 primary and many other derived morphological characters. None of the characters commonly used to differentiate the various segregates recognized in the literature or by us was found to be significantly affected by environmental factors, but several of them (e.g. flower-length, pod-length, absolute leaflet-shape) show continuous variation which renders them of very little taxonomic value. Characters such as heterophylly, tendril form, petal colour, pod colour, seed conspicuousness in the pod and seed texture may be used to separate four main taxa: *V. lathyroides*, *V. angustifolia*, *V. segetalis* and *V. sativa*.

The taxonomic status of these will be discussed in a later paper dealing with breeding and hybridisation data.

INTRODUCTION

Vicia sativa L. agg. is widespread over much of Europe, western Asia and North Africa as a native plant and, due to its frequent cultivation for green manure and fodder, it has become naturalized over an even wider area of the northern hemisphere.

The taxonomy of this species aggregate, and indeed its distinction from some close relatives, has been confused ever since Linnaeus' time. Much of this confusion is due to the inbreeding which is predominant in the aggregate and, in more recent times, to the large number of cultivated strains which have been bred and then grown on a field scale, and which have subsequently escaped from cultivation and intermingled with the native populations. The work described here is part of an attempt to place the taxonomy of the aggregate on a more logical basis than hitherto, with particular reference to the taxa occurring in the British Isles and adjacent parts of the Continent.

Vicia sativa agg. may be separated from all other European species of the genus by its annual habit; 1- to few-flowered, shortly pedunculate inflorescences; leaves with *c* 3-8 pairs of leaflets and a terminal, usually branched tendril; glabrous, usually reddish-purple corollas; equal calyx-teeth; and smooth seeds with a hilum occupying $\frac{1}{8}$ to $\frac{1}{4}$ the circumference.

Its closest relative, at least in western Europe, is *V. lathyroides* L., which is smaller in all its parts, has leaves with usually fewer leaflets and unbranched tendrils, and has tuberculate seeds. This species is, however, very often confused with small plants of *V. sativa*, particularly in the field, and for this reason it has been included in the present survey.

V. lutea L., another closely related species, differs from *V. sativa* in its unequal calyx-teeth; yellow corollas; strongly pubescent, deep pods; and seeds with a hilum $\frac{1}{3}$ to $\frac{1}{2}$ the circumference. Variants of *V. sativa* with white or yellow corollas occasionally occur and have sometimes been misidentified as *V. lutea*, but the calyx, seeds and pods of the latter species are distinctive.

At maturity most individuals of *V. sativa* agg. are much-branched, sprawling or climbing plants

bearing 1- to 2-flowered inflorescences in most of the upper leaf-axils. The shape of the leaflets on the lower leaves is often markedly different from that of those on the upper leaves which bear flowers in their axils; plants with this character well developed are termed heterophyllous. The leaves on the primary shoot of the young seedling are usually different again from any of those on the floriferous shoots, both in the shape of the leaflets and in the possession of a simple tendril or in lacking a tendril. The primary shoot never bears flowers; these are formed on the lateral shoots which develop from the lowest few nodes of the primary shoot, and on similar secondary or higher-order laterals. The overall vegetative vigour of a plant is an expression not only of the size of each shoot but of the numbers and orders of the laterals, which soon over-top the short-lived primary shoot.

In many cases the production of high-order laterals continues throughout the growing season. In certain plants very short laterals are formed low down near the ground, late in the season, when most of the older laterals possess ripe or ripening fruits. These short laterals bear small leaves and often very small flowers, which may be cleistogamous and give rise to small, few-seeded pods. In yet other plants, laterals produced very close to ground level become subterranean and develop as whitish shoots with rudimentary leaves and minute, whitish, cleistogamous flowers. The latter form whitish-brown, 1- to 2-seeded, subterranean pods, often in great quantity, which are thus conspicuously different from the earlier epigeal ones and contain seeds often also distinguishable from those formed above ground. Subterranean seed-production is typical of the taxon known as *V. amphicarpa* Dorthes, and we shall use the term amphicarp to describe the feature.

V. lathyroides is a less vigorous plant with usually far fewer branches and less pronounced differences in leaf-shape between main and lateral branches. Cleistogamy and amphicarp have not been observed and, moreover, the primary shoot does on a few occasions bear one or two flowers. Most of these differences are probably related to the ephemeral life-cycle of this species.

PREVIOUS CLASSIFICATIONS OF *VICIA SATIVA* AGG.

In the past *V. lathyroides* has almost always been recognized as a species distinct from *V. sativa* agg. In British Floras the latter has either comprised a single species with or without subspecies and varieties, or two species, *V. sativa sensu stricto* and *V. angustifolia* L., which differ in size, leaflet-shape, flower-colour and fruit-shape and -colour. The former treatment was adopted, for instance, in *Flora Anglica* (Hudson 1762), *English botany* (Syme 1864) and *Flora of the British Isles*, 2nd ed. (Tutin 1962); the latter in *The English flora* (Smith 1825), *The British flora* (Hooker 1830) and *Flora of the British Isles*, 1st ed. (Tutin 1952). *V. angustifolia*, whether treated as a species or a subspecies of *V. sativa*, was frequently separated into two varieties usually known as var. *angustifolia* and var. *bobartii* (E. Forst.) Koch (e.g. Tutin 1952). The former variety is also known as var. *segetalis* (Thuill.) Koch, and it appears, in fact, that var. *bobartii* is the type variety and hence the one to be known as var. *angustifolia*. Var. *segetalis* is a more robust plant than var. *bobartii*, and in several characteristics falls somewhere between the latter and *V. sativa*.

Continental authors have shown a similar degree of variation in their treatment of *V. sativa* agg., but because of the greater number of variants found in southern Europe the situation is much more confused. Rouy (1899), for example, recognized six distinct taxa in the aggregate, which he called *V. communis* Rouy. These taxa were termed 'formes', intermediate in rank between subspecies and variety, and among them a further ten varieties and three sub-varieties were recognized. Ascherson & Graebner (1909) divided *V. sativa* into four subspecies, which were largely equivalent to Rouy's formes (although two of the latter were reduced to synonymy), but in addition they recognized a very large number of varieties and other infra-specific categories.

