# STUDIES ON *ALCHEMILLA FILICAULIS* BUS., *SENSU LATO*, AND *A. MINIMA* WALTERS.

## INTRODUCTION, AND

## I. MORPHOLOGICAL VARIATION IN *A. FILICAULIS.*, *SENSU LATO*

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### Abstract

*Alchemilla filicaulis* Bus., *A. vestita* (Bus.) Raunk. and *A. minima* Walters form a critical group within the *A. vulgaris* L. aggregate. The results of a biosystematic study of variation in morphology, habit and cytology are presented in a series of papers. These indicate that *A. vestita* should be treated as a subspecies of *A. filicaulis* but *A. minima* should be maintained as a species.

In paper I morphology and habit are considered. Density of the indumentum of the flower-stem and leaves is genetically determined but greater variation occurs in the more hairy plants, subsp. *vestita*, than in the less hairy subsp. *filicaulis*. Plants of intermediate hairiness may be genotypes or environmentally-induced variants. Colour of the stipules and leaf shape are genetically determined but can be modified by environmental factors. Lowland, meadow and rock-ledge plants are tall with few shoots; a dwarf much branched genodeme occurs in close-grazed upland grassland. Such ecogenodemes are analogous to the ecotypes of sexual species and important in the evolution of apomicts.

### Introduction

In recent years a number of papers have been published on the taxonomy and distribution of the British species of the apomictic *Alchemilla vulgaris* L. aggregate by Walters (1949, 1952), Bradshaw (1957), Bradshaw & Walters (1961) and Bradshaw (1963). In Britain there are twelve named taxa and a critical group temporarily referred to as the Lawers '*acutidens*' (see Clapham, Tutin, & Warburg, 1962). Several species of the *Alchemilla vulgaris* aggregate were shown to be obligate apomicts by Strasburger (1905) and Murbeck (1901). All the British taxa are thought to be obligate apomicts. Walters' paper (1949) illuminated some of the difficulties associated with the group formed by *A. filicaulis* Bus., *A. vestita* (Bus.) Raunk. and *A. minima* Walters. Of the first two, Walters wrote 'The morphological difference is very slight – the only " good " character appears to be the hairiness of the inflorescence – nevertheless, the two can with rare exceptions be satisfactorily separated in the field, and exhibit somewhat different geographical ranges.' Exactly how ' good ' needed to be ascertained, as field collections made between 1951 and 1954 contained several plants of intermediate hairiness not readily assignable to either taxon. Furthermore dwarf plants of these two taxa from closely grazed habitats are very similar to *A. minima*. In the field, the latter proved not so easy to separate from the former as suggested by Walters (1949), so that further study of the dwarf populations was needed to ascertain the proportions of genotypic and environmentally induced dwarfs.

The present work is based on a biosystematic study of these taxa with particular reference to variation in morphology, habit and cytology. As a result of these investigations certain changes of status are recommended.

The new designations and reasons for the changes are briefly given here in order that these names can be used throughout the papers in which fuller explanations will appear.

*Watsonia* **5** (5), 1963.

Satisfactory separation of *A. filicaulis* and *A. vestita* by morphological characteristics is not possible because of intermediates. The two taxa do exhibit somewhat different ecological and geographical distributions; and it is accordingly proposed that they be ranked as subspecies of *A. filicaulis* Bus., viz :

(1) subsp. *filicaulis*

(2) subsp. *vestita* (Bus.) M. E. Bradshaw stat. nov. (*A. filicaulis* Bus. forma *vestita* Bus., Bull. Herb. Boiss. **1**, app. 2, 23 (1893).

*A. minima* Walters is retained at specific rank.*

## I. MORPHOLOGICAL VARIATION IN *A. FILICAULIS* BUS., *SENSU LATO*

*A. filicaulis*, *sensu stricto*, was first described by Buser (1893). From it he separated ' Une f. *vestita*.' As his description is rather long and not easily accessible the following shortened translation is given :

Plant small to medium sized, rhizome medium thick. Lower part of stem and petioles usually with spreading hairs; upper part of stem and pedicels glabrous. Leaves variously clothed with spreading hairs often only on the veins below and folds above. Earliest petioles and leaves often ± glabrous, later petioles with spreading hairs. Base of the petioles and stipules usually wine-red. Leaves medium (3–9 cm wide, 2·5–8 cm long), ± reniform in outline, with wide basal sinus, somewhat blue-green, paler below, lobes 7 or incompletely 9, round or ± triangular, toothed all round; teeth (9–) 11–13 (–15), subacute, somewhat connivent, all ± equal except the small terminal tooth. Stems (5–) 20–30 (–40) cm, ascending, slender. Inflorescence medium, flowers large, 3–4 mm, clusters not very dense.

Of the forma *vestita* Buser continued ' (la plante entière plus ou moins velue) a été constaté en outre dans les Cevennes, en Normandie, au Jura (Reculet). Dans ces localités la forme semble se présenter comme une race indépendante, à l'exclusion du type, tandis qu'au Salève on ne la rencontre qu'en individus égrenés et rares parmi la forme normale fréquente.' Raunkiaer (1906) raised this forma to specific rank, no doubt impressed by its frequency in Denmark.

### 1. VARIATION IN HAIRINESS

### (*a*) *The flowering stem*

It has already been indicated that the hair cover on plants of *A. filicaulis*, *sensu lato*, varies from dense to slightly hairy. A measure of this hairiness is most conveniently made on the flowering stem, where the density of the indumentum usually decreases from the base upwards. This change, however, may be slight, in which case the plant will be either densely hairy throughout, or with all but the basal internodes glabrous. The hairiness of the flower-stems was measured by direct visual comparison of the density of the indumentum on the internodes with a set of six standards. This method was of sufficient accuracy, and easier to apply than an analysis based on the number of hairs per unit length of stem, which would have wasted too much time obtaining a degree of exactitude which was not necessary.

### (*i*) *Method*

The flower-stems were classified in the following way. Standards were set up to provide six *classes* of degree of hairiness of the stem in Fig. 1.

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* In his latest paper, Rothmaler (1962) treats these three taxa as varieties of *A. filicaulis*.

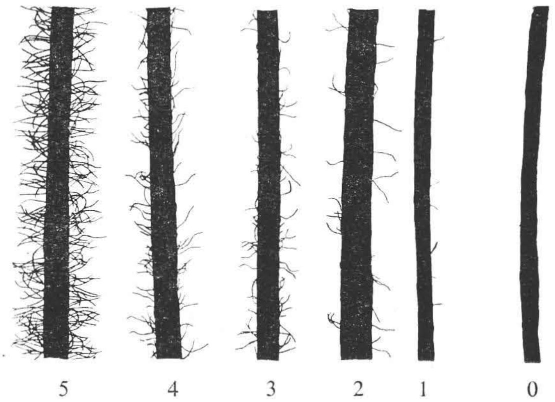

Fig. 1. Classes of hair density on internodes of the flower-stem. Drawing based on a photograph (× 4).

