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Bradshaw, Margaret Elizabeth (1959) *Variation in alchmilla vulgaris agg*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/8839/

VARIATION IN ALCHEMILLA VULGARIS AGG.

BY

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B.Sc. (LEEDS)

- being a thesis presented in candidature for the Degree of Doctor of Philosophy in the University of Durham, 1959.

ACKNOWLEDGEMENTS

The writer wishes to express her thanks to Dr. S.M. Walters and Professor D.H. Valentine. To the former for introducing her to the Genus Alchemilla, for guidance and much encouragement whilst learning the group and continued interest. To Professor Valentine for the initial interest which made this full-time study of Alchemilla possible, and for offering valuable advice and criticism throughout the course of this work and during the preparation of this thesis.

Thanks are also due to the Technical staff of the Department of Botany of the Durham Colleges in the University of Durham for advice and assistance in the preparation of the illustrations.

Finally, the writer is indebted to the Nature Conservancy for providing a grant during the period 1954-57 enabling her to study in the Durham Colleges and to the Research Fund of the Durham Colleges for generously contributing towards field expenses.

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INTRODUCTION

The first outstanding contribution to the study of Alchemilla vulgaris agg. was undoubtedly that of Robert Buser in Geneva. He was the first to appreciate fully the significance of the small differences in morphology which separate the species, and to recognise their different ecological and geographical ranges. The major part of his taxonomic treatment of the Alchemillas of Central Europe was published in the last decade of the 19th century, principally 1893 and 1895, just before Murbeck's (1897-1901) study of the embryology and reproduction. This work of Murbeck marked the beginning of the modern study of apomixis. Together with the studies of Strasburger (1905) it was established that several species of A. vulgaris agg. were apomictic. Embryo development was aposporous and pollen production bad. Strasburger found good pollen in A. pentaphylla and some species of A. alpina with which hybrids were formed, some were reported to be apomictic. Earlier Buser (1895) had also named these as hybrids though then, he did not know of the mode of reproduction.

Lindberg's taxonomic study of the Scandinavian species followed in 1909.

Thus, by the end of the first decade of the 20th century the general mode of reproduction had been established and many discrete taxonomic units with ecological and geographical ranges similar to sexual species had been recognised. The ground work had been prepared for further advances, but this was the time of the development of the study of the genetical basis of speciation with the emphasis on sexual species. Apart from the extension of the taxonomic studies principally those of Rothmaler (several papers between 1934-44) no detailed or experimental work in Alchemilla was published till 1943, when Samuelsson's phytogeographic study of Scandinavian Alchemillas and Turesson's experimental investigation appeared.

Up to this time and even today the constancy and uniformity of apomictic species has been stressed. By cultivation of many plants of several species Turesson clearly revealed the existence of morphological and physiological variation within the species of Alchemilla. Although Lindberg had indicated that some variation maybe found within species, the range and amount was not anticipated. This raised the big problem of what is the basis of this variation since the species are obligate aposporous apomicts which presumably are absolutely true breeding.

Meanwhile, interest in apomixis research has been steadily increasing. This is evident in Gustafsson (1946, 47) and more recently Nygren (1954). Much of this has been the study of polymorphic species complexes such as *Poa*, *Sorbus*, *Calamagrostis* and others.

Walters' paper (1949) had established some order in the classification of the British *Alchemilla* species and raised again the doubtful nature of the status of *A. filicaulis* and *A. vestita*; two species separated by a variable character of hair cover and slightly different geographical ranges. Further-more they formed dwarf variants very similar to the newly described *Alchemilla minima* Walters, only known from one small area.

The work presented in this thesis is an extension of Turesson's cultivation and cytological investigations to a group of morphologically related species to determine the range of genotypic and phenotypic variation and if possible to determine or suggest the basis of the variation exhibited. Then, on the basis of these results and with ecological and geographical data to reconsider the taxonomic status of the members of the group.

Apomixis

The terminology given by Gustafsson (1946) and used by Nygren (1954) has been used, and only a few terms of particular importance will be considered now. Apospory is used in the sense of Rosenberg (1907) to mean that a cell outside the embryo-mother-cell gives rise to the embryo-sac; this is somatic apospory of some authors. Diplospory (Edman 1931) is used for those cases in which the embryo-mother-cell forms the embryo-sac, gametic or generative apospory according to some authors.

The slight change made by Stebbins (1950, p. 383) in his modification of Gustafsson's classification of apomixis (1946, p. 9):- the substitution of "archesporial cells" for "embryo-mother-cells" is of vital importance in the consideration of Alchemilla for it is a debatable point whether the cells from which the functional embryo is formed should be regarded as generative or somatic since the archespore is multicellular. As a true embryo-mother-cell is formed, (but does degenerate) the decision of Gustafsson to regard the form of apomixis in Alchemilla as aposporous has been accepted.

Evidence for apomixis in *Alchemilla vulgaris* agg.

The cytological evidence for apomixis is based on the work of Murbeck (1901) and Strasburger (1905) on the embryology and pollen development in *Alchemilla*. Both worked on several species in the *A. alpina* agg. and *A. vulgaris* agg.; though Murbeck examined more in the latter group, including *A. glaucescens*, *A. glabra*, *A. monticola*, *A. subcrenata*, *A. acutiloba*, and *A. filicaulis*.

Embryology. Murbeck followed the development of the embryo in considerable detail. The archesporial tissue is multicullar but only one true embryo-sac-mother cell has been observed. This increases in size and enters a meiotic-like prophase, no further development takes place and this cell degenerates. The other archesporial cells divide several times by mitosis. Those near the true embryo-sac-mother cell may develop in one of two ways: enter meiotic-like prophase and then degenerate or develop aposporously by mitotic divisions to give a binucleate embryo-sac which forms a normal looking gametophyte – only one embryo is formed.

Gustafsson referred to this as the *Alchemilla* type of stabilised apospory. When the archespore is multicellular it is difficult to demarcate between diplospory and apospory. Since a true embryo-mother-cell is formed (but degenerates) this is regarded as apospory by Gustafsson (1946) and somatic apospory by Liljefors (1953) and Rutishauser.

Embryo and especially endosperm development has been observed by Murbeck (1901), Strasburger (1905) and the author to commence before the flowers open. Murbeck (1901) states that the endosperm is tetraploid due to the fusion of the polar nuclei.

Pollen formation. Production of pollen in an obligate, ~~autogamous~~ apomictic plant may be regarded as a vestigial activity of no consequence in the continuance of the species. Therefore it is not surprising that there is considerable variation in the quality of the pollen produced.

In Alchemilla the sexual species A. pentaphylla forms a useful standard with which to compare the pollen of A. vulgaris. The grains are oblong in optical section with two nuclei, one ± round the other elliptical, both stain well in aceto-carmine and presumably are typical of good fertile pollen. (FIG. 1.)

Nothing has been published of the development of pollen in A. vulgaris since the work of Strasburger (1905) and Murbeck (1901). Murbeck observed that pollen development varied in the different species. In A. alpina

FIG. 1. Pollen grains of *Alchemilla pentaphylla* (x 370)

FIG. 2. Pollen grains of *Alchemilla glabra*. (x 370)

FIG. 3. Tetrad of *Alchemilla vestita* and the burst pollen-mother-cell wall. (x 485)

pollen-sacs are sometimes disorganised before the pollen-mother-cells have formed; of the pollen-mother-cells formed 20-50% die away in early prophase. Tetrads arise in some cases but no fully developed pollen grains are differentiated. In A. glabra (alpestris) (and A. speciosa) tetrad division occurs in nearly every pollen-mother-cell. The greater part of the pollen dies away but in other cases the pollen grain contains two cells and reaches such a state of development that one is tempted to regard them as capable of germination. Murbeck regarded the state in A. monticola, A. filicaulis and A. acutiloba as intermediate between A. alpina and A. glabra types.

These observations are supported by my investigations though only one nucleus has been observed in pollen grains in A. glabra, the grains are more or less round in optical section, vary slightly in size and appear degenerate when compared with those of A. pentaphylla. (FIG. 2).

In the A. filicaulis agg. meiosis appears to take place in all pollen-mother-cells to give four daughter cells. Although comparatively few bivalents are formed, the chromatic material divides to form diads and then tetrads of approximately equal size with little evidence of lost material. (FIG. 3) Just in one case six daughter nuclei were observed. Fuller details of meiosis are given below.

It is after the tetrad stage that degeneration occurs, this has not been followed closely. When the anther opens only rarely are free pollen grains found; these are ± round, vary in size and intensity of staining and have a single poorly defined nucleus. Most usually there is a hard pollen-mass, yellow-black in colour, which is broken with difficulty. In aceto-carmine this is a dark brown amorphous mass, with a yellow-green liquid; occasionally a few free degenerate pollen grains are present.

These pollen grains differ so much from the pollen grains of the sexual species A. pentaphylla that it seems unlikely that they are fertile. Examination of a number of stigmas on which pollen-grains or masses had settled never showed any grains attached to the stigmas in preparations, no signs of pollen tubes were seen. Murbeck (1901) found the same state in A. vulgaris, but in Aphanes which is pseudogamous attached pollen-grains and pollen tubes were observed; he concludes that the pollen grains of A. vulgaris did not germinate.

Intermediate between this state and A. pentaphylla are the African Alchemilla species examined by Hjelmquist (1956). Though a large amount of free pollen grains is produced, these too are apomictic. Hjelmquist found that the pollen grains passed through a stage with two nuclei before the elliptical vegetative nucleus degenerated and the generative nucleus became granular and highly stainable; no further development was observed and Hjelmquist concluded that this pollen became non-functional. Some giant pollen grains were observed.

The occurrence of apomixis in Alchemilla vulgaris is based on the evidence of aposporous embryo development in several species and the generally poor, apparently non-functional pollen. The study of the embryology is far from exhaustive but the degenerate quality of the pollen suggests that apomixis is obligate; extensive investigations are needed to prove this. The large number of comparatively uniform species separated by small differences is characteristic of many apomictic species e.g. Taraxacum and Hieracium.

Cytology of Alchemilla vulgaris agg.

Cytological studies of A. vulgaris agg. have proved very difficult. The chromosome numbers, so far, indicate the species are high polyploids. The chromosomes are small and it is difficult to spread these sufficiently to obtain accurate counts. Chromosome numbers of A. vulgaris agg. have been listed by Löve and Löve (unpubl.) and are given below.

glaucescens Wallr. (hybrida (L) Mill.=minor Huds.auct = pubescens (Lam.) Bus.)	c.103-110	Turesson	1957
	(?) 32	Mattick (in Tischler	1950)
acutiloba Opiz.	c.100	Ehrenberg	1945
	c.105-109	Turesson	1957
	(?) 64	Strasburger	1905
subcrenata Bus.	96	Löve &Löve	1956b, 1948
	c.104-110	Turesson	1957
xanthochlora Rothm. (=vulgaris Bus. non L.)	c.105	Turesson	1957
gracilis Opiz.	c. 93	Ehrenberg	1945
	c.104-110	Turesson	1957
cymatophylla Juzep.	c.106-107	Turesson	1957
sarmatica Juzep.	c.105-106	Turesson	1957
subglobosa C.G. West.	c.102-108	Turesson	1957
vestita (Bus.) Raunk. (= minor auct)	96	Löve & Löve	1956b
	c.110	Turesson	1957

filicaulis Bus.	96	Löve & Löve	1956b
	c.103-110	Turesson	1957
monticola Opiz.	101	Ehrenberg	1945
	c.103-109	Turesson	1957
glabra Neygen.	96	Löve & Löve	1956b
	c.100	Ehrenberg	1945
	c.102-110	Turesson	1957
obtusa Bus.	c.103	Turesson	1957
wichurae (Bus.) Stef.	c.103-106	Turesson	1957
	(?)64	Löve & Löve	1956b
murbeckiana Bus.	c.102-109	Turesson	1957
	(?)64	Löve & Löve	1956b
oxyodonta Bus.	c.165-168	Turesson	1957
	(?)64	Löve & Löve	1956b
glacialis Oskarss.	c.144	Löve & Löve	(unpubl.)
borealis Sam.	c.130-152	Turesson	1957
glomerulans Bus.	96	Jørgensen, Sorensen & Westergaard	1958
	c.101-109	Turesson	1957
	(?)64	Bøcher Löve & Löve	1938b, 1956b.

Turesson's figures appear to be the most accurate but even these are not absolutely exact and the values are within the margin of the counts given. However the accuracy is sufficient to show several species have a number 2n = c. 105-106 whilst others probably have several numbers between 2n = 100 and 110. The values 2n = 93 and 96 are undoubtedly counts from insufficiently spread plates, the latter an obvious multipule of 8 which has been considered to be the basic number.

Values of 2n = 64 and 2n = 130-152, 165-168, 144 are certainly distinct, and scarcely counts for other values published. Strasburger's early counts should be checked though a preliminary examination of A. pentaphylla by the author indicated that his number is probably accurate.

The two sets of values for A. wichurae, A. murbeckiana, A. oxyodonta and A. glomerulans call for comment. Löve and Löve's and Bøcher's figures are 2n = c.64 whilst Turesson's are 2n = c.100-110 and c.165-168. Differences of this magnitude are unlikely to be errors in counting if the material has been identified correctly (this is not certain). There may be some significance in the fact that Turesson's material was of Scandinavian origin whilst Bøcher's was from Greenland and Löve and Löve's was from Iceland; though the material of Jørgenson et al., was also from Greenland. Obviously some rechecking is needed here. Further consideration will be given to the cytology later. (p. 48).

ALCHEMILLA FILICAULIS AGGREGATE

For the purpose of this thesis only, the three species A. filicaulis Bus., A. vestita (Bus.) Raunk. and A. minima Walters are grouped together as the A. filicaulis aggregate. Under the binomial A. filicaulis Bus s.l. are the two taxa known as A. filicaulis Bus. and A. vestita (Bus.) Raunk.. Buser (1893) first described the species A. filicaulis and separated from it "Une f. vestita". As his description is rather long and not easily accessible I have prepared the following [illegible]

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 ones with spreading hairs. Base of the petioles and stipules usually wine-red. Leaves medium (3-9 cms wide, 2.5-8 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) sub-acute, somewhat connivent, all ± equal except the small terminal tooth. Stems (5)20-30(40) cms., 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, a l'exclusion du type, tandis qu'au Salève on ne la rencontre qu'en individus égrenés et rares parmi la forme normale fréquente." This forma was raised to specific rank by Raunkiaer (1906) no doubt because of its greater frequency than the type in Denmark. In Britain both species occur, *A. vestita* being more wide-spread and frequent than *A. filicaulis* s.st... In his paper Walters (1949) says the morphological difference between *A. vestita* and *A. filicaulis* is very slight --- the only 'good' character appears to be the hairiness of the inflorescence" (see FIG. 4) but field collections made in N. England between 1951 and 1954 contained plants of intermediate hairiness not readily assignable to either taxon. Clearly the distinction between these species was not at all clear. A thorough investigation into the nature of the distinguishing characters of both these species was needed. Are the plants of intermediate hairiness phenotypic extremes of both species or genotypes of an intermediate character?

Very similar to dwarf forms of *A. filicaulis* s.l. is *A. minima* Walters. Walters (1949) separated this as a

FIG. 4. Inflorescences of (a) *A. filicaulis* s.st. upper internodes and branches glabrous. (b) *A. vestita* all parts hairy.

species from populations which had been assumed to consist of phenotypic dwarf specimens of the more widely distributed 'normal species'. Walters drew attention to the need for extensive cultivation experiments to test this assumption. Accordingly investigation has been made into the whole range of variation found in the very similar segregates which can be included in A. filicaulis agg.; these are A. filicaulis Bus. s.l. including A. filicaulis s.st. and A. vestita (Bus.) Raunk., and A. minima Walters.

I. VARIATION IN ALCHEMILLA FILICAULIS s.l.

A. Variation in hairiness

(1) The inflorescence stem

It has already been indicated that the hair cover on plants of A. filicaulis s.l. varies from dense throughout to glabrescent. A measure of this is most conveniently made on the inflorescence stem, where the density of the indumentum usually decreases from the base to the distal branches, This change may be slight, in which case the whole plant is pubescent, or so great that all but the basal internodes are glabrous.

a) Method

The inflorescences were classified in the following way. Standards were set up to provide six classes of hairiness as in FIG. 5. Internodes II, IV, VI, and VIII were then scored for hairiness on this scale, other internodes being scored where necessary. Since some inflorescences have more internodes than others comparison was made over the lowest six internodes only.

The grade of hairiness of the inflorescence corresponds to the decrease in hairiness of the internodes along the inflorescence, since internode II is usually densely hairy, it was assumed to be class 5 in all cases for this purpose.

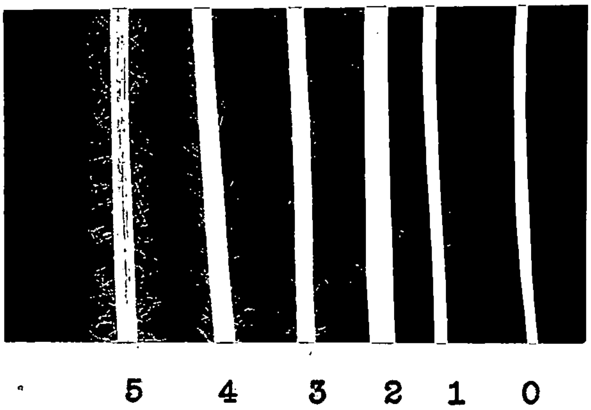


FIG. 5. Classes of hairiness on internodes of the inflorescence. (x 4)

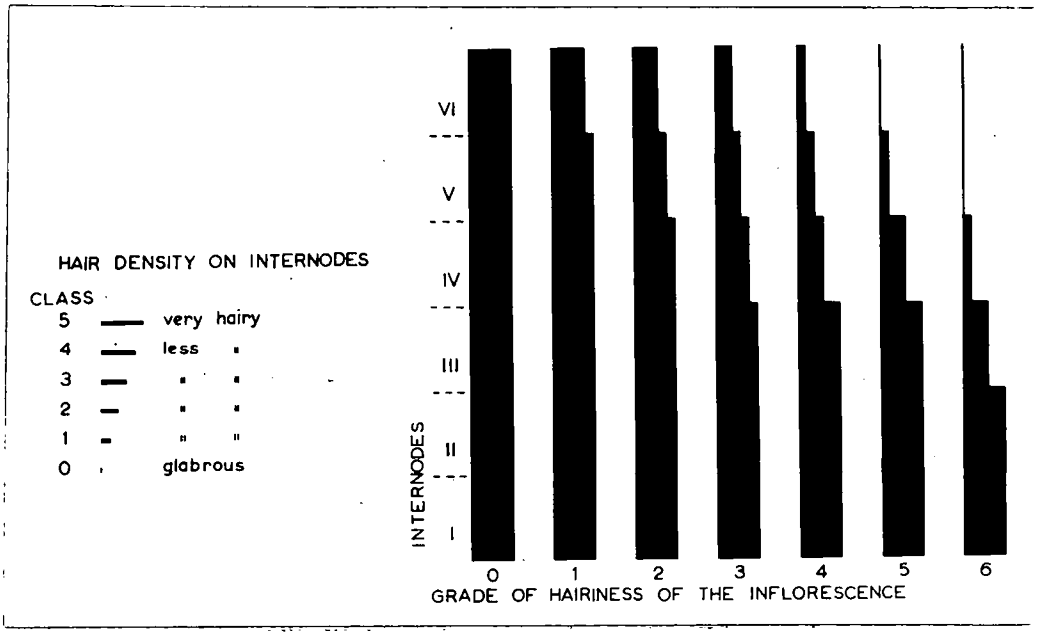


FIG. 6.

The grade for each inflorescence was calculated as the difference between the class of the VIth internode and the most hairy state, (class 5). In FIG. 6, grade 0 is class 5 throughout; in grade 5 the VIth internode is glabrous, the difference between this class (0) and the most hairy state (5) is 5 i.e. the grade. In grade 6 internode V as well as VI is glabrous. This gives seven grades of hairiness of the inflorescence (0-6).

It should be noted that in grades 0-4 the internodes above the sixth (VI) may be hairy; in grade 6, internodes below the fifth (V) may be glabrous, and in some cases the most hairy internode may be less than class 5.

All scoring was done on fully expanded inflorescences of the main summer growth in which most flowers were open.

Inflorescences arise in the axils of radical leaves on a prostrate rhizome; the lowest internode was usually found to be c.0.5 cm. long and was sometimes glabrous. Occasionally the lowest internode collected was extremely short, the next internode appearing more similar to the usual first internode; in these cases the very short internode was not scored, the next being regarded as internode I.

Comparison of the hairiness of plants in the following analyses is based on this method so that the index of 'hairiness of the inflorescence' which is used is one of the 7

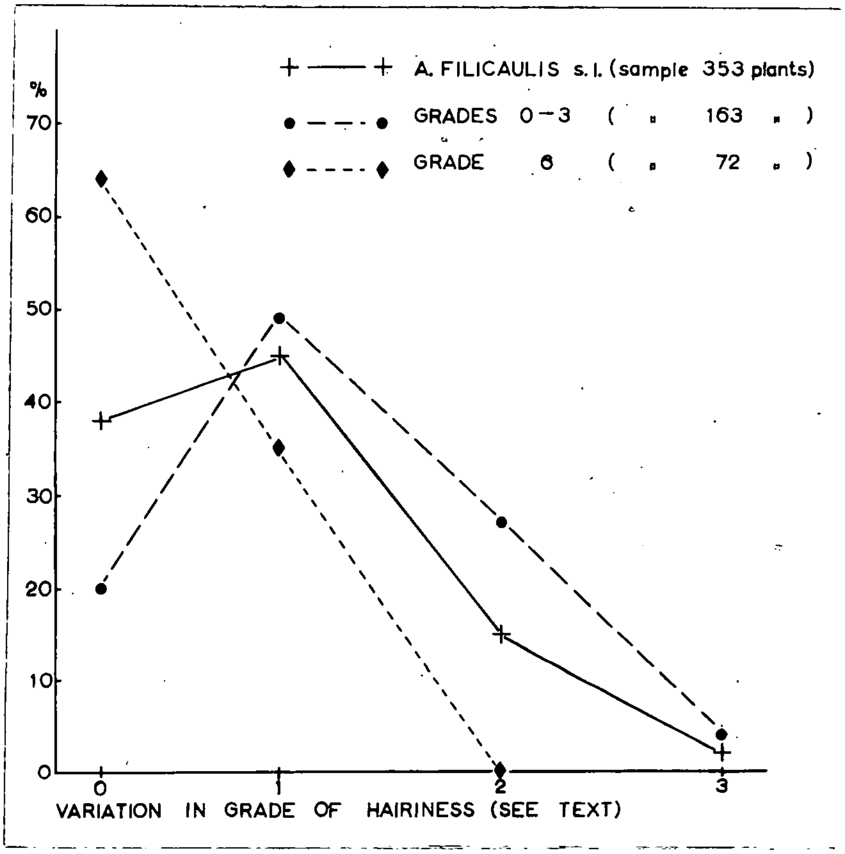


FIG. 7. Variation in grade of hairiness of two or more inflorescences on the same plant.

grades described above (FIG. 6).

b) Variation in the grade of hairiness of the inflorescences of individual plants. (i.e. variation within a plant.)

Preliminary studies showed that a slight variation may occur in the grade of hairiness of the inflorescences on a single plant. Comparisons were made between the two or three inflorescences available on 21 plants collected in the field. 67% had inflorescences all of the same grade of hairiness, whilst 33% showed a difference of one type between the two or three inflorescences which were scored; e.g. a plant with inflorescences of hairiness grades 0 and 1 or 3 and 4 or 4 and 5 etc. shows a variation within the plant of one grade, those with 0, 1, 2 or 1, 1, 3 show a variation of 2 grades etc. Examination of a larger number of plants in cultivation has shown that greater variation in the grade of hairiness of the inflorescence does occur within a single plant; this is shown in (FIG. 7).

c) 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 inflorescences per plant in the last year, and one inflorescence per plant in the other year(s). (FIG. 8).

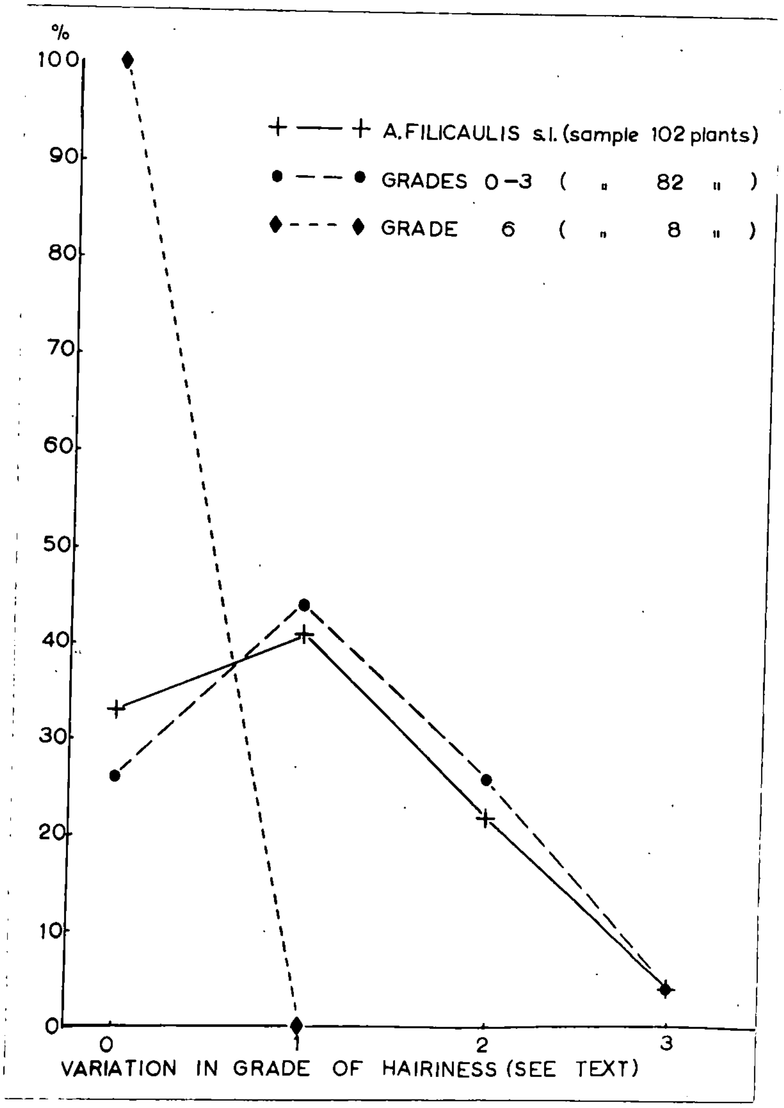


FIG. 8. Variation in grade of hairiness of the inflorescences from year to year.

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 inflorescence 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 inflorescences 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 inflorescence found in A. filicaulis s.l.

d) 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 1 containing 10 plants each. Three mature inflorescences were collected from each plant and scored for hairiness by the method described. Results are given below (TABLE 1) and as histograms. (FIG. 9).

TABLE 1

Parent	inflor. grade	family	number of plants with means of each grade of hairiness.						
	M	M	0	1	2	3	4	5	6 grades
4/38/371	0	.65	7	13					
4/28/326	2	.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				

M = mean, usually of 3

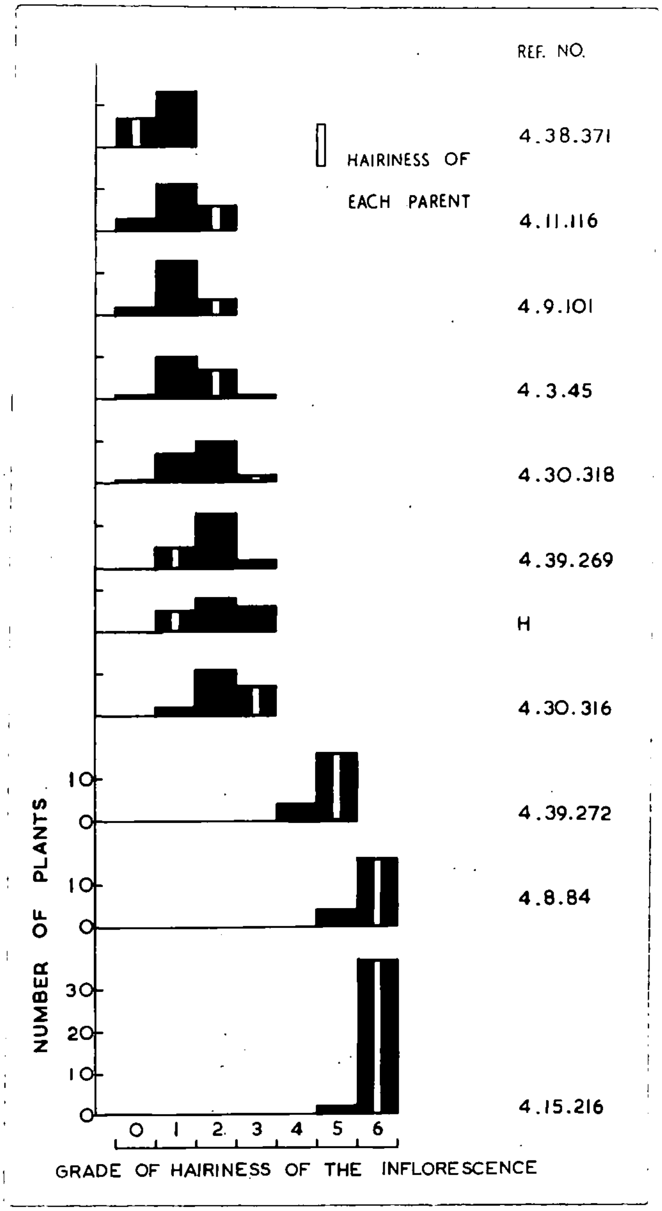


FIG. 9. Variation within families.