The most important taxonomic studies of recent years have been made by Mettin & Hanelt (1964), who divided the aggregate into six species: *V. sativa*, *V. angustifolia*, *V. amphicarpa*, *V. incisa* Bieb., *V. cordata* Wulfen ex Hoppe and *V. macrocarpa* (Moris) Bertol. Later (Hanelt & Mettin 1966) they added a seventh species, *V. pilosa* Bieb. The first two of these are the two species which have been recognized by British authors, and the second of them was divided by Mettin & Hanelt into subsp. *angustifolia* and subsp. *segetalis* (Thuill.) Gaud.

Ball (1968) based his treatment for *Flora Europaea* on the work of Mettin & Hanelt, but preferred to consider the segregates as subspecies of *V. sativa*. Under this scheme *V. angustifolia* must be called

subsp. *nigra* (L.) Ehrh. Moreover, Ball included *V. pilosa* with it, so that he recognized a total of only six subspecies. They are: subsp. *sativa*, subsp. *nigra*, subsp. *amphicarpa* (Dorthes) Asch. & Graeb., subsp. *cordata* (Wulfen ex Hoppe) Asch. & Graeb., subsp. *incisa* (Bieb.) Arcangeli and subsp. *macrocarpa* (Moris) Arcangeli.

Much important work on this aggregate has also been carried out by Yamamoto (e.g. Yamamoto 1966). The results of his breeding experiments have important taxonomic implications but Yamamoto has not sought to use these to propose modified systems of classification.

Plitmann's (1967) valuable contribution on Middle-Eastern species of annual *Vicia* includes a careful survey of *V. sativa* agg. In it he, like Ball (1968), recognized the main variants as subspecies of *V. sativa*, but subsp. *pilosa* is not treated (not occurring in the region concerned) and subsp. *cordata* and *incisa* are amalgamated as a single subspecies. Moreover, in the main text, *V. segetalis* is placed with subsp. *cordata* rather than with subsp. *angustifolia* (= *nigra*), although a 'corrigendum' (p. 128) reverses that decision. In the *Flora of Turkey*, Davis & Plitmann (1970) recognized the same five subspecies.

Most previous systems of classification of the *Vicia sativa* aggregate have been based on a small, subjective selection of characters, both quantitative and qualitative, with little regard to their mode of variation. Some of the most frequently used characters, notably flower and pod length, are in fact continuous variables and the points in the scale of variation used by different authors to separate the taxa has varied a great deal (cf. Figs. 2 & 3). They have probably been selected for use because they are readily observable on herbarium material, whereas many other characters (often taxonomically more useful) are usually poorly preserved or demand floral dissection.

The work reported here has, therefore, sought to determine the pattern of variation in the morphological characters, as well as their points of discontinuity (if any) and the existence of any correlation between them, and has attempted to ascertain to what extent any groups so defined correspond with the segregates which have been recognized in the past.

For convenience we shall in this paper use the classification (i.e. the delimitation of the segregates and their nomenclature) of Mettin and Hanelt, but in addition shall recognize *V. segetalis* Thuill. as a distinct species. It is in several ways as distinct from *V. angustifolia* as are some of the other species and, in the British Isles at least, it has in fact been confused with *V. sativa* more frequently than with *V. angustifolia*. It is likely that only *V. angustifolia* of the above species is native in northern Europe, including the British Isles, but *V. sativa* and *V. segetalis*, and to a lesser extent *V. cordata* and *V. amphicarpa*, are cultivated there and occur as escapes from cultivation. The last two, however, have not to our knowledge been found wild in the British Isles. The decline of *V. sativa* as a cultivated plant in the British Isles has been documented by Killick (1975). We shall not be concerned with the other three taxa (*V. pilosa*, *V. incisa* and *V. macrocarpa*).

The main characters which may be used to separate these five segregates of *V. sativa* agg. and *V. lathyroides* are best summarized in the following key:

- | | | |
|---|---|------------------------|
| 1 | Seeds tuberculate | <i>V. lathyroides</i> |
| 1 | Seeds smooth | |
| 2 | Plants with subterranean stems bearing cleistogamous flowers and whitish, few-seeded pods | <i>V. amphicarpa</i> |
| 2 | Plants without subterranean stems | |
| 3 | Pods constricted between seeds | <i>V. sativa</i> |
| 3 | Pods not constricted between seeds | |
| 4 | Calyx-teeth longer than calyx-tube | <i>V. cordata</i> |
| 4 | Calyx-teeth shorter than calyx tube | |
| 5 | Plant markedly heterophyllous | <i>V. angustifolia</i> |
| 5 | Plant not or scarcely heterophyllous | <i>V. segetalis</i> |

MATERIALS AND METHODS

Seed samples of wild, known origin were collected personally or by colleagues, or were obtained from the seed exchange schemes of various botanic gardens. The 45 samples so gathered are listed with their chromosome numbers in Hollings & Stace (1974, Table 2). In addition, a large number (*c* 160) of samples of cultivated material was used, mostly of agricultural origin from various seedsmen and research stations. We feel this is justified because, as previously stated, many of the 'wild' populations found in the British Isles today originate as escapes or relics from such sources. For most of the work only about 30 or 40 of the cultivated strains were utilized. Since these plants are annuals, fairly regular re-sowing and seed harvest had to be carried out, although seed viability can last for several years in laboratory conditions. Representatives of all samples used were grown under field conditions and specimens were dried and pressed to provide a comprehensive herbarium. Flowers were more difficult to preserve adequately as they fade and wither very rapidly. Freshly opened flowers were therefore dissected into their component organs and spread out flat on the adhesive surface of transparent, self-adhesive tape, which was then inverted and mounted on stiff cards. These preserve the floral organs indefinitely for measurement and examination.

Measurements were standardized as far as possible, particularly in relation to the part of the plant sampled. Floral measurements are means from at least 10 freshly open flowers; leaf and fruit characters are means of 20 measurements. Seeds were measured with the aid of a Vernier travelling microscope or Vernier screwgauge. Where possible, leaf measurements were taken from the lowest flowering node, unless otherwise noted; stipules were scored from the two nodes below the lowest flowering node (where they are best developed).