Internodes II, IV, VI and VIII were thus scored for hairiness according to this scale, other internodes being scored where necessary. Since some flower-stems have more internodes than others comparison was made over the lower six internodes only. The *grade* of hairiness of the flower-stem corresponds to the decrease in hairiness of the internodes of the flower-stem, and since internode II is usually densely hairy, it was assumed to be class 5 in all cases. Therefore, the *grade* for each flower-stem was calculated as the difference between the class of the VIth internode and class 5. In Fig. 2, in grade 5 the VIth internode is glabrous, the difference between this class (0) and the most hairy state (5) is 5; in grade 0, all internodes are class 5, so that there is no difference between the class of internode VI and the most hairy state (5). This gives seven grades of hairiness of the flower-stem (0–6). It should be noted that in grades 0–4 the internodes above the sixth (VI) may be hairy; in grade 6, internode V as well as VI is glabrous, internodes below the fifth (V) may be glabrous; also, in some cases the most hairy internode may be less hairy than class 5.

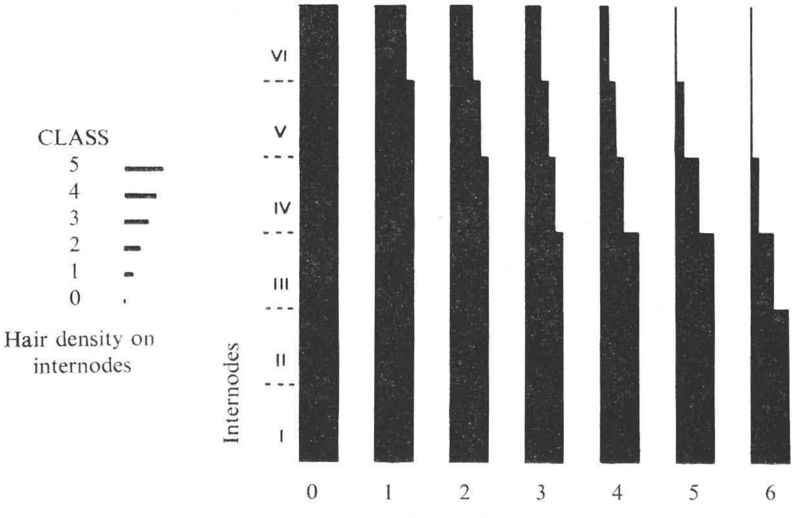

Fig. 2. Diagrammatic representation of the seven grades of hairiness of the flower-stems.

### (*ii*) *Variation in the grade of hairiness of the flower-stem of individual plants* (*i.e. variation within a plant*)

Preliminary studies showed that a slight variation may occur in the grade of hairiness of two or more flower-stems on the same plant. For example, the grade of hairiness may be 0 and 1, or 3, 4 and 3, in both plants the variation is one grade; those plants with 0, 1, 2 or 1, 1, 3 show a variation of 2 grades, etc. Analyses of 353 plants are shown in Fig. 3. In the whole sample, 83% showed either no variation or a difference of only one grade between the two or three flower-stems which were scored. When the more glabrous (Grade 6) and more hairy (Grade 0–3) plants were plotted separately, it was clear that most variation occurred in the more hairy plants.

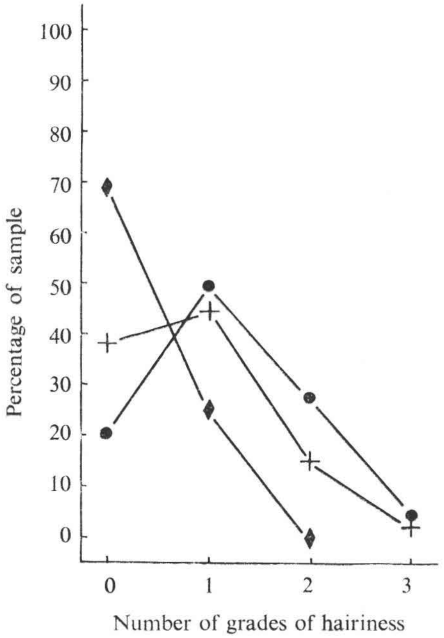

Fig. 3. Variation in grade of hairiness of two or more flower-stems on the same plant. Crosses, *A. filicaulis, sensu lato* (353 plants); dots, grades 0–3 (163 plants); diamonds, grade 6 (72 plants).

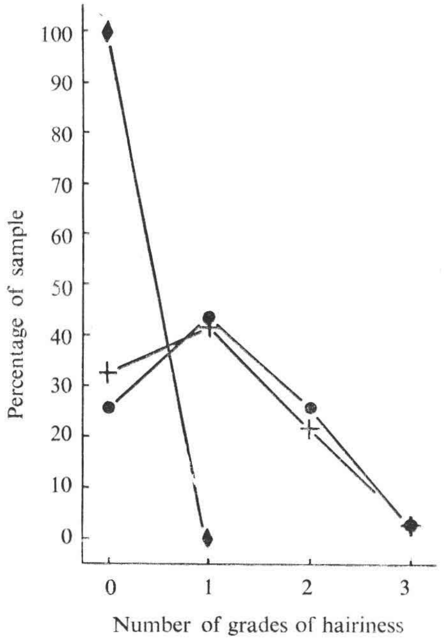

Fig. 4. Variation in grade of hairiness of the flower-stems on the same plant from year to year. Crosses, *A. filicaulis, sensu lato* (102 plants); dots, grades 0–3 (82 plants); diamonds, grade 6 (8 plants).

### (*iii*) *Variation from year to year*

This analysis was made on 102 plants grown in the garden for three (in some cases two) years. In most cases it is based on the mean of three flower-stems per plant in the final year, and one flower-stem per plant in the other year(s). (Fig. 4).

Whilst 74% show variation of no more than 1 grade, 26% have greater variation; this is somewhat higher than was found within the plants and no doubt is in part due to the analysis being based on a single flower-stem from each plant in the earlier years, thus giving an over-estimation of the difference.

In both of these analyses the more hairy plants, grades 0–3, show greater variability than the less hairy grade 6.

From the above observations on plants grown under similar conditions in the garden, it is clear that there is some fluctuation in the density of the indumentum between the several flower-stems of each plant and on the same plant from year to year. The less hairy plants are least variable, but even in the more variable hairy plants the oscillation is over only a portion of the total range of hairiness. Thus this method of analysis does provide a means of discriminating between the various degrees of hairiness of the flower-stem found in *A. filicaulis, sensu lato.*

### (*iv*) *Variation within families*

Offspring of plants of different hair density were raised from seed. As far as possible, 20 plants of each family were grown in boxes of John Innes Compost No. 1 containing 10 plants each. Three mature flower-stems were collected from each plant and scored for hairiness by the method described. Results are given below (Table 1).