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.

e) 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 an 0 grade 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 inflorescence in <u>A. filicaulis</u> s.l. 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 off-spring with little variation and shows very well that the intermediate character is probably 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 genetical but is more probably phenotypic 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 <u>grades</u> used in classification of the inflorescences with the taxonomic names in current usage. Grades 0-3 may be regarded as A. vestita and grade 6 as A. filicaulis s.st.; grades 4-5 are intermediate in character. It is in this sense that the binomials will be used below unless it is stated otherwise. The limitations and status of each will be fully considered later.

f) Variation in plants grown under field and garden condition

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 glabrous plants do require special mention; some of these with glabrous or nearly glabrous inflorescences in the field produced more normal, grade 6 inflorescences after cultivation. These were all plants of high altitudes and will be discussed fully after variation in hairiness of the leaf has been considered.

(2) Other parts of the inflorescence

Variation in hair density is not limited to the main branches of the inflorescence 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; the density decreases, but rarely are all the urceoles on the inflorescence without hairs; though in grade 6 there may be no more than one or two hairs on a few urceoles only.

(3) 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 the 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,

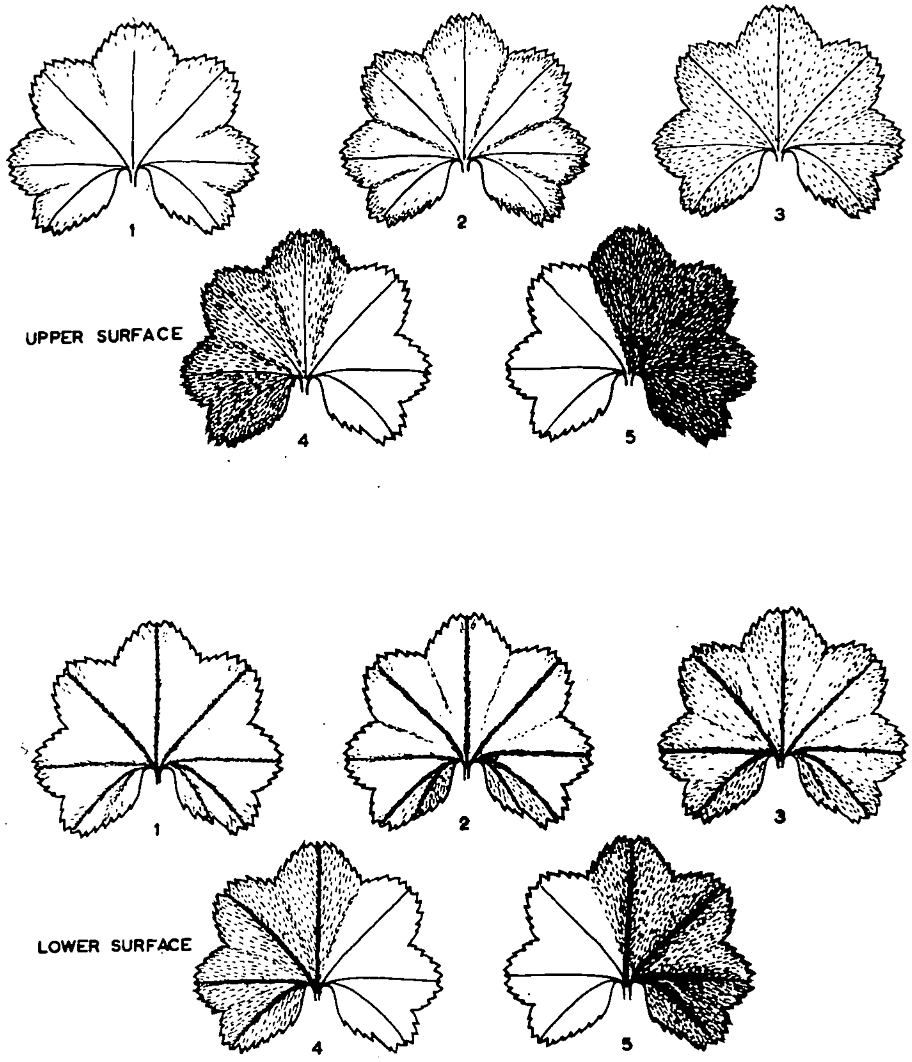


FIG. 10. Grades of hairiness of upper and lower leaf surfaces. In grades 4 and 5 hairs are shown on a portion of the leaf only.

so a series of standards had to be used. These were chosen for upper and lower surfaces of the leaf as in FIG. 10.

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

TABLE 2.

Grade of hairiness of the inflorescence.	Lower surface mean*.	Upper surface mean*.
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

* means are of one leaf of several plants with inflorescences of each grade of hairiness.

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

Results of scoring 218 garden and field plants assessed on one inflorescence and one leaf are given in TABLE 3.

TABLE 3.

Grade of hairiness of the inflorescence.

		0	1	2	3	4	5	6
Grade 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

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

Now that hairiness of the inflorescence and leaf have been considered generally and in detail, certain almost glabrous plants can be considered. These formed a very small proportion (16) of all the plants collected in the field. In most cases the lower surface of the leaves were hairy only on the nerves, the inflorescences 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 s.st. In plant 6/28/201 the petioles and leaves became hairy as in A. filicaulis s.st. but the inflorescences remained glabrous. This was the only plant in which the absence of hairs appears to be genetically determined. Details of variation in five plants are given in TABLE 4.

TABLE 4

Plant	Year		Leaf hairiness			Inflorescence hairiness class						
			Petiole	Lamina lower	upper	Internodes 1	2	3	4	5	6	urceoles
6/22/172	56	f	class 1	1,distal 2/3 nerve	2	0	1	0	0	0		few on most
	57	g	" 2-3*	"	2	.	1	.	0	.	0	few
	58	g	–	–	–	0	4	3	0	.	0	–
6/28/201	56	f	" 1	1 "	2	.	0	.	0	.		most hairy
	57	g	" 2+3*	"	2	.	0	.	0	.	0	few on most
	58	g	–	–	–	0	2	0	0	0	0	–
						.	0	.	0	.	0	
						.	0	.	0	.	0	
6/28/202	56	f	" 1	1,distal 1/2 nerve	1 few	.	0	.	0	.	0	few on most
	57	g	" 2-4*	1, " 2/3 "	2	.	1	.	0	.	0	very few
	58	g	" 4	1	–	.	3	.	2	.	0	–
						.	3	.	3	.	1	
						.	3	.	0	.	0	
6/28/203	56	f	0 hairs	1, " 1/4 "	1 few	.	0	.	0	.	0	0
	57	g	class 3-5*	1, " 3/4 "	2	.	4	1	0	.	0	few on some
	58	g	hairy	1	–	.	4	.	4	.	2 1	–
						.	4	.	2	1	0	
6/26/181	56	f	class 2	1, " 3/4 "	3	.	0	.	0	.		?0
	57	g	" 5	2, " 3/4 "	3	.	1	2	0	.	0	few on most

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

B. 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 lobe; 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 s.l. 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. (see FIG. 11).

Leaves of five representative plants from four samples of twenty raised from different parent plants are shown in FIG. 12. 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 that

FIG. 11. Variation in leaf shape, 3 leaves from each of 5 plants.

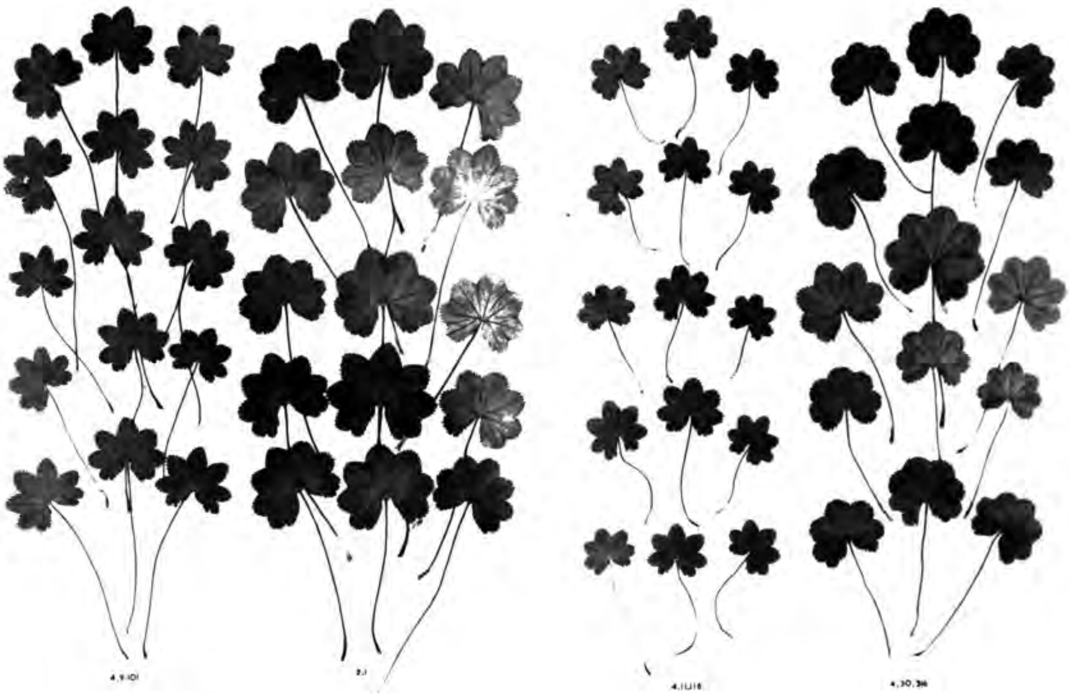


FIG. 12. Variation in leaf shape between families. 3 leaves from each of 5 plants in each family.

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 on the median lobe of a well grown leaf; though the ratio of length : ½ the 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.

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.

TABLE 5.

Code no.	No. of plants	length of lobe: ½ breadth	s.e.
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

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' and c.350' the last two are from high altitude pasture c.2000'. Further investigation may show that leaf-lobe shape is associated with habitats.

C. Variation in stipule colour

In A. filicaulis s.l. 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 concoloured forms without the pigment are found.

Cultivation has shown that the presence or absence of anthocyanin is genetically determined. All the offspring of three concolour 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 taxa in A. filicaulis s.l. 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.

Cultivation 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 19).
e) as d), these plants were kept short (1" above soil level) by cutting throughout the summer.

Results are given in TABLE 6.

TABLE 6.

Code No.	Garden plot		Boxes		
A. vestita	a(20pl.)	b(20pl.)	c(20pl.)	d(40pl.)	e(20pl.)
4/3/45	3	2-, 2	2, 2+	3	2=
4/12/173	2+, 3	1, 2-	2-, 2		
4/39/270				3(20pl.)	2-, 2
4/30/318				2, 3	2-, 2
4/9/101				2+, 3	2
A. filicaulis					
4/15/216	3	2=, 2		2, 3	2+(10pl.)

pl. = plants; 1 = no wine colour; 3 = deep wine red;

2± = intermediate intensity of 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 similar 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.

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

		Map reference No.
nr. Malham	several plants	34/68
Scarborough	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.

Morphological Delimitation of A. vestita and A. filicaulis s.st. and the intermediate

A. vestita and A. filicaulis s.st. have been separated on the single character of hair density, in particular that of the inflorescence. This hair density has been shown in the preceding observation and cultivation experiments to be genetically determined; but it is subject to phenotypic variation which is most marked in the more hairy plants.

On the basis of this data it is now possible to define more exactly the limitations in the morphological characters of the three genodemes.

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.

A. filicaulis s.st. usually has inflorescences with hairiness grade 6 and the lower surface of the leaf grade 1 or 2. Thirty plants in cultivation and 92% (of 203 plants) of the off-spring of type 6 parents had this grade of hairiness of the inflorescence, i.e. with internode V. glabrous. The remaining 8% of the off-spring of type 6 parents had some hairs (class 1) on internode V. It is not yet known if these are phenotypes or genotypes. Internode IV is often glabrous or with a low hairiness value (class 1 or 2). Usually internodes IV 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 A. filicaulis s.st. but this is not so, as these internodes may be less hairy. No attempt has been made to sub-divide the less hairy forms within A. filicaulis as in most cases these appear to be phenotypic states (p. 27).

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 > 90% of the plants referable to A. filicaulis s.st. are separable from other plants of A. filicaulis s.l. on the basis of inflorescence hairiness supported by leaf hairiness.

A. vestita. forms the other end of the hairiness scale. All observations have shown a large amount of variation of a phenotypic nature but it is not possible to say whether the wide variation seen in the families is mainly phenotypic or partly genotypic. It seems best to include in A. vestita all those plants with inflorescences 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 *A. filicaulis* s.st.

As im the inflorescence the leaves show a greater range of variability than in *A. filicaulis* s.st.; in 100 plants hairiness of the lower surface of the leaf was

grade 5 in 25 plants
" 4 in 43 "
" 3 in 36 "
" 2 in 6 " .

Thus 95% were within the more hairy half of the scale (grade 3-5) only 5% were of the most glabrous grades (1 and 2).

The intermediate between the lower limit of hairiness of *A. vestita* and the upper limit of *A. filicaulis* s.st. are those plants with inflorescences of hairiness grade 4 and 5. These are not so frequent as the other genodemes.

In cultivation the grade of hairiness of the inflorescence was maintained over several years with slight variations between grades 4 and 6. It was only possible to raise off-spring of one plant (grade 5); all these were of grade 4 and 5. Although so near to *A. filicaulis* s.st., no plant had a mean of grade 6, though single infloresences on some plants were this grade. This evidence does show that the intermediate is a genodeme.

The leaves are also intermediate in the grade of hairiness of the lower surface.

D. Variation in the habit of A. filicaulis s.l.

Considerable variation in the size of plants of A. filicaulis s.l. 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 phenotypic dwarfs or not.

A preliminary experiment to test this was set up. Habitat samples were obtained mainly from pasture, but also from long grass and woodland, from nine sites between 450' in East Durham and 2,500' on the Pennine escarpment near Cross Fell to the west, all about latitude 54° 40'; and from 2000' 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 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 inflorescence branches.
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 inflorescences.

In 3, 4 and 5 the mean value of three measurements per plant was used. Results are given in TABLE 7.

Sample 5/36-40 from Ingleborough differs greatly from the other samples in the high number of inflorescences and short petioles, which are characteristic of A. minima. It was surprising that all the plants in the sample were of this kind; and since no A. filicaulis s.l. plants were included, this sample will be considered no further here, but will be included in the section on A. minima later. In the other samples the originally dwarf plants attained a greater size in cultivation than in the field.

Pasture and long grass samples have been considered in relation to altitude in FIG. 13. It is clear that there is correlation between the size of plant (as measured by petiole length and leaf breadth) and altitude. A steady decrease in size is found in the pasture plants as the altitude increases, the absence of pasture samples between 1000' and 2000' emphasises the significance of the difference between the lowland and montane samples.

The two samples from meadows show the same correlation with altitude, and somewhat surprisingly fit into the curve of the pasture plants with little distortion.

In a similar manner, correlation is shown between the altitude and the number of shoots produced per plant. (FIG. 14). This time correlation is positive, the plants of high altitude producing more shoots than those of low alti-

TABLE 7

Code No.	Habitat	Alt.	Mean shoot number, s.e.	Mean petiole length, s.e.	Mean leaf breadth, s.e.	Mean inflorescence number.
4/8	wood	950'	4.6 ± 0.32	13.3 ± 0.57	6.4 ± 0.35	2.8
6/50	rough grass	450'	3.1 ± 0.11	13.1 ± 0.11	7.3 ± 0.24	4.3
4&6/46	pasture	500'	4.1 ± 0.22	12.5 ± 0.25	6.6 ± 0.20	4.2
4/3	"	950'	5.4 ± 0.42	12.3 ± 0.71	6.8 ± 0.36	3.3
4/9&11	"	950'	3.9 ± 0.47	12.2 ± 0.45	6.2 ± 0.45	4.5
4&6/39	meadow	1300'	4.8 ± 0.36	12.0 ± 0.58	6.6 ± 0.28	2.1
4/21&5/53	pasture	2000'	5.7 ± 0.45	10.0 ± o.40	5.1 ± 0.10	4.4
5/46	"	2500'	7.3 ± 0.44	8.7 ± 0.42	4.7 ± 0.19	2.4
5/50	"	2000'	6.4 ± 0.67	9.2 ± 0.39	4.4 ± 0.21	3.2
5/36&40	"	2000'	4.7 ± 0.45	1.9 ± 0.17		15.7

s.e. = standard error

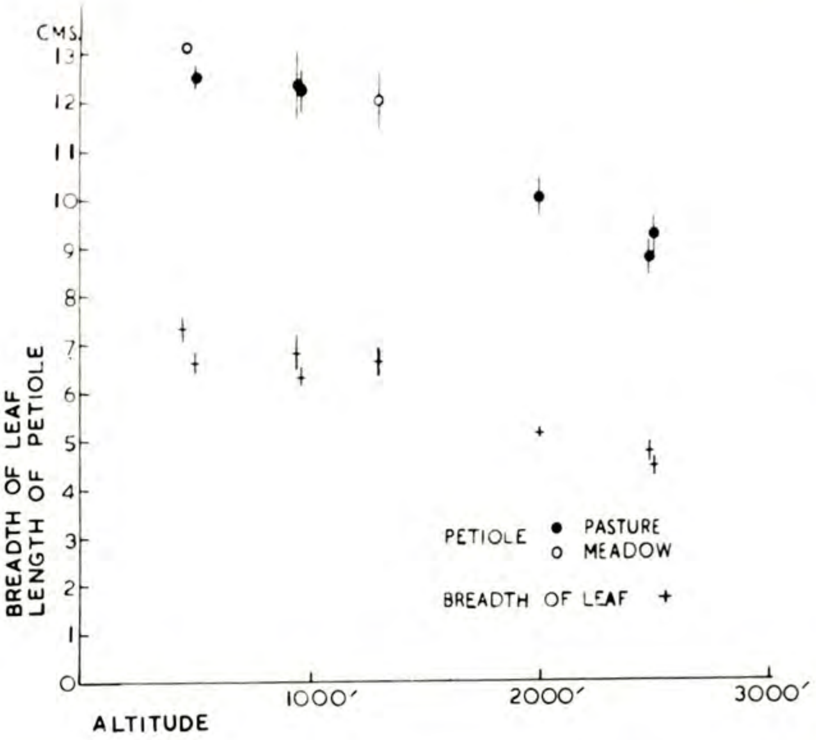


FIG. 13.

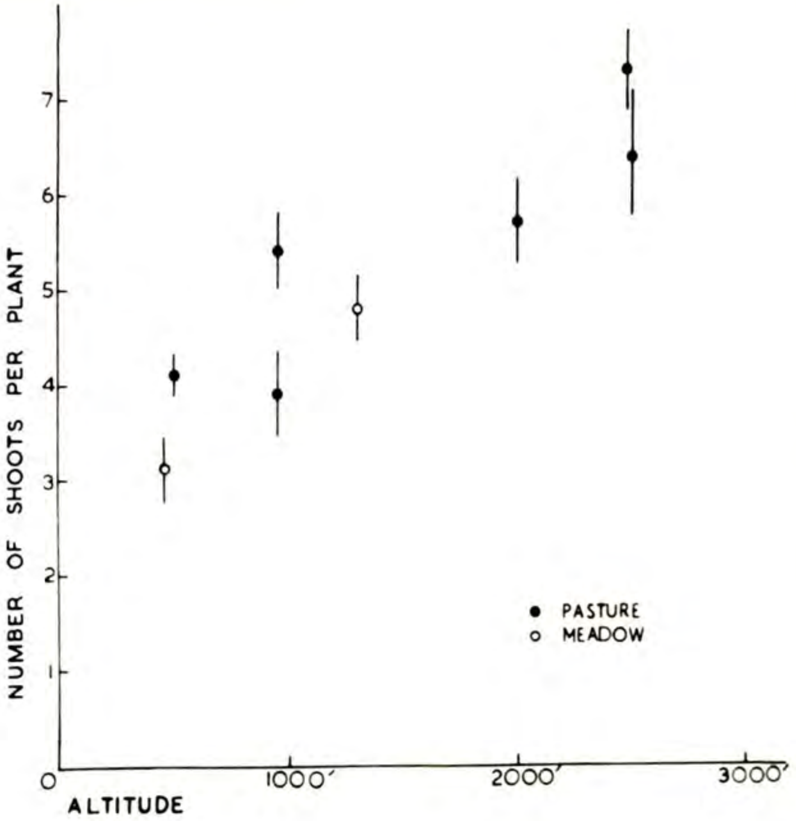


FIG. 14.

(Standard error is given as a vertical line above and below the mean.)

tudes; variation within samples was greater here but significant differences were found between high and low samples. Meadow plants were significantly different from each other and again fitted in with the curve for the pasture plants.

The 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 other habitats at 950', the petioles are slightly but not significantly longer. The number of the inflorescences per plant have 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. (FIG. 15).

In this experiment comparison has been made between the attainment of plants grown under uniform conditions for only a short period (March-August, 4 months). However most of the stock plants from which the cuttings were taken had been in cultivation for several years ($1\frac{1}{2}$-$2\frac{1}{2}$) and have retained characteristic differences. Therefore it appears reasonable to assume that these differences are genetically determined.

FIG. I5 Ecogenodemes of A. filicaulis s.l..Ten transplants grown under similar conditions from (C) 2500', (D) 950', (E) 500'.

Obviously comparison of seed progenies is required to prove this. Early attempts to raise these were thwarted by poor germination, but some families are now being grown. The following figures were obtained for seedlings after approximately five months growth. (TABLE 8, FIG. 16).

TABLE 8.

Code No.	No. of plants	Altitude	Mean Shoot No., s.e.
4/15/216	24	950'	1.0
4/8/89	24	950'	1.0
4/30/318	24	950'	1.325 ± 0.153
4/33e	24	1200'	1.17 ± 0.01
4/39/272	24	1300'	1.2 ± 0.137
5/4/29	24	1800'	1.42 ± 0.134
5/6/46	24	2000'	1.8 ± 0.195
5/45/247	12	2000'	1.17 ± 0.179
5/45/248	12	2000'	1.17 ± 0.179
5/46/261	12	2400'	2.52 ± 0.405
5/47/267	20	2400'	3.35 ± 0.325

The families from some of the high altitude parents have a higher mean value for the number of shoots per plant (2.52, 3.35 and 1.8) than those of the lower altitudes (up to 1300'); the differences in the means are not great and in some cases variations within the families are large. On

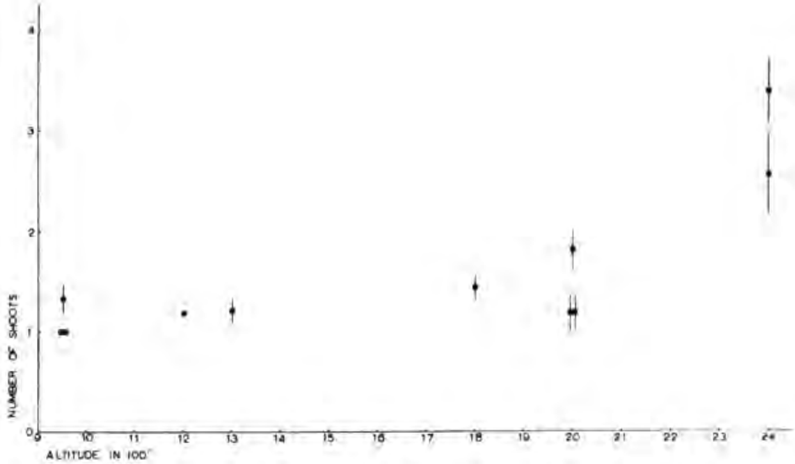


FIG. 16. Variation in mean number of shoots per family with altitude.

(Standard error is given as a vertical line above and below the mean.)

the whole the findings do support those of the transplant experiment. Further comparisons will be made when these plants are mature.

This variation in size and habit is closely connected with environmental factors; as is to be expected in closely grazed habitats the A. filicaulis s.l. plants are small; so far, in all lowland samples this character appears to be only phenotypic in nature, but at the higher altitudes the dwarfing is at least partially genotypic. This gives a cline in size and habitat which is most obviously correlated with altitude. Inseparable from altitude are the associated climatic factors, temperature, exposure and their effects on the soil, all of which must have influenced the development of the clines. In the pasture samples the increase in altitude is accompanied by more intensive grazing; the montane habitats, from which the samples were taken, are very much more closely grazed by sheep than the lower pastures, and may have been subject to close grazing for a long time. Under these combined environmental factors a low, much branched variant has evolved which is well suited to the habitat.

It is difficult to assess the relative importances of the biotic and altitudinal factors. It seems reasonable to assume that the altitudinal factors have been important in the development of the cline, since variation is continuous over the whole altitudinal range of the grazed samples and also in those from the long grass habitats; though other environmental conditions are not equivalent here, since the higher is subject to mowing and some grazing whilst the lower is not. No doubt grazing has been important at the higher altitudes since field observations have shown that rock-ledge plants (2000'+) which are protected from grazing are about the same size as the more lowland plants.

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 <u>Achillea lanulosa</u>, investigated by Clausen, Keck and Hiesey (1948), which shows a similar correlation between plant height and altitude, forming several ecotypes in isolated localities between c.4000' and 10,000'; or <u>Plantago maritima</u> where Gregor (1939) recognised ecoclines related to ecological gradients. In <u>A. lanulosa</u> the ecotypes are geographically isolated but in <u>P. maritima</u> where variation is continuous, separation is difficult, and each end of the cline may be regarded as an ecotype. In <u>Alchemilla filicaulis</u> s.l. the evidence so far obtained suggests a parallel with the ecoclines found in <u>P. maritima</u>, 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, these differed in respect to habit, time of flowering and mildew resistance as follows:

A. filicaulis

Type	Habitat	Flowering	Mildew
Lapland	small low tussock	earliest	very severely damaged
Scanian	compact well formed tussock	latest	severely damaged
Uppland	" " " "	intermediate	" "
Smaland	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.

The work on A. filicaulis presented above suggests that the delimitation of distinct agamotypes(ecogenodemes) by Turesson may be due to the method of sampling which was apparently discontinuous, and that in at least some groups, a more or less continuous clinal series may exist, as in some outbreeding species.

E. Cytology of *A. filicaulis* s.l.

A knowledge of the cytology of the group is clearly important from the stand-point of taxonomy and variation. A short review of the cytological data already published on *A. vulgaris* agg. is given above. (p. 10) A more detailed study of *A. filicaulis* s.l. follows.

Method

Root-tips for mitosis. Some root-tips were taken from potted plants in the garden, but the best results were obtained from roots grown by a simple water-culture method.

1. All the roots except young actively growing ones were removed from the rhizome of a healthy shoot.

2. The rhizome was suspended in a beaker of water.

3. After a few weeks (time varied) many new adventitious roots had developed.

4. Yellow tipped roots several mms. long were cut off the plants and pre-treated with 0.002 M. solution of Hydroxyquinoline in corked tubes.

5. The tubes were immersed in running water (about 15°C.) to keep a constant low temperature, for 4 hours.

6. The hydroxy-quinoline was pipetted off and replaced by a fixative of one part of glacial acetic acid to three parts of absolute alcohol.

7. The tubes were then placed in a domestic refrigerator (temp. c.$4^{o}C.$) for 3-6 days. Walker (1956) reports that this gives a better spread of chromosomes. Tubes were stored in a deep-freeze refrigerator.

Staining. It proved difficult to get well spread and stained chromosome plates. The best results were obtained with aceto-carmine as the stain.

8. Staining and maceration were combined in a technique used by Proctor (1955). The roots were heated in about 1 cc. of aceto-carmine in a test-tube, in which a cleaned needle was standing, in a boiling water-bath for 3-5 mins.

9. The root-tip was cut off on a slide and thoroughly pounded with a flat-sided needle in a drop of aceto-carmine.

10. A clean cover-slip was applied, and tapped with a needle to help to spread the cells. The slide was heated over a spirit lamp until a slight amount of boiling occurred at one corner only.

11. Then the cells were squashed by pressing as hard as possible with the thumb onto a folded filter paper over the coverslip. (Care must be taken to press directly downwards; any lateral pressure will cause shearing of the cells). After staining slides were passed through

an acetic-alcohol series and made permanent by mounting in Euporal.

In some cases maceration was aided by the use of hydrochloric acid, but this tended to reduce the staining to some extent; in item 8 the aceto-carmine contained 1 drop of normal HCl. to each 9 drops of aceto-carmine, heating was continued for 5 minutes.

Some roots were embedded in wax, sectioned at 12 μ and stained in gentian-violet; though the differentiation was good, the chromosomes were too crowded to obtain an accurate count.

<u>Meiosis</u>. <u>Alchemilla</u> flowers from April to September and even November in cultivation. Flower buds were collected during this period (preferably in April) when the inflorescences were still very compact. The flower buds were separated and fixed in 3 parts abs. alc.
1 part glacial acetic acid.
1 part chloroform.

for at least 24 hours. Material was stored at -10°C.

<u>Staining</u>.

1. The four anthers were dissected out of a young flower about 2 mms. long, and placed in a drop of aceto-carmine on a slide.

2. The anthers were split and the walls removed from the slide; at the correct stage the pollen-mother-cells float out as separate round cells.

3. Two clean needles were rubbed together in the stain to provide a little iron.

4. A cover slip was put on and gently tapped to spread the pollen-mother-cell. Only a small drop of aceto-carmine must be used or else the pollen-mother-cell will flow to the margin of the cover slip and be lost, more stain can be added from the edge of the cover-slip if air gaps remain.