Optical densities of wing and standard petals were taken from known weights of tissue (approx. 0.5 g) extracted in 5 ml of 1% methanolic HCl. Optical density at 530nm was determined for each sample using an Eel Spectrometer and corrected to a value for 1g of tissue. 1% methanolic HCl was used as a blank standard.

Cultivation experiments were carried out in crowded (10 plants per 5 inch pot) and isolated (1 plant per 5 inch pot) conditions, in constant (15°C, 16h day, 40% rel. humidity) glasshouse or changing outdoor conditions, and in four types of soil (sand, loam, clay, John Innes No. 1 compost). The cultivation experiments therefore comprised 16 different treatments. The soil types were prepared with regard to texture only; in particular it should be noted that the sand was low in calcium and thus resembled the soil of inland sandy heaths rather than that of most maritime dunes.

DEFINITION OF CHARACTERS INVESTIGATED

The characters chosen for this survey included most of those which had been used taxonomically in the past, plus many which clearly varied and might therefore be of taxonomic value. From this basic list many additional characters were derived, either ratios or measurements from different parts of the plant. The list is clearly by no means exhaustive, as the measurements of a flower such as that of *Vicia* can be extended almost indefinitely. Moreover, many other, mainly qualitative, characters were omitted from the detailed study, e.g. detailed patterns of testa coloration, presence of a blackish spot (extra-floral nectary) on the stipules, as well as a number of very variable quantitative features, e.g. plant height.

The following 50 primary characters were scored, 37 being quantitative and 13 qualitative.

a. *Flowers:*

1. Flower length, from base of calyx to apex of lateral petal
2. Number of flowers per node
3. Cleistogamy, as one of three categories: cleistogamous flowers absent; aerial cleistogamous flowers present; subterranean cleistogamous flowers present

b. *Calyx:*

4. Calyx-tube length, from base of mid-ventral tooth to base of calyx-tube
5. Calyx-tube width, across base of calyx-teeth of opened-out calyx
6. Midventral calyx-tooth length, from base to apex along mid-vein
7. Midventral calyx-tooth width, across base

- c. *Standard petal:*
8. Petal length, from base of claw to apex of limb along mid-line
 9. Petal-limb length, from apex of limb to its junction with claw along mid-line
 10. Petal-limb width, across widest point
 11. Petal-claw length, from base to its junction with limb
 12. Petal-claw apical width, at its junction with limb
 13. Petal-claw greatest width, at widest point
 14. Petal-notch depth, from tip of petal-lobes to base of notch
 15. Optical density at 530nm of pigment from 1g tissue in 5ml 1% methanolic HCl
- d. *Lateral petals:*
16. Petal length, from base of longer claw to apex of limb
 17. Petal-limb length, from apex of limb to its junction with claws
 18. Petal-limb width, across widest point
 19. Long petal-claw length, from base to its junction with limb
 20. Short petal-claw length, from base to its junction with limb
 21. Optical density at 530nm of pigment from 1g tissue in 5ml 1% methanolic HCl
- e. *Keel:*
22. Keel-pouch length, along greatest length parallel to claws
 23. Keel pouch depth, from dorsal opening to ventral suture
 24. Keel-claw length, from base to junction with pouch
 25. Keel-pouch pigmentation extent, from dorsal opening to further edge of dark pigmentation
- f. *Androecium:*
26. Stamen-tube length, along mid-ventral line
 27. Stamen-tube width, across widest point when opened out
 28. Free filament length, from its junction with stamen-tube to its junction with anther
- g. *Gynoecium:*
29. Ovary length, from base to its junction with style
 30. Ovary width, across widest point
 31. Style length, from its junction with ovary to base of style
- h. *Pod:*
32. Pod length, from its junction with pedicel to base of beak
 33. Pod depth, from dorsal to ventral suture
 34. Pod colour, as five categories: yellow; yellow-brown; brown; brown-black; black
 35. Seed conspicuousness, as smooth or moniliform pods
 36. Number of seeds per pod
 37. Pod pubescence, as glabrous or pilose
- i. *Seeds:*
38. Seed length, across widest point parallel to hilum
 39. Seed depth, across widest point from dorsal (hilum) to ventral side
 40. Seed width, across widest point at right angles to both 38 and 39
 41. Testa colour, as five categories: white; yellow; green; brown; black
 42. Testa mottling, as mottled or unmottled
 43. Testa texture, as smooth or tuberculate
- j. *Leaves:*
44. Leaf length, from base of petiole to point of attachment of apical leaflets
 45. Leaflet number
 46. Leaflet length, from base of apex along midrib, including mucro if present
 47. Leaflet width, across widest point
 48. Leaflet-apex shape, as five categories: acute; obtuse; truncate; truncate-emarginate; emarginate (Fig. 1)
 49. Stipule-tooth number, as mean number of primary teeth per stipule
 50. Tendril type, as short and simple or long and branched.

Of the various ratios derived from these primary characters only the heterophylly index, designed to measure the difference in leaf-shape between leaflets on upper and lower leaves, requires further explanation. The heterophylly index is defined as the ratio of average leaflet ratio of the leaf on the eighth node/average leaflet ratio of the leaf on the first node of the first lateral shoot, where average leaflet ratio is the ratio of average leaflet length/average leaflet width.

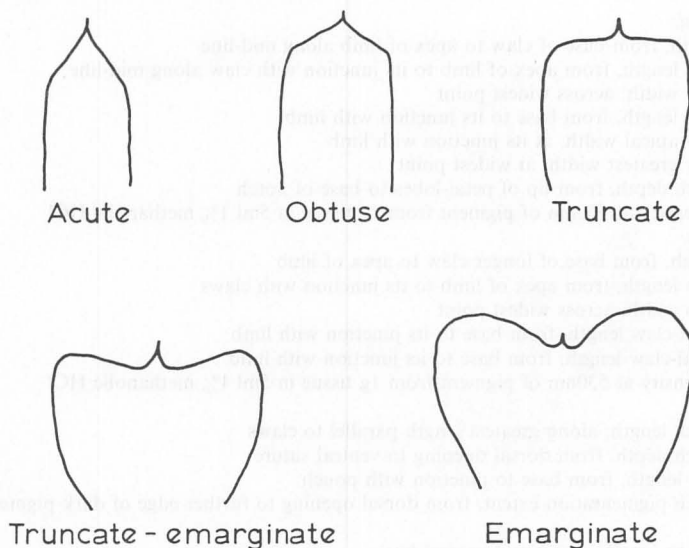


FIGURE 1. Terms used to describe leaflet-apex shapes

RESULTS

MORPHOLOGICAL CHARACTERS

As expected, no single character, either primary or derived, affords complete separation of the six taxa defined in the Introduction.