TABLE 1

Variation in hairiness of the flower-stems within families. (grade mean, usually of three flower-stems per plant)

| *Code number* | *Hairiness grade* | | *Frequency of each grade of hairiness in each family* | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Parent* | *Family* | | | | | | | |
| | | | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
| 4/38/371 | 0 | 0·65 | 7 | 13 | | | | | |
| 4/28/326 | 2 | 0·8 | 4 | 18 | 1 | | | | |
| 4/11/116 | 2 | 1·1 | 3 | 11 | 6 | | | | |
| 4/9/101 | 2 | 1·2 | 2 | 13 | 44 | | | | |
| 4/3/45 | 2 | 1·4 | 1 | 10 | 7 | 1 | | | |
| 4/30/318 | 3 | 1·7 | 1 | 7 | 10 | 2 | | | |
| 4/39/269 | 1 | 1·85 | | 5 | 13 | 2 | | | |
| H | 1 | 2·0 | | 5 | 8 | 6 | | | |
| 4/30/316 | 3 | 2·25 | | 2 | 11 | 7 | | | |
| 4/39/272 | 5 | 4·8 | | | | | 4 | 16 | |
| 4/8/84 | 6 | 5·8 | | | | | | 4 | 16 |
| 4/15/216 | 6 | 5·9 | | | | | | 2 | 37 |
| 4/16/207 | 6 | 6·0 | | | | | | | 10 |
| Sc. 8 | 6 | 6·0 | | | | | | | 13 |
| 4/10/109 | 6 | 6·0 | | | | | | | 5 |
| 52/1 | | 1·0 | 5 | 11 | 4 | | | | |

In line with the earlier observations, least variation occurred in the more glabrous families with means of 5·8, 5·9 and 4·8 (families 4/8/84; 4/15/216 and 4/39/272). In addition three small families of 5, 10 and 13 plants respectively and means of grade 6 showed no variation. Other nearly uniform families are at the other end of the scale with means of 0·5 and 0·65 (families 4/11 and 4/38/371). The families with means between 0·8 and 2·25 were much more variable, even containing plants of three or four grades of hairiness. One would have liked more examples of families with the grade mean of 0, 4 or 5. The range of variation found in all these families is of the same order of magnitude as that found within individual members of the families; in no case does it exceed the maximum range found in individuals.

### (*v*) *Variation in hair character of parents and offspring*

In the same families, comparison was made between the hairiness of the parent (the mean over a number of years) and the variation found in the families (as above). As before the greatest similarity was found in the more glabrous families (4/8/84; 4/15/216 and 4/39/272). The one family of a grade 0 parent showed a shift of the mean towards grade 1, but other families of parental grade 0–3 are those with a wide range in the offspring. This spreads over 2–4 grades usually ranging about the mean of the parent, but rarely is the mean of the offspring the same as that of the parent.

Care must be taken when drawing conclusions from these breeding experiments because the most hairy (0) and intermediate grades (4–5) are represented by only one family each. It is clear that determination of the hairiness of the flower-stem in *A. filicaulis, sensu lato* is largely genetical. In the least hairy plants this is within quite narrow limits. Family 4/39/272 is of particular interest; this is a plant of the dubious intermediate grade. Here the hair character is maintained in the offspring with little variation and shows very well that the intermediate character is not improbably genetically determined. Results of breeding from grades (0–) 1–3 suggest that these grades should be grouped together; the method of analysis reveals an amount of variation which may be genotypic but is more probably environmental in origin. This is supported by the evidence of wide variation within single plants and the fluctuation above or below the grade of the parent.

At this stage it is convenient to correlate the grades used in classification of the flower-stem with the taxonomic treatment recommended at the beginning of this paper. Grades 0–3 may be regarded as subsp. *vestita* and grade 6 as subsp. *filicaulis;* grades 4–5 are intermediate in character.

### (*vi*) *Variation in plants grown under field and garden conditions*

The preceding observations have been made on plants grown under garden conditions. Investigations were also made on the hairiness of plants as collected in the field and after a period of cultivation in the garden for one or more years. These 30 plants gave 57% showing no variation and 33% with variation of 1 grade; the remaining 10% varied 2 or 3 grades; this suggests that on the whole variation with change of growing conditions is within the range found in individual plants. Certain rather sparsely hairy plants do require special mention; some of these with glabrous or nearly glabrous flower stems in the field produced more normal, grade 6 flower stems after cultivation. These were all plants of high altitudes and will be discussed fully after variation in hairiness of the leaf has been considered.

## (*b*) *Other parts of the flower-stem*

Variation in hair density is not limited to the main branches of the flower-stem only. On the pedicels (ultimate inflorescence branches) hairiness is of the same nature as the rest of the branches, being absent in the more glabrous grades. Hairiness of the urceole shows a similar series. Urceoles in the more hairy grades are usually also densely hairy. In other grades the density decreases, but rarely are all the urceoles on the flower-stem without hairs, though in grade 6 there may be no more than one or two hairs on a few urceoles only.

## (*c*) *The leaves*

Variation occurs in the hairiness of the petiole and of the upper and lower leaf surfaces. No detailed analysis was made on the hair density of the petiole but a series from densely hairy in the grade 0–3 plants to sparsely hairy or almost glabrous in grade 6 does occur.

More detailed work was done on the lamina of the leaf. Mature summer leaves were compared. Only in the most densely hairy plants are the hairs apparently evenly distributed over the surfaces of the leaf; in less hairy leaves decrease of hair cover is localised so that hairs persist on the folds and ends of the lobes of the upper surface and the veins and basal lobes of the lower. Such a distribution of hairs cannot be measured quantitatively, so a series of standards had to be used. These were chosen for upper and lower surfaces of the leaf as in Fig. 5.

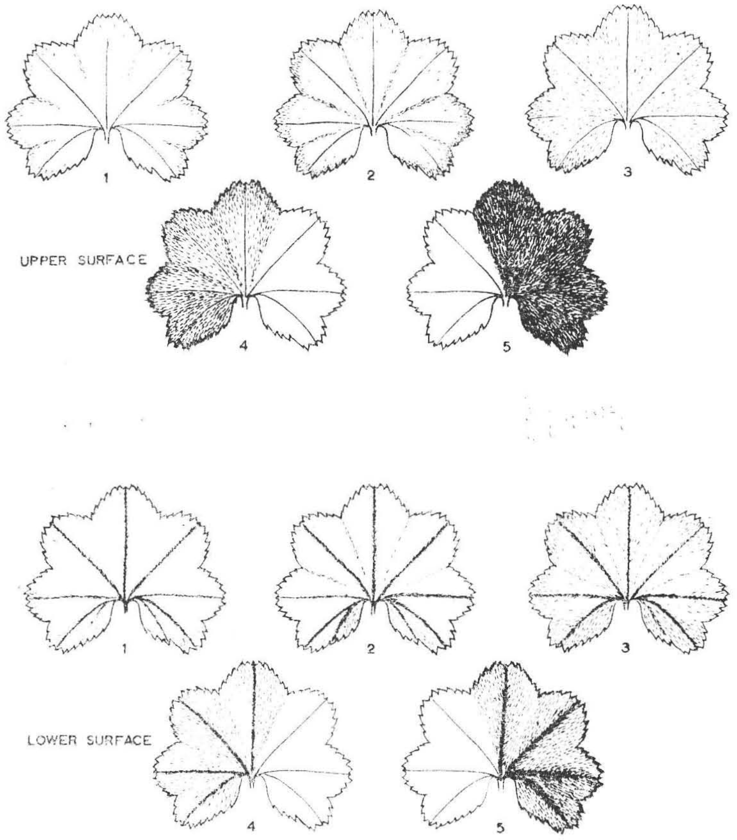

Fig. 5. Classes of hairiness of upper and lower leaf surfaces. In classes 4 and 5 hairs are shown on a portion of the leaf only.