5. The slide was heated over a spirit-lamp till the aceto-carmine bubbled at one corner of the slide.

6. The cells were well squashed by direct pressure with the thumb over filter paper.

7. The slide was warmed again if the staining was not sharp enough. In both cases slides were examined in the temporary state for suitable plates; only slides with some promising cells were made permanent.

Examination and later work was considerably facilitated by the phase-contrast lighting; this improved the differentiation between chromosomes and cytoplasm which was never very good when an ordinary light system was used. This was done using a Cooke, Troughton and Simms phase contrast microscope. The best plates were photographed using a Reichert Zetopan microscope, with a phase-contrast immersion objective or a Zeiss using ordinary light.

Since the chromosomes numbers were all high (2n = c. 100), enlarged photographic prints were used as a base on which to ink-in the chromosomes as observed under the microscope; this method is described by Manton (1950).

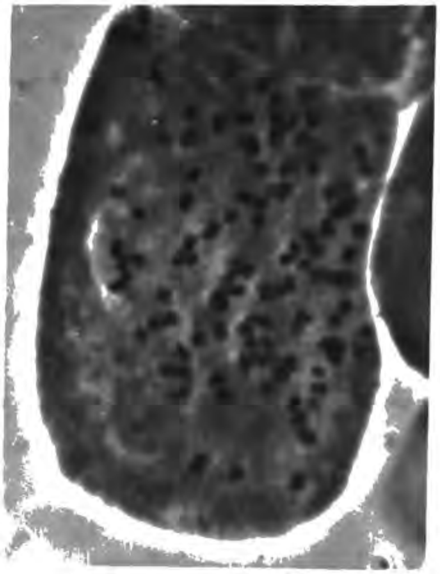
Results

The high number of chromosomes and difficulty of getting them well spread, made it almost impossible to obtain exact counts; somatic counts from the root-tips presented the least difficulties and are given below.

(1) Mitotic counts.

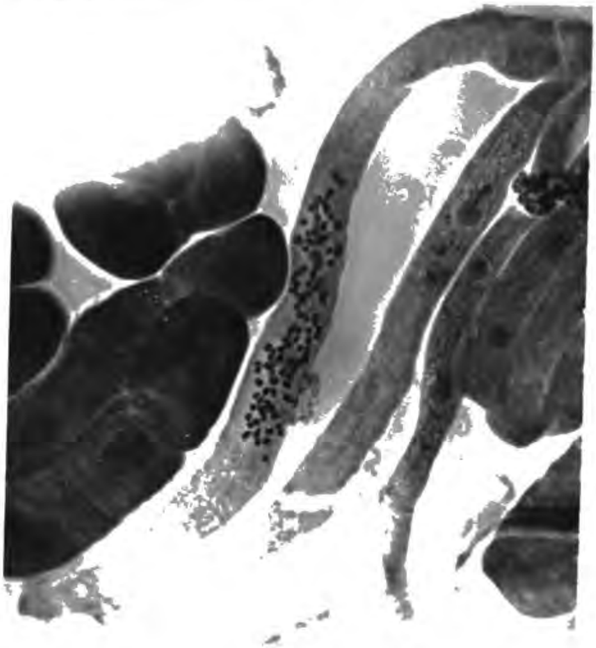
Species	Code No.	Chromosome counts
A. vestita	4/9/101	105 ± 2
		105 ± 2
		104 ± 2
A. vestita	4/24/300a	104 ± 1
		105 ± 2
		106 ± 1 (FIG. 17)
		101 ± 1
		106 ± 1
A. vestita	4/39/269a	104 ± 2
		104 ± 1
		105 ± 1
		104 ± 1
A. vestita	4/30/318b	106 exact. (FIG. 18)
A. vestita montane	5/45/250a	105 ± 2
A. filicaulis s.st.	3(60) n	152 ± 3 (FIG. 19)
	" m	150 ± 2

FIG. 17. (a)



(b)

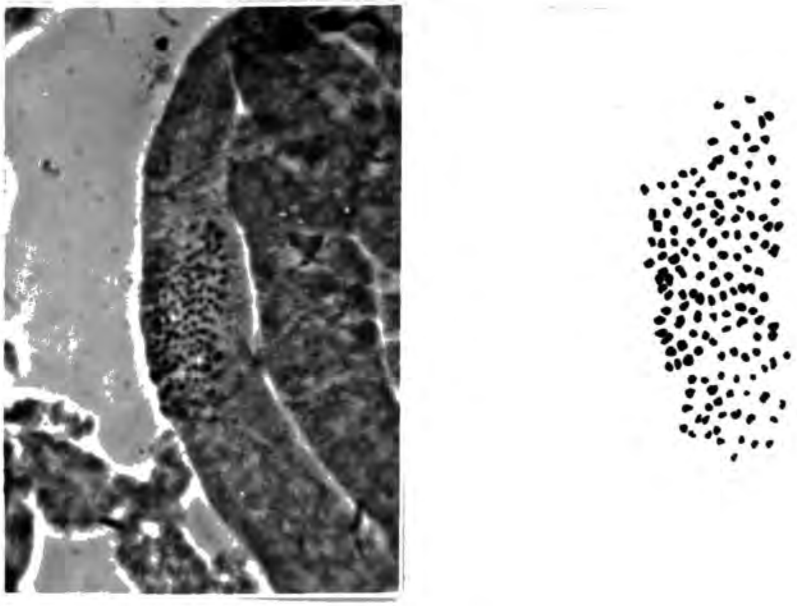
FIG. 18. (a)



(b)

A. vestita (a) Mitotic metaphase (b) Explanatory diagram

FIG. 17. 2n = 106±1 (x 1940) **FIG. 18.** 2n = 106 (x 1160)



(a) (b)

FIG. 19. A. filicaulis s.st. (3(60)m) (a) mitotic metaphase $2n = 150 \pm 2$. (x 1140). (b) Explanatory diagram of (a).

The probable margin of error is given in each case. The count for 4/30/318 is thought to be exact. Plates with explanatory diagrams of some of these are given below. FIGS. 17, 18 and 19.

(2) Meiotic counts

Preparation of pollen-mother-cell squashes was relatively easier than the root-tips and stain differentiation was better, but the interpretation was much more difficult. In all cases there were many univalents, and it was not easy to determine which were bivalents or even if multivalents were present; no certain cases of the latter were found. Certain closely associated pairs of chromosomes have been queried as probable bivalents, whether they are interpreted as such or regarded as univalents makes no difference to the total chromosome number. All interpretations are made in the light of somatic counts obtained from the root-tips. In general, when the larger chromatin bodies were regarded as bivalents and the smaller as univalents, the total chromosome number obtained was near the somatic value of the species; thus this interpretation seems justified and does give some idea of the number of bivalents which usually occur. It is essential to know the somatic value when studying meiotic figures as other interpretations could easily be made; because of this all chromosome numbers are approximate only.

FIG. 20. (a) (b)

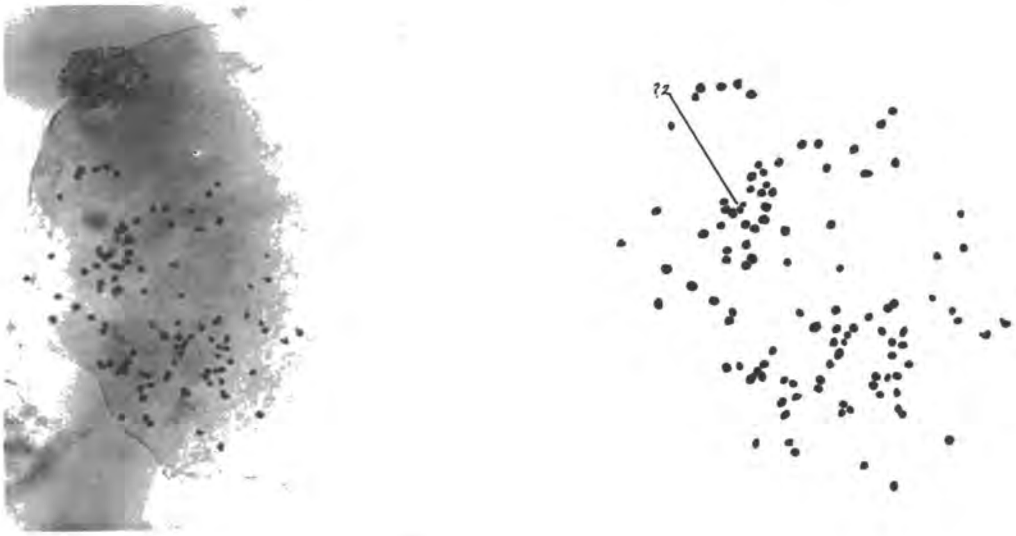
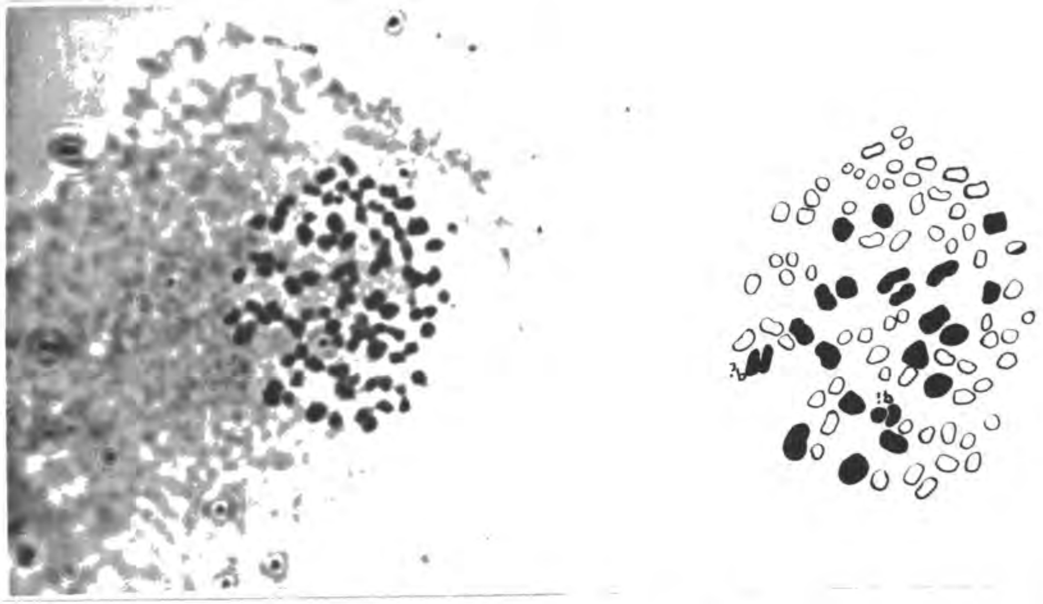


FIG. 21. (a) (b)



Meiosis in A. vestita. FIG. 20. (a) First anaphase or second metaphase showing 109 or 110 univalents. (x 800).

FIG. 21. (a) First metaphase showing 21 (II) + 66 (I). (x 1600)
(b) Explanatory diagram of (a) in each figure.

Species	Code No.	2n		
A. vestita	4/2/31	109 ?+1	?anaphase	
	4/45/414b	c.108	metaphase	I 23 II, 62 I
A. filicaulis s.st.	4/3/55a	c.103	"	I 22 II, 59 I
		c.103	"	I 19 II,65 I
A. filicaulis s.st.	3(60)b	c.150	diakinesis	20 II,c.110 I

Each plate will be considered separately. In the explanatory diagrams, the univalents are outlined, the bivalents and closely associated chromosomes are blacked in.

A. vestita 4/2/31 (FIG. 20 a and b) this was very well squashed and is probably a late anaphase, though it could be regarded as a metaphase II. All the chromatid bodies are much the same size and if interpreted as single chromosomes give 2n = 109 or 110; which is near the number obtained for the somatic counts in the species and the same as that given for *A. vestita* by Turesson.

A. vestita 4/45/414b (FIG. 21 a and b). This is a metaphase plate with 21 II and 66 I. giving 2n = 108.

A. filicaulis s.st. The only somatic count of British material is of somewhat atypical material 3(60) which is considered separately below, Turesson has published values 2n = 101-110. for Scandinavian plants. Interpretation of the meiotic figures of British material has been based on the assumption that this has approximately the same range of numbers.

FIG. 22. (a) (b)

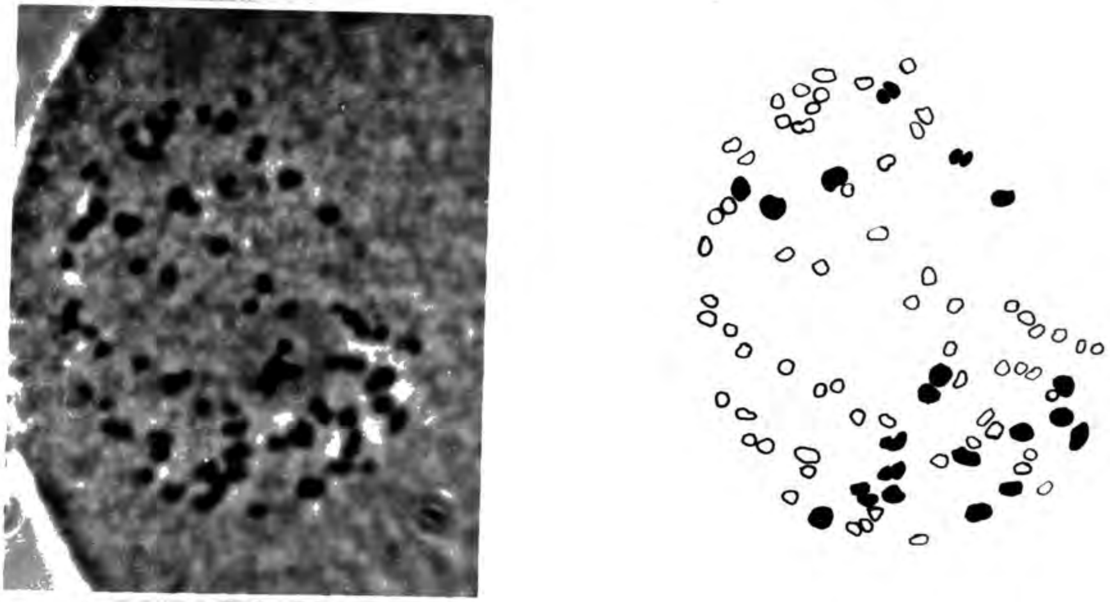
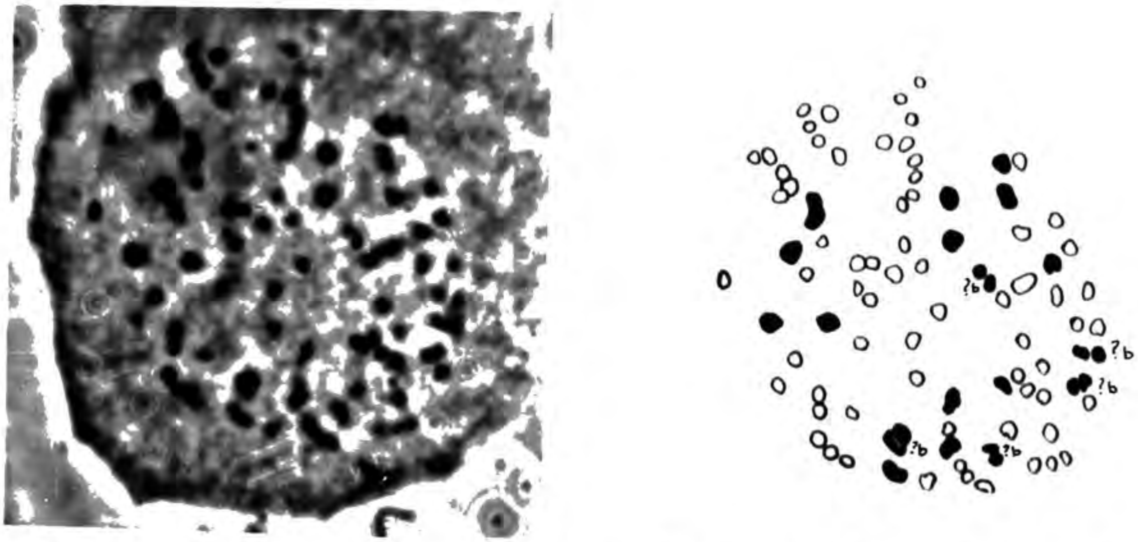


FIG. 23. (a) (b)



Meiosis in A. filicaulis s.st; first metaphase showing in FIG. 22. 20 (II) + 63 (I) (x 1900) FIG. 23. 18 (II) + 67 (I) (x 1475) (b) Explanatory diagram of (a) in each figure.

A. filicaulis s.st. 4/3/55a (FIG. 22). A fairly straight forward metaphase I with 20 II and 63 I giving 2n = 103.

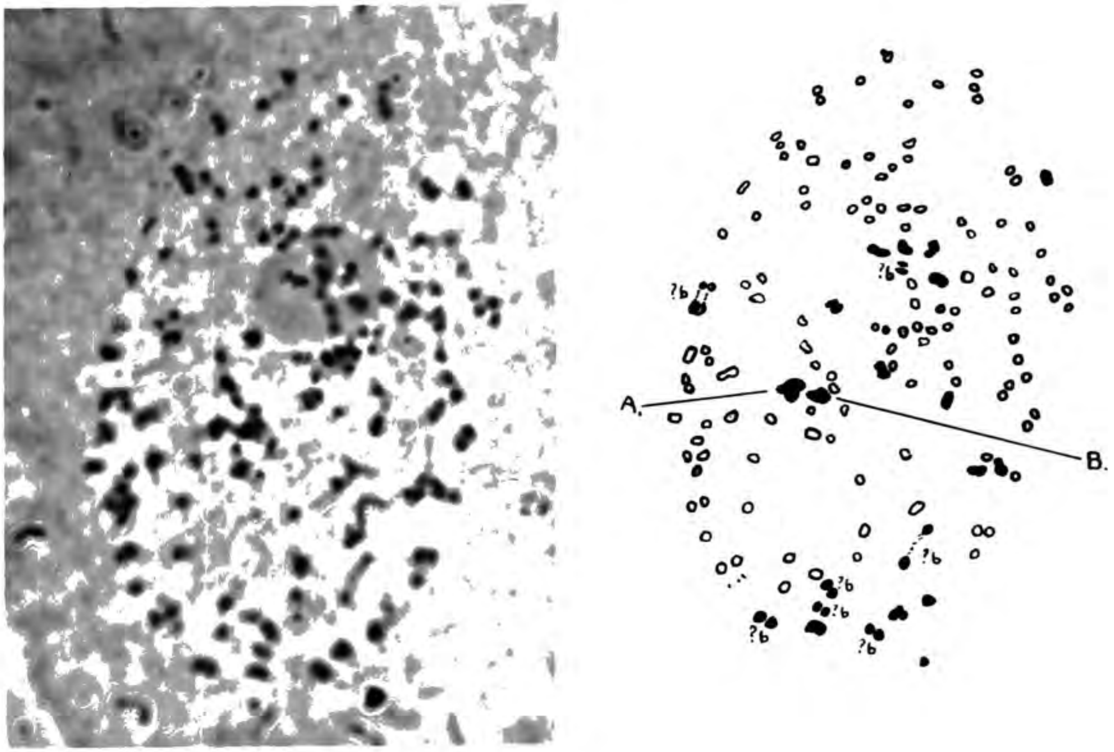
Same plant (FIG. 23) also a metaphase I plate with 2n = 103. 18 II and 67 I.

Although the number of bivalents varies the total number of chromosomes is 2n = 103, it is of particular interest to know if the somatic count is the same, but a countable preparation was not obtained.

A. filicaulis s.st. 3(60)b (FIG. 24 a and b). The presence of the nucleolus and indication of an outer membrane suggests that this is at diakinesis or maybe metaphase I. The diffuse nature of the chromatin bodies makes their interpretation as univalents or bivalents difficult and hence the total number uncertain. Two clusters A and B probably consist of a total of 6 or 7 chromosomes. Of the other bodies, if the larger are interpreted as bivalents, the probable values are 20 II and 117 I giving a total of 159, if all are considered as univalents the total is 144; one above and the other below the somatic value of 2n = c.150.

(3) Cytology of A. vestita

The mean values obtained for lowland plants of A. vestita were:



(a) (b)

FIG. 24. Meiosis in *A. filicaulis* s.st. (3(60)b).
(a) probably diakinesis showing 20 (II) + 117 (I) but see text. (x 1550). (b) Explanatory diagram of (a).

Somatic counts 2n = 104, 105, 105, 106.

Meiotic counts 2n = c.108, c.109.

Inspite of the closeness of the somatic numbers and the difficulty of getting exact counts, it is very probable that several chromosome numbers do occur in the species. Turesson (1957) obtained a range of numbers between 101 and 110 for several species of A. vulgaris agg. He gave 2n = 110 for the only two plants of A. vestita which he examined.

A count was obtained for only one of the dwarf montane plants, this gave 2n = 105, which is within the range of the lowland plants.

(4) Cytology of A. filicaulis s.st.

The only count obtained of a British lowland plant was from a pollen-mother-cell, 2n = c.103. Turesson (1957)found a range of numbers:

2n =	102	103	104	105	106	107	108	109	110
No. of plants	2	6	1	7	5	1	3	4	2

This overlaps the range found in A. vestita. Most interesting and surprising is the value 2n = 150-152 obtained for a A. filicaulis s.st. plant, 3(60), which represents a Scottish mountain population. These plants have the usual A. filicaulis s.st. hair character and wine-red base, but the leaves have very short broad lobes and sharply pointed, somewhat connivent teeth, rather similar to A. wichurae; the leaves tend also to be more shiny and crisp than in other A. filicaulis s.st. plants. They could easily be recognised in the field from amongst other plants of A. vulgaris agg.

The question may be raised here, should this plant be regarded as A. filicaulis s.st.? Morphologically it has some of the characters of the "acutidens" aggregate which contains the only other plants known to have a similar chromosome number, viz. A. oxyodonta 2n = 165-168, A. borealis (syn. A. transpolaris) 2n = 130-152 (Turesson 1957), Unlike this A. filicaulis s.st. plant these species all have adpressed hairs, a distinguishing feature of considerable importance in the taxonomy of A. vulgaris agg. From the morphological point of view 3(60) is best regarded as A. filicaulis s.st.

The chromosome numbers obtained by Turesson (1957) and myself for A. vestita and A. filicaulis s.st. agree well and show no major differences in the cytology of the two taxa, except in the case already mentioned. Both have a range of numbers which are similar to those found in several distinct morphological species in A. vulgaris agg. (Turesson 1957). The difference in hair density which separates

A. filicaulis s.st. from A. vestita is not correlated with any constant difference in the chromosome numbers of these taxa.

So far no counts are available for the genodeme of intermediate hairiness, though it is possible that Turesson's A. vestita may contain some of these.

(5) Cytology of the ecogenodemes

A chromosome count of one example of the dwarf montane ecogenodemes is clearly an insufficient basis for any conclusions on the correlation between chromosome numbers and 'ecotypic' variation. If it is representative of the dwarf ecogenodeme then there would appear to be no major cytological differences between the ecogenodemes. Further data on the same kind of variation are provided by Turesson (1956). He worked with six species (but not A. filicaulis), and also found statistically significant differences in stem and petiole length, and leaf size between genodemes. His analysis was very similar to that described above. (p. 39). Later (1957) he published chromosome counts of many species but it is not clear if the numbers are those of the plants used in the earlier work or not. Turesson did not give the chromosome numbers of his morphological genodemes individually; neither is it known if the plants used in his experiment all came from the same or different types of habitat. Turesson concluded "Our Alchemillas apparently do not adapt themselves to different habitats by any change in chromosome numbers". Difference in habitat is implied by the wide latitudinal range of the original samples. Only by obtaining exact counts of several plants of each genodeme will it be possible to determine if this kind of variation is correlated with differences in the chromosome numbers.

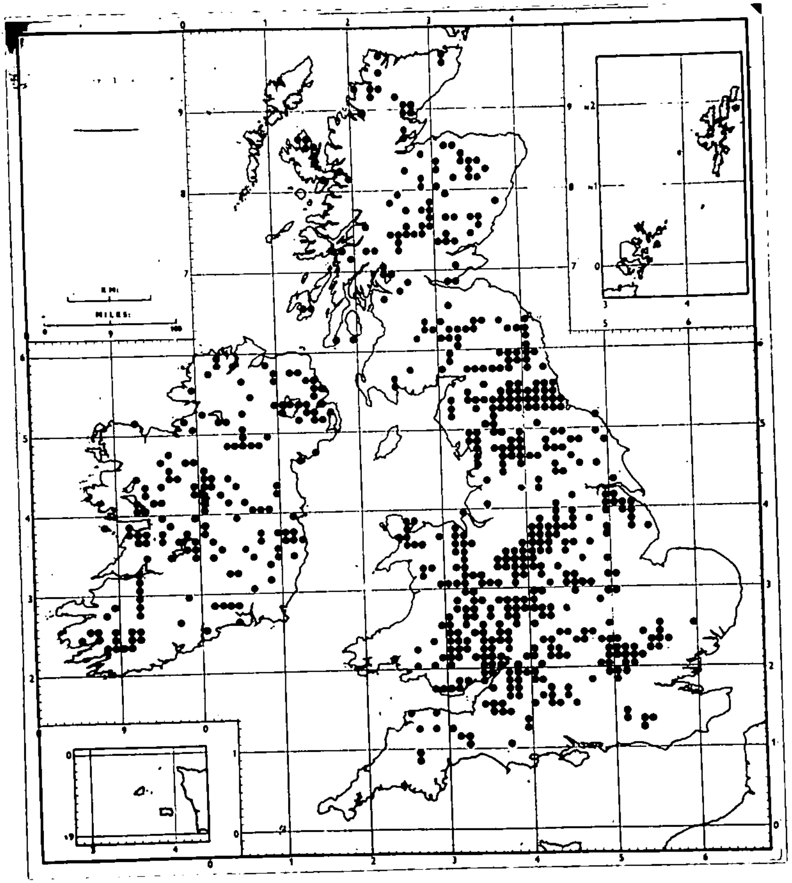


FIG.25. A. vestita

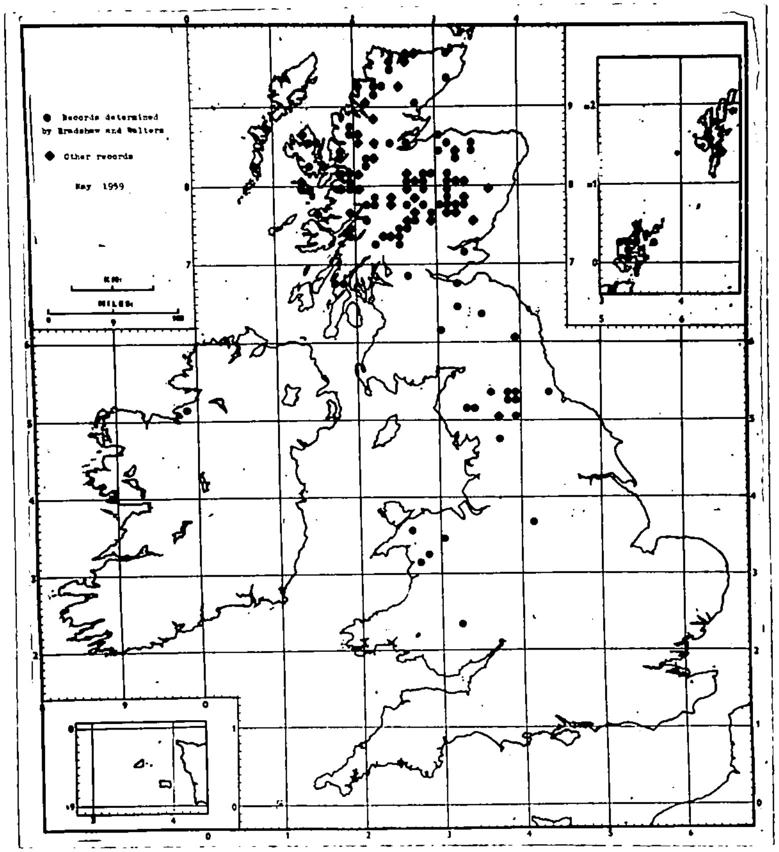


FIG.26. A. filicaulis s.st.

II. Distribution of the segregates of A. filicaulis s.l.

(1) In Britain

A. filicaulis s.l. is the most widespread of the British Alchemilla species. At least since the work of Wilmott (1922), the two main segregates A. vestita (A. minor Huds.) and A. filicaulis s.st. have been treated as separate species; thus their individual distribution patterns are well known. A. vestita is the most widely distributed Alchemilla in Britain and nearly all records for A. vulgaris agg. in southern England refer to this plant. A. filicaulis s.st. is constantly more northern and is largely restricted to mountain habitats.

This is clearly shown in the maps. (FIG. 25 and FIG. 26). These are based on field records obtained by the Botanical Society of the British Isles Maps Scheme - determined by S.M. Walters or myself and from herbarium material. Careful selection of intermediate material was not made until the later stages of collection of the records so that the maps are based on A. filicaulis s.l. separated into two groups A. vestita and A. filicaulis s.st. only.

In order to assess the frequency of each of these segregates and the intermediate, an analysis was made of a series of populations ranging from Leicester to North-west Scotland. The areas selected were those where adequate populations of *Alchemilla* were thought to exist; unfortunately it has not been possible, so far, to examine populations in the south of England and Wales and in Ireland.

Sampling. A population was taken to consist of all the *A. filicaulis* s.l. plants growing in a ± uniform community, usually not exceding two acres, except in some Scottish mountain areas. Details of associated species and habitats are given later. Sampling was done between late June in the south and mid-August in the north, when a mature summer leaf and inflorescence were collected from twenty plants as well dispersed over the population area as possible and not closer together than two feet; it was not always possible to collect twenty good inflorescences.