The quantitative characters fall into two main categories, with continuous and discontinuous distributions. In the former case the histograms obtained mostly show normal or near-normal distributions (Fig. 2), although sometimes slightly skewed, but a few show evidence of multimodal curves (e.g. flower length, Fig. 3). Some of these probably indicate artificial clustering, caused by the rounding up and down of figures, but others are the results of separate curves, with different modes from the various taxa, superimposed on each other. These separate, unimodal curves, however, overlap greatly and such characters are not alone reliable for delimiting taxa, despite the fact that they have been much used by previous authors. In fact they merely serve to illustrate an increase in size of most vegetative and reproductive parts across the aggregate, from *V. lathyroides* at the lower end of the scale to *V. sativa* at the upper.

The only quantitative characters showing truly discontinuous distributions are two ratios: optical density of lateral petals/optical density of standard petal (characters 21/15) (Fig. 4), and heterophylly index (Fig. 5). A low optical density ratio (1/8 to 1/13) indicates a conspicuous difference between the pigmentation of the lateral (dark) and standard (light) petals, while a high one (1/1 to 1/4) indicates little difference. A high heterophylly index (4—5.5) represents a plant with relatively broad leaflets on lower leaves and narrow leaflets on upper (flowering region) leaves, and a low index (0.5—2.5) represents a plant with relatively little change in leaflet shape. Because of the disjunction of both of these characters, each separating the aggregate into two groups, they can be equally expressed qualitatively as concolorous and bicolorous flowers and as isophyllous or heterophyllous stems, although we do not claim that with wider samples than ours intermediates would not be found in both characters.

Many quantitative characters, especially various floral dimensions and seed measurements, are strongly correlated. Such straight-line relationships illustrate the fairly constant shape of these organs irrespective of absolute size or of the segregate, and are particularly well-marked in characters of the gynoecium, androecium and keel (Fig. 6), probably due to the importance of maintaining the critical floral dimensions needed in the floral biology of the aggregate. They are therefore of little taxonomic use.

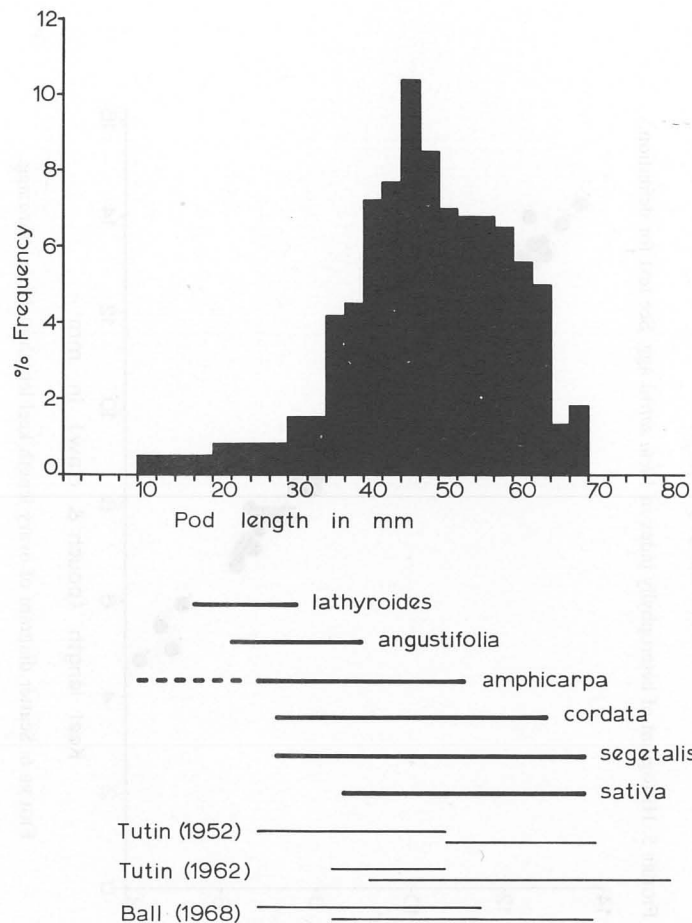


FIGURE 2. Histogram of pod lengths of *Vicia sativa* agg. The thick lines below the histogram indicate ranges in our material exhibited by each of the six segregates (exceptional ranges in broken lines) as delimited by Mettin & Hanelt (1964) except that we have for the purpose included all strains producing cleistogamous flowers under '*V. amphicarpa*'. The thin lines below these represent the ranges of *V. angustifolia* (left) and *V. sativa* (right) given in three representative Floras.

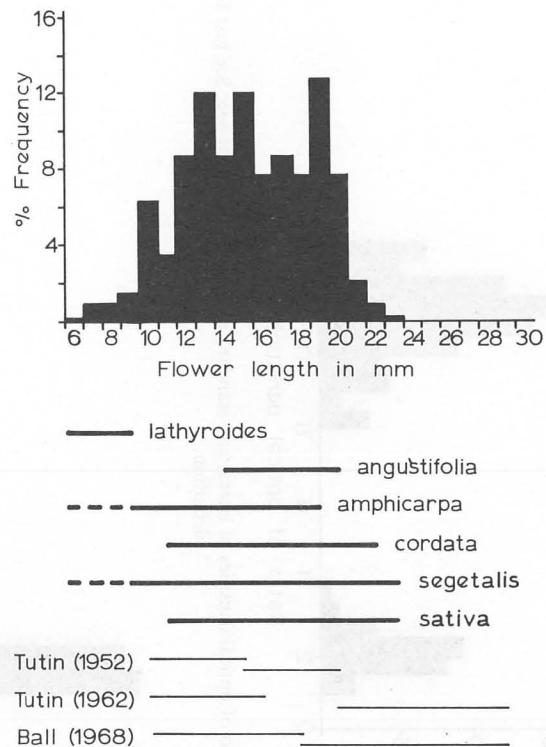


FIGURE 3. Histogram of flower lengths of *Vicia sativa* agg. Thick and thin lines below the histogram as in Figure 2.