Preliminary investigations of the hairiness of both leaf surfaces of plants of different grades of hairiness of the flower-stem showed a close correlation between the lower surface and the flower-stem grade (Table 2).

TABLE 2

Correlation of flower-stem hairiness. Mean values for class of leaf hairiness of several plants with flower-stems with the same grade of hairiness.

| *Flower-stem grade* | *Leaf* | |
|---|---|---|
| | *Lower surface* | *Upper surface* |
| 0 | 4·4 | 4·4 |
| 1 | 3·0 | 3·4 |
| 2 | 2·7 | 2·75 |
| 3 | 2·7 | 3·3 |
| 4 | 1·75 | 2·75 |
| 5 | 1·3 | 2·7 |
| 6 | 1·1 | 3·1 |

Further comparisons between flower-stem and leaf hairiness (lower surface) were made on cultivated plants. Observations on three leaves per plant showed very little variation within the plant, even in the hairy ones. Means of these supported the preliminary findings of correlation between the hairiness of the flower-stem and the leaf, e.g. in family 4/38/371 of flower-stem hairiness 0–1, leaf class was consistently 4; i.e. maximum flower-stem hairiness with near maximum leaf hairiness. In Sc. 8 and 4/15/216, both of grade 6 flower-stem, leaf hairiness is of minimum density.

Results of scoring 218 garden and field plants assessed on one flower-stem and one leaf are given in Table 3.

These results support those from the families at both ends of the series and, as with the hairiness of the flower-stem, greater variability was found in the intermediate grades.

TABLE 3

Correlation of flower-stem hairiness and hairiness of the lower surface of the leaf.

| | *Grade of hairiness of the flower-stem* | | | | | | |
|---|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
| *Class of hairiness of the lower surface of a leaf.* 1 | | | | | | 5 | 41 |
| 2 | | | 3 | 3 | 2 | 9 | 16 |
| 3 | 1 | 9 | 14 | 12 | 8 | 12 | 6 |
| 4 | 12 | 16 | 10 | 5 | 5 | 4 | |
| 5 | 6 | 13 | 4 | 2 | | | |
| Total | 19 | 38 | 31 | 22 | 15 | 30 | 63 |

Certain almost glabrous plants can now be considered. These formed a very small proportion (16) of all the plants collected in the field. In most cases the lower surfaces of the leaves were hairy only on the nerves; the flower-stems were glabrous, including all or most of the urceoles. All were very dwarfed when collected and of high montane habitats, including very wet flushes. After cultivation for 2–3 years they increased in size and all but one developed the hairs typical of the more glabrous variants of *A. filicaulis, sensu stricto*. In plant 6/28/201 the petioles and leaves became hairy as in *A. filicaulis, sensu stricto*, but the flower-stem remained glabrous. This was the only plant in which the absence of hairs appeared to be genetically determined. Details of variation in five plants are given in Table 4.

## 2. VARIATION IN LEAF SHAPE

From the beginning of these investigations it was apparent that there was considerable variation in the shape of the leaf, especially in that of the lobes; but this was difficult to measure and too variable to assess qualitatively. Only when leaves of families were available did the genotypic nature of the variation become clear.

Three mature leaves were collected from samples of twenty plants of different families. Though the general shape of the leaf in *A. filicaulis, sensu lato*, is reniform, the angle of the basal sinus does vary a little; of greater significance is the variation in the length of the lobes, most obviously in the median lobe. This may be broad and shallow or long and narrow or even with a truncate end. Leaves of five representative plants from four samples of twenty raised from different parent plants are shown in Fig. 6. The relative length of the lobe decreases in the order 4/9/101, 4/11/116, 2/1, 4/30/316. The great similarity within each family clearly shows the genotypic nature of this character. This range is shown in plants of the grade 0–3 hairiness range; from general observations it is known

TABLE 4
Hairiness of five dwarf montane plants when collected and in cultivation

| *Code no.* | *Date* | *Leaf hairiness* | | | *Flower-stem hairiness* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Petiole* | *Lamina* | | *Internodes* | | | | | | | *Urceoles* |
| | | | *lower* | *upper* | | I | II | III | IV | V | VI | |
| 6/22/172 | 1956 f | class 1 | class 1, distal 2/3 nerve | class 2 | class | 0 | 1 | 0 | 0 | 0 | | few on most |
| | 1957 g | class 2–3* | class 1, distal 2/3 nerve | class 2 | class | . | 1 | . | 0 | . | 0 | few |
| | 1958 g | — | — | — | class | 0 | 4 | 3 | 0 | . | 0 | — |
| 6/28/201 | 1956 f | class 1 | class 1, distal 2/3 nerve | class 2 | class | . | 0 | . | 0 | . | | most hairy |
| | 1957 g | class 2–3* | class 1, distal 2/3 nerve | class 2 | class | . | 0 | . | 0 | . | 0 | few on most |
| | 1958 g | — | — | — | class | 0 | 2 | 0 | 0 | 0 | 0 | — |
| | | | | | class | . | 0 | . | 0 | . | 0 | |
| | | | | | class | . | 0 | . | 0 | . | 0 | |
| 6/28/202 | 1956 f | class 1 | class 1, distal 1/2 nerve | 1/few | class | . | 0 | . | 0 | . | 0 | few on most |
| | 1957 g | class 2–4* | class 1, distal 2/3 nerve | class 2 | class | . | 1 | . | 0 | . | 0 | very few |
| | 1958 g | class 4 | class 1, distal 2/3 nerve | — | class | . | 3 | . | 2 | . | 0 | — |
| | | | | | class | . | 3 | . | 3 | . | 1 | |
| | | | | | class | . | 3 | . | 0 | . | 0 | |
| 6/28/203 | 1956 f | 0 hairs | class 1, distal 1/4 nerve | 1/few | class | . | 0 | . | 0 | . | 0 | 0 |
| | 1957 g | class 3–5* | class 1, distal 3/4 nerve | class 2 | class | . | 4 | 1 | 0 | . | 0 | few on some |
| | 1958 g | hairy | class 1, distal 3/4 nerve | — | class | . | 4 | . | 4 | . | 2 1 | — |
| | | | | | class | . | 4 | . | 2 | 1 | 0 | |
| 6/26/181 | 1956 f | class 2 | class 1, distal 3/4 nerve | class 3 | class | . | 0 | . | 0 | . | | ? 0 |
| | 1957 g | class 5 | class 2, distal 3/4 nerve | class 3 | class | . | 1 | 2 | 0 | . | 0 | few on most |