Analysis. After pressing, each inflorescence was scored for hairiness type as described earlier (p. 16). In the light of the cultivation and breeding experiments which showed the range of variation which could be expected in each segregate, plants were grouped into the three segregates, as described above. (p. 35).

i.e.	*A. vestita*	hairiness	grades	0-3
	intermediate	"	"	4-5
	A. filicaulis s.st.	"	"	6

The percentage of each in each population was then determined. The distribution of the three groups is shown

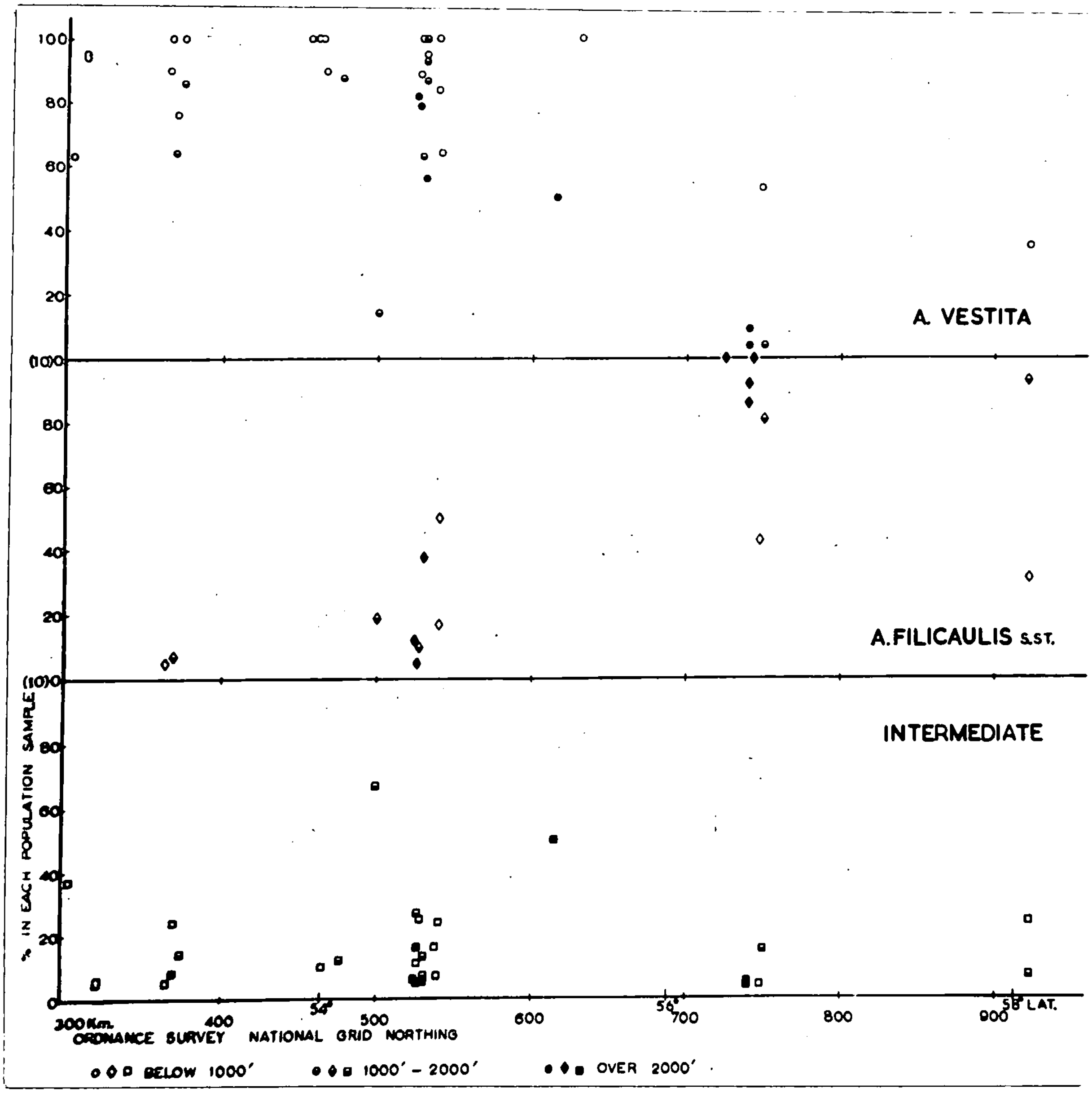


FIG. 27. Proportion of each segregate of A. filicaulis s.l. in population samples from Leicestershire (300km.N.) to N.W. Scotland (920Km.N.)

in FIG. 27) in which the percentage of each per population is plotted against the latitude as expressed by the Ordnance Survey National Grid northings. Each group is treated independently without any attempt to link it with the percentage of the other groups in the same population.

A. vestita and A. filicaulis s.st. contrast strongly and confirm the picture given in the maps. High proportions of A. vestita are most common in the south. A. filicaulis is in greatest frequency in Scotland, the most southern records of A. filicaulis in these samples were in Derbyshire, (O.S. Northing Km 365 which represents one plant in each population). Its occurrence is more frequent in the North of England (500-550 Km. North); here the plant occurs in several populations at frequencies between 5% and 20%, and reaches 50%. The difference in distribution is further emphasised when the altitudinal range of the plants is considered.

From Leicester to Swaledale (300-500 Km. N) none of the localities examined were above 1000'. A. vestita is predominant in all except the Swaledale population; the only records of A. filicaulis s.st. are at the higher levels of 950' and 1000'. In N. England both species occur over a large altitudinal range, A. vestita from 450' to 2,500', A. filicaulis s.st. from 500' to 2500'; but eight out of nine populations with -80% *A. vestita* are no higher than 1500' whilst half the recorded plants of *A. filicaulis* s.st. occur at or above 2000'. In South Scotland (610 Km. N.) *A. filicaulis* s.l. is very local in its occurrence; *A. vestita* occurs up to 2000', a very little *A. filicaulis* s.st. was found in one locality only, at 750'.

In Central and North Scotland (740 and 920 Km. N.) *A. filicaulis* is generally more common. At high altitudes (2000' +) in the Central Highlands *A. filicaulis* s.st. is the more common but some plants of *A. vestita* are usually present. At lower altitudes (c. 1000') *A. vestita* is the more common but the proportion varies. In N.W. Scotland the localities are comparatively low (-1000') *A. filicaulis* s.st. is common, but again the proportion in the populations varied.

These details of the altitudinal distributions of the two groups support the spatial patterns (FIGS. 25 and 26); illustrating that *A. filicaulis* s.st. is restricted to a more northern and more montane distribution than *A. vestita*.

The intermediates are found throughout the spatial and vertical range of the populations sampled (FIG. 27 lower graph), and in most cases the proportion is small (-30%). Only three populations were found in which the intermediates were common; these are in Swaledale (500 Km. N.) and Teesdale (530 Km. N.), (this sample was too small for inclusion in the graph), and Midlaw Burn (615 Km. N.). The first two are woodland habitats and also contain a small proportion of A. filicaulis s.st. Intermediates from those populations keep their character in cultivation and breeding. From the results of all the cultivation work it is very probable that the intermediate is over-recorded in these field samples since the score will include phenotypic variants of A. vestita and A. filicaulis s.st., as well as genotypic intermediate types.

Further discussion of the distribution patterns is left until the ecology of the groups has been considered.

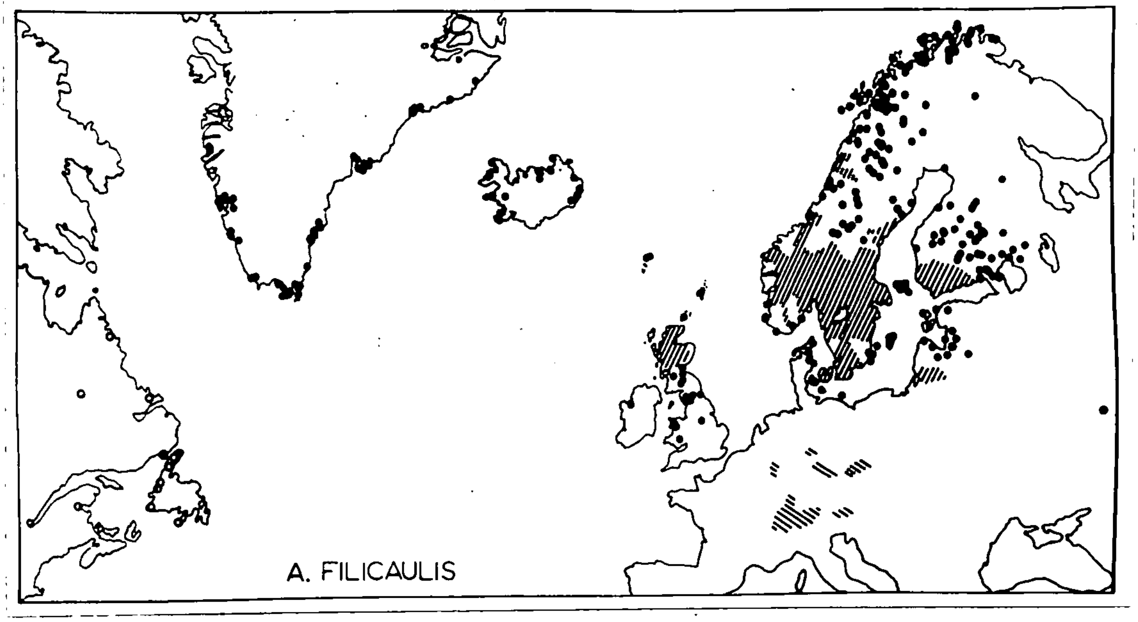
(2) Outside Britain

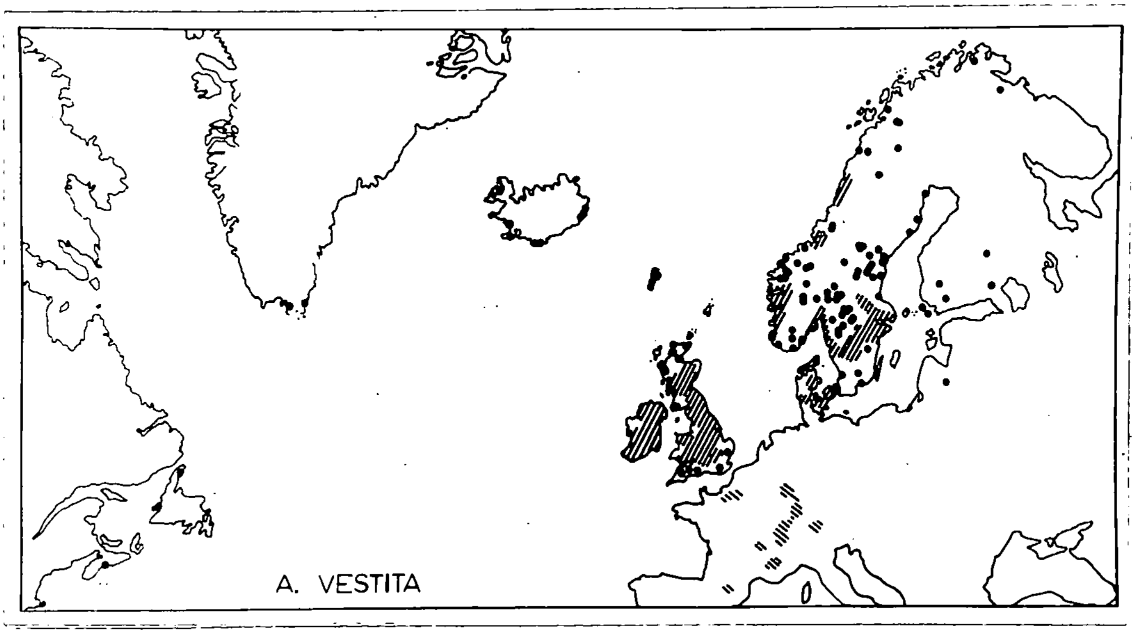
Details of the total distribution of the segregates of A. vulgaris agg. are often incomplete because of the lack of individual records of more than the most distinct and widespread segregates of this critical aggregate and would appear to be under-recorded especially in Central Europe where other larger and apparently better grown plants are plentiful.

Furthermore, in some countries A. filicaulis s.l. is not subdivided into the two taxa; where A. filicaulis s.st.

and A. vestita are both recorded plants of intermediate hair-types (4-5 described above) will be included in both taxa. Naturally the validity of literature records depends upon the authors and the intensity of Alchemilla study in this country in question. Consequently published records should be used only with considerable discretion and backed up by examination of field records and herbarium material wherever possible.

The distribution maps (FIGS. 28 and 29) are based on published records and herbarium specimens, and the data fall into three categories; reliable records based on herbarium material seen by the author, probably reliable literature data and thirdly, published data which require confirmation. The distribution in Scandinavia and the Baltic countries is based on Samuelsson (1943), the data for the latter countries and Denmark are supported by the appropriate floras and papers. (Raunkiaer 1906, Juzepczuk 1941 and Zamalis 1933). This is probably the most complete and accurate in Europe. Most records in France, Switzerland and Austria are based on Buser (1893) and herbarium specimens (!), no doubt these, too, are authentic but probably very incomplete. Later (1895) Buser only recorded A. filicaulis from the Valais, he may have included one or even both taxa under this name following some confusion in nomenclature between 1893 and 1895.





FIGS. 28 and 29. World distribution of *A. vestita* and *A. filicaulis*.

● ////// Verified or apparently reliable records.

\\\\\\ Probably reliable records.

○ Unverified records, reliability unknown.

There is very little reliable information for Germany and the Low Countries; recent work by De Langhe and Reichling (1954) and Sougnez (1957) gives *A. filicaulis* s.st. in the mountainous S.E. of Belgium and Luxembourg, the former authors say *A. vestita* is absent from this area. This does not support the data given by Samuelsson that "*A. vestita* has a rather well linked field of distribution.... through Normandy, Belgium, Netherland to N.W. Germany with fingers into the Thuringen Mountains, and through Holstein to Great Britain". For *A. filicaulis* s.st. he gives the mountain regions of W. Germany. Floras for these areas do not separate the two taxa; and details should be regarded as provisional only. In East Germany *A. filicaulis* s.st. is known from Pommern, otherwise little data is available. The taxa do appear to be absent from the Central East European countries, neither Pawlawski (1947) nor Juzepczuk (1941) record them in their intensive studies. Soó and Jávorka (1951) do not record them for Hungary but *A. filicaulis* is included in the Carpathians in an earlier paper by Soó and Palitz (1936), this requires investigation. They are not recorded for Transilvania in Savulescu, (1956) where several *Alchemilla vulgaris* species are recorded,or other Balkan countries, Italy or Spain.

The absence of really critical, comprehensive studies in France, Germany and the Low Countries gives very disjunct distributions for both taxa in Central Europe, *A. filicaulis* s.st. may truly be limited to the mountain areas; but, since *A. vestita* is so frequent in lowland England and south Scandinavia a greater frequency is to be expected at least in the adjacent parts of the mainland. On the other hand, *A. vestita* is not frequent in the south east of England, which has the most 'Continental' climate in the island; so, like *A. filicaulis*, *A. vestita* may be montane in Central Europe and lowland records such as that near Paris are local introductions.

In the wider Atlantic area; both taxa occur in the Faeroes and Iceland; details of their distribution are taken from Lindberg (1909) based on herbarium material. Distribution of *A. filicaulis* s.st. in Greenland is based on Bøcher (1933) and herbarium material (!), the species occurs in his 'high perennial field community' and is truly native. *A. vestita* is recorded from two localities only, Naniseq Fiord (60°. 33') (Devold and Scholander, 1933) and Julianehaale. (Lindberg, 1909). As no details of the habitats are available, these are best regarded as adventives.

The distribution of both taxa in N. America is based on herbarium material determined by Walters and the author;

and unverified records in Hultén (1958). A number of these records are from apparently natural habitats viz. A. filicaulis from 'turfy limestone barrens', 'springy and bushy slopes', 'In a damp thicket under limestone crest, 650 M.' and 'on moist gravelly soil with sedges and grasses', these are all in Newfoundland; one record in Labrador 'Hades Hills 56° 58' Lat., N. sous les Alnus de la berge, le long d'un minuscule ruisseau ombrage' appears to be of truly native plants. Other records are of more open habitats including harbours, roadsides and other sites near human settlements where it is difficult to determine the status of the plant.

The status of A. vestita is much more difficult to determine, plants from 'gravel by a brook' in the St. John Highlands and 'dry open places near first pond near Curling' both in Newfoundland may be truly native. Other records from Newfoundland and E. Canada are more doubtful.

The presence of good A. filicaulis s.st. in natural vegetation in Greenland establishes its amphi-atlantic status; probably it is also native in America, at least in Newfoundland. The available data for A. vestita in both countries are such that it is not possible to decide its status, it is probably best to regard it as an adventive until substantial evidence for its native status is obtained.

The total geographical range of undoubtedly native A. filicaulis s.st. is amphi-atlantic, arctic-montane in accordance with Hultén's classification (1954 and 1958). Since A. vestita is probably only native in Europe including Iceland it is best classified as European, boreal-montane (Hultén 1954, Group 12). Both species show distinct Atlantic tendencies. (Hultén's group 19); Samuelsson considered them to belong to an oceanic group.

Distribution of the intermediate outside Britain is completely unknown. Plants of intermediate type are known in Swedish collections, but it is not possible to tell if these are genotypes or phenotypes.

III. ECOLOGY OF THE SEGREGATES OF *A. FILICAULIS* s.l.

(1) In Britain

The geographical and altitudinal distribution of *A. filicaulis* s.st. coincides with a portion of the wider distribution of *A. vestita*; as there is no clear demarcation, it is very necessary to know if the two taxa can be separated on the basis of their ecological requirements.

It has not been possible to cover the whole range of the taxa in Britain but notes on the habitat and associated species have been made in a number of regions including those where the ranges overlap. The number of samples in each region varies from three to twenty six; as far as possible the range of habitats in which the species occur has been covered and in some areas. e.g. North Pennines, details of several examples of each type have been recorded.

Collection and analysis of ecological data

The methods of sampling populations of *A. filicaulis* s.l. are the same as are described above (p. 61) and most habitats are those used in the population study. Notes were made on the type of soil, slope, aspect and altitude and the associated species. The assessment of the floristics of each community follows the method used by Poore (1955) using a quadrat of appropriate size for the vegetation and scoring each species according to the Domin scale.

Cover c.100%	10	Abundance - Cover c. 20%	5
75%	9	c. 5%	4
50–70%	8	Scattered cover very small	3
33–50%	7	less	2
25–33%	6	scarce	1
		isolated	x

Additional lists without quantitative assessment were made in some cases, especially rock-ledges and mountain habitats where the flora was very heterogeneous.

Gregariousness. Under natural conditions A. filicaulis s.l. rarely forms dense clumps or stands such as are found in the case of A. acutiloba and A. monticola. Usually the plants of A. filicaulis s.l. are well dispersed each with a few shoots. In the close grazed montane habitats where the more branched dwarf ~~ecotypes~~ ecogenodemes occur, dense mats of shoots may be found.

Plant communities. Full details of the floristics of about ninety habitats are given in TABLES 9 a,b,c; 10. Map grid references, localities and code numbers are given in Appendix A. All but five contain A. vestita, twenty-nine contain A. filicaulis s.st. As the variation in climate and edaphic factors is appreciable over the latitudinal range cover, each area will be considered separately first; a summary of the more constant species in each area is given in TABLE 11. Subsequently the findings for each taxa will be compared.

TABLE 11 Constancy values of the more frequent species in each areawhere populations were studied as in TABLES 9 and 10. The constancy of a species is shown by the % of populations in which it occurs in each area.

A. vestita

I	TABLE	9a	nos.	1 - 6	Leicestershire
II	"	"	"	7 - 17	Derbyshire
III	"	"	"	18 - 20	Wales
IV	"	"	"	22 - 27	Yorkshire (excluding Swaledale & Teesdale)
V	"	9b	"	28 - 31	East Durham
VI	"	"	"	32 - 57	North Pennines below 1350'
VII	"	9c	"	58 - 71	" " above 1350'
VIII	"	"	"	72 - 76	South Scottish Uplands and Central Highlands
IX	"	"	"	77 - 80	Central Highlands (montane)
X	"	"	"	86 - 88	North West Scotland

A. filicaulis

XI	TABLE	10	nos.	32 - 34	woods
XII	"	"	"	9 - 92	Derbys and East Durham
XIII	"	"	"	48 - 76	North Pennines and South Scotland
XIV	"	"	"	77 - 85	Central Highlands
XV	"	"	"	86 - 88	North West Scotland

TABLE II

	A.vestita										A.filicaulis				
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Achillea millefolium	17	36	100	33	75	50	36	20	.	.	.	33	46	.	.
Ajuga reptans	17	54	33	33	75	31	.	.	.	.	100	.	.	.	.
Alchemilla alpina	.	.	.	.	.	.	.	.	100	33	.	.	.	100	33
A. acutiloba	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.
A. filicaulis	.	9	.	.	25	31	36	60	50	100	100	100	100	100	100
A. glabra	.	54	.	83	25	88	85	80	100	100	100	33	62	86	100
A. glomerulans	.	.	.	.	.	19	.	.	50	.	.	.	8	43	.
A. minor	.	.	.	51	.	.	.	.	.	33	.	.	.	.	33
A. monticola	.	.	.	.	.	31	.	.	.	.	.	.	.	.	.
A. subcrenata	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.
A. vestita	100	100	100	100	100	100	100	100	100	100	100	100	100	29	100
A. wichurae	.	.	.	33	.	12	.	.	100	67	.	.	.	100	67
A. xanthochlora	.	9	33	33	.	62	.	60	.	.	100	.	15	.	.
Bellis perennis	17	64	67	17	75	58	.	20	.	67	33	67	31	.	67
Campanula rotundifolia	17	36	33	83	.	39	43	.	50	.	33	67	31	72	.
Carex caryophyllea	17	36	67	67	50	58	64	40	25	.	.	100	77	14	.
C. flacca	50	82	33	83	100	31	7	20	.	67	.	67	39	14	67
C. pulicaris	.	.	.	.	.	.	.	.	50	.	.	.	29	72	33
Centaurea nigra	50	55	.	33	100	58	.	.	.	.	100	33	31	.	.
Cerastium vulgatum	67	64	.	.	75	62	79	60	25	67	67	67	54	14	67
Cirsium palustre	67	.	.	.	.	.	.	20	.	33	.	.	.	.	33
Conopodium majus	17	55	.	67	.	88	.	20	.	.	67	33	31	.	.
Euphrasia agg.	.	.	67	33	.	31	29	20	75	67	.	33	.	82	67
Galium cruciata	.	46	.	50	75	12	7	.	.	.	67	67	.	.	.
G. verum	33	73	.	50	75	19	.	80	.	.	.	100	.	.	.
Geranium sylvaticum	.	.	.	17	.	27	.	20	.	.	67	.	.	.	.
Geum rivale	.	27	.	17	.	27	29	.	50	33	33	.	.	72	33
Leontodon hispidus	33	64	67	.	75	62	21	.	.	.	67	67	39	.	.
Lotus corniculatus	100	91	33	67	50	73	7	60	.	67	33	100	46	29	67
Luzula campestris	67	73	67	83	50	69	57	.	.	33	67	100	54	.	33
Plantago lanceolata	67	73	67	50	75	88	21	100	.	67	33	33	62	29	67
Polygomum viviparum	.	.	.	.	.	7	14	.	75	33	.	.	14	72	33
Potentilla erecta	83	55	33	50	.	46	36	60	.	67	67	33	46	29	67
Poterium sanguisorba	.	64	.	67	.	15	.	.	.	.	.	.	.	.	.
Prunella vulgaris	83	46	100	33	25	35	43	60	.	100	67	.	62	.	100
Ranunculus acris	100	55	100	83	75	62	43	60	25	33	33	67	39	43	33
R. bulbosus	.	36	.	67	50	62	7	.	.	.	67	33	.	.	.
Rumex acetosa	83	55	33	50	75	38	43	60	50	.	67	67	.	.	.
Sanguisorba officinalis	67	18	.	.	.	23	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	.	.	.	.	.	.	.	20	75	67	.	.	.	72	67
S. oppositifolia	.	.	.	.	.	.	.	.	25	33	.	.	.	72	33
Selaginella selaginoides	.	.	.	.	.	.	.	.	.	100	.	.	14	29	100
Senecio jacobaea	50	55	.	67	100	35	.	20	.	.	.	.	.	.	.
Succisa pratensis	33	64	100	50	25	44	.	20	.	33	67	67	23	14	33
Taraxacum agg.	33	36	.	33	50	66	7	20	.	33	.	100	39	29	33
Thymus drucei	.	27	33	67	25	31	64	20	50	100	.	100	54	57	100
Trifolium medium	17	9	.	.	75	4	.	.	25	33	.	.	.	.	33
T. pratense	83	55	33	67	75	58	.	60	.	.	67	67	23	.	.
T. repens	17	64	100	67	25	62	64	100	25	33	33	33	77	29	22
Veronica chamaedrys	33	64	100	50	75	50	14	60	.	.	67	100	31	.	.
Viola riviniana	50	36	67	17	25	62	64	.	75	100	100	33	46	57	100
Agrostis tenuis	.	27	100	50	25	38	43	80	.	100	33	.	62	.	100
Anthoxanthum odoratum	67	91	33	83	50	92	29	60	25	67	67	67	62	57	67
Briza media	67	64	33	83	100	54	7	20	.	67	.	67	46	.	67
Cynosurus cristatus	83	36	100	17	50	42	.	80	.	.	.	67	46	.	.
Dactylis glomerata	50	73	33	50	100	69	.	40	.	.	100	100	15	.	.
Deschampsia caespitosa	50	.	.	33	25	38	21	20	100	33	33	.	23	72	33
Festuca ovina & rubra	83	100	67	100	50	92	79	80	100	100	67	100	85	72	100
F. vivipara	.	.	.	.	.	.	.	.	75	33	.	.	.	43	33
Lolium perene	.	.	.	.	75	.	.	.	.	.	.	.	.	.	.
Holcus lanatus	83	82	67	33	50	62	.	80	.	33	100	67	39	.	33
Koeleria gracilis	.	55	.	67	25	15	7	.	.	.	.	67	15	.	.
Poa trivialis	67	9	.	17	50	12	14	20	.	.	.	.	.	.	.
Nardus stricta	.	.	.	.	.	.	7	40	50	.	.	15	57	.	.