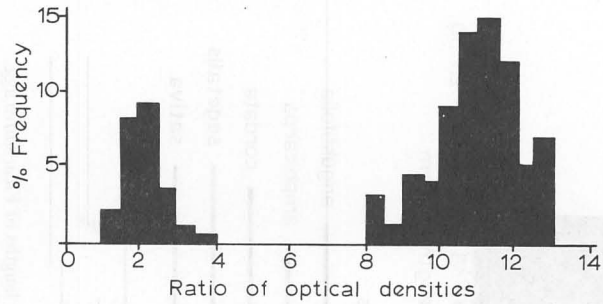


FIGURE 4. Histogram of ratio of optical densities of lateral and standard petals in *Vicia sativa* agg. See text for definition.

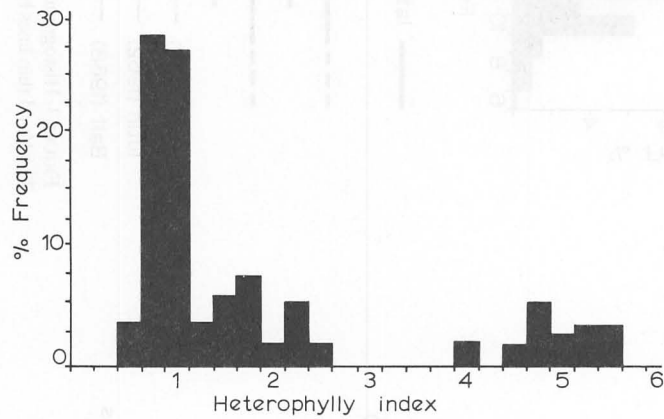


FIGURE 5. Histogram of heterophylly index in *Vicia sativa* agg. See text for definition.

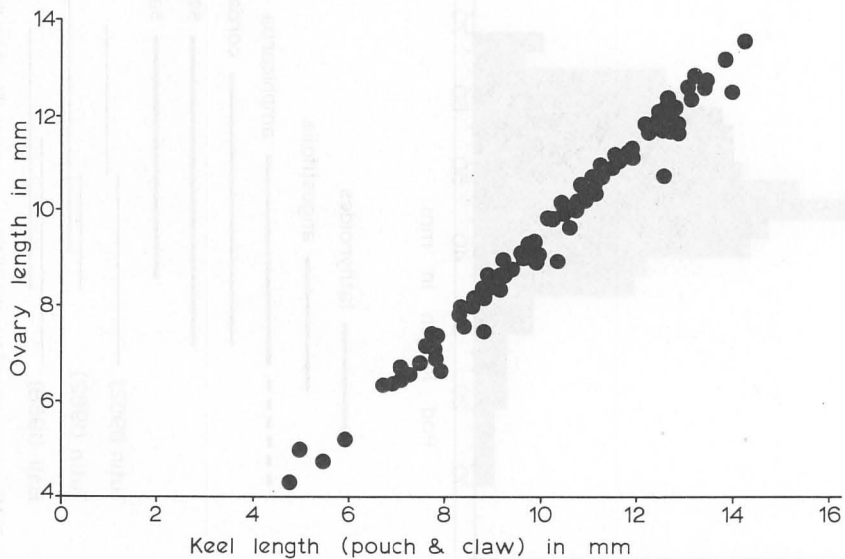
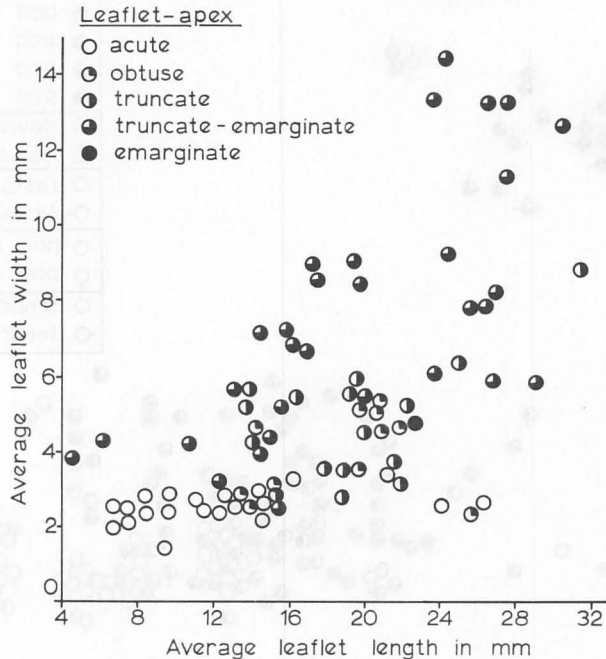


FIGURE 6. Scatter diagram of ovary length/keel length in *Vicia sativa* agg.

FIGURE 7. Scatter diagram of leaflet width/leaflet length in *Vicia sativa* agg.

On the other hand, most pod and leaf dimensions are rather poorly correlated, indicating that leaflets (Fig. 7) and pods vary greatly in shape. These variations are not closely correlated with the characters used to define the segregates, and are thus no more useful for delimiting them than are the absolute dimensions.

Certain characters are, however, correlated with the two discontinuous variables (heterophylly index and optical density ratio) and serve to further discriminate between separate groups of plants. Plants with a high heterophylly index have mostly smaller pods (Fig. 8), seeds and leaves and fewer stipule-teeth than plants with a low heterophylly index. Furthermore, whereas isophyllous plants exhibit a wide range of flower length, strongly heterophyllous plants fall into two groups with respect to this character: one with flowers 6–9mm and one with flowers 14–19mm long (Fig. 9). Fig. 9 also shows that strongly heterophyllous plants possess concolorous petals, while isophyllous plants possess bicolorous ones. The other floral character which has been used by several previous workers in the aggregate, ratio of calyx-tooth length/calyx-tube length, is not in itself a very useful discriminant (Fig. 10) and is not very well correlated with other characters. For example, although plants with a high heterophylly index all have calyx-teeth/calyx-tube ratios equal to or less than 1.0 (100 in Fig. 11), plants with a low heterophylly index may have ratios well below or well above 1.0 (Fig. 11). The calyx-teeth/calyx-tube ratio is also not well correlated with any of the important qualitative characters such as smooth or moniliform pods.