f = field, g = garden, * = 3 leaves

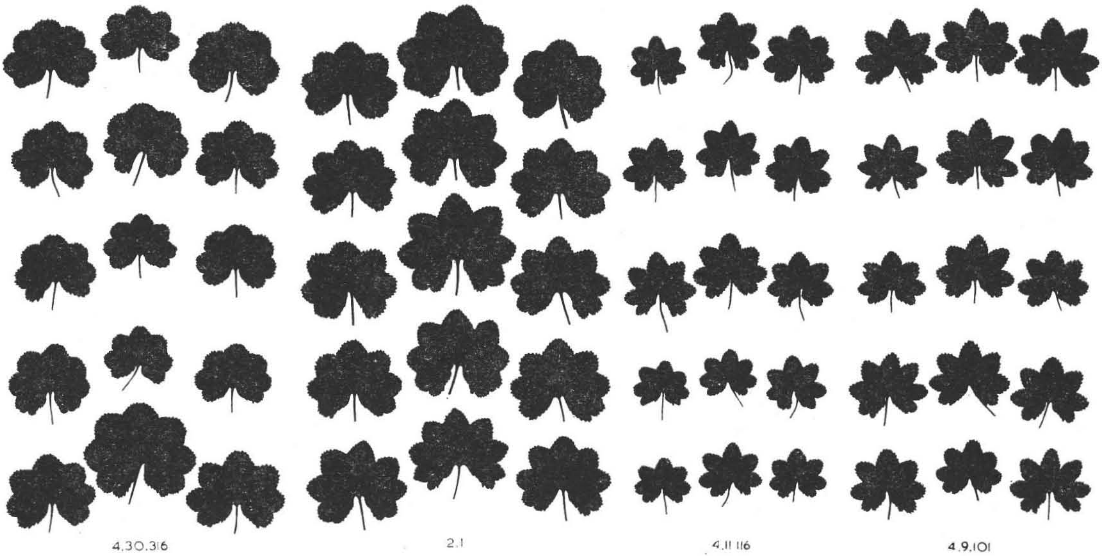

Fig. 6. Variation in leaf-lobe shape between families. Three leaves from each of five plants in each family.

that a range of leaf shapes is also found in plants of the other hair groups. It would appear that this variation is quite independent of the variation in hairiness.

A preliminary analysis of the variation in the shape of the leaf-lobe has been made. Measurements were made of the median lobe of a well grown leaf; though the ratio length/($\frac{1}{2}$ greatest breadth) makes no allowance for the degree of curvature of the sides of the lobes, it does differentiate between the long and narrow, and short and broad lobes. Analysis of *c.* 100 herbarium specimens showed that there is considerable variation in lobe shape; the values obtained were between 0·58 and 3·26 with a mean of 1·36. Although the sample was not random, it showed there is considerable variation in the lobe size throughout Britain, without local concentrations of any one size.

TABLE 5
Variation in shape of the median lobe of the leaf in several populations.

| | *Population code no.* | *No. of plants* | *Length of lobe / ½ breadth.* | |
|---|---|---|---|---|
| | | | *mean* | *s. d.* |
| | 4/39 | 6 | 0·77 | 0·11 |
| mixed | 4/44-52 | 9 | 0·9 | 0·04 |
| | 4/9-11 | 10 | 1·03 | 0·07 |
| | 4/22 | 7 | 1·1 | 0·16 |
| | 4/3 | 9 | 1·1 | 0·20 |
| | 4/8 | 9 | 1·1 | 0·21 |
| | 5/48 | 10 | 1·18 | 0·06 |
| | 5/45 | 12 | 1·2 | 0·13 |

Values for some populations of uneven size from different habitats but grown under the same garden conditions for one or two years are given in Table 5. The range of variation within the populations is usually wide (e.g. 0·7–1·7), but some populations are less variable and centre about different means : e.g. the mixed collection with 0·9 ± 0·04 and 5/48 with 1·18 ± 0·06. Whilst the first two samples (Table 5) are from long rough grass at 1300 ft and *c.* 350 ft the last two are from high altitude pasture at *c.* 2000 ft. Further investigation may show that leaf-lobe shape is associated with habitats.

## 3. VARIATION IN STIPULE COLOUR

In *A. filicaulis*, *sensu lato*, the base of the petiole is usually wine-red due to anthocyanin; the colour may extend along the stipules and usually occurs on the rhizome. Occasionally concolourous forms without the pigment are found.

Cultivation and breeding have shown that the presence or absence of anthocyanin is genetically determined. All the offspring of three concoloured plants, (60, 20, 20 plants respectively) were without the pigment. Offspring of pigmented plants were coloured but the intensity varied considerably. This variation is found in both subspecies in *A. filicaulis*, *sensu lato*. It was noticeable in wild material that the deeply coloured plants were most frequently found in long grass, whilst plants of open or grazed habitats were more variable and usually less deeply coloured. Experiments have supported these observations. Samples of seedlings from several plants were grown under the following conditions :

(a) in grass which was allowed to grow tall (meadow).
(b) in grass which was kept short with a lawn mower.
(c) open soil in the garden.
(d) boxes (see page 308).
(e) as (d), these plants were kept short (2·5 cm above soil level) by cutting throughout the summer.

Results are given in Table 6.

TABLE 6
Variation in colour of the base of the petiole

| *Code number* | *Garden plot* | | | *Boxes* | |
|---|---|---|---|---|---|
| subsp. *vestita* | a (20 pl.) | b (20 pl.) | c (20 pl.) | d (40 pl.) | e (20 pl.) |
| 4/3/45 | 3 | 2 –, 2 | 2, 2 + | 3 | 2 – — |
| 4/12/173 | 2 +, 3 | 1, 2 – | 2 –, 2 | | |
| 4/39/270 | | | | 3 (20 pl.) | 2 –, 2 |
| 4/30/318 | | | | 2, 3 | 2 –, 2 |
| 4/9/101 | | | | 2 +, 3 | 2 |
| subsp. *filicaulis* | | | | | |
| 4/15/216 | 3 | 2 – —, 2 | | 2, 3 | 2 + (10 pl.) |

a tall grass
b short grass
c open soil
d open soil
e short grass
pl. = plant
1 = no wine colour
2 = intermediate
3 = deep wine-red

This shows that the wide variation in the intensity of the wine colour is correlated with the conditions in which the plants are grown. In the shade produced by closely associated plants (a and d) the bases of the plants are deep wine-red (3). Under simulated grazed conditions (b and e) the colouring is slight – maybe only a very little on the rhizome or stipules, rarely is it completely absent. Widely spaced plants grown in open soil (c) were intermediate in colour. It seems probable that the quantity of pigment present is correlated with the amount of light which reaches the base of the plants.