TABLE 9a

	1	2	3	4	5	6		7	8	9	10	11	12	13	14	15	16	17		18	19	20		22	23	24	25	26	27	
Coryl ave	.	.	.	.	.	.		.	.	.	.	+	.	.	.	+	+	+	36					.	.	.	+	+	.	
Crata mon	.	.	.	.	.	.		.	.	.	.	+	.	.	.	x	+	.	27					.	.	.	.	.	.	
Fraxi exc	.	.	.	.	.	.		.	.	.	.	.	.	.	.	+	+	.	18					.	.	.	.	+	.	
Achil mil	1	.	.	.	.	.	17	.	2	.	.	1	.	.	3	.	.	2	36	+	+	+	100	.	2	+	.	.	.	33
Agrim eup	.					.						.				.	.			+	.	.	33	.	1	.	.	.	.	17
Ajuga rep	.	.	.	.	.	1	17	1	.	.	x	4	.	.	1	1	1	.	55	+	.	.	33	.	.	.	1	1	.	33
Alche fil		.	.					.	.	x	.	.	.	.	.	.	.	.	9	.	.	.		.	.	.	.	.	.	
A. gla		.		.	.			1	.	2	.	1	.	.	3	.	x	3	55	.		.		.	3	+	2	2	1	83
A. min	.							.	.	.	.	.	.	.	.	.	.	.						.	.	.	3	3	2	51
A. ves	2	2	1	+	3	1	100	1	1	1	1	2	x	3	4	1	2	3	100	+	+	+	100	+	3	+	2	1	1	100
A. wic	.	.	.	.		.		.	.	.	.	.	.	.	.	.				.	.			.	.	+	1	.	.	33
A. xan	.	.	.	.	.	:		.	.	.	.	.	.	1	.	.	.	.	9	+	.	.	33	.	2	+	.	.	.	33
Anemo nem	.	.	.	.	.	.		.	.	1	.	.	.	.	1	.	.	.	18	.	.	.		.	.	.	1	.	.	17
Belli per	.	.	.	.	.	3	17	3	3	3	2	2	.	3	1	.	.	.	64	+	+	.	67	+	.	.	.	.	.	17
Campa rot	.	.	.	.	.	1	17	.	2	1	2	.	.	.	.	1	.	.	36	.	.	+	33	.	1	+	2	2	x	83
Carda pra	.	.	.	+	.	.	17											.		.	+	.	33	.	.	.	.	.	.	
Carex car	.	.	.	.	.	2	17	.	2	2	.	.	.	.	2	2	.	.	36	.	+	+	67	.	.	+	1	1	3	67
C. fla	2	.	.	.	1	2	50	2	.	2	2	4	2	4	3	.	2	2	82	.	+	.	33	+	1	+	1	1	.	83
C. hir	2	.	.	+	2	.	50						.		.	.														
C.panicea	2	.	1	.	.	.	33	.	.	.	.	.	.	.	.	.	.	.						.	.	+	.	.	4	33
Centa nig	3	.	2	+	.	.	50	1	.	1	x	.	3	.	3	1	.	.	55					.	.	+	3	.	.	33
Ceras vul	1	.	1	+	1	.	67	2	1	1	.	1	1	.	.	1	1	.	64	.		.								
Chrys leu	.	.						1	.	.	.	.	.	.	1	.	.	.	18	+	.	.	33	.	.	+	.	2	.	51
Cirsi arv	1	1	.	.	1	1	67	.	1	.	2	.	.	.	1	1	.	x	46	.	.	+	33	.	.	.	1	.	1	33
C. pal	1	.	1	+	1	.	67	1	.																		.	.		
C. vul	.	.	.	.	.	1	17	1	.	.	.	.	.	.	.	.	.	x	18	.		.		+	1	.	.	.	.	33
Conop maj	.	1	.	.	.	.	17	1	.	3	1	.	3	.	2	.	.	2	55					+	1	.	1	2	.	67
Euphr agg																				.	+	+	67	.	.	.	1	1	.	33
Filip ulm	.	.	3	.	.	.	17	2	.	.	.	.	.	.	2	.	.	.	18					.	1	.	1	.	.	33
Galiu cru	.							.	.	1	.	.	.	.	1	1	2	x	46	.		.		+	1	+	.	.	.	50
G. her	.	.	.	.	.	1	17																							
G. pum								.	.	.	.	.	.	.	.	.	2	.	9					.	1	.	1	.	1	50
G. ver	1	.	.	.	1	.	33	.	2	1	1	.	3	3	.	3	2	4	73					+	1	+	.	.	.	50
Geum riv								3	.	.	.	1	.	.	1	.	.	.	27					.	.	+	.	.	.	17
Helia cha								.	.	.	.	.	2	.	.	5	3	3	36					+	.	.	3	.	.	33
Herac sph	.	1	.	.	.	.	17	1	.	1	.	.	2	.	1	.	.	.	36					.	.	.	1	.	.	17
Hiera pil	.	.	.	.	.	2	17	.	2	.	1	.	.	.	.	2	.	.	27	.	+	.	33	+	.	.	1	.	2	50
Hypoc rad	.	.	.	+	.	.	17	.	.	.	x	.	.	.	.	.	.	.	9											
Lathy pra	1	1	1	.	.	.	50	.	.	.	.	.	.	.	1	.	.	.	9					.	1	.	1	.	.	34
Leont aut								.	.	1	1	.	.	1	.	.	.	.	27	+	+	.	33							
L. his	1	.	1	.	.	.	33	2	1	1	2	.	2	3	3	.	.	.	64	+	+	.	67							
Linum cat								.	2	1	.	.	.	.	.	.	.	.	18	.	+	+	67	+	.	.	1	.	1	50
Lotus cor	3	2	2	+	1	1	100	1	4	1	2	.	4	4	3	3	2	4	91	.	+	.	33	.	2	+	2	.	1	67
Luzul cam	3	2	1	.	3	.	67	3	3	2	3	4	.	3	2	.	3	.	73	+	.	+	67	+	1	+	3	2	.	83
Plant lan	1	.	1	+	.	4	67	4	3	3	2	.	3	2	3	.	.	4	73	+	.	+	67	+	3	+	.	.	.	50
P. med	.	.	.	.	.	3	17	.	.	3	5	.	.	3	1	.	.	.	36					+	1	+	.	.	.	50
Polyg vul								.	+	1	2	.	x	.	.	.	.	.	36	.	.	+	33	+	.	.	.	.	.	17
Poten ere	3	1	x	.	1	2	83	1	.	2	.	3	.	.	.	2	2	3	55	+	+	.	33	.	.	.	1	3	1	50
P. ste	.	.	.	.	1	2	33	.	.	.	x	3	.	.	1	1	.	2	46	.	+	.	33	.	1	.	1	.	1	50
Poter san								.	.	3	3	.	3	.	4	4	4	3	64					.	3	+	2	.	3	67
Primu ver						1	17	1	.	1	.	.	.	.	2	1	.	3	46	+	.	.	33	+	1	+	.	.	x	67
P. vul																				+	.	.	33	.	.	.	3	2	.	34
Prune vul	1	2	.	+	1	3	83	5	2	2	1	.	.	.	.	1	.	.	46	+	+	+	100	.	.	+	1	.	.	33
Ranun acr	3	4	3	+	1	2	100	3	2	2	.	.	.	3	1	.	1	.	55	+	+	+	100	+	1	+	1	2	.	83
R. bul								.	2	.	3	2	.		1	.	.		36					+	.	+	.	2	1	67
R. fic	.	.	1	+	.	.	33																	+	1	.	.	.	.	33
R. rep	1	2	.	+	.	.	50	3	.	.	.	.	.	.	.	.	.	.	9					.	.	+	.	.	.	17
Rumex ace	3	3	1	+	4	.	83	3	.	3	2	2	.	.	1	.	.	2	55	.	.	+	33	+	3	+	.	.	.	50
Sangu off	3	.	3	+	.	1	67	4	.	3	.	.	.	.	.	.	.	.	18											
Senec jac	2	.	.	.	1	2	50	1	.	3	1	.	.	2	.	1	1	.	55					+	x	+	1	.	.	67
Stach off	2	.	.	.	1	3	50	1	.	2	2	.	.	.	.	.	.	3	36					.	3	.	.	1	.	17
Stell gra	3	.	.	.	.	.	17	1	.	.	.	.	.	.	.	.	.	.	9											
Succi pra	2	.	.	.	.	4	33	1	.	6	.	.	2	.	3	1	2	5	64	+	+	+	100	.	.	+	4	8	.	50
Tarax agg	.	.	1	+	.	.	33	.	1	2	1	.	3	3	.	.	.	3	36					+	.	.	1	.	.	33
Teucr sco								.	.	.	.	.	.	.	.	2	2	4	27											
Thymu dru								.	.	3	x	.	.	.	.	2	.	.	27	.	.	+	33	+	.	+	2	.	1	67
Trifo pra	.	3	3	+	3	2	83	4	.	2	2	.	.	2	1	.	1	.	55	.	.	+	33	+	1	+	2	.	.	67
T. rep	2	.	.	.	.	.	17	4	3	2	2	.	.	4	.	2	1	.	64	+	+	+	100	+	.	+	.	2	1	67
Veron cha	.	1	.	.	3	.	33	2	.	1	x	.	.	.	1	1	1	2	64	+	+	+	100	.	1	+	2	.	.	50
Viola riv	1	1	.	.	4	.	50	.	.	.	.	1	.	.	.	2	1	2	36	+	+	.	67	.	.	.	1	.	.	17
Agros ten								5	.	.	.	4	.	.	.	.	2	.	27	+	+	4	100	+	.	+	.	4	.	50
Antho odo	5	6	4	.	6	.	67	4	6	5	4	7	6	5	.	6	7	7	91	.	.	3	33	+	6	+	3	3	.	83
Briza med	2	.	2	+	.	3	67	3	6	4	4	.	4	4	.	4	.	.	64	+	.	.	33	+	4	+	3	.	x	83
Cynos cri	5	.	3	+	1	5	83	5	7	5	.	.	.	5	.	.	.	.	36	+	+	4	100	.	.	+	.	.	.	17
Dacty glo	.	4	.	.	1	2	50	5	.	3	.	4	6	6	.	4	3	7	73	+	.	.	33	+	6	.	3	.	.	50
Desch cae	4	.	.	.	2	3	50														.			.	4	.	.	.	x	33
Festu ovi	.	.	.	.	.	4	17	5	.	7	[illegible]	4	4	.	.	[illegible]	7	6	100	.	+	[illegible]	67	+	.	+	7	5	7	100
F. rub	6	7	5	.	7	2	83		7	.	.	.	.	.	.	.	.	.					[illegible]	.	2	+	.	.	.	33
Holcu lan	4	5	3	+	2	.	83	4	5	3	4	4	4	.	.	4	3	5	82	.	+	3	67	.	5	+	.	.	.	33
Helic pub	.	.	.	.	.	2	17	.	4	2	.	.	.	6	.	5	2	.	46					.	5	+	3	.	.	50
Koele gra								.	6	1	4	.	3	.	.	4	.	3	55					+	4	+	.	.	2	67
Poa pra								.	.	.	.	.	2	.	.	.	3	.	18	+	.	.	33							
P. tri	6	5	.	+	1	.	67	.	.	.	.	7	.	.	.	.	.	.	9					+	.	.	.	.	.	17
Sesle cae																								.	.	+	8	.	5	5(
Zerna ere								.	.	.	.	2	4	.	.	4	.	.	27											

Alchemilla vestita

Leicestershire (TABLES 9a, nos. 1-6; 11, I).

The seven habitats studied in various parts of the county are representative of the communities in which A. vestita occurs. (TABLE 12).

TABLE 12.

No.	Habitat	Soil	pH	Aspect	Altitude
1	rough pasture in Quercus wood.	friable clay loam	5.1	level	200'
2	meadow near 1.	friable clay loam	5.0	90°	200'
93*	rides of Quercus wood.	clay-wet	-	level	500'
3	rough grass, grazed.	clay-loam-silt wet	-	90°	200'
4	wet pasture.	clay-loam-silt wet	6.4	225°	280'
5	damp, pasture.	clay-loam	5.8	90°	350'
6	pasture, Crataegus scrub.	slightly clayy loam	5.8	0°	350'

In all localities except Loddington Reddish, A. vestita was in closed grassland. In the two Bogs the substratum was wet; the two Swithlands wood sites were both adjacent to a mature Quercus woodland but not shaded. A few plants were recorded in the open vegetation of a much disturbed ride in Loddington Reddish wood. In all cases clay predominated in the soil, though in the 'bog' habitats the soil was blacker with silt. Only the Botcheston Bog locality has a nearly southern aspect; the driest habitat at Ulverscroft Mill faces north. The pH range is 5.0-6.4.

Full details of the associated species of six habitats are given in TABLE 9a. The most constant of these are listed in TABLE 11. Nine of these species are of high constancy in most areas, but Trifolium repens is rather lower. Poa trivalis, Sanguisorba officinalis and Cirsium palustre are more frequent here than in the other areas; these are plants of dampish habitats.

Derbyshire (TABLE 9a, nos. 7-17; 11, II).

A. vestita is not uncommon in natural grassland, especially on the limestone so the habitats studied are a sample only. (TABLE 13).

Only the first of these habitats is not in the Carboniferous limestone area. All are grassland of some kind, though it was not possible to examine the hay meadows. The species was not found in the woodland examined but was present in the more open scrubland of Corylus and Crataegus, found on the steep sides of the valleys. In most cases the plants grow on the rich brown loam over the limestone. pH 5.6-6.5. As in Leicester the southern aspects appear to be avoided and only the Monsal Head habitat which is on clay, is south facing. Details of the associated and constant species are given in TABLE 9a and 11.

TABLE 13.

No.	Community	Soil	pH	Aspect	Slope	Altitude
7	cattle grazed pasture	clay with silt over shale damp	6.3	0°	5°	450'
8	pasture	-	-	0°		500'
9	rough pasture, rocky	dark-brown loam	6.0	0°	10°	1000'
10	rough grass-pasture	rich brown clay loam	5.6	180°	15°	550'
11	pasture, scattered trees.	brown loam	5.8	90°	20°-40°	600'
12	rough grass	-	-	90°	25°-30°	700'
13	rough grass, roadside	brown loam	-	level		950'
14	rough grass	rich, brown loam	6.5	0°	5°-10°	750'
15	rough grass with limestone out-crops	dark-brown loam	6.2	270°	25°	1000'
16	" "	dark brown peaty	5.8	0°	30°	950'
17	" "	" "	6.0	0°		950'

All the most constant species are well represented except *Ranunculus acris*; in addition *Ajuga reptans*, *Bellis perennis*, *Carex flacca*, *Galium verum*, *Leontodon hispidus*, *Poterum sanguisorba*, *Succisa pratense*, *Veronica chamaedrys*, *Briza media* and *Dactylis glomerata* have high constancy values. *Alchemilla glabra*, *Conopodium majus* and *Leontodon hispidus* which are more common further north, are present in half of these south Pennine localities.

North Wales (TABLES 9a, nos. 18-20, 11, III)

Only four populations of *A. vestita* were found during a week's botanising in North East Wales. TABLE 14.

TABLE 14.

No.	Community	Soil	pH	Aspects	Slope	Altitude
18	pasture		5.4	0°	5°	350'
94*	calcareous flush below limestone	dark-grey, wet	-	270°	5°-8°	c.1000'
19	flushed pasture	dark-brown creamy loam	6.2	270°	2°	1000'
20	dry pasture, *Crataegus* scrub	reddish slightly sandy loam	5.2	270°	10°	1000'

The distribution of *A. vestita* appears to be rather strictly limited to moist base-rich pasture or flushes with a pH range 5.6-6.2. Three populations were on or below Ordovician limestone and the fourth on a north facing pasture below woodland on Carboniferous limestone; it was not found in woodland. The main associated species of the pasture are *Achillea millefolium*, *Prunella vulgaris*, *Ranunculus acris*, *Taraxacum* agg. *Trifolium repens*, *Veronica chamaedrys*, *Agrostis tenuis* and *Cynosurus cristatus*. These are similar to the constants found in Leicestershire, Derbyshire and Yorkshire in TABLES 9a and 11. The wet base-rich flush community contained the usual species, including: *Achillea ptarmica*, *Angelica sylvatica*, about 10 species of *Carex*, *Chrysosplenium oppositifolium*, *Filipendula ulmaria*, *Juncus* species, *Molinia caerulea*, *Pinguicula vulgaris* etc.

Yorkshire (excluding Swaledale and Teesdale)(TABLES 9a, nos. 22-27, 11 IV)

A. vestita is widespread and frequent in parts of Yorkshire. In the West Riding the six habitats studied are all on limestone, pasture, rough grassland or rocky outcrops. (TABLE 15). *A. vestita* is common in close-grazed limestone. The only East Yorkshire population is on west facing semi-natural, grazed grassland on chalk at 500'. The soil is a shallow dark brown loam pH 7.0. The associated flora is very similar to that of the West Yorkshire habitats and has been included with them in TABLE 9a.

TABLE 15.

No.	Habitat	Soil	pH	Aspect	Slope	Altitude
22	pasture	brown loam with flints on chalk	7.0	270°	20°	500'
23	rough grass on limestone outcrop	dark brown loam	6.4	90°	15°	750'
24	rough grass	" " "	6.0	180°	5°-10°	1250'
25	*Corylus* scrub on limestone outcrop	1-4" black peaty	-	315°	10°	1000'
26	pasture	-	6.4	315°	10°	1000'
27	rough pasture on moraine	brown peaty	-	90°	c.20°	1200'

Though these habitats in the west are between 750'-1250' *A. vestita* does occur at higher altitudes; again only one habitat faces south. Three of the species generally constant in other areas are low here (TABLE 9a and 11) *Holcus lanatus*, *Plantago lanceolata* and *Cerastium vulgatum*; but a number of additional species have high frequencies. *Alchemilla glabra*, *Campanula rotundifolia*, *Carex flacca* 83%; *Carex caryophyllea*, *Conopodium majus*, *Poterium sanguisorba*, *Prunella vulgaris*, *Ranunculus bulbosus*, *Senecio jacobaea*, *Trifolium pratensis*, *Thymus drucei*, and *Koeleria gracilis* 67%.

TABLE 9b

	28	29	30	31		32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	
Betul pub						+	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Coryl ave						+	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Crata mon	.	.	.	+	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	3	.	.	.	.	8
Fraxi exc						+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	12
Prunu pad						+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Sorbu auc						+	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Achil mil	.	+	+	+	75	.	.	.	.	+	+	x	.	+	.	x	.	.	2	.	2	.	1	.	.	.	1	2	x	x	2	50
Ajuga rep						+	2	1	.	+	.	.	.	+	.	.	.	.	.	.	.	.	x	.	.	.	1	1	.	.	.	31
Alche acu						.	.	.	.	+	3	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
A. fil	.	x	.	.	25	+	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	.	.	.	.	.	x	3	31
A. gla	2	.	.	.	25	+	1	2	3	+	1	2	3	+	3	1	2	3	3	1	x	.	.	.	2	+	3	2	2	2	3	88
A. glo						.	.	.	.	.	.	.	.	+	.	x	.	.	5	.	.	.	.	.	.	.	.	x	.	.	x	19
A. mon						.	.	.	.	.	.	.	.	.	.	3	x	1	1	.	x	.	.	.	.	+	.	.	2	.	x	31
A. sub						.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	4
A. ves	3	+	+	2	100	+	4	2	3	+	2	5	5	+	3	1	2	3	3	2	1	3	3	4	5	+	4	2	2	2	1	100
A. wic						.	.	.	.	.	.	.	.	.	.	.	4	x	.	.	1	.	.	.	.	.	.	.	.	.	.	12
A. xan						+	1	1	2	.	1	.	.	+	3	x	x	3	3	.	x	.	.	.	2	+	.	x	.	.	2	62
Anemo nem						+	3	1	.	.	.	.	.	+	.	x	.	.	3	.	.	.	.	.	.	.	.	.	.	.	x	27
Belli per	.	+	+	+	75	+	.	.	.	+	+	.	.	+	.	.	x	2	.	2	2	.	x	.	1	+	3	3	.	2	2	58
Calth pal	.	.	+	.	25	.	.	.	.	.	.	.	.	+	.	.	x	.	1	.	.	.	.	.	4	.	.	.	.	.	.	15
Campa rot						.	1	.	.	.	.	.	.	+	1	1	.	.	.	1	.	2	2	.	.	+	1	.	1	.	.	39
Carex car	.	+	+	.	50	.	.	.	+	.	.	.	.	+	.	1	1	.	.	2	2	3	1	2	.	+	3	4	2	3	1	58
Care fla	+	+	+	+	100	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	x	2	x	.	.	.	3	3	.	x	31
C.panicea	+	.	.	.	25	.	.	.	.	.	.	.	.	+	.	.	1	3	3	.	.	x	.	2	.	+	x	4	3	3	x	48
Centa nig	+	+	+	+	100	+	3	2	+	+	+	.	.	+	.	.	2	.	.	.	2	4	2	2	.	.	2	x	.	.	2	58
Ceras vul	+	+	+	.	75	+	2	.	.	+	+	1	.	+	2	.	1	x	1	1	1	.	2	.	.	.	1	2	.	.	1	62
Cirsi arv						+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	x	1	.	.	.	.	x	.	19
Conop maj						+	.	3	+	+	+	3	3	+	6	3	2	2	3	3	1	5	2	2	1	+	2	.	2	.	2	88
Euphr agg						.	.	.	.	.	.	.	.	.	.	.	2	2	2	.	.	.	1	.	.	.	.	1	x	2	1	31
Filip ulm	+	.	.	.	25	+	.	.	+	+	.	.	.	+	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	19
Galiu cru	.	+	+	+	75	+	2	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
G. ver	.	+	+	+	75	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	+	.	1	.	2	2	19
Geran syl						+	.	2	+	.	.	3	.	+	4	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	27
Geum riv						+	.	.	.	+	.	3	.	+	.	.	.	.	3	.	.	.	.	x	.	.	.	1	.	.	.	27
Hiera pil						.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	.	2	.	.	+	1	.	2	.	2	23
Herac sph	+	.	.	.	25	.	.	.	.	.	+	x	.	+	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	19
Hypoc rad						.	.	.	.	.	+	.	.	+	3	.	x	.	.	2	.	.	2	2	.	+	2	.	2	.	2	42
Lathy pra	.	.	.	+	25	+	.	.	.	+	.	.	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
Leont aut	.	+	+	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	.	+	.	3	x	2	.	23
L. his	.	+	+	+	75	+	.	1	+	.	.	.	.	+	.	.	2	3	3	2	1	2	2	.	.	+	.	3	x	2	2	62
Linum cat	.	+	+	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.	8
Lotus cor	.	+	+	.	50	.	.	2	+	+	+	x	2	+	.	2	1	.	3	5	.	1	4	2	.	+	2	2	2	.	2	73
Luzul cam	.	+	+	.	50	+	2	.	+	+	+	.	.	+	2	3	.	2	.	2	.	4	2	1	.	+	2	.	2	1	2	69
Orchi mas						+	.	.	.	.	.	.	.	+	.	x	.	.	x	.	.	x	2	x	.	.	.	.	.	.	1	31
Oxali ace						+	3	3	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
Pimpi sax	.	.	+	+	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	x	.	.	1	.	.	.	1	19
Plant lan	+	.	+	+	75	+	.	.	+	+	+	1	1	+	4	4	3	3	.	3	2	5	2	3	2	+	3	2	2	4	2	88
Poten ere						.	1	2	+	.	.	.	.	.	.	1	x	.	.	2	2	3	.	2	.	+	.	.	2	.	1	46
P. ste	.	+	+	.	50	+	.	2	+	+	.	2	x	.	.	.	.	.	.	1	.	.	2	.	.	+	1	.	.	.	.	39
Poter san	.	.	.	+	25	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	2	1	.	.	.	.	.	.	.	.	15
Primu ver	.	+	.	+	50	+	.	2	+	+	.	.	.	+	.	.	.	.	.	1	.	x	2	.	.	.	.	.	.	.	.	31
Prune vul	.	.	.	+	25	.	.	.	.	+	.	.	1	+	.	.	.	.	.	.	2	1	.	2	.	.	.	4	2	3	.	35
Ranun acr	+	+	+	.	75	+	.	.	.	+	+	.	.	+	.	1	3/	1	2	1	2	.	.	2	2	+	2	x	.	.	1	62
R. aur						+	.	.	.	.	.	.	.	+	.	.	.	1	x	.	.	.	x	.	.	.	.	.	.	.	1	23
R. bul	.	+	+	.	50	+	2	.	+	+	+	.	.	+	3	.	2	1	.	2	.	4	2	.	.	+	2	.	2	2	.	62
R. fic	+	3	.	.	50	+	3	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
Rhina min						.	.	.	.	.	.	.	.	+	2	.	2	3	2	.	.	.	.	.	.	.	.	.	.	.	.	19
Rubus fru	.	+	+	.	50	.	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Rumex ace	+	+	+	.	75	.	3	1	.	.	+	6	.	+	3	1	3	.	3	.	.	.	.	.	3	.	.	.	.	.	.	38
Sangu off						.	.	.	.	.	.	.	.	.	.	.	2	.	.	x	.	.	3	.	.	.	1	x	.	.	1	23
Senec jac	+	+	+	+	100	.	.	.	+	+	+	.	.	.	.	1	.	.	.	2	2	.	.	2	.	+	2	.	.	.	.	35
Stach off						.	2	3	.	+	.	.	.	.	.	.	.	.	.	.	.	5	.	2	.	.	.	.	.	.	.	19
Stell gra						+	2	1	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
Succi pra	+	.	.	.	25	+	.	4	+	+	.	.	.	+	.	x	.	.	2	.	2	.	.	5	.	.	3	.	.	.	1	44
Tarax agg	.	+	+	.	50	.	.	.	+	+	+	5	.	+	.	1	2	1	.	.	2	.	3	.	1	+	1	2	x	2	2	66
Thymu dru	.	+	.	.	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	+	3	2	1	2	2	31
Trifo med	+	+	+	.	75	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	4
T. pra	+	+	+	.	75	+	.	1	.	.	+	.	2	+	4	2	3	1	1	3	.	1	.	.	1	+	.	.	.	.	2	58
T. rep	.	.	.	+	25	.	2	.	.	+	+	.	.	+	.	1	2	3	.	1	.	.	.	2	2	+	1	3	2	3	2	62
Trolli eur						+	.	.	.	.	.	.	.	+	.	.	x	2	2	.	2	.	.	.	.	.	.	1	.	.	.	27
Veron cha	.	+	+	+	75	+	2	.	+	.	+	2	.	+	2	2	.	.	2	1	.	2	.	.	1	+	.	.	.	.	.	50
Viola lut						.	.	.	.	.	.	.	.	+	.	1	x	.	1	x	.	.	.	.	.	.	.	x	.	.	.	23
V. riv	.	.	+	.	25	+	3	2	+	.	+	.	.	+	.	1	.	.	x	.	.	2	2	.	.	+	1	x	1	x	x	62
Agros ten	.	.	+	.	25	.	3	.	.	.	.	.	2	.	.	.	x	.	.	.	.	1	.	3	.	2	2	3	3	4	.	38
Antho odo	+	.	+	.	50	+	.	2	5	+	+	3	1	+	4	5	3	3	3	3	2	5	4	2	4	3	2	2	3	.	3	92
Briza med	+	+	+	+	100	.	.	.	2	.	.	.	.	.	x	3	.	3	2	3	x	3	3	2	.	2	2	.	.	3	3	54
Cynos cri	.	+	+	.	50	.	.	.	.	+	+	.	.	.	.	.	3	3	.	4	2	2	.	2	.	3	4	.	.	.	3	42
Dacty glo	+	+	+	+	100	+	3	2	3	+	+	6	2	+	4	2	4	.	.	.	3	2	.	.	6	2	3	.	.	.	2	69
Desch cae	+	.	.	.	25	+	.	.	3	.	.	2	.	+	.	.	.	3	3	.	2	.	.	.	.	.	4	3	.	3	.	38
Festu ovi	.	+	+	.	50	+	.	3	7	+	+	4	.	+	5	8	3	+	5	9	.	6	6	7	7	5	7	4	8	5	7	}92
F. rub						.	.	.	.	.	+	.	.	.	.	.	+				3			.						2		
Loliu per	+	+	+	.	75	+	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Holcu lan	.	.	+	+	50	+	3	3	3	+	+	4	4	+	5	.	.	2	.	.	.	6	.	3	4	3	.	.	2	.	.	62
Helio pra						.	.	.	.	.	.	2	.	+	.	.	.	.	.	.	.	.	.	.	.	.	3	7	.	.	2	19
H. pub						+	.	.	2	.	+	.	.	+	.	.	.	2	2	2	.	3	.	.	.	.	.	.	.	.	2	35
Koele gra	.	+	.	.	25	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	3	2	.	.	2	.	.	.	.	15
Poa pra	.	.	+	.	25	.	4	.	.	+	+	3	3	.	.	.	3	6	.	3	.	.	.	.	6	.	.	.	.	.	.	35
P. tri	.	+	+	.	50	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	12
Siegl dec	.	+	+	.	50	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	2	.	1	.	.	15

East Durham (TABLES 9b, nos. 28-31, 11,V).

A. vestita is only frequent on or near the magnesian limestone though it is scattered throughout the area. (TABLE 16).

TABLE 16.

No.	Habitat	Soil	pH	Aspect	Slope	Altitude
29	Limestone pasture Crataegus scrub	creamy, brown friable loam	6.2	180°	10-20°	500'
30	rough grass Crataegus scrub	rich brown loam	6.8	level		275'
31	pasture	"	-	"		400'
28	rough grass, wet	"	6.7	0°	5°	450'

In all cases the soil is a rich brown loam though at Cassop the water table is high.

Details of the associated species are in TABLES 9b and 11. Only four of the more constant species have high frequencies here, but several other species occur in three of the four habitats. Galium cruciata, Galium verum and Dactylis glomerata are more characteristic of the Derbyshire and West Yorkshire areas than the north. A. glabra, A. xanthochlora, Conopodium majus found in Pennine areas are noticeably absent.

The Pennine area of Swaledale, Teesdale and Weardale

The forty habitats in this area consist of woodland, scrub, rough grass, meadows, pastures and flushes, between 600' and 2475'. On the basis of their floristic composition the mountain pasture and flush communities can be separated from the valley habitats at 600'-1350'. As there are several samples of each community a more detailed analysis is possible than in the other areas.

The Valley area. 600'-1350' (TABLES 9b, nos. 32-57; 11, VI)

Woodland is rather a courtesy title, as only Park End wood has a closed canopy but here the trees are mainly old Betula pubescens and Corylus avellana, and A. vestita is only in the outer region where the shade is light. Mill Bank is more or less closed scrub of Betula pubescens and Corylus avellana. Brockers' Gill is a relatively open area in a mixed deciduous wood of Fraxinus excelsior, Ulmus glabra, Acer pseudoplatenus and Corylus avellana. The Swaledale locality may have been more dense woodland once, but now is herb-rich grassland with mature trees of Fraxinus excelsior at the top of the slope and Corylus avellana and Alnus glutinosa below. (TABLE 16).

TABLE 17

No.	Habitat	Soil	pH	Aspect	Slope	Altitude
32	rough grass, some trees	rich brown loam	6.1	315°	5°-25°	950'
33	open wood	medium brown loam on shale	5.4	270°	5°-15°	1000'
34	*Betula* wood	rich medium loam	5.4	180°	10°-15°	850'
35	Open *Corylus* scrub	dry sandy loam	5.4	0°	0°-5°	900'

Details of the ground flora are in TABLE 7b (32-35) several characteristic woodland species are present: *Anemone nemorosa**, *Endymion non-scripta*, *Fragaria vespa*, *Geranium sylvaticum*, *Luzula pilosa*, *Mercuralis perennis*, *Oxalis acetosella*, *Primula veris**, *Ranunculus ficaria**, *Stachys officinalis**, *Stellaria graminea**, *Stellaria holostea*; many of these species are also found in the meadow lists. *A. filicaulis* s.st. is also found in two of the woodland habitats.

Rough grassland seems to be the best description for the heterogeneous habitats of roadside verges, woodland ride and limestone spoil heap since grasses predominate and none are mown or grazed. (TABLE 18).

TABLE 18.

No.	Community	Soil	pH	Aspect	Slope	Altitude
36	rough grass ride in conifer wood	dark-brown loam	-	level	level	600'
37	rough grass, roadside	slightly sandy loam	6.4	270°	5°	650'
38	sparse rough grass, laneside	damp dark-brown loam	6.2	270°	30°-40°	1350'
39	rough grass on spoil heaps	mid-brown, stony loam	7.4	level	level	900'

The soils are medium loams with quite a high base-status inferred from the pH 6.2-7.4. Floristics in TABLE 9b (36-39) show that the tussocky grasses Dactylis glomerata and Holcus lanatus are frequent and Rumex acetosa, Trifolium pratense, Veronica chamaedrys are more constant than in the other valley habitats.