Many of the qualitative characters, both those systematically scored and many more not so, exhibit a reticulate-type variation, obeying Vavilov's (1951) Law of Homologous Series. Thus they are found in almost infinite combination with other such characters, and show extensive parallels between related taxa, so that they are of very little value in orthodox taxonomy. Characters of this type are testa colour, patterns of testa mottling, albinism, pubescence, and presence or absence of a black spot on the stipules.

A number of qualitative characters are, however, fairly closely correlated with each other and with various quantitative characters. Plants with tuberculate seeds mainly have small, dark, smooth pods; small, concolorous flowers; a high heterophylly index; and simple tendrils. The rest of the aggregate

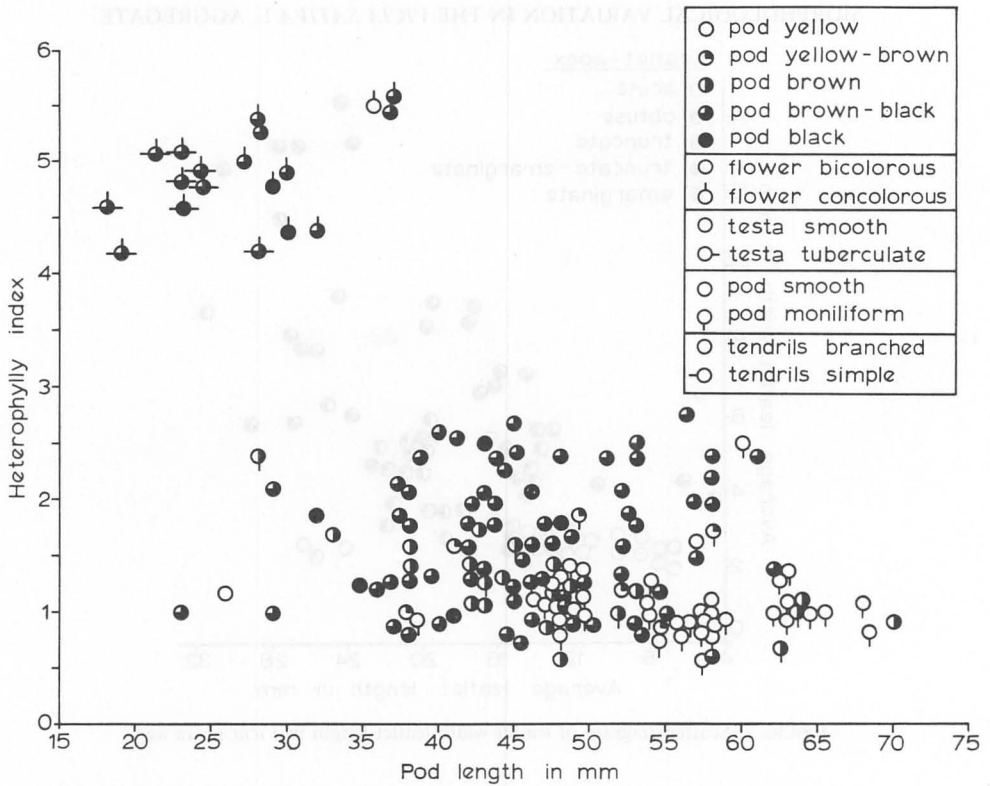


FIGURE 8. Scatter diagram of heterophylly index/pod length in *Vicia sativa* agg.

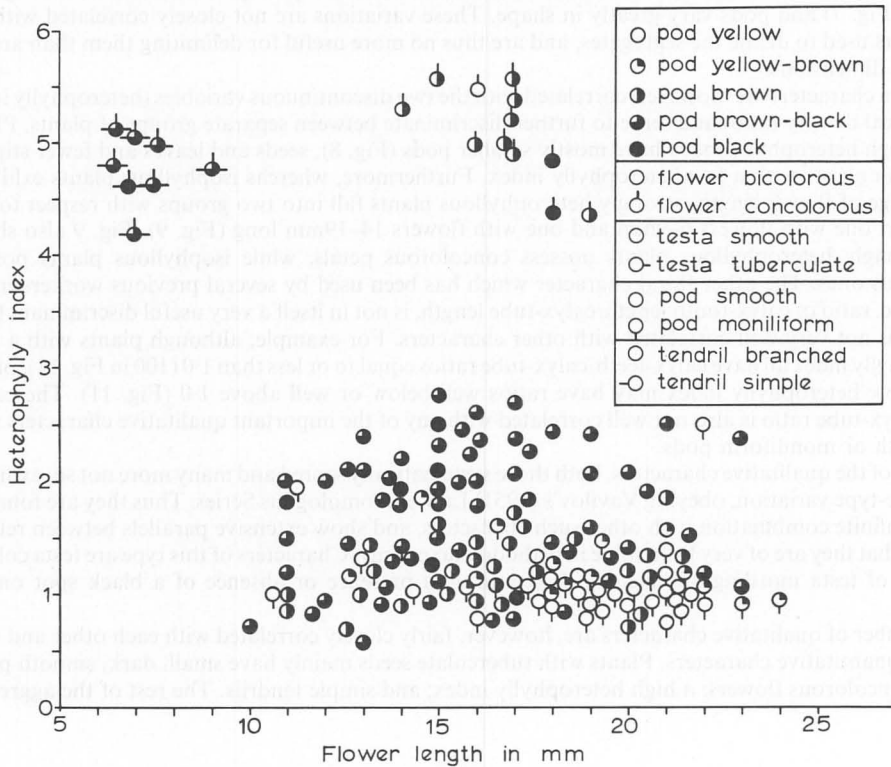


FIGURE 9. Scatter diagram of heterophylly index/flower length in *Vicia sativa* agg.