Concolourous plants are readily recognised in rough grass, meadow and woodland habitats; they are difficult to determine in open or grazed habitats, since genetically determined coloured plants may be so lacking in colour that only careful examination, preferably followed by cultivation, will separate the concoloured genotypes. They are very difficult to determine in herbarium material. Only a few concoloured plants have been confirmed during these studies, and then occurrence is sporadic.

| | | Map reference No. |
|---|---|---|
| Nr. Malham, Yorks. | several plants | 34/68 |
| Scarborough, Yorks. | 1 plant | 54/08 |
| Upper Teesdale | 1 plant | 35/83 |
| S. Scottish Uplands | 3 plants | 36/0612 |
| Central Highlands | 1 plant | 27/6544 |
| W. Pennines | 2 plants | 35/7131 |

Only around Malham is this form known to be at all frequent. Further cultivation experiments on grazed plants will undoubtedly show that the concoloured plant is more widespread.

## 4. MORPHOLOGICAL DELIMITATION OF SUBSP. FILICAULIS, SUBSP. VESTITA AND THE INTERMEDIATE

The subsp. *filicaulis* and subsp. *vestita* have been separated by the single character of hair density, in particular that of the inflorescence. This hair density has been shown in the preceding observations and cultivation experiments to be genetically determined; but it is subject to variation which is most marked in the more hairy plants. On the basis of these data it is now possible to define more exactly the limitations in the morphological characters of the two taxa and their intermediate. This, of course, is based on the hair character only, since there is no evidence that the observed variation in leaf shape is in any way correlated with the variation in hair density.

Subsp. *filicaulis* usually has flower-stems with hairiness grade 6 and the lower surface of the leaf class 1 or 2. Thirty plants in cultivation and 92% (of 203 plants) of the offspring of type 6 parents had this grade of hairiness of the flower-stem, i.e. with internode V glabrous. The remaining 8% of the offspring of type 6 parents had some hairs (class 1) on internode V. It is not yet known if the hairiness of these plants is environmentally induced or genetically determined. Internode IV is often glabrous or with a low hairiness value (class 1 or 2). Usually internodes II and III are densely hairy and so the abrupt change between III and IV is very noticeable; at first, it was thought that this was characteristic of subsp. *filicaulis* but this is not so, as these internodes may be less hairy. No attempt has been made to subdivide the less hairy forms within subsp. *filicaulis* as in most cases these appear to be environmentally-induced states (p. 311). The leaves are very uniform in hairiness of the lower surface, which is hairy only on the nerves or also on the lowest lobes; a very small proportion are thinly hairy all over.

From the preceding data over 90% of the plants referable to subsp. *filicaulis* are separable from other plants of *A. filicaulis*, *sensu lato*, on the basis of flower-stem hairiness supported by leaf hairiness.

Subsp. *vestita* forms the other end of the hairiness scale. All observations have shown a large amount of variation of an environmentally determined nature but it is not possible to say whether the wide variation seen in the families is mainly the same or partly genotypic. It seems best to include in subsp. *vestita* all those plants with flower-stems of hairiness grades 0–3; this includes plants densely hairy throughout, and those moderately hairy (class 2) on internode VI and maybe glabrous in the upper branches. Though it is apparent in the breeding experiment that the most hairy plants are a little less variable than the others, there is no reason why these plants should be considered to be anything more than equivalent to the most glabrous members of subsp. *filicaulis*. As in the flower-stem the leaves show a greater range of variability than in subsp. *filicaulis*; in 110 plants hairiness of the lower surface of the leaf was :

class 5 in 25 plants
class 4 in 43 plants
class 3 in 36 plants
class 2 in 6 plants

Thus 95% were within the more hairy half of the scale (classes 3–5) class only 5% were of the most glabrous classes (1 and 2).

The intermediates between the lower limit of hairiness of subsp. *vestita* and the upper limit of subsp. *filicaulis* are those plants with flower-stems of hairiness grade 4 and 5. These are not so frequent as the other genodemes. In cultivation the grade of hairiness of the flower stem was maintained over several years with slight variations between grades 4 and 6. It was only possible to raise offspring of one plant of grade 5; all these were of grade 4 and 5. Although so near to subsp. *filicaulis*, no plant had a mean of grade 6 though single flower-stems on some plants were this grade. (The leaves are also intermediate in the class of hairiness of the lower surface).

## 5. VARIATION IN THE HABIT OF A. FILICAULIS, SENSU LATO

Considerable variation in the size of plants of *A. filicaulis*, *sensu lato*, was very obvious in field samples collected from grazed pasture, meadow and wood over a wide altitudinal range. Walters' recognition (1949) of *A. minima* as a dwarf species opened up the question of whether in fact these other assumed dwarf variants of more ' normal ' species were environmental dwarfs or not.

A preliminary experiment to test this was set up. Habitat samples were obtained mainly from close-grazed pasture, but also from long grass and woodland, from nine sites between 450 ft (138 m) in East Durham and 2,500 ft (723 m) on the Pennine escarpment near Cross Fell to the west, all about latitude 54° 40′N; and from 2,000 ft (610 m) on Ingleborough where *A. minima* grows. As far as possible equivalent-sized pieces of unbranched rhizome of ten plants from each habitat were planted in boxes of John Innes Compost No. 1 in March, 1957. The plants were grown under similar conditions until August and then scored for the following characters :

1. number of rhizome branches.
2. number of flower-stems.
3. length of the petioles of three well-developed leaves.
4. breadth of the lamina of three well-developed leaves.
5. length of the three longest flower-stems.

In 3, 4 and 5 the mean value of three measurements per plant was used. Results are shown as graphs in Figs. 7 and 8.