Meadows. Unlike the larger Alchemilla species such as A. glabra, A. xanthochlora and A. monticola, A. vestita is not frequent in meadows and even when present it is well dispersed and never graded as common. (TABLE 19). Although the first of these samples is not really a meadow it is best included here on the basis of floristics as in TABLE 9b (40-45).

TABLE 19.

No.	Habitat	Soil	pH	Aspect	Slope	Altitude
40	rough grass on stream in meadow		-	270°	-	1350'
41	meadow	brown	5.6	180°	20°	900'
42	meadow	rich brown loam	6.2	90°	0°-10°	1100'
43	meadow	rich brown loam	7.2	180°	5°	1250'
44	meadow	dark brown loam, wet	5.4	270°	5°-15°	1450'
45	flushed meadow	dark brown loam, wet	6.4	270°	c.5°	1400'

Several additional species are frequent in these meadows, viz. Achillea ptarmica, Cirsium heterophyllum, Orchis mascula, Ranunculus auricomus, Rhinanthus minor, Saxifraga granulata, Trollius europeus; several grasses are present but only Phleum pratense is not recorded for the other habitats. The soil is usually a rich brown loam, brown-earth type, well drained since most habitats are on sloping ground, generally facing south-west and north-east.

Pastures. A. vestita is most frequently found in this area, in close grazed pasture including open grazed scrub, usually, with Crataegus monogyna, Corylus avellana, Rosa species and Salix species. (TABLE 20).

TABLE 20.

No.	Community	Soil	pH	Aspect	Slope	Altitude
46	pasture with *Rosa*	red-brown, slightly sandy loam	5.8	0°	10°	750'
47	pasture much disturbed	mid-brown loam	5.4	0°	5°	850'
48	rough pasture	rich brown loam	6.0	180°	10°-20°	900'
49	pasture with *Crataegus*	mid-brown loam	5.4	180°	10°-20°	950'
50	damp pasture with *Crataegus*, *Salix*, *Rosa*	"	5.8	225°	5°-10°	950'
51	rough pasture	damp, black-brown	6.2	0°	5°	950'
52	" "	loam				
52	" "	-	-	135°	25°	1000'
53	pasture, occasional *Crataegus*	moist, brown loam	6.6	225°	10°	1000'
54	pasture on river terrace	brown, slightly sandy loam	6.4	180°	25°	1200'
55	pasture	brown loam	6.6	225°	15°-20°	1100'
56	"	dark-brown, slightly peaty, sandy loam	6.3	180°	c.3°	1350'
57	pasture on limestone outcrop	mid-brown loam slightly sandy	5.8	225°	5°-10°	1275'

Although the soils are all loams, there is a little more variety in colour, mainly connected with the wetter conditions. Only two habitats have a rather peaty soil, these are Brockholm - a slightly sandy riverside alluvial at 1200' pH 6.2 and a base-rich area, pH 6.3 with earthworms and moles in the general acid vegetation below (N) of Cronkley Scar at 1350'.

A few herbs are more frequent here than in the other habitats in the area, TABLE 9b (46-57); these are *Carex caryophyllea*, *Carex flacca*, *Galium verum*, *Leontodon autumnalis*, *Pimpinella saxifraga*, *Thymus drucei* and *Agrostis tenuis*. *A. filicaulis* s.st. occurs in five of these habitats.

These valley communities have the greatest variety of species; eighteen have constancy values of 76%:- *A. glabra*, *A. xanthochlora*, *Conopodium majus*, *Geranium sylvaticum*. *Hypochaeris radicata*, *Taraxacum* agg., *Plantago lanceolata* and *Deschampsia caespitosa* are more frequent here than further south; *Cirsium arvense*, *Cirsium palustre*, *Galium cruciata*, *Galium venum* and *Poterium sanguisorba* are less frequent here. (TABLE 11, VI)

In spite of the variety of plant communities the soils are much the same, brown-earth type with a top soil

TABLE 9c

	58	59	60	61	62	63	64	65	66	67	68	69	70	71		72	73	74	75	76		77	78	79	80		86	87	88	
Achil mil	.	.	.	x	.	2	.	2	2	.	.	.	4	.	36	.	.	.	1	.	20									
Alche alp																						5	4	+	3	100	.	.	+	33
Alche fil	.	.	.	.	x	x	.	.	.	x	.	x	x	.	36	x	.	.	1	1	60	2	3	.	.	50	+	x	+	100
A. gla	2	1	1	2	.	.	2	1	x	1	3	x	3	x	85	1	2	.	1	2	80	1	1	+	2	100	+	x	+	100
A. glo																						.	1	+	.	50				
A. min																											+	.	.	33
A. 'acutid'																						.	1	.	.	25				
A. ves	3	3	3	x	x	2	2	2	x	1	2	x	3	.	100	2	2	3	1	1	100	1	1	+	2	100	+	x	+	100
A. wic																						1	2	+	2	100	+	.	+	67
A. xan																.	1	3	2	.	60									
Belli per																3	.	.	.	.	20						.	2	+	67
Campa rot	2	2	2	.	x	2	.	.	1	.	.	.	.	.	43							1	.	.	1	50				
Carda	.	.	.	.	x	.	2	x	1	.	2	.	2	1	50															
Carex car	x	2	5	4	x	x	.	2	3	.	.	.	4	.	64	.	.	.	4	3	40	2	.	.	.	25				
C. den	.	.	x	x	.	.	1	.	.	1	.	.	.	.	29	4	.	.	.	2	40	1	.			25	+	.	.	33
C. fla	.	.	.	2	.	.	.	.	.	.	.	.	.	.	7	2	.	.	.	.	20						+	3	.	67
C. panicea	.	2	3	.	.	.	.	.	.	.	.	.	.	.	14	3	.	.	.	2	40	1	.	.	.	25				
C. pul	.	.	.	x	.	.	.	2	.	.	.	.	.	.	14	2	.	.	.	2	40	1	2	.	.	50	+	.	.	33
Ceras vul	2	2	2	.	.	2	1	.	2	1	2	x	2	1	79	1	1	.	1	.	60	1	.	.	.	25	.	1	+	67
Cirsi arv	x	.	.	x	.	.	.	1	.	.	.	x	.	.	29	.	1	.	3	.	40									
Cochl off	.	.	2	.	x	.	.	.	.	.	.	.	2	1	29							.	.	.	2	25				
Euphr agg	.	.	.	.	x	x	.	1	1	.	.	.	.	.	29	.	.	.	.	1	20	1	1	+	.	75	.	1	+	67
Filip ulm	.	.	.	.	.	.	1	.	.	.	.	.	.	.	7							.	.	.	2	25	+	1	.	67
Galiu pum	.	2	2	1	x	.	.	1	2	.	.	.	.	.	43							1	.	.	.	25				
G. ver																1	2	.	2	2	80									
Genti ver	.	.	2	x	x	.	.	.	.	.	.	.	.	.	21															
Geum riv	3	x	.	.	x	.	.	1	.	.	.	.	.	.	29							.	.	+	3	50	.	1	.	33
Herac sph																.	1	.	.	.	20				4	25	.	.	+	33
Hiera pil	.	2	.	.	.	.	.	.	.	.	.	.	.	.	7												+	1	+	100
Linum cat	.	.	.	.	.	.	.	.	.	.	.	.	.	1	7							.	.	.	3	25	+	1	+	100
Leont aut	.	.	.	.	.	.	2	.	.	1	.	.	.	.	14	1	x	.	.	.	40									
Lotus cor	.	2	.	.	.	.	.	.	.	.	.	.	.	.	7	.	2	.	1	1	60						.	2	+	67
Luzul cam	.	2	2	3	x	3	.	1	3	.	.	.	3	.	57												.	1	.	33
Plant lan	.	2	2	x	.	.	.	.	.	.	.	.	.	.	21	x	2	2	1	1	100						.	1	+	67
P. mar																											.	1	+	67
Polyg viv	.	2	2	.	.	.	.	.	.	.	.	.	.	.	14							1	2	.	1	75	.	.	+	33
Poten ere	2	2	1	.	.	.	.	3	2	.	.	.	.	.	36	2	.	.	1	2	60						.	1	+	67
Prune vul	2	.	2	.	.	1	1	x	.	.	.	x	.	.	43	3	.	.	1	2	60						+	2	+	100
Ranun acr	.	.	.	2	x	.	1	.	1	.	1	.	.	2	43	2	.	.	1	1	60	.	.	.	3	25	.	.	+	33
R. rep	.	.	.	.	x	.	.	.	.	x	.	.	.	.	14	.	.	2	.	.	20									
Rumex ace	.	.	.	.	.	x	.	.	3	.	1	x	2	3	43	.	2	1	1	.	60	.	.	+	3	50				
Sagin pro	.	.	.	.	.	.	.	.	1	.	.	x	4	.	21	1	.	.	1	.	40						.	1	+	33
Saxif aiz																.	.	.	.	2	20	.	4	+	1	75	+	.	+	67
S. hyp	.	.	.	.	x	.	.	.	1	.	.	.	1	.	21							1	.	.	2	50				
Sedum vil	.	.	.	.	.	.	1	.	.	1	1	.	.	.	21															
Selag sel	.	.	1	1	x	.	.	.	.	.	.	.	.	.	21							.	1	.	.	25	+	1	+	67
Sibba pro																						1	1	.	.	50				
Thymu dru	3	3	3	3	x	4	.	4	4	.	.	.	1	.	64	.	.	.	.	1	20	.	1	.	2	50	+	3	+	100
Trifo rep	2	.	2	2	x	2	1	.	2	.	.	x	3	.	64	1	4	4	3	2	100	1	.	.	.	25	.	3	.	33
Veron cha	.	.	.	.	x	.	.	.	.	.	.	x	.	.	14	.	1	1	1	.	60									
Viola lut	.	2	2	2	x	.	.	.	.	.	.	.	.	.	29															
V. riv	1	2	2	2	x	x	1	1	1	.	.	.	.	.	64							1	1	.	+	75	+	2	+	100
Agros ten	6	3	2	.	.	3	.	3	.	.	.	x	.	.	43	1	5	.	3	3	80						+	5	+	100
Antho odo	.	.	.	2	.	5	.	3	.	.	.	x	.	.	29	4	3	.	5	.	60	4	.	.	.	25	.	4	+	67
Briza med	.	.	.	.	.	.	5	.	.	.	.	.	.	.	7	.	.	.	.	3	20						.	2	+	67
Cynos cri																3	4	.	4	3	80									
Desch cae	.	.	.	.	.	.	4	.	4	.	.	7	.	.	21	.	.	.	2	.	30	4	3	+	2	100	+	.	.	33
Festu ovi		6	4			7	4	7	7	4	.	.	.	4	79	3	5	.			80		4			100	+	6	+	100
F. rub	7	.	.	9	8	.	.	.	.	.	.	.	.	.					5	4										
F. viv																						7		+	3	75	.	.	+	33
Holcu lan																2	5	.	3	2	80						.	2	.	33
Nardu str	.	.	.	.	.	.	2	.	.	.	.	.	.	.	7	4	.	.	.	3	40	4	7	.	.	50				
Poa tri	.	.	.	.	.	.	.	.	.	.	5	x	.	.	14	.	.	3	.	.	20									
Sesle cae	.	4	3	.	.	4	.	.	.	.	.	.	.	.	21															

of medium loam, sometimes a little sandy, sometimes slightly peaty, pH 5.4-7.4. The meadow soils have an excellent crumb structure.

It is interesting to note that 17 of the 21 samples on sloping ground face south, south-west, or west, further south, southern aspects appear to be avoided.

North Pennine montane area > 1350' (TABLES 9c, nos. 58-71; 11, VIII)

In addition to the altitudinal difference the samples included here are separated on a floristic basis; most striking are the species which are absent or rare: *A. xanthochlora, Bellis perennis, Centaurea nigra, Conopodium majus, Hypochaeris radicata, *Leontodon hispidus, *Ranunculus bulbosus, Succisa pratensis, Trifolium pratense, Veronica chamaedrys, Briza media, *Dactylis glomerata and *Holcus lanatus.

A few other species are present only up to 1750' Hieracium pilosella, Helianthenum chamaecistus and Lotus corniculatus and Plantago lanceolata up to 1800'. These species are more frequent at lower altitudes, and perhaps these habitats should be included in the "valley group".

All the habitats are on limestone outcrops or base-rich flushes in the general peat cover of the Yoredale series of the Carboniferous limestone. All are heavily grazed by sheep. (TABLE 21).

TABLE 21.

No.	Habitat	Soil	pH	Aspect	Slope	Altitude
59	pasture	well drained, sugar limestone	7.4	135°-315°	5°-10°	1750'
60	pasture	well drained, sugar limestone	7.2	all	-	1800'
61	pasture	well drained, limestone	5.7	all	-	1850'
62	pasture	well drained, limestone	5.8	315°	20°	2000'
63	pasture	well drained, limestone	-	180°	c. 5°	2400'
58	pasture	moist, black, peaty loam	6.7	all	-	1750'
66	pasture	moist, dark brown loam	5.7	270°	c. 5°	2450'
65	pasture	moist, dark brown loam between limestone	6.2	270°	10°-15°	2275'
70	pasture	black, peaty loam	6.0	all	c. 5°	2475'
69	flush	very wet, black peaty	6.1	270°	10°-20°	2400'
67	flush	very wet, silty iron soil	-	270°	c. 5°	2375'
68	flush	very wet, silty dark brown	6.1	270°	c.30°	2400'
64	flush	very wet, black silt	5.6			
71	flush	moist, black silt	5.6	90°	15°-20°	2400'

A. vestita is not present on the main areas of sugar limestone; the two sugar-limestone habitats listed above are comparatively small and surrounded by peat, which probably keeps them more moist than the larger sugar-limestone areas. A. vestita grows on the sides not the almost level top. In the flushes A. vestita grows in water saturated conditions. A similar habitat was found in the south Scottish Uplands area, and this habitat (No. 71) has been included with the Pennine montane group.

The main associated species are A. glabra, Carex caryophyllea, Cerastium vulgatum, Luzula campestris, Thymus drucei, Viola riviniana and Festuca spp. In addition there are a few characteristic species of less frequent occurrence, Cardamine hirsuta, Galium pumilum, Saxifraga hypnoides, S. stellaris, Sedum villosum and Selaginella selaginoides. A. filicaulis s.st. occurs in five of these habitats also.

Scotland

The Scottish localities which were visited are very variable, so that an analysis on a floristic basis is probably better than a too rigid adherence to their geographical distribution. Whilst the high montane and N.W. Scottish habitats form two distinct groups, the other habitats are very similar to those in the N. Pennines.

Already attention has been drawn to the similarity of the flush habitat at 2400' on White Coomb (71) and the N. Pennine flush communities with which it is grouped in TABLE 9c. *A. vestita* was not recorded from this type of habitat in the Central Highlands though it may occur there.

The lower Central Highlands and Southern Uplands. (TABLE 9c, nos. 72-76; 11,VIII)

Five samples are grouped together because, in addition to the constant species, a number of others are more characteristic of the English localities especially in the N. Pennines. *A. xanthochlora*, *Galium verum*, *Plantago lanceolata*, *Potentilla erecta*, *Prunella vulgaris*, *Rumex acetosa*, *Trifolium pratense*, *Veronica chamaedrys*; whilst other Scottish species are absent. (TABLE 22).

TABLE 22.

No.	Habitat	Soil	pH	Aspect	Slope	Altitude
72	damp flushed pasture	moist brown loam	5.9	270°	5°	750'
75	pasture with *Pteridium*	ochre brown loam	5.5	135°	10-15°	750'
76	flushed grassland	-	-	90°	c10°	1000'
73	rough grass	light brown loam	5.5	180°	c 3°	550'
74	grassy parts in deciduous wood	-	-	-	-	500'

The first three habitats are close grazed - *Festuca Agrostis* grassland, in the 750'-1000' range; two are damp flushed areas, whilst the others are drier and appear to be moderately base-rich. Of the associated species *A. filicaulis* is present in all, *A. xanthochlora* is quite frequent, *Galium verum* is high.

Broadmeadow (No. 73) at 550' is south facing, rough grass on a mid-brown loam (drift), and is rather similar to the meadow communities in the North Pennines.

In the Newark Castle habitat (No. 74) *A. vestita* was growing by a lane and in grassy clearing in a mixed oak wood (*Quercus robur*, *Ulmus glabra*, *Fraxinus excelsior* and *Betula pubescens*). The ground flora was that of grassland rather than a typical woodland flora.

In the Southern Uplands. *A. vestita* was not at all common, it was found in only these few lowland habitats and by mountain streams at about 2000' in the White Coomb area. *A. filicaulis* also occurs in three of these localities.

The Central Scottish Highlands (TABLE 9c, nos 77-80; 11, IX)

The other habitats in this region are all rock-ledge or montane grassland between 2500' and 2750'. Though subject to some grazing this is not severe as in the North

Pennines. Only the presence or absence of species was recorded on the rock-ledge habitats because of the great heterogeneity of these chomophyte communities; it may be a matter of chance which species happen to be in the site listed. (see Poore, Thesis 1954). Full details are given in TABLE 9c (77-80), the main associated species are A. alpina, A. glabra, A. wichurae, Euphrasia species, Polygonum viviparum, Saxifraga aizoides, Deschampsia caespitosa, (Deschampsia alpina) and Festuca species including Festuca vivipara, several other species characteristic of Scottish mountain vegetation are also present in small quantity. (TABLE 23).

TABLE 23.

No.	Habitat	pH	Aspect	Slope	Altitude
77	rough grass	5.8	225°	20°-25°	2750'
78	wet flushes in Nardus grassland	-	315°	10°-30°	2750'
79	rock ledges in gully	-	225°	-	2500'
80	rock ledges in gully	-	0°	-	2400'

The soil is largely derived from micaceous schist rocks, is mainly grey-brown in colour, the single pH 5.8 agrees well with rock ledge soils in the same area tested by Poore (Thesis) which gave pH 5.4-5.9.

North-West Scotland (TABLES 9c, nos. 86-88; 11, X)

These three are all at low altitude 500'-1000' and associated with outcrops of Durness limestone. The main associates are shown in Table 9c, these contain a number of Arctic-alpines (A. filicaulis, A. wichurae, Plantago maritima, Polygonium viviparum, Saxifraga aizoides, Saxifraga oppositifolia, Thalictrum alpinum and Dryas octopetala) and other species of high frequency which are more frequent in other lowland habitats to the south - mainly Bellis perennis, Lotus corniculatus, Potentilla erecta, Prunella vulgaris, Agrostis tenuis, Briza media. Of the other Scottish Alchemilla species A. glomerulans is absent but A. minor occurs here on the limestone. (TABLE 24).

TABLE 24.

No.	Habitat	Soil	pH	Aspect	Altitude
86	pasture	yellowish clay, shallow	7.4	0°	500'
87	pasture	peaty clay	7.0	225°	700'
88	pasture	yellow clay shallow	7.6	315°	1000'

The soil is mainly derived from the limestone and in No. 86 and 88 is a rather yellowish clay, the other habitat is darker with peat and is slightly more acidic pH 7.0

against pH 7.4 and 7.6. Aspects vary slightly south-west, north-west and north.

These field records were made within the main areas of distribution of A. filicaulis s.l. It can be seen in FIG. 25 that the frequency of A. vestita decreases towards the south and south-east of Britain.

Some habitat details are available from the county Floras. South of the Thames and east of Dorset it is very rare and indeed is now absent from Kent (v.c. 15 and 16). In central southern England it is more frequent; but again it is absent from the south-west and from south-west Wales. As in other areas A. vestita is found in grassland; pastures, commons, meadows and woods. More exact details of the habitats are not available here and are generally missing from herbarium sheets. It should be noted that the habitats are usually damp and presumably shaded since borders of woods and grassy places within them are mentioned. It would be interesting to know if south facing slopes are avoided as in Leicestershire.

These studies show that A. vestita occurs most frequently in neutral and base-rich grassland, flushes, rock-ledges and open woodland. This neutral grassland is determined by the absence of domination by species characteristic of acid or base-rich grassland. The close similarity of the communities throughout much of the range is shown by the number of constant species in Table 11. Most striking is the relatively high number of species in all but some of the montane communities and the absence of dominant species; the grasses have the highest abundance-cover value but rarely does any one species form more than 50% of the community and usually several grasses are present in small quantity. The montane grassland communities of the North Pennines and Southern Scotland approximate to an Agrostis-Festucetum type, and in these the number of species is fewer. Very similar to the grassland communities is the open scrub-land of Crataegus monogyna, Corylus avellana and Salix species, A. vestita is also in open woodland, where the light intensity is high, as in Betula pubescens - Corylus avellana woodland; and near or along sides in more dense woodland.

In all these habitats A. vestita is on medium loam or clay associated with limestone or glacial drift usually of mull type, pH (5.2) 5.4 - 6.8 (7.8). The wetter and montane soils mostly contain some silty peat but the acidity is still within the above range.

Aspect appears to be important in the south since few south-facing localities were recorded in Leicestershire and Derbyshire. Though no details of aspect are available from the Flora records, many of the habitats in the south-east are damp or shaded. These conditions are also found in the Leicestershire and Derbyshire habitats. Farther north where the climate is cooler and wetter aspect is less important. However, plants on a shallow soil over magnesian limestone on a south facing slope in East Durham died down during the hot dry summer of 1955. This frequently happens in the Botanic Gardens at Cambridge, the plants do not thrive in very dry conditions.

On the other hand A. vestita is found in water saturated flushes dominated by mosses at c.2000'; here the soil is on only slightly acid, silty peat, pH 5.8.

In the Scottish Highlands A. vestita is on rock ledges or rough grassland and by streams. The soils are immature and contain much micaceous schist. The few samples studied faced south-west through west-north but insufficient is known to judge if aspect is important

To sum-up, in Britain A. vestita is frequent in hill grassland with base-rich soils. It is locally common in natural or semi-natural grassland on slightly acid soils (pH $>$ 5.0); pasture, meadow and rough grassland including roadsides and mountain ledges. It is present in open woodland and along rides in more closed woods. It is not generally common in chalk grassland, and appears to be absent from sandy soils and acid peaty conditions which include much hill grassland, heaths and moors. Although it grows in man-made open habitats such as roadsides and quarry spoil heaps it is not an aggressive synanthropic species like *A. xanthochlora* and *A. acutiloba*, for example.

(b) *A. filicaulis s.st.*

Of the 29 habitats in which *A. filicaulis* s.st. was recorded 24 also contain *A. vestita*. Only in the Central Highland area was *A. filicaulis* s.st. recorded alone. It is apparent that the ecological requirements of *A. filicaulis* s.st. must be very similar to those of *A. vestita*, but the latter has a much wider range; it is worth drawing together the details of the *A. filicaulis* s.st. habitats to see if the species is more limited than *A. vestita* in its ecological as well as its geographical range.

A. filicaulis s.st. is most frequent in Scotland, It occurred in some habitats in all three areas in which *A. vestita* occurred, viz. high mountain rock-ledges and grassland, lowland limestone grassland in the north-west, and 'neutral' and *Festuca-Agrostis* grassland often associated with flushes below 1000'.

TABLE 10

	9 22 29	32 33 34	48 49 50 57 56 62 63 67 69 70 72 75 76	77 78 81 82 83 84 85	86 87 88
Betul pub		+ . 5 67			
Coryl ave		+ . 9 67			
Fraxi exc		+ . 1 67			
Prunu pad		+ . 1 67			
Sorbu auc		+ . 2 67			
Achil mil	+ 33		. 1 . 2 x . 2 . . 4 . 1 . 46		
Ajuga rep		+ 2 1 100			
Alche alp				5 4 3 + 3 + + 100	. . + 33
A. fil	x + x 100	+ x x 100	x x x 3 x x x x x x x 1 1 100	2 3 3 + 1 + + 100	+ x + 100
A. gla	2 . . 33	+ 1 2 100	. . . 3 2 . . 1 x 3 1 1 2 62	1 1 2 + 2 . + 86	+ x + 100
A. glo			. . . x 8	. 1 . . 1 + . 43	
A. ves	1 x + 100	+ 4 2 100	3 3 4 1 2 x 2 1 + 3 2 1 1 100	1 1 29	+ x + 100
A. wic				1 2 1 + 2 + + 100	+ . + 67
A. xan		+ 1 1 100	. . . 2 . . . . 2 . 15		
Anemo nem	1 . . 33	+ 3 1 100	. . . x 8		
Belli per	3 . + 67	+ . . 33	. x . 2 2 . . . . . 3 . . 31		. 2 + 67
Campa rot	1 + . 67	. 1 . 33	2 2 . . . x 2 31	1 . 1 + 1 . + 72	
Carex car	2 + + 100		3 1 2 1 3 x x . . 4 . 4 3 77	2 14	
C. dem			. . . . 1 . . 4 . 2 23	1 . 2 1 . . + 57	+ . . 33
C. fla	2 . + 67		x 2 x x . . . . . . 2 . . 39	. . . . . . + 14	+ 3 . 67
C. pan			x . 2 x 3 . . . . . 3 . 2 46	1 . 2 4 . . . 43	
C. pul			. . . . 2 . 2 29	1 2 2 1 . . + 72	+ . . 33
Centa nig	1 . . 33	+ 3 2 100	4 2 2 2 31		
Ceras vul	1 + . 67	+ 2 . 67	. 2 . 1 . . 2 1 + 2 1 . . 54	1 14	. 1 + 67
Conop maj	3 . . 33	+ . 3 67	5 2 2 2 31		
Dryas oct					+ . + 67
Euphr agg	. + . 33		. 1 . 1 2 x x 1 46	1 1 1 + 1 + . 86	. 1 + 67
Filip ulm		+ . . 33		. . . . . . + 14	+ 1 . 67
Galiu cru	1 . + 67	+ 2 . 67			
G. ver	1 + + 100		. . . 2 2 . . . . . 1 . 2 31		
Geran syl		+ . 2 67			
Geum riv		+ . . 33	. . x . . x 15	. . 1 + 1 + + 72	1 . . 33
Hiera pil	. + . 33		. 2 . 2 15		+ 1 + 100
Leont aut	1 . + 67		. 1 . . 2 . . 1 . . 1 . . 31		
L. his	1 . + 67	+ . 1 67	2 2 . 2 2 . . . . . 1 . . 39		
Linum cat	1 . + 67		. . . . x 1 15	. . . + . . . 14	+ 1 + 100
Lotus cor	1 + + 100	. . 2 33	1 4 2 2 . . . . 1 1 46	. . . + . . + 29	. 2 + 67
Luzul cam	2 + + 100	+ 2 . 67	4 2 1 2 1 x . . . 3 . . . 54		. 1 . 33
Orchi mas			x 2 x 1 31		
Oxali ace		+ 3 3 100		1 14	. . + 33
Pimpi sax	. + . 33		1 1 x 1 31		
Plant lan	3 . . 33	+ . . 33	5 2 3 2 4 . . . . . x 1 1 62	. . 1 + . . . 29	. 1 + 67
Polyg viv			. . . 2 14	1 2 2 + 1 . . 72	. . + 33
Poten ere	2 . . 33	. 1 2 67	3 . 2 1 . . . . . . 2 1 2 46	. . 2 . x . . 29	. 1 + 67
Primu ver	1 . + 67	+ . 2 67	x 2 29		
Prune vul	2 + . 67		1 . 2 . 3 . 1 . + . 3 1 2 62		+ 2 + 100
Ranun acr	2 . + 67	+ . . 33	. . . 1 . x 2 1 1 39	. . 1 + 1 . . 43	. . + 33
R. bul	. . + 33	+ 2 . 67	. x . . 2 . . . 1 23		
R. fic		+ 3 . 67	4 2 15		
Rumex ace	3 . + 67	. 3 1 67	. . . . . . x . + 2 . 1 . 31		
Sagin pro			. . x . 1 . . . + 4 1 1 . 46		. 1 + 67
Saxif aiz			. . . . 2 14	. 4 2 3 2 . + 72	+ . + 67
S. opp				. 2 2 2 2 . + 72	. . + 33
Selag sel			. . . . . . + ... 14	. 1 . + . . . 29	+ 1 + 100
Sibba pro				1 1 . . x . . 43	
Siler aca				. 3 . + 3 . . 43	
Succi pra	6 + . 67	+ . 4 67	. . 5 1 . . . . 3 23	. . . . . . + 14	. . + 33
Tarax agg	2 + + 100		. 3 . 2 2 . . . . 1 x . . 39	. . . + . . + 29	. . + 33
Thali alp				. . 1 + 3 . . 43	. . + 33
Thymu dru	3 + + 100		. 3 . 2 2 + 4 . . 1 . . 1 54	. 1 3 . 2.. + 57	+ 3 + 100
Trifo pra	2 . + 67	+ . 1 67	1 . . 2 . . . . 2 23		
T. rep	2 . . 33	. 2 . 33	. . 2 2 3 + 2 . + 3 1 3 2 77	1 . 2 29	. 3 . 33
Veron cha	1 + + 100	2 + . 67	2 . . . . + . . + . . 1 . 31		
Viola riv	. + . 33	+ 3 2 100	2 2 . x x + x 46	1 1 1 . . . + 57	+ 2 + 100
Agros ten		. 3 . 33	1 . 3 . 4 . 3 . + . 1 3 3 62		+ 5 + 100
Antho odo	5 + . 67	+ . 2 67	5 4 2 3 . . 5 . + . 4 5 . 62	4 . . 3 4 . + 57	. 4 + 67
Briza med	4 . + 67		3 3 2 3 3 . . . . 3 46		. 2 + 67
Cynos cri	5 . + 67		2 . 2 3 . . . . . . 3 4 3 46		.
Dacty glo	3 + + 100	+ 3 2 100	2 . . 2 15		
Desch cae		+ . . 33	. . . . 3 . . . 7 . . 2 . 23	4 3 . . 5 + + 72	+ . . 33
Festu ovi	7 + + 100	+ . 3 67	6 6 7 7 5 8 7 4 . . 3 5 4 }85	} 4 . } . . +	+ 6 + 100
F. rub			. . 2 . .	}7 . }5 . + . 72	
F. viv				} . . } . + . 43	. . + 33
Holcu lan	3 + . 67	+ 3 3 100	6 . 3 . . . . 2 3 2 39		. 2 . 33
Koele gra	1 . + 67		. 3 2 15		
Nardu str			. . . . 4 . 3 15	4 7 . 5 4 . . 57	

High Mountain Habitats (TABLES 10,nos. 77-85; 11,XIV)

A. filicaulis occurs on rock-ledges and grassland in most of the high mountains of Scotland. Studies were made in the Central Highlands of seven habitats, some of which also contained A. vestita and are included in the habitats considered earlier. Details of the habitats are given below. (TABLE 25).