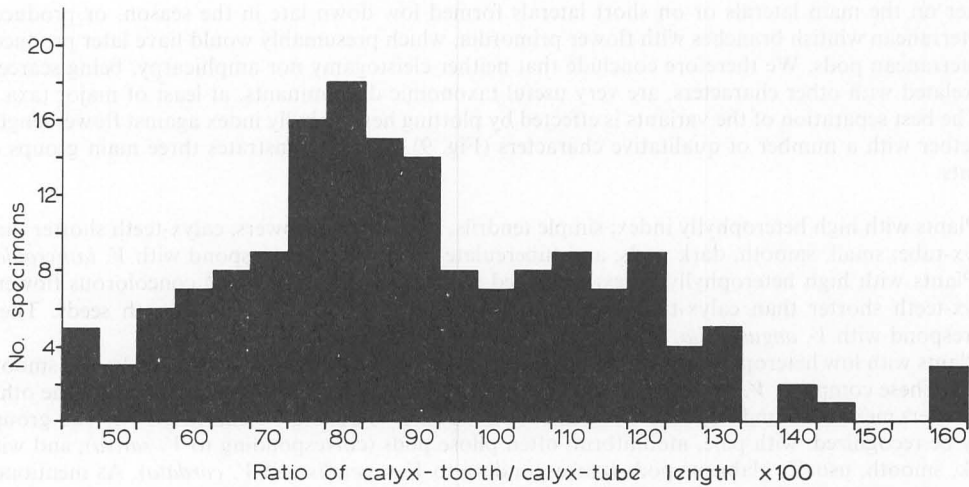


FIGURE 10. Histogram of ratio ($\times 100$) of calyx-tooth length to calyx-tube length in *Vicia sativa* agg.

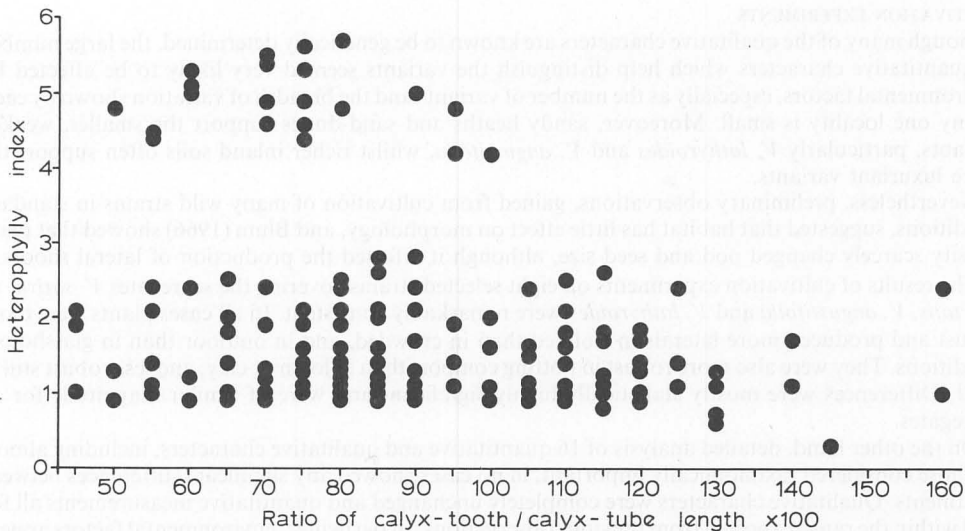


FIGURE 11. Scatter diagram of heterophylly index/ratio ($\times 100$) of calyx-tooth length to calyx-tube length in *Vicia sativa* agg.

have smooth seeds and (usually) branched tendrils. Pods which are moniliform are usually also pale-coloured and pilose; whilst those which are smooth are usually glabrous and dark-coloured, although dark, moniliform pods and pale, smooth pods do occur. The shape of the leaflet apex is to some extent correlated with leaflet width, acute and obtuse apices being confined to narrow leaflets, but emarginate apices are found on very narrow as well as very broad leaflets, and leaflet apex shapes are not well correlated with the characters usually used to separate the segregates.

Cleistogamous underground flowers, supposed to be indicative of *V. amphicarpa*, occur on only one of the living strains studied (from Turkey). On this plant the aerial flowers are also small and cleistogamous, which is not the case in most plants of *V. amphicarpa* described in the literature. Other strains, with smooth or moniliform and pale or dark pods, with bicolorous or concolorous, large or small flowers, and with isophyllous or heterophyllous stems, produced aerial cleistogamous flowers,

either on the main laterals or on short laterals formed low down late in the season, or produced subterranean whitish branches with flower primordia, which presumably would have later produced subterranean pods. We therefore conclude that neither cleistogamy nor amphicarpy, being scarcely correlated with other characters, are very useful taxonomic discriminants, at least of major taxa.

The best separation of the variants is effected by plotting heterophylly index against flower length, together with a number of qualitative characters (Fig. 9). This demonstrates three main groups of plants:

1. Plants with high heterophylly index; simple tendrils; concolorous flowers; calyx-teeth shorter than calyx-tube; small, smooth, dark pods; and tuberculate seeds. These correspond with *V. lathyroides*.
2. Plants with high heterophylly index; branched tendrils; larger (14–19mm) concolorous flowers; calyx-teeth shorter than calyx-tube; rather small, smooth, dark pods; and smooth seeds. These correspond with *V. angustifolia*.
3. Plants with low heterophylly index; branched tendrils; bicolorous flowers; larger pods; and smooth seeds. These comprise: *V. sativa*, *V. segetalis*, *V. cordata* and *V. amphicarpa*. These vary in the other characters mentioned under groups 1 and 2, but on the basis of qualitative characters two sub-groups may be recognized: with pale, moniliform, often pilose pods (corresponding to *V. sativa*); and with dark, smooth, usually glabrous pods (corresponding to *V. segetalis* and *V. cordata*). As mentioned above, *V. amphicarpa*, as usually defined (on the basis of amphicarpy), cannot be accommodated in this system of grouping.

CULTIVATION EXPERIMENTS

Although many of the qualitative characters are known to be genetically determined, the large number of quantitative characters which help distinguish the variants seemed very likely to be affected by environmental factors, especially as the number of variants and the breadth of variation shown by each in any one locality is small. Moreover, sandy heaths and sand-dunes support the smaller, weaker variants, particularly *V. lathyroides* and *V. angustifolia*, whilst richer inland soils often support the more luxuriant variants.