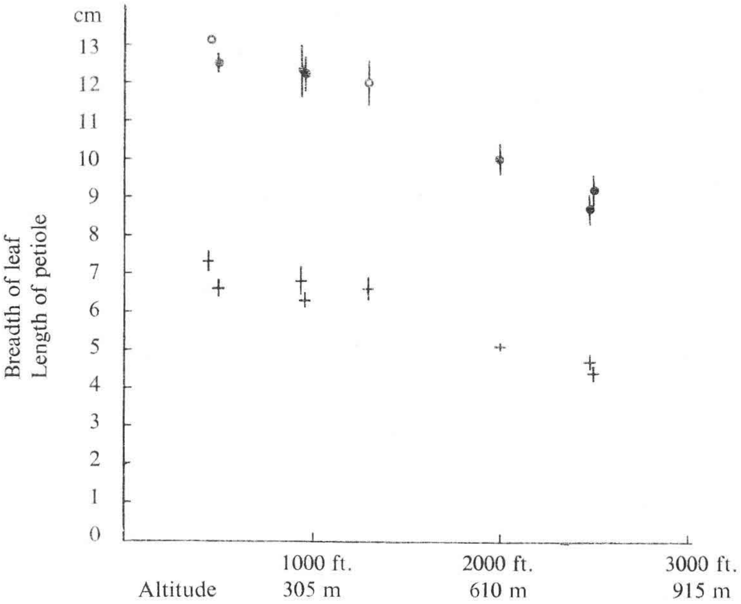

Fig. 7. Variation in breadth of leaf and length of petiole of population samples from various altitudes after cultivation. Leaf measurements, plain crosses; petiole measurements, solid dots (pasture) and open circles (meadow). (Standard deviation is given as a vertical line above and below the mean).

The sample from Ingleborough differed greatly from the others in the high number of flower stems (15·7) and short petioles, which are characteristics of *A. minima*. It was surprising that all the plants in this sample were of this kind; and, since no *A. filicaulis*, *sensu lato*, plants were present, this sample will be considered no further here, but will be included in a later paper on *A. minima*. In the other samples, although the dwarf plants attained a greater size in cultivation than in the field, a correlation between size of plant (as measured by petiole length and leaf size) and altitude was revealed. Fig. 7 shows the steady decrease in size found in the pasture plants as the altitude increases; the absence of pasture samples between 1,350 ft (411 m) and 2,000 ft (610 m) emphasises the difference between the lowland and montane populations. Additional correlation exists between the numbers of shoots produced per plant and altitude (Fig. 8). This is positive, the plants of high altitudes producing more shoots than those of low altitudes; variation within samples was greater here but significant differences were found between high and low samples.

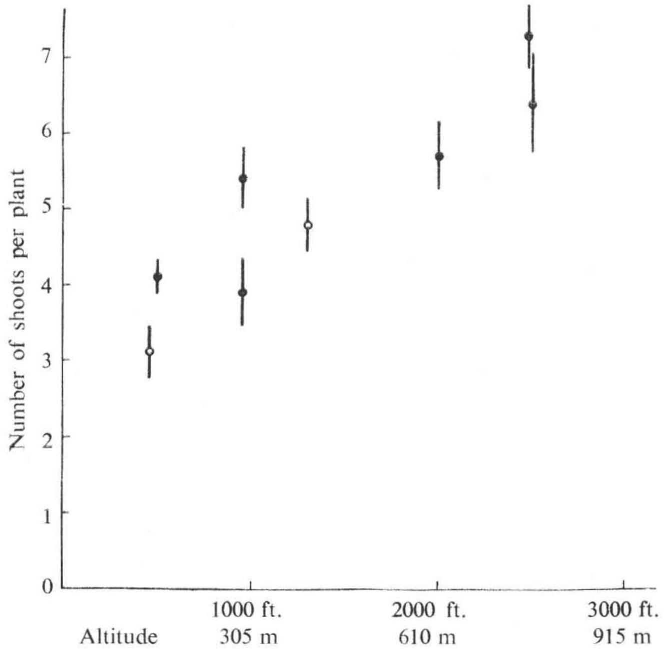

Fig. 8. Variation in the number of shoots produced per plant after cultivation of population samples from various altitudes; solid dots, pasture, open circles, meadow. (Standard deviation is given as a vertical line above and below the mean).

The two samples from meadows show the same correlation with altitude, and somewhat surprisingly fit with little distortion into the curve of the pasture plants. A single woodland sample was not included in the graphs because of the greater difference in the nature of the habitat. The number of shoots and breadth of the leaves are very similar to those of samples from the other habitats at 950 ft (290 m); the petioles are slightly but not significantly longer. The number of the flower-stems per plant has not been considered any further because there did not appear to be any obvious correlation with any of the other factors.

The combined effect of these variables is that the montane plants form shorter, more dense clumps, whilst the more lowland plants are taller, less branched and hence less compact.

Two of these pasture samples from 2,500 ft (723 m) and 950 ft (290 m) have been grown in a garden plot for several years. The low, dense growth habit has been maintained by seven of the ten plants from 2,500 ft (723 m); the other three became taller and of lowland habit. This was revealed in the first year in the plot and has been maintained. Subsequent inspection of the data used in Figs. 7 and 8 did, in fact, show that these plants had leaf measurements slightly greater than the means of the samples. All plants in the 950 ft (290 m) sample maintained the lowland type of growth.

Seed progeny samples have been grown, and were analysed in a similar way in their second year. Table 7 shows that the characteristics of the parents are maintained in the families. Families 1, 2 and 3 from the highest altitudes show the characteristic low dense habit. Those from 2,000 ft (610 m) and 1,350 ft (411 m) have maintained the same low growth for four years but had produced fewer shoots per plant than families 1–3 in two years. The number of shoots was not recorded in later years. Although family 6 is from 1,800 ft (549 m) it is of more lowland form and taller in cultivation. The lowest pasture family (7) from 1,200 ft (366 m) is of lowland stature. Four families from a lower pasture and other habitats maintained the lowland form of their parents. These results confirm that the habit characters are genetically determined.

TABLE 7
Analysis of the number of shoots per plant and leaf size in several families

| *No.* | *Code no.* | *Alt. (ft.)* | *Habitat* | *No. of plants* | *Shoot no.* | *Petiole length (cm)* | | *Leaf breadth (cm)* | | *Height after 4 years* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | **Parent* 1957 | *Offspring* 1959 | **Parent* 1957 | *Offspring* 1959 | |
| 1 | 5/47/267 | 2,400 | pasture | 20 | 9·8 ± 0·41 | 3·1 | 7·4 ± 0·28 | 3·5 | 3·9 ± 0·29 | short |
| 2 | 5/46/261 | 2,400 | pasture | 10 | 10·2 ± 0·76 | 3·5 | 5·5 ± 0·40 | 3·6 | 3·9 ± 0·15 | short |
| 3 | 5/6/46 | 2,000 | pasture | 20 | 12·3 ± 0·34 | 2·8 | 6·8 ± 0·48 | 3·8 | 4·0 ± 0·07 | short |
| 4 | 5/45/247 | 2,000 | pasture | 10 | 3·5 ± 0·45 | 1·6 | 6·7 ± 0·34 | 2·7 | 5·4 ± 0·43 | short |
| 5 | 5/1/13 | 1,350 | pasture | 20 | 5·4 ± 0·30 | 2·3 | 6·9 ± 0·32 | 3·4 | 4·5 ± 0·21 | short |
| 6 | 5/4/29 | 1,800 | pasture | 20 | 4·8 ± 0·34 | 5·8 | 7·5 ± 0·33 | 4·9 | 5·4 ± 0·21 | medium |
| 7 | 4/33e | 1,200 | pasture | 20 | 6·3 ± 0·53 | 10·0 | 11·1 ± 0·50 | 5·4 | 6·1 ± 0·12 | tall |
| 8 | 4/15/216 | 950 | grass | 20 | 3·9 ± 0·32 | 11·5 | 10·3 ± 0·34 | 7·3 | 6·7 ± 0·40 | tall |
| 9 | 4/39/272 | 1,300 | meadow | 10 | 3·7 ± 0·42 | 10·0 | 10·1 ± 0·34 | 7·2 | 7·4 ± 0·13 | tall |
| 10 | 4/30/318 | 950 | meadow | 20 | 4·7 ± 0·44 | | not available | | | tall |
| 11 | 4/8/89 | 950 | wood | 20 | 4·9 ± 0·22 | 12·2 | 11·0 ± 0·88 | 7·4 | 6·8 ± 0·56 | tall |