TABLE 25.

No.	Habitat	pH	Aspect	Altitude
77	rough grass	5.8	225°	2750'
78	rough grass,flush	-	315°	2750'
81	" "	-	90°	2250'
82	" "	-	90°	2250'
83	scree	-	0°	2500'
84	rock ledge	-	135°	2800'
85	" "	-	-	2500'

The rough grassland communities consist mainly of Festuca species including Festuca vivipara, Deschampsia alpina, Anthoxanthum odorata with some Nardus stricta. Other associated species given in TABLE 10, include Alchemilla alpina, A. glomerulans, A. wichurae, Campanula rotundifolia, Carex pulicaris, Euphrasia species Geum rivale, Polygonium viviparum, Saxifraga aizoides.

North West Scotland. (TABLES 10, nos. 86-88; 11,XV)

Both taxa are frequent in close-grazed Agrostis - festuca grassland on the Durness limestone; several Arctic-alpine species are present in addition to the usual associated species. The three habitats are described above (p. 93).

Other lowland habitats in Scotland. (TABLES 10, nos. 72-76; 11,XIII)

A. filicaulis grows with A. vestita in three of the five habitats described above (page 90), these are close-grazed Agrostic-Festuca grassland with the usual associated species. The floristies of these three habitats are very similar, and the communities are of a 'neutral' type. A. vestita, A. glabra, Carex caryophyllea, Cerastium vulgatum, Galium verum, Lotus corniculatus, Plantago lanceolata, Potentilla erecta, Prunella vulgaris, Ranunculus acris, Trifilium repens, Agrostis tenuis, Anthoxanthum odoratum, Cynosurus cristatus, Festuca ovina and rubra, Nardus, and Sieglingia decumbens.

The proportion of A. filicaulis s.st. varies greatly, at Keltney (No. 76) it is 80%, at Garth (No. 75) equal to A. vestita and in South Scotland (No. 72), [A. filicaulis and in South Scotland (No. 72)] A. filicaulis s.st. is rare. The first two localities are associated with the limestone (pH 5.5) the third a flush, is rather silty, (pH 5.9).

Northern England

Hill pasture and outcrops (TABLES 10,nos. 48-57; 11, XIII)

Details of five habitats are available; these are below 1300' all are pasture associated with limestone, three below limestone outcrops (pH 6.0, 5.4, 5.8): one a rocky outcrop and the fifth a base-rich pocket (pH 6.3) in Nardus grassland. Three other localities are all limestone outcrops.

The main associated species are:-
A. vestita, Carex caryophyllea, Carex flacca, Centaurea nigra, Cerastum vulgatum, Conopodium majus, Leontodon hispidus, Lotus corniculatus, Luzula campestria, Plantago lanceolata, Taraxacum agg., Thymus drucei, Anthoxanthum odoratum, Briza media, Cynosorus cristatus, Dactylis glomerata, Festuca species.

Montane habitats about 2000' are all on or near limestone outcrops on Mickle Fell, Cronkley Fell and Knock Fell, (TABLES 10, nos. 56-70; 11,XII). The associated species are very restricted A. glabra, A. vestita, Cerastum vulgatum, Trifolium repens, Agrostis species.

The woodlands (TABLES 10,nos. 32-34; 11,XI) are in Swaledale and Teesdale, altitude 950', 1000' and 850' respectively; as mentioned before the Swaledale habitat is nearer meadow conditions with few trees, Brocker's Gill (No. 33) is more closed and Park End is *Betula-Corylus* woodland; the soil is fairly acidic (pH 5.4, 5.8, 5.4). The ground flora is rich with a number of woodland species generally absent from the other habitats; *Ajuga reptans*, *Anemone nemorosa*, *Endymion non-scriptus*, *Oxalis acetosella*, *Ranunculus ficaria*, *Stellaria holostea*.

Rest of England. (TABLES 10,nos. 9, 29, 92; 11,XII)

These three localities in East Durham and Derbyshire are on limestone, two are in rocky pastures, the other is a limestone cliff in Lathkill dale, Derbyshire. In all cases the soil is shallow and only slightly acidic (pH 6.7, 6.0, 6.0). Both Derbyshire habitats are north facing. The associated flora is similar to that of the lower Teesdale habitats, e.g. No. 57.

This survey shows that *A. filicaulis* s.st. grows in a smaller range of habitats than *A. vestita*. It occurs on rock-ledges and in the higher Scottish mountains in mixed-grass communities. At lower altitudes (1500') and in Northern England it appears to be limited to neutral grassland on limestone or base-rich soils, rock-ledges, pasture and woodland. Unlike *A. vestita* this species is absent from rough-grassland including roadsides, meadows and most lowland pastures. This species is almost confined to natural habitats and is even less associated with man than *A. vestita*.

Only in some of the habitats in the Scottish Central Highland group is *A. filicaulis* s.st. not accompanied by *A. vestita*. In some of these both species are together, in two *A. filicaulis* is absent. *A. filicaulis* is generally more common in this area and it may be that here *A. vestita* is restricted in its habitats; *Saxifraga hypnoides* occurs only with *A. vestita*, *Saxifraga oppositifolia* and *Thalictrum alpinium* only with *A. filicaulis* s.st.; sites with *A. vestita* face north and west, those of *A. filicaulis* s.st. only face north and east. These differences are worth noting, but, of course, the number of samples is much too small to draw any further conclusions.

McVean, in an analysis of Scottish vegetation has observed (in letter) that *A. vestita* and *A. filicaulis* s.st. seem to replace each other for no obvious reason.

(c) *A. filicaulis* s.l. plants of intermediate hairiness

The plant with inflorescences of hairiness intermediate between *A. vestita* and *A. filicaulis* s.st. described above (p. 24) was found throughout the range of the two taxa. These records are, of course, of phenotypic intermediates, it was not possible to cultivate all of these and so far only a few genotypes are known. The phenotype was found in thirty six samples which are listed in TABLE 26.

TABLE 26.

numbers as in TABLES 9 and 10.

Leicestershire 1, 2, 4, 6,

Derbyshire 9, 10, 11, 15, 16.

Yorkshire 25.

East Durham 30.

N. Pennines below 1350' 32, 33, 34, 35, 41, 44, 45, 48, 49, 50, 56.

N. Pennines above 1350' 62, 63, 64, 70.

Scotland 71, 75, 76.

Central Highlands 77, 78, 81, 85.

N.W. Scotland 86, 87, 88.

The plant communities, altitude and soil cover the same range as in A. vestita and there appears to be no strong aspect preference. It is not so restricted as A. filicaulis s.st. since it also occurs in meadows and rough grassland at low altitudes.

Phenotypic intermediates are slightly more common in populations containing both taxa than those with A. vestita only (21/36: 15/36).

Two of the three populations with the genotypic intermediate also have both the other taxa; both habitats are woodland type in Swaledale (No. 32) and Teesdale (No. 33). The third, also in Teesdale (No. 45) is meadow, with A. vestita only. Obviously, more details of populations containing the genotype are needed before any useful conclusions can be drawn.

(2) Outside Britain

The difficulties of obtaining details of the ecology of both taxa are very similar to those mentioned above in connection with the geographical distribution. The amount of detail available varies considerably and is generally greater for A. filicaulis s.st. since this taxon is more frequent in the northern countries which have been more thoroughly studied.

In all countries A. filicaulis s.st. is a grassland plant. In Greenland (Bøcher 1933 and 1954) it is in Salix and Alnus scrub and a 'field with high perennials' community. In Scandinavia it occurs in all type of natural meadow, with a preference for wet ones, and also in deciduous woodland. In mountains it goes up to the tree line and in parts considerably higher. Rarely it is on roadsides and ditches. (Sam. 1943).

In central Europe, in the mountain regions of the Alps, Cevennes and Ardennes, grassy places and borders of woods; Buser adds 'xerophyte, dry grass patches, poor warm pastures ..... hillocks.'

Habitat details for N. America were obtained from herbarium material at Montreal and Ottawa. The habitats are quite varied rocky and stony ground by streams, sea cliffs; meadows,roadsides and margins of conifer woods being near human habitation; in the following habitats A. filicaulis may be truly native: 'turfy limestone cliffs ' and ' on moist gravelly soil with sedges and grasses' in Newfoundland.

A. vestita habitats are described only from Scandinavia where it is found in all types of grass community (natural meadow and open deciduous woodland) and more rarely on road and ditch sides, in fact in the same habitats as A. filicaulis s.st., but it is generally more restricted. No details are available of the one locality in Greenland (Devold and Scholander 1933); in N. America the habitats are similar to those for A. filicaulis mainly ruderal and less natural, though in one given as 'grassy woods' and another 'gravel by brook' in the St. John Highlands in

Newfoundland, A. vestita may be native.

Both taxa occupy very similar habitats in Britain and Europe and Greenland. But in Britain neither appears to be xerophytic - the description applied by Buser. In fact one is absent from southern Britain and the other, A. vestita appears to avoid the drier sunnier slopes in the south. It must be remembered that Buser's dry and sunny habitats are montane and so conditions are probably not so dry as in parts of S. Britain. Samuelsson (1943) considers neither species to be synanthropic in Scandinavia and the same is largely true in Britain. In America, however, both are often associated with man and may be synanthropic but not to the same extent as A. xanthochlora and others.

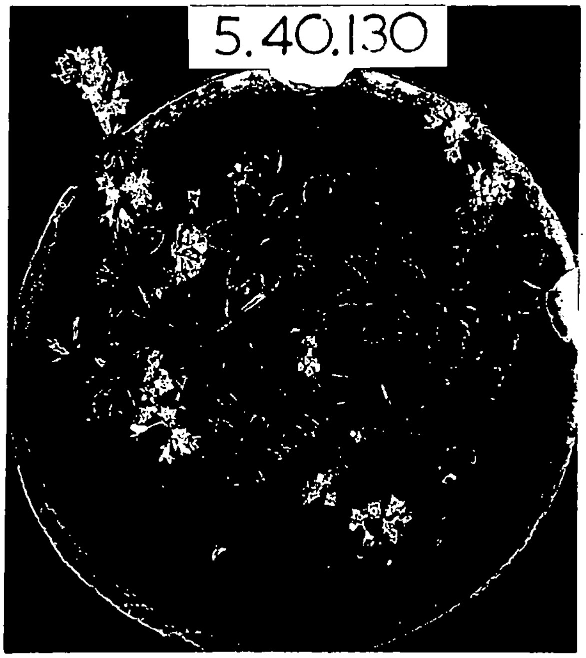


FIG. 30. *A. minima* Walters.
(pot 10 cms. diam.)

IV. ALCHEMILLA MINIMA. WALTERS

Reference has been made from time to time to the third taxon included in A. filicaulis agg. This is A. minima Walters., a dwarf plant very similar to the extremely dwarfed montane plants of A. filicaulis s.l. FIG. 30.

Even though Walters described the species accurately and well (1949) it is not easy to separate from A. filicaulis s.l. in the field; it was considered that by the cultivation of more material along with that of dwarf A. filicaulis the differences could be better established. Also, at the commencement of this work, A. minima was only known from Ingleborough c.1000'-2000' in Craven 34/7574, yet dwarf A. filicaulis agg. plants are plentiful in other hill areas. Extensive cultivation experiments were thus needed to see if any of these plants were referable to A.minima. The results of these latter experiments have already been described. (p. 40).

In no case was A. minima found off the Simon Fell - Ingleborough range though it is now known to be frequent in suitable habitats down to 950'.

Comparison of A. minima and the dwarf ecogenodeme of A. filicaulis s.l.

Comparison of the morphology and habit of A. minima

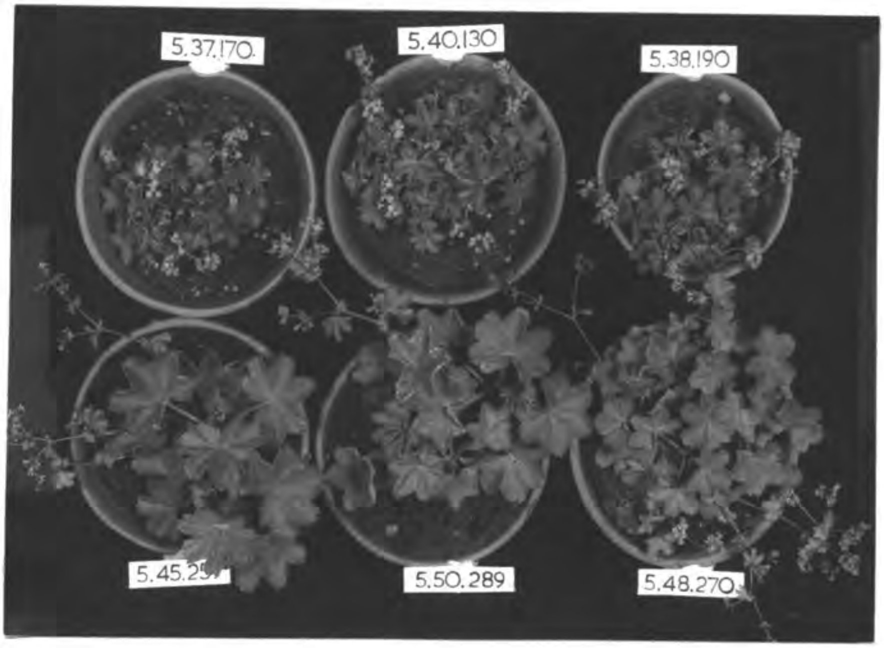


FIG. 31. Habit of A. minima (top row), A. filicaulis s.l. (bottom row). (larger pots 10 cms. diam.)

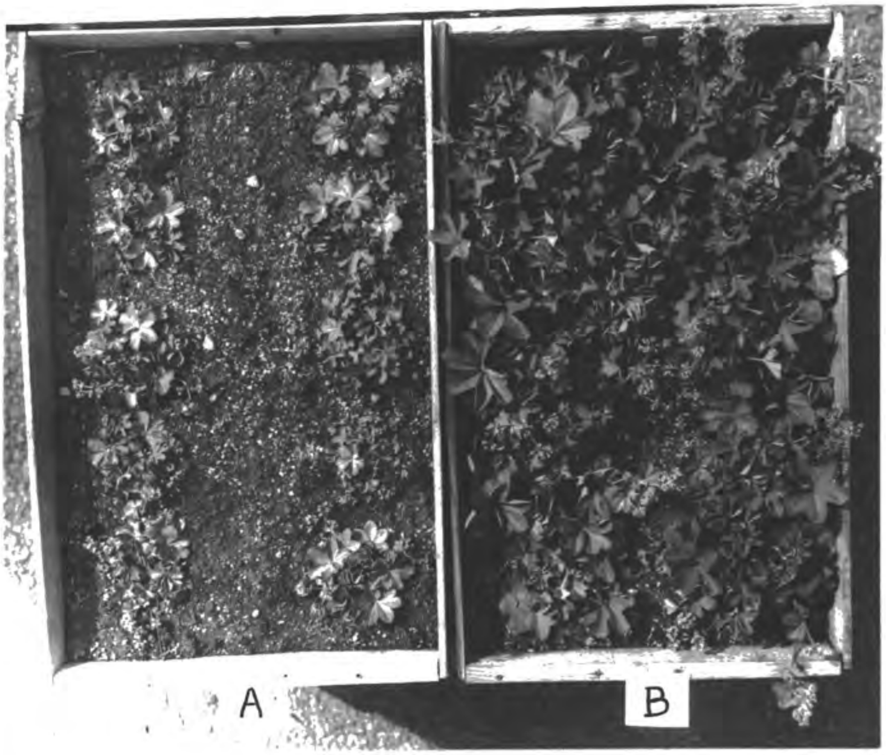


FIG. 32. Habit of A. minima (A), A. filicaulis (B) (width of boxes 24 cms.)

and dwarf montane _A. filicaulis_ s.l. is based on transplants grown in pots under ± similar conditions in the Botanic Garden at Durham for a year and other transplants grown in boxes as described above (p. 40). Some differences in the general appearances can be seen in the photographs, (FIG. 31 and 32) and measurable differences are given in TABLES 27 and 28.

TABLE 27.

Pots

		A. minima		_A. filicaulis_ s.l.	
		25 plants		29 plants	
		mean	s.e.	mean	s.e.
1.	petiole length:lamina length	0.8	± 0.029	1.16	± 0.031
2.	lobe length:lamina length	0.51	± 0.010	0.4	± 0.009
3.	depth of V between lobes:lamina length	0.21	± 0.023	0.14	± 0.006

TABLE 28.

Boxes

		A. minima		*A. filicaulis* s.l.	
		10 plants		3x10 plants	
		mean	s.e.	mean	s.e.
1.	No. of shoots.	4.7	± 0.45	5.7	± 0.45
				7.3	± 0.44
				6.4	± 0.67
2.	length of petiole	1.9	± 0.17	10.0	± 0.40
				8.7	± 0.42
				9.2	± 0.39
3.	breadth of leaf	2.3	± 0.18	5.1	± 0.10
				4.7	± 0.19
				4.4	± 0.21
4.	No. of inflorescences	15.7	± 2.22	3.8	± 0.39
				1.9	± 0.47
				3.2	± 0.66

In the following comparison *A. minima* will be considered first in each case.

The rhizomes are longer and more slender due to the longer internodes; in cultivation it produced slightly fewer branches (TABLE 28). In *A. minima* the leaves are ± prostrate giving a plant a few centimetres high; in

A. filicaulis s.l. the leaves are more erect in cultivation so the length of the petiole gives an approximate measure of the height of the plant. (TABLE 28).

The base of the plant is usually without any wine-red pigment, in contrast to A. filicaulis s.l. where it is usually present.

In A. minima the young and mature leaves are usually blue-green, the lamina of mature leaves tends to be recurved and rather stiff, the lobes are V shaped in cross section. (FIG. 31).

A. filicaulis s.l. is less blue - often pure green, the lobes are more open and the lamina flatter and not stiff. These differences are well shown in the photograph. (FIG. 32). Leaves of A. minima are much smaller (TABLE 28), usually with five full lobes, in A. filicaulis another pair of basal lobes is more frequently well developed. Other differences in size are between leaf and petiole length, length of the median lobe and lamina and depth of the incision between the lobes are in TABLE 27. The longer lobes of A. minima have fewer teeth than A. filicaulis s.l., 9(11) : 11(13) on the median lobe. A. minima produced many inflorescences (TABLE 28), these were more slender and slightly shorter (usually 5 internodes) than A. filicaulis s.l. (usually at least 6 internodes).

No obvious differences were noted in the flowers and fruits.

The hair characters of the A. filicaulis s.l. plants have already been considered. Both A. filicaulis s.st. and A. vestita dwarf variants are known; some of the former were very glabrous when collected in the field. The leaves in A. minima on the lower surface were almost all grade 1, the upper surface grade 2, (FIG. 10), in only one case were the leaves more hairy, grades 3 and 4 respectively.

Comparable analysis of the hairiness of the inflorescence is difficult because of the shorter inflorescences. In all cases the first internode was glabrous - this is often so in A. filicaulis s.l.; frequently internode II was glabrous. In ten plants the inflorescence was grade 6, that of A. filicaulis s.st. The inflorescences of the other plants were hairy to the top; twelve were placed in grades 0-3, and three in grades 4-5, though this is based on 4 or 5 internodes only in most cases. Although direct comparison cannot be made with A. filicaulis s.l. it is clear that there is similar variation in the hairiness of the inflorescences.

Chromosome counts were obtained of pollen-mother-cells of two plants of A. minima. 5/40/129 $2n = \begin{cases} c.105 \\ c.108 \end{cases}$

$$5/39/106 \quad 2n = \left\{\begin{array}{l} c.103 \\ \left.\begin{array}{l} c.\ 98 \\ c.\ 99 \end{array}\right\} \text{probably too low} \end{array}\right.$$

These are within the range for *A. filicaulis* s.l. (2n = 101-110) and near the values obtained for a montane *A. vestita* plant.

$$5/45/250 \quad 2n = \left\{\begin{array}{l} c.105 \\ c.109 \end{array}\right.$$

Distribution of *A. minima*

All the dwarf montane plants of the *A. filicaulis* agg. from mountains other than Ingleborough became larger in cultivation and so belong to *A. filicaulis* s.l.. So far *A. minima* is known only from the close grazed and often wet flushed limestone grassland on Ingleborough between 950' and 2000'.

It appears to be frequent in these lower habitats on the west side of Ingleborough and it should be looked for over a wider area including the adjacent hills. Although no plants of *A. filicaulis* s.l. were collected in the population samples from c.2000', *A. filicaulis* s.l. does grow in this area and *A. filicaulis* s.st. has been recorded from the west side of Ingleborough.

Ecology of *A. minima*

A. minima appears to be confined to closely grazed, base-rich flushes or wet Festuca-Agrostis grassland - on or just below the limestone strata of the Carboniferous limestone series of Ingleborough. Details of the habitat factors are listed below TABLE 29.

TABLE 29.

	Habitat	Soil	pH	Aspect	Slope	Altitude
1.	above limestone	moist, dark-brown peaty loam, shallow	5.9	225°	c.20°	2000'
2.	depressions in limestone pavement	"	5.2	180°	c.5°	2000'
3.	wet flush below limestone	wet, dark-brown peaty loam	-	180°	-	2000'
4.	"	"	6.7	180°	c.15°	2000'
5.	"	"	6.1	270°	c.10°	2000'
6.	"	"	6.5	270°	c.10°	950'

In all cases the soil is a rather peaty dark brown loam associated with limestone but obviously leached (pH 6.1-5.9). The lower acidity of the wetter habitats (pH 6.1-6.7) must be due to base rich flushing from the limestone strata.

The associated species are listed in TABLE 30.

In all the communities Festuca ovina, Trifolium repens, Thymus drucei and Euphrasia agg. are present.

The five montane communities also contain *Achillea millefolium*, *Cerastium vulgatum*, *Galium pumilum*, *Sagina procumbens*. *Deschampsia caespitosa* and *Agrostis tenuis* are frequently present. This community is rather similar to those found in the high montane habitats of *A. filicaulis* s.l. in the N. Pennines (cf. p.87). The habitat at 950' altitude contains a number of species characteristic of lower hill pastures e.g. *Hypochaeris radicata*, *Leontodon autumnalis* and *Leontodon hispidus*. *Poterium sanguisorba* and *Carex panicea* not found in the higher communities.

TABLE 30.

	1	2	3	4	5	6
Alchemilla glabra	.	.	1	+	.	.
A. minima	+	3	3	3	3	+
A. vestita	.	.	.	.		+
Achillea millefolium	+	2	2	1	2	.
Bellis perennis	+	.	4	4	2	+
Cardamine	.	.	2	2	1	.
Carex caryophyllea	.	3	3	3	.	+
C. panicea	.	.	.	.	.	+
Campanula rotundifolia	+	.	2	1	2	.
Cerastium vulgatum	+	2	2	2	3	.
Erophila verna	+	1	.	.	.	.
Euphrasia agg.	+	1	2	1	2	+
Galium pumilum	+	1	2	1	3	.
Hypochaeris radicata	.	.	.	.	.	+
Juncus effusus	.	.	.	.	1	.
Leontodon autumnalis	.	.	.	.	.	+
L. hispidus	.	.	.	.	.	+
Lotus corniculatus	.	.	.	2	.	+
Luzula campestris	+	4	.	.	1	.
Minuatia verna	+	1	.	.	.	.
Plantago lanceolata	.	.	1	2	.	+
Potentilla erecta	+	.	.	.	.	+

TABLE 30 (continued)

	1	2	3	4	5	6
P. sterilis	+	2	2	1	.	.
Poterium sanguisorba	.	.	.	.	.	+
Prunella vulgaris	.	.	3	2	.	+
Ranunculus acris	+	.	2	2	2	+
R. bulbosus	.	2	.	3	2	.
Rumex acetosa	.	2	.	.	3	.
Sagina procumbens	+	2	2	2	1	.
Thymus drucei	+	3	3	3	4	+
Trifolium repens	+	2	2	3	3	+
Veronica chamaedrys	+	.	.	.	1	.
V. serpylifolium	.	.	.	.	1	.
Viola riviniana	.	1	.	.	2	.
Agrostis tenuis	.	4	5	5	.	4
Anthoxanthum odoratum	.	.	.	2	.	.
Briza media	.	.	4	.	.	3
Deschampsia	4	1	.	4	3	3
Cynosurus cristatus	.	+	.	3	2	3
Festuca ovina	8	9	7	8	9	5
Helictotrichon pratense	5	.	.	.	3	.
Koeleria gracilis	+	.	.	.	4	.

The main points of difference are summarised below:

	A. minima	A. filicaulis
Rhizome	long and slender, internodes long, few branches	compact and thicker, internodes short, often much branched.
Petioles	usually shorter than leaf lamina.	longer than leaf lamina.
Lamina	usually blue green.	not so blue-green, usually pure green.

	A. minima	A. filicaulis
Lobes	½ radius of lamina, usually 5, deep V between lobes.	less than ½ radius of lamina usually 7, shallow V between lobes.
Teeth	usually 9	usually 11
Inflorescences	many, very slender, usually 5 internodes.	fewer, less slender, usually 6 internodes.
Distribution	? endemic, Ingleborough.	? endemic, N. Pennine mountains.
Ecology	base-rich flushed grassland.	montane grassland and flushes.

The status and probable origin of A. minima will be discussed later.

V. OTHER *A. FILICAULIS* s.l. PLANTS

During the course of this work a number of plants have been collected which have some morphological affinities with *A. filicaulis* s.st. but are far from typical. These are best described and compared with more typical *A. filicaulis* s.l. individually. Descriptions are based on cultivated plants.

The Malham plant 4/27

Comparison with typical *A. filicaulis* s.l.

Plant more robust, height of basal leaves 25-30 cms.; leaves more orbicular, 7-8 (9) cms. wide, 6-7 cms. long, 9 (11) lobes, mid-green not blue-green, coriaceous, slightly undulating. Lobes round, $\frac{1}{5}-\frac{1}{4}$ radius of the leaf; teeth large somewhat connivent. Petioles all well covered with adpressed hairs but not dense, leaves with few hairs on folds above and nerves below. Stipules brown, base of petioles wine-red. Stems erect 30-35 cms., stouter, clothed with adpressed hairs on 3 basal internodes. Flowers large 4 mm. diam., urceoles U shaped, some with a few hairs. Known only from a small population near Malham House.

Filicaulis 8 collected by Dr. S.M. Walters as dwarf *A. glomerulans* from the east side of Creag na Caillich 5.7.47.

Plant robust, height of basal leaves 25-30 cms. Leaves orbicular - reniform 7-8 cms. wide, 6-7 cms. long, 9 lobed green-blue green, coriaceous, slightly undulating. Lobes round, $\frac{1}{4}$-$\frac{1}{5}$ radius of leaf, teeth large, more acute than 4/27, somewhat connivent. Petioles of main summer leaves glabrous, younger petioles with scattered loosely adpressed hairs; leaves with few hairs on folds above, ± glabrous on nerves below. Stipules brown, base of petioles wine-red. Stems 30-35 cms. stout erect with adpressed hairs only on lowest internode, Flowers large 4 mms. diam., urceoles U shaped without hairs. $2n =$ c.150.

So far, only the one plant is known from Creag na Caillich in Scotland.

These two variants are very similar in all characters except hairiness, Filicaulis 8 being very much less hairy. Both have the general appearance of *A. filicaulis* s.st., but deviate particularly in the hair character, also the more robust habit and fuller, undulating leaves. From the small amount of material available so far, one cannot be certain that they should be regarded as one taxon; nor is it at all certain whether they should even be included in *A. filicaulis* s.l.

These plants closely resemble A. versipila Bus. (1895) a sub-glabrous species known only in the Alps, at least as far as can be ascertained from Buser's report.

Group 6/18 These plants were collected from a roadside verge in Shetland by W. Scott and appeared to be well grown plants of A. filicaulis s.st. After one year of cultivation the plants were very atypical but in the 2nd year a closer resemblance was shown. The main differences were the more yellow-dark green colour and strong red coloration of stems and fruiting inflorescence on the sun-side, a characteristic common in some species but not usually noticeable in A. filicaulis s.l. Leaves pleated and somewhat funnel-shaped, so that the lobes appear to be narrow. Teeth slightly more acute. Stem stouter and more branched, spreading hairs similar to the intermediate type.

The plant still looked atypical in the second year of cultivation, but because of the difference between this and the previous year, observation over at least another is advisable.

DISCUSSION

In the preceding sections evidence of genotypic and phenotypic variation in A. filicaulis s.l. has been presented, together with ecological and geographical data.

It is abundantly clear that though the species is an obligate apomict, the individual plant populations are by no means uniform. Genotypic variation occurs in the hair cover, leaf shape, stipule colour; also plant size and habit, and chromosome number.