Nevertheless, preliminary observations, gained from cultivation of many wild strains in standard conditions, suggested that habitat has little effect on morphology, and Blum (1966) showed that plant density scarcely changed pod and seed size, although it affected the production of lateral shoots.

The results of cultivation experiments on eight selected strains covering the segregates *V. sativa*, *V. segetalis*, *V. angustifolia* and *V. lathyroides* were remarkably consistent. In all cases plants were more robust and produced more laterals in isolated than in crowded, and in outdoor than in glasshouse, conditions. They were also more robust in potting compost than in loam or clay, and less robust still in sand. Differences were mostly statistically highly significant and were of similar magnitude for all segregates.

On the other hand, detailed analysis of 16 quantitative and qualitative characters, including almost all those considered taxonomically important, in no cases showed any significant differences between treatments. Qualitative characters were completely unchanged and quantitative measurements all fell well within the range expected from previous observations. In particular, environmental factors appear to have negligible or no effect on flower, pod and leaf measurements; heterophylly index; flower, seed and pod colour; seed texture and conspicuousness in pod; and tendril branching.

CONCLUSIONS AND DISCUSSION

The cultivation experiments show that the complex pattern of variation found in *V. sativa* agg. is not the result of phenotypic responses to different habitats but is genetically determined.

The quantitative characters mostly vary in such a way that the four British segregates, *V. lathyroides*, *V. angustifolia*, *V. segetalis* and *V. sativa*, differ by increasing size of most of their parts (in the order of taxa given). However, there is a wide measure of overlap so that these characters are not alone sufficient for distinguishing the segregates.

In particular, flower length and pod length have been much used in the past as discriminants. Figs. 2 and 3, besides providing a breakdown of the ranges of variation shown in our material by the individual

segregates, also illustrate, by reference to three selected treatments, the very variable interpretation which has been placed on these characters by past workers. It should be noted that, in these selected treatments, *V. segetalis* was nomenclaturally contained in *V. angustifolia*, but that a proportion of *V. segetalis* plants was probably included under *V. sativa*. Flower length alone may be useful in distinguishing *V. lathyroides* from the other taxa, except that cleistogamous, late-season flowers of the latter frequently fall into the size range of normal *V. lathyroides* flowers. In general, vegetative characters, particularly absolute measurements of leaves and the shape of the leaflet apex, are of little taxonomic value.

Two quantitative characters which appear to be good discriminants, heterophylly index and colour difference in standard and lateral petals, may for convenience be scored qualitatively, as explained previously. These, and certain other qualitative characters, notably seed conspicuousness, pod colour and seed texture, are the best diagnostic characters in the aggregate and can be used to separate the four segregates. It is arguable that this effects a very artificial separation, in that a few discontinuous characters have been carefully chosen from a much greater number of continuous variables, but it is the taxonomist's aim to search for discontinuities and, where they are found, express them in taxonomic terms by naming the discrete units so separated.

V. cordata is usually separated from *V. angustifolia* and *V. segetalis* on the basis of the calyx-teeth/calyx-tube ratio and chromosome number, *V. cordata* having $2n = 10$ and a ratio over 1.0 (100 in Figs. 10 & 11), the latter two having $2n = 12$ and a ratio under 1.0. However, in a previous paper, we (Hollings & Stace 1974) failed to find precise correlation between these two characters, and, moreover, plants of *V. sativa* also have a calyx-tooth/calyx-tube ratio varying from below to above 1.0. Thus on morphological features alone *V. cordata* is scarcely worthy of recognition. On the basis of our observations, plants corresponding with *V. cordata* can be quite easily accommodated in *V. segetalis*, which agrees well with the preliminary conclusion of Plitmann (1967), but not with his later decisions.

V. amphicarpa, delimited simply by the presence of subterranean pods originating from cleistogamous flowers, is otherwise very variable both in morphology and in karyotype (Hollings & Stace 1974). The recognition by Rouy (1899) of two varieties, var. *pseudosativa* and var. *pseudoangustifolia* (amphicarpous variants of *V. sativa*-like and *V. angustifolia*-like plants respectively) reinforces the opinion that '*V. amphicarpa*' as normally understood is not a taxon but a series of variants of other taxa possessing only amphicarpity in common.

The four segregates revealed by our studies may be distinguished by the following diagnoses:

V. lathyroides: Strongly heterophyllous; tendrils simple; flowers 6–9 mm, concolorous (usually dull purple); pods 18–30 mm, brown to black, smooth, glabrous; seeds tuberculate.

V. angustifolia: Strongly heterophyllous; tendrils branched; flowers 14–19 mm, concolorous (usually bright pink); pods 23–38 mm, brown to black, smooth, glabrous; seeds smooth.

V. segetalis: More or less isophyllous; tendrils branched; flowers 9–26 mm, bicolorous (with standard petals paler than lateral petals); pods 28–70 mm, brown to black, smooth, usually glabrous; seeds smooth.

V. sativa: More or less isophyllous; tendrils branched; flowers 11–26 mm, bicolorous (with standard petals paler than lateral petals); pods 36–70 mm, yellowish to brown, moniliform, often pilose; seeds smooth.

As stated in the Introduction, it is likely that only the first two of these are native in the British Isles.

On the basis of morphological characters there is not a strong argument for separating *V. lathyroides* from the rest of this aggregate. However, there are differences in the suspected pattern of karyotype evolution of *V. lathyroides* from that of the rest (Hollings & Stace 1974), and there is a strong breeding barrier between it and the other taxa (Hollings & Stace, unpublished).

V. angustifolia, *V. segetalis* and *V. sativa* are not genetically isolated, and their rather complex pattern of variation is almost certainly the result of extensive inbreeding and, in this country at least, of the cultivation and subsequent escape of many non-native variants. These segregates (as well as others such as *V. macrocarpa*, *V. pilosa* and *V. incisa*) therefore represent groups of variants representing modes in a spectrum of largely continuous variation. Although they are usually separable by the characters given above, plants of intermediate status, or with one or two anomalous characters, are not

uncommon. Indeed they are to be expected from an application of the Law of Homologous Series, which proves to be a useful concept in this group of plants and applies to karyotype variation as well as to morphological characters. The most appropriate rank for the main segregates will be discussed in a later paper dealing with breeding and hybridisation data.

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