*The measurements were made in different years, therefore comparative values between the parents and between the families should be considered, not the direct parent-family value.

This variation in size and habit is closely connected with environmental factors; as is to be expected the *A. filicaulis*, *sensu lato*, plants are small in closely grazed habitats; so far, in all lowland samples, this character appears to be only environmentally induced, but at the higher altitudes probably the majority of the dwarf *A. filicaulis*, *sensu lato* plants of the close grazed montane habitats (above 1,500 ft, 458 m) are the dwarf, much-branched variant. The cline in size and habit shown in Figs. 7 and 8 and Table 7 is most obviously correlated with altitude and hence, the associated factors of climate, temperature, exposure and their effects on the soil. In the pasture habitats the grazing pressure is very important. All the montane habitats are very much more closely grazed by sheep than the lowland pastures, and may have been subject to this close grazing for a long time, probably several centuries.

It is difficult to assess the relative importance of the biotic and altitudinal factors in the evolution of this variant. The low-growing, much-branched variant is so obviously well adapted for survival under high grazing pressure that it appears to be axiomatic that grazing pressure has been of great importance. This is confirmed by field observations on rock-ledge plants protected from grazing which are similar in size and habit to the more lowland plants. It seems reasonable to assume that altitudinal factors also have been of some importance in the development of the cline, since variation is continuous over the whole altitudinal range of samples from the long grass habitats as well as those from the grazed habitats.

The gradual variations found in these two characters, size and shoot number, form clines similar to those known in sexual species; for instance the well known example of *Achillea lanulosa*, investigated by Clausen, Keck & Hiesey (1948), which shows a similar correlation between plant height and altitude, forming several ecotypes in isolated localities between *c.* 4,000 ft (1,220 m) and 10,000 ft (3,050 m); or *Plantago maritima* where Gregor (1939) recognised ecoclines related to ecological gradients. In *A. lanulosa* the ecotypes are geographically and morphologically isolated but in *P. maritima* where variation is continuous, separation is difficult, and each end of the cline may be regarded as an ecotype. In *Alchemilla filicaulis*, *sensu lato*, the evidence so far obtained suggests a parallel with the ecoclines found in *P. maritima*, with the possibility of a separation into a dwarf montane and a tall ecotypic variant or ecogenodeme.

The existence of genodemes within the species in *Alchemilla vulgaris* agg., similar to the ecotypes in sexual species, was first demonstrated by Turesson (1943). The initial work, based on eleven species, was qualitative and showed variation in morphological and physiological characters in several species, from widely spaced localities in Sweden; those within *A. filicaulis* differed in habit, time of flowering and mildew resistance as follows:

| *Type* | *Habitat* | *Flowering* | *Mildew* |
|---|---|---|---|
| Lapland | small low tussock | earliest | very severely damaged |
| Scania | compact well formed tussock | latest | severely damaged |
| Uppland | ,, | intermediate | ,, |
| Småland | loose spreading tussock | ,, | less attacked |
| Gotenburg | large, loose spreading | late | slight |

Photographs of two types were given. Turesson regarded this species as the most variable of those which he studied.

Later work on seed progenies of some species has confirmed the genotypic nature of some of these characters (Turesson 1956). In the earlier work Turesson introduced the term ' agamotype ' for the different genodemes, which he regarded as equivalent to the ecotypes of the sexual species. This work revealed the genetic heterogeneity of species, which had been regarded as uniform and monotypic apomicts. Recently, Grun (1955) has shown that morphological variation also occurs in the obligate apomict *Poa nervosa*.

## ACKNOWLEDGMENTS

I am pleased to record my thanks to Professor D. H. Valentine and Dr. S. Max Walters for encouragement and their interest in the work presented in this and the subsequent papers in this series. I wish to thank the Nature Conservancy and Research Fund Committee of the Durham Colleges for financial assistance while this work was being done, Professor Valentine for providing working space in the Department of Botany, and the Laboratory staff for technical assistance.

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## APPENDIX—LOCALITIES

Key to code numbers, a/b/c, where, a = year b = population and locality, and c = number of the individual plant.

| *Code No.* | *Year* | *Locality* | *O.S. Nat. Grid. ref.* |
|---|---|---|---|
| 2/1/ | 1952 | Craven | 34/720780 |
| 4/3/ | 1954 | Weardale | 35/964392 |
| 4/8/ | 1954 | Teesdale | 35/922274 |
| 4/9/ | 1954 | Teesdale | 35/921273 |
| 4/10/ | 1954 | Teesdale | 35/861303 |
| 4/11 | 1954 | Craven | 34/910633 |
| 4/11/ | 1954 | Teesdale | 35/921273 |
| 4/12/ | 1954 | Teesdale | 35/930258 |
| 4/15/ | 1954 | Teesdale | 35/922274 |
| 4/16/ | 1954 | Teesdale | 35/926270 |
| 4/22/ | 1954 | Teesdale | 35/866313 |
| 4/28/ | 1954 | Weardale | 35/875388 |
| 4/30/ | 1954 | Weardale | 35/900378 |
| 4/38/ | 1954 | Bishop Auckland | 45/214294 |
| 4/39/ | 1954 | Teesdale | 35/865309 |
| 4/45/ | 1954 | E. Durham | 45/338384 |
| 5/1/ | 1955 | Teesdale | 35/855284 |
| 5/4/ | 1955 | Teesdale | 35/833273 |
| 5/6/ | 1955 | Teesdale | 35/837264 |
| 5/44 and 45/ | 1955 | Mickle Fell | 35/815247 |
| 5/46-52/ | 1955 | Knock Fell | 35/7130 |
| 6/22/ | 1956 | Ben Lawers | 27/658444 |
| 6/26/ | 1956 | Ben Lawers | 27/635405 |
| 6/28/ | 1956 | Ben Lawers | 27/6443 |
| H | 1946 | Scarborough | 54/08 |
| Sc. 8 | | Borghamn, Sweden | |