As this variation occurs in plants which are presumably absolutely true-breeding several problems arise:-

a) what is the mechanism of variation?
b) are new genotypes still being formed?
c) when and how did these variants arise?

The basis of the variation depends upon the mode of origin of the embryo. Of the four methods by which new genotypes can arise in apomictic genera given by Gustafsson (1947), hybridisation and segregation can only take place when fertilisation is still able to occur. The obligate nature of the apomixis and the aposporous mode of embryo formation in Alchemilla (see p. 5), combined with apparently infertile pollen would appear to exclude any possibility of hybridisation taking place.

Other methods by which new genotypes may arise are:-

(1) polyploidy.

(2) mutation.

(3) autosegregation.

1) All Alchemilla vulgaris species are high polyploids. Within A. filicaulis s.l. the chromosome numbers of most of the plants examined are in the range 2n = 101-110.

Two cases with a higher number have been found; a population represented by 3(60) with 2n = c.150 and a single plant (Fil 8) which is doubtfully referable to A. filicaulis s.l. also with 2n = 150. This figure may be considered to be triploid if the lower value is "diploid", this is not an exact multiple but the loss of a few chromosomes amongst so many may be of insignificant effect.

It is difficult to see how an increase of half the chromosome number can have come about in an aposporous apomict. If fertilisation could take place, fusion of a haploid (n = c.50) pollen nucleus with a diploid egg (2n = c.100) would give the required value c.150, but in the present method of reproduction this does not seem possible. Similar higher values are known also for A. transpolaris Juz. (synonym, A. borealis Sam. ined.), 2n = 130-152 and A. oxyodonta, 2n = 165-168. In these cases their origin may have been in the early stages of the formation of the Alchemilla species but 3(60) is morphologically so near to A. filicaulis s.st. that a more recent and closer link seems to be called for.

2) Mutations. Gustafsson (1947) gives several reasons why it seems probable that those apomicts which lack the capacity of fertilisation will be stuffed with recessive changes of various kinds; some chromosomal, others genic. Although dominant mutations are rare, and recessive mutations in polyploids, which are at least partially autopolyploids, have little chance of showing visible effects until sufficient mutants of the same kind have accumulated, the obligate apomict has time on its side. The very lack of gene exchange and action of natural selection results in the accummulation of all mutations. Bantu and Wood reported some dominant mutations in Cladocera clones formed by parthenogenetical reproduction for more than 350 generations. As A. filicaulis s.l. was probably formed in the early Quaternary period (see below) there has been plenty of time for accumulation of many mutations.

3) Autosegregation of Gustafsson (1947) "this takes place in ovules where the egg-cells are not fertilised, and implies female changes or rearrangements of the genotype". The term is ± equivalent to subsexual segregation of Darlington (1937).

Small change in the chromosome number is the simplest form; it is best known in Taraxacum, (Sörenson and Gudjönsson (1946). In A. filicaulis s.l. a range of chromosome numbers occurs, 2n = 102-110 and it was hoped that these would be found to be correlated with the morphological variation already observed.

The less hairy A. filicaulis s.st. and the hairy A. vestita have a range of chromosome numbers which overlap 2n = 102-110 and 2n = 104-110 respectively. Only one count of a dwarf montane ecogenodeme plant was obtained; this was of A. vestita and had 2n = c.105, which comes within the range obtained for the lowland (< 2000') plants with 2n = 104-109. Obviously more counts are needed.

Some further data from very similar work are provided by Turesson (1956) who found significant differences in stem and petiole length and leaf size between biotypes in six species of A. vulgaris (not including A. filicaulis.). Later (1957), he published chromosome counts but it is not clear if the numbers were those of plants used in the earlier work or not. Even, if they were, he does not give the numbers of his morphological variants individually. Only by obtaining exact counts will it be possible to determine if this kind of variation is correlated with differences in the chromosome numbers. Even then, interpretation will not be easy, since the reduction in chromosome number may be due to the loss of different chromosomes. Thus plants with the same number of chromosomes will have different genomes and hence (if the loss is reflected in the external morphology) show variation in several factors.

Autosegregation without change in the chromosome number is more difficult to conceive. On a first consideration it is reasonable to expect that segregation depends on the formation of chiasmata and crossing-over and hence meiosis, in the formation of the embryo. The critical stage is, of course, the formation of the gametophyte; does meiosis take place or are all divisions mitotic? Meiosis is usually in diplospory in which the gametophyte arises directly or indirectly from a macrospore-mother-cell (embryo-mother-cell), the unreduced chromosome number being maintained by restitution nuclei or pseudo-homeotypic divisions. Segregation may be expected in some diplosporous apomicts. What of the aposporous apomicts? Embryo formation from a somatic cell by mitotic division would appear to provide no opportunity for segregation.

In Alchemilla an intermediate state exists, the archespore is multicellular, so one may regard all these cells as potential embryo-mother-cells. A central cell enlarges and enters meiotic prophase and then degenerates, other archesporial cells after one or two mitotic divisions may enter meiotic prophase and degenerate or develop aposporously into embryo sacs by mitotic divisions, only one reaches maturity.

Gustafsson (1946) regards this as 'the Alchemilla - type of stabilised apospory' since an abortive true embryo-mother-cell was formed in the first instance.

If the embryo is always formed in this way segregation appears to be excluded completely.

This mode of embryology is very similar to that found in Sorbus (Liljefors 1934 and 1954) and, of course, Aphanes arvensis (Böös 1924). Both authors found that the meiotically directed aposporous cells can pass through the complete meiotic-cycle and form reduced embryo-sacs capable of fertilisation; Böös (l.c.) found that the true embryo-mother-cell sometimes goes through meiosis. A re-examination of the embryology of A. arvensis by Hjelmquist (1959) has shown that normal reduced embryo-sacs and aposporous unreduced embryo-sacs are formed, thus apomixis in A. arvensis is facultative. There is a tendency to apomixis in the two diploid species A. microcarpa and A. floribunda.

An interesting series from somatic apospory to diplospory is found in Elatostema (Fagerlind 1944). As in Alchemilla the archespore is multicellular and secondary embryo-sacs may be formed in several ways:-

1. Apospory. The embryo-mother-cell enters meiosis and degenerates, the aposporous embryo-sac is formed from a neighbouring cell by mitotic divisions (c.f. *Alchemilla*.)

2. No meiotic tendencies in any tissue. a) *Apospory*. The embryo-sac arises directly from an archesporial cell. b) *Diplospory* - rarely a embryo-mother-cell arises from the archesporial tissue.

3. Diplospory; the embryo-sac arises from a true embryo-mother-cell by restitution nuclei, pseudohomeotypic or mitotic divisions. Transitional stages are found.

In view of this evidence and the fact that *Alchemilla* shows stronger meiotic tendencies in the nucellus tissue than *Elatostema*, further examinations should be made of the embryology, especially of the more variable micro-species of *A. vulgaris* agg. e.g. *A. filicaulis* s.l. It does not seem likely that sexual reproduction will be found in those species which have already been examined because of the poor pollen and absence of evidence of pollination. Discovery of the occasional occurrence of diplospory could provide the mechanism for segregation. Only a few of the many species of *A. vulgaris* agg. have been studied, furthermore these are the more widespread species; examination of pollen, in the first instance, of the many species of smaller range in Central or Eastern Europe may reveal better pollen and maybe diploids or low polyploids and evidence of sexual reproduction which could be followed by embryological studies.

This problem of segregation cannot be left without the mention of what may be a 'very long shot', that of somatic crossing-over. This has been known in Diptera for a long time and evidence is accumulating of its occurrence in Fungi. (Pontecorvo. 1959). There is little evidence of it in higher plants so far and indeed, it would be very difficult to distinguish from other types of variation.

Thus on a theoretical basis several sources of variation can be postulated. Of these, polyploidy does not seem to be important in determining the kind of interspecific variation found in <u>A. filicaulis</u> s.l. but may be important in the larger changes which lead to the formation of subspecies and new species.

The many small variations, mostly of a quantitative nature, found in <u>A. filicaulis</u> s.l. are more probably based on a combination of the other three sources of variation; mutation, segregation and change in chromosome number.

There is no reason to think that the mutation rate in apomicts should differ greatly from that in amphimictic plants; but the greatest difference is one of profound importance; once formed, the mutations, good and bad, will tend to accumulate, they will not be lost as in inbreeding systems or to a less extent out-breeding systems. The greatest draw-back is the high polyploid state which will tend to mask all but dominant mutations. A mutation to a dominant allele will be expressed in the phenotype at once; but such mutations may be expected to be relatively uncommon. The greatest effect on the phenotype is likely to be due to changes in alleles which are partial dominants only. As similar alleles accumulate so a gradual variation will appear in the phenotype. In Alchemilla several types of variation are of this gradual kind, e.g. leaf shape, lobe shape, hairiness. In aposporous apomicts recessive mutations are unlikely to be revealed unless the homozygous state is reached, a lengthy process. An intermediate state occurs when the heterozygote produces a distinct phenotype from that of the dominant or recessive.

The build up of similar mutations may be expected to be slow, but, if the period is long enough this will be accomplished eventually. Should segregation take place the effect would be to speed-up the appearance of variants especially in the cases of co-dominants and recessive mutations. Somatic crossing over would be particularly important in the former.

It is clear from this review that there is very little real evidence of the basis of variation, only further cytological and embryological investigations may show the correctness of the various mechanisms for the source of variation which have been postulated.

There is another alternative which should be considered now; it is the possibility of facultative apomixis at some period in the formation of the present day species. Pollen is so bad that it seems unlikely that facultative apomixis could occur today. Some species like Agropyron scabrum (Hair, 1956) are known to contain the whole range of methods of reproduction, sexual, facultative and obligate apomixis. A period of facultative apomixis may have occurred and have given rise to at least some of the variants now found within the species framework. No direct evidence of this is available in the A. vulgaris agg. so far, though apomixis in Aphanes arvensis has been shown to be facultative (Hjelmquist 1959). It is also worth mentioning that hybrids between the sexual species A. pentaphylla and some species of the A. alpina agg. were considered to be obligate apomicts by Buser and Strasburger (1905). This evidence does not favour the possibility of a period of facultative apomixis, but it is dangerous to draw analogies in this way without more definite evidence. Examination of the distribution pattern of the genodemes in A. filicaulis s.l. may throw light on their time and mode of origin.

Plant geography has long been an important factor in taxonomy, and more recently population studies have been used in the study of biosystematics.

In line with current phyto-geographical opinion Samuelsson (1943) suggested a centre of origin for the older species of the large A. vulgaris aggregate in the Alps or Central Eurasiatic regions on the basis of the high number of species in those areas today and the distribution of the more widespread species. These latter reached Greenland and maybe North America as native species and so are considered to have migrated in the early Quaternary period. It is well known that many of these species are morphologically very uniform over their whole range e.g. A. minor, A. subcrenata, A. acutiloba; although variations of the kind described above do occur, they do not burst the species boundary. This general uniformity of each species suggests that these boundaries were fixed i.e. the species were apomictic before migration to their present stations began. Although there are many segregates in the central Eurasian area whose distribution is little known it is unlikely that any have a distribution of wide geographical significance to the north-west since the Alchemillas have been intensively studied in those areas.

A. filicaulis s.l. has a wide distribution in north-west Europe and reaches Greenland and north America and so may be regarded as one of the earlier formed species.

It is not easy to apply the same principle of 'age and area' to genodemes within the species boundary when so many factors are unknown; however, the distribution patterns of the genodemes, some of which are widespread, others rare and sporadic, may be of significance.

Variation in hairiness and leaf shape are the most widespread and frequent. Most information is available for the hair variants since this has long been used by taxonomists to split the aggregate into two taxa which correspond approximately to hair grades 6 and 0-3. (see above p. 35). When divided on this basis, two patterns of distribution are obtained which are sufficiently dissimilar to suggest independent migrations. The presence of only A. filicaulis s.st. as a native plant on the west of the Atlantic suggests that this originated as a distinct genodeme earlier than A. vestita, which is more Atlantic and less northern and in Europe only. The distinction is emphasised by the physiological differences implied by the different ecological tolerances of each taxon shown in the more northern - arctic range of *A. filicaulis* s.st. and the greater frequency of *A. vestita* in south Britain and France; but there is a margin of overlap, where one taxon replaces the other without any apparent reason, as in Scotland. (see page 102 above). Plants of intermediate hairiness will be considered later.

Another widespread variation is in leaf shape. Unfortunately little is known of this outside Britain where preliminary analyses indicate that wide variation, at least in lobe shape, occurs throughout the British range of *A. filicaulis* s.l. and it is independent of the hair character. There appears to be no geographical segregation of the leaf shapes comparable to that of the hair types - though this may be revealed when more data are available. Although no details are available outside Britain, it is almost certain that Buser would have made use of the leaf character in his taxonomic treatment if it were associated with significant distribution patterns, as in the species: *A. monticola* Opiz. *A. acutiloba* Opiz and *A. xanthochlora* Rothm.

Thus on the basis of the data available so far, separation of *A. filicaulis* s.l. into two taxa on the basis of hairiness takes precedence over leaf variation since it is supported by distinct distribution patterns and ecological distinctions. No doubt A. filicaulis s.st. arose with the other widespread species of A. vulgaris agg. in the early Quaternary period. Since both taxa are contained in the general morphological frame-work of A. filicaulis s.l. it is more likely that A. vestita arose from A. filicaulis s.st. than as an entirely independent species. On the question, whether these segregates were facultative or obligate apomicts at this time, it is difficult to understand how one set of characters (i.e. hairiness) should remain fixed whilst another (leaf shape) continued to vary. More probably A. filicaulis s.st. and the other early segregates of Alchemilla vulgaris agg. at any rate, were obligate apomicts from the time of their emergence as distinct taxa (c.f. the hybrids between A. pentaphylla and A. alpina agg.).

A. vestita could have arisen as a mutant or by some form of autosegregation early in the history of the species, probably the former producing an abrupt variant.

The more gradual variation in hairiness found in both taxa and the range of variation in the leaf shapes may be due to the gradual accumulation of mutants or autosegregation. Genic segregation could give these results - but there does not appear to be much possibility of this in aposporous embryology. The occurrence of diplospory (as described above p. 124) could provide the mechanism.

These genodemes will have been subject to the usual action of natural selection, and probably some information on the time of their formation may be obtained from the examination of variation within and between populations. Wide variation within all populations would indicate that the genodemes were formed before the populations, which are partially isolated. A narrow range of variation which differs between populations could indicate more recent formation of the genodemes.

There is some evidence to show that the range of variation within most populations is wide; but in some it is more limited and centred about a mean, which differs between populations giving some with broad shallow or long lobed leaves.

The existence of ecogenodemes supports the idea of continued production of variants by mutations or autosegregation. So far these are known from areas of intensive grazing and rigorous climatic conditions. Certainly they are post-glacial and if the grazing factor has been important (as would appear to be the case), maybe within historic times. It seems unlikely that grazing would be severe before the development of blanket bog which reduced the area of these habitats drastically, or that the number of herbivores would be sufficiently high before man introduced sheep - though deer may have been numerous. It is likely that these comparatively base-rich areas have always been subject to heavier grazing pressure than the surrounding vegetation. (Pearsall, 1950).

Similar ecogenodemes of A. xanthochlora from Ingleborough and A. glabra from Knock Fell are known.

Reference can now be made to the plants of intermediate hairiness. These were separated in this study because they were found to breed true; but phenotypic intermediates arise from genotypes of A. filicaulis s.st. and A. vestita; whether these breed true is not yet proven. These phenotypes make it impossible to recognise genotypic intermediates without cultivation experiments, and consequently their distribution is only known in Britain, where they are rare and scattered. The limited data available indicates a polytopic origin rather than dispersal from one centre: the very low frequency in each of the populations suggests a recent origin probably from one or the other taxa. In all cases the intermediate occurs in mixed populations of both taxa.

Rather similar in frequency and distribution are several genodemes which differ from normal A. filicaulis s.l. by a single character.

Concoloured plants which lack the wine-red pigment at the base of the petioles and on the stipules are known in both hair segregates. They occur scattered in Northern England and Scotland, usually in ones or twos. Malham is the only area where they are at all frequent; here several plants occur in two populations about four miles apart. Though the greater frequency may be due to cloning it is not known if they have spread from a single locality.

A few plants referable to A. filicaulis s.st. but with adpressed instead of spreading hairs are known from one locality in Scotland. "adpressipilosa" forms are known in several species of Alchemilla, e.g. A. acutiloba, minor, monticola (Sam. 1943). In each case only one or two examples are known.

Only one glabrous variant proved to be genotypic; this too, is in Scotland. Other plants collected as glabrous A. filicaulis s.l. variants became more hairy after a few years in cultivation and are now referable to A. filicaulis s.st. All were extremely dwarfed when collected.

With this group should be included the genodeme 3(60) which has broad shallow lobes and the chromosome number 2n =c.150. So far it is known from the Craig-na-Caillach - Meall-nam-Tamachan range only. The area is about the same size as that occupied by the Malham concoloured plants, but is open to sheep along the whole range; it is likely that they have helped in the dispersal of the plants which were common on the sheltered ledges used by sheep.

Like the intermediate hairiness genodeme, these genodemes are scattered and of low frequency and so are probably fairly recent in origin.

The genetic mechanism for the production of adpressed instead of spreading hairs may well be a fairly simple one, since the same genodeme has arisen in several species of *Alchemilla vulgaris* agg. Probably it is a single gene mutation.

Only the 3(60) genodeme is known to have a different chromosome number 2n = c.150. So far it is only known in the one area, and if it is indeed so restricted, its spread may have been rapid and its origin recent.

A number of more atypical plants have been found and described above. These have some characteristics in common but require further observation before it can be decided to which segregate they belong and what status they should be given.

A. minima

Cultivation experiments have shown that A. minima is worthy of specific status. The similarity of morphological characteristics with A. filicaulis s.l. suggests a close relationship but as before we have no proof. Chromosome numbers are of the same order. An interesting parallel can be drawn between these species and certain pairs of species in the Alps. A. minima possesses several morphological characteristics often found in the immature stages of typical large plants of A. filicaulis s.l., such as the truncate,deeply divided leaf lobes and shortage of hairs. To a lesser extent the dwarf ecogenodemes of A. filicaulis s.l. exhibit characteristics of the early stages of development of the larger plants. e.g. the long-lobed leaves. Phenotypic dwarfs, particularly those from high wet flushes (see p. 27) show these characters, but lose them when grown under garden conditions and a larger size is obtained. In A. minima the character appears to have become stabalised, a state comparable to that of neoteny in the animal kingdom.

Buser (1894) noticed similar series in several groups of species in the Alps e.g. A. demissa and A. coriacea, A. intermedia and A. colorata, A. fissa and A. flexicaulis. In each pair the first-named is the dwarf, in all, the few lobes of the small leaves tend to be truncated and deeply divided by toothless incisions; the few teeth are usually long. All were 'subnivale' in distribution. He discusses several other cases including some in *A. alpina* agg., on the basis of certain anatomical characters he was of the opinion that the taller lowland plants had developed from the subnivale dwarfs. Available data for *A. minima* and *A. filicaulis* s.l. genodemes supports a different view. *A. minima* and the dwarf ecogenodemes are limited in distribution, all grow in extreme climatic conditions where the extreme phenotypic dwarfs of larger ecogenodemes show that the full potentialities are not attained. It seems more likely that *A. minima* may have evolved from such stock by one of the mechanisms discussed above (p.121) or at an earlier date in the wet flushes probably above the tree line (where the extreme phenotypes occur) and spread into the close grazed grasslands as the habitats became available.

TAXONOMIC STATUS AND CLASSIFICATION OF THE SEGREGATES OF THE A. FILICAULIS AGGREGATE

The classification of apomictic groups presents the modern biosystematists with a number of intractable problems. On the one hand, are the apomictic groups which are in an active state of evolution so that a stable classification of all the variants is practically impossible. On the other, are those obligate apomictic groups in which hybridisation cannot occur; here the situation is more stable, and in fact the taxa appear to have many of the desirable characters of the "classical" species ..... constancy, invariability and distinctness. If the biosystematist's criteria of the species concept based on gene-exchange is applied to obligate apomicts each individual becomes a species! Keen-eyed classical taxonomists have already described very many species in certain groups e.g. Hieracia, Rubi. The treatment required has been formulated by Valentine and Löve (1958), "The classification to be aimed at is thus one which takes into account biosystematic discoveries, but is based mainly on the taxonomic criteria of morphology, ecology and geographical distribution, and which makes use of the whole taxonomic hierarchy from species down to forma with or without the prefix agamo-."

The major problem in the treatment of obligate apomictic groups is the large number of units which have been or may be described. These are of different kinds, some morphologically distinct and eco-geographically well defined, others less clear in one or both respects. These units are generally referred to as species, but some authors prefer to use the term microspecies since the differences between each are small, whilst Turesson introduced the special term agamospecies. Whichever terminology is used the same rank is given to each of the units, whereby failing to separate the well defined taxa from the indistinct. Use of infra-specific categories would over-come this difficulty and produce a hierarchical system which indicates probable relationships within the A. vulgaris aggregate.

Though each apomictic group must be treated on its own merits, comparable treatment between the groups should be aimed at .... but this is difficult to achieve because of the immense task of knowing several obligate apomictic groups sufficiently well, e.g. Euhieracium, Taraxacum, Alchemilla. Are the taxonomic units ... those with binomials ... in Alchemilla vulgaris agg. equivalent to those in Taraxacum e.g. T. officinale or T. paludosum, T. laevigatum etc.? Recent evidence of variation within the species of A. vulgaris agg. stresses the point at what level shall the species status be granted?

In *A. vulgaris* agg. many taxa are differentiated by several morphological and maybe physiological characters and are eco-geographically well characterised. The British and Scandinavian taxa are nearly all widespread in Europe; moreover they show significant geographical distributions (arctic-alpine, oceanic, continental etc.) which are strikingly parallel to those of normal sexual species of a widespread Eurasiatic genus. Since these *Alchemilla* taxa are distinguishable by the characteristic taxonomic criteria used in orthodox taxonomy it is appropriate to use the same system here. The prefix agamo- may be added to denote the apomictic state of reproduction especially when this is of particular relevance in the context. Thus the taxa already recognised, such as *A. monticola* and *A. subcrenata* are agamospecies, the term already introduced by Turesson for this rank in the revision of his special terminology for apomictic groups (1943). Just as in amphimictic groups not all taxa possessing a binomial fulfil the desired requirements for specific rank, even within one apomictic group the agamospecies are of different kinds; it would be useful if some distinction could be made to show their relative taxonomic importance by use of the infraspecific criteria of orthodox taxonomy.

It has been shown above that *A. filicaulis* s.st. and

A. vestita are only poorly distinguished morphologically on the basis of hair cover. Although variation in other morphological characters does occur (e.g. leaf shape) only this one is known to be correlated with eco-geographical differences; almost certainly some physiological differences are correlated with these. On the basis of eco-geographically significant variation and indistinct morphological boundaries these two taxa are best regarded as subspecies of *A. filicaulis* Bus. and we thus have agamospecies *A. filicaulis*, subspecies *filicaulis* and subspecies *vestita*. Recently, Rothmaler (1952 and 1958) has ranked these two taxa as varieties, but in view of the existence of other variants which are considered below, subspecific rank is more suitable.

A. minima however, differs from *A. filicaulis* Bus. in several morphological characters and geographical distribution and fully justifies specific rank.

Within the agamospecies are the smaller units - the ecogenodemes and genodemes in both subspecies of *A. filicaulis* Bus. described above and the variants of Turesson (1943, 56). The evidence so far indicates a surprisingly close parallel with the ecotypic system in amphimictic species so that these genodemes may similarly be regarded as units of micro-evolutionary change in the sense of Gilmour and Heslop-

Harrison (1954). Whilst the system of classification of the biosystematist based on gene-exchange criteria cannot be used, Turesson's term agamotype is available. This he used to cover groups analogous to the climatically and edaphically specialised groups of sexual species covered by the term ecotype.

Whether such agamotypes should be given a name is a very debatable point not limited to apomictic groups. Usually the biosystematist attempts to fit his units (demes, ecotypes etc.) into the existing system of classification of the orthodox taxonomist. Following this practice with the material under discussion, at least the ecogenodemes of both species of _A. filicaulis_ Bus., would rank as varietatis. The much branched dwarf montane variant could be named varietas _nana_ and the tall lowland variant, varietas _typica_. However, the morphological differences are very slight and not sharply defined (though in some respects more obvious than between subspecies). In addition in most cases they are masked by phenotypic variation, this makes the material almost impossible to classify without facilities for cultivation. It is inevitable that var. _nana_ would be applied to phenotypic as well as genotypic dwarfs in field and herbarium determinations. For these reasons it would appear undesirable to give a name to these genodemes; on the other hand, a name is useful for reference purposes and undoubtedly does emphasise the presence of such micro-evolutionary units. A matter of particular importance, as inspite of the work of Turesson, Alchemilla agamospecies are still regarded as being constant and uniform.

Finally, there are three variants which are morphologically distinct in a particular character but sporadic or occasional in occurrence. In the systematists' terminology these correspond to the rank of 'forma'; thus we have

forma adpressipilosa
f. denudata
f. concolor, (this refers to the absence of wine-red coloration at the base of the plants).

The first two have been recognised as varieties of certain agamospecies of A. vulgaris agg. by Lindberg and Buser respectively but the rank of 'forma' is more appropriate. Though these differ in only a single character, each is much less critical than the distinguishing characters of the ecotypic variants, and recognisable in most fresh and herbarium material.

APPENDIX A

No. in Table.	Map grid reference no.	Locality	Population code no.
1	43/5312	Swithland Wood	5/19
2	43/539130	" "	5/20
3	42/548978	Narborough bog	5/17
4	43/486045	Botcheston bog	5/18
5	43/5108	Groby	5/22
6	43/5110	Ulverscroft Mill	5/21
7	43/233677	Coomb farm	5/23
8	43/193695	Ashford	5/27
9	43/171699	Taddington	5/29
10	43/182715	Monsal	5/33
11	43/180732	Heydale	5/30
12	43/172744	Cressbrooke	-
13	43/180688	Sheldon roadside	5/28
14	43/172740	Ravendale	5/32
15	43/174735	"	5/31
16	43/176654	Lathkill	5/24
17	43/182656	"	5/25
18	33/265228	Llanyblodwell	5/56
19	33/1229	Tyn-y-fron, Llanrhaiadr	5/58
20	33/1229	" "	5/59
22	44/852547	Huggate	5/15
23	34/910633	Janet's Foss	5/34
24	34/895673	Malham House	5/35
25	34/7376	High Wood Pasture	5/41
25	34/736765	Ravenscar	-
27	34/910662	Gordale Head	-
28	45/338384	Cassop	4/45 & 50
29	45/321378	Quarrington	4 & 6/46
30	45/325310	Bishop Middleton	
31	45/339384	West Cornforth	7/1
32	35/907004	Swaledale	6/7
33	35/922274	Brockers Gill Wood	4/8 & 15
34	35/925257	Park End Wood	-
35	35/914265	Mill Beck	4/13
36	45/060381	Thornhope	4/16
37	45/113313	Hamsterly-Bedburn roadside	-
38	35/875388	Black Dene Lane	4/28
39	35/963392	Kells Bank	4/2
40	35/863309	West Under Hurth sike	-
41	35/926381	Park House	-
42	35/881285	East Force Garth	-

No. in Table.	Map grid reference no.	Locality	Population code no.
43	35/839299	Widdy Bank farm	4/41
44	35/865309	West Under Hurth	4 & 6/39
45	35/864308	" " "	-
46	35/931257	Crook Hill	4/12
47	35/914266	Hungry Hall	-
48	35/964392	Thrush nest	4/3
49	"	" "	-
50	35/921273	Brockers Gill	4/9 & 11
51	35/900378	Daddry Shield	4/30
52	35/947238	Bowbank	-
53	35/926270	Woodside	4/16
54	35/847297	Brockholm	-
55	35/932268	Stony Gill	-
56	35/855284	Cronkley 1	5/1
57	35/861305	Youth Hostel	4/10
58	35/846284	Cronkley 2	5/2
59	35/842278	Cronkley 3	5/3
60	35/833273	Cronkley 4	5/4
61	35/838271	Cronkley 5	5/5
62	35/837264	Cronkley 6	5/6
63	35/815247	Mickle Fell	5/45
64	35/744315	Moss Burn flush	5/52
65	35/715308	Knock Fell	5/50
66	35/717311	" "	5/51
67	35/717312	" "	5/47
68	35/717312	" "	5/49
69	35/717312	" "	5/46
70	35/717312	" "	5/48
71	36/163155	Midlaw Burn	6/14
72	36/063128	Devil's Beef Tub	6/12
73	36/414301	Broadmeadows	6/17
74	36/422289	Newark Castle	6/16
75	27/758484	Garth	6/24
76	27/7649	Keltney	6/25
77	c.27/635405	Ben Lawers, S.W.Corrie	6/26
78	c.27/658444	Coire nam Buidheag	6/22
79	26/657435	Meall Garbh	
80	27/489435	Allt Cashlie (Poore, Thesis 1954)	-
81	27/2726	Beinn Laoigh	6/35
82	27/2726	" "	-
83	27/272265	" "	-

No. in Table.	Map grid reference no.	Locality	Population code no.
84	21/3754	Bidean nam Beinn (Walters)	
85	27/564375	Creag na Caillich	6/32
86	29/262216	Tralagill	6/29
87	29/2522	Inchnadamph	6/31
88	29/278191	Loch Mhaolach-coire	6/30
92	43/179657	Lathkill	-
93*	43/7702	Loddington Reddish	5/16
94*	33/120290	Tyn-y-fron, Llanrhaiadr	5/57

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