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

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ABSTRACT

By transplant experiments and by growing seed progenies, it has been shown that *A. minima* differs from the dwarf ecogenodemes of *A. filicaulis* in several morphological characters, in habit and in ecological requirements. The chromosome numbers of both are within the same range, $2n = c.$ 103–108. *A. minima* occurs on Whernside and Ingleborough in north England and is endemic. The dwarf ecogenodemes of *A. filicaulis* are known from the north Pennines only and may also be endemic.

INTRODUCTION

The third taxon in this critical group within the *A. vulgaris* aggregate is *A. minima* Walters. This small plant is very similar to the dwarf ecogenodemes of *A. filicaulis, sensu lato,* found in close-grazed montane grassland in the north Pennine hills (Bradshaw 1963a, p. 316). Leaves from field collections of both are shown in Fig. 1. The plants are difficult to separate in the field and it was hoped that the diagnostic characters could be better established by cultivation experiments. Also, *A. minima* was known only from Ingleborough, yet dwarf *A. filicaulis* plants are plentiful in other hill areas. Cultivation experiments were needed to show if any of these plants were referable to *A. minima.*

MORPHOLOGY AND HABIT

The morphological characters of *A. minima* are most clearly appreciated when compared with the dwarf ecogenodeme of *A. filicaulis.* Transplants of both from the field were grown in pots and boxes (as described by Bradshaw, 1963a, p. 308) for one year under similar conditions in the Botanic Garden at Durham. Some differences in the general appearance can be seen in Plate 2 and measurable differences are given in Tables 1 and 2.

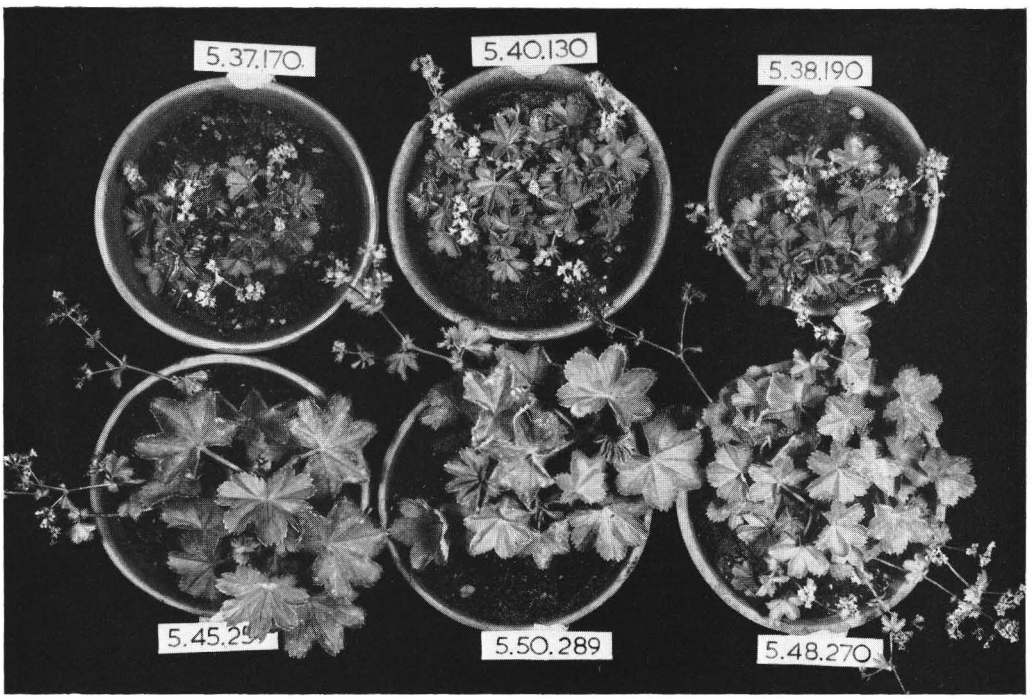
TABLE 1. Measurements of plants cultivated in pots

Characters	*A. minima* (*25 plants*)	*A. filicaulis dwarf ecogenodeme* (*29 plants*)
1. Petiole length: lamina length	0·8 ± 0·03	1·16 ± 0·03
2. Lobe length: lamina length	0·51 ± 0·01	0·4 ± 0·009
3. Depth of incision between lobes: lamina length	0·21 ± 0·02	0·14 ± 0·006

(a) *Rhizome and habit*

The rhizomes are more slender in *A. minima* and longer because of the longer internodes. In *A. minima* the leaves are more or less prostrate giving a plant a few centimetres high; in *A. filicaulis* the leaves are more erect, so that the length of the petiole gives an approximate measure of the height of the plant (Table 2).

PLATE 2



Plants from closely grazed grassland after 9 months cultivation. Top row : *A. minima* from Ingleborough area. Bottom row: *A. filicaulis* from Mickle Fell and Moor House National Nature Reserve.

[*facing page 76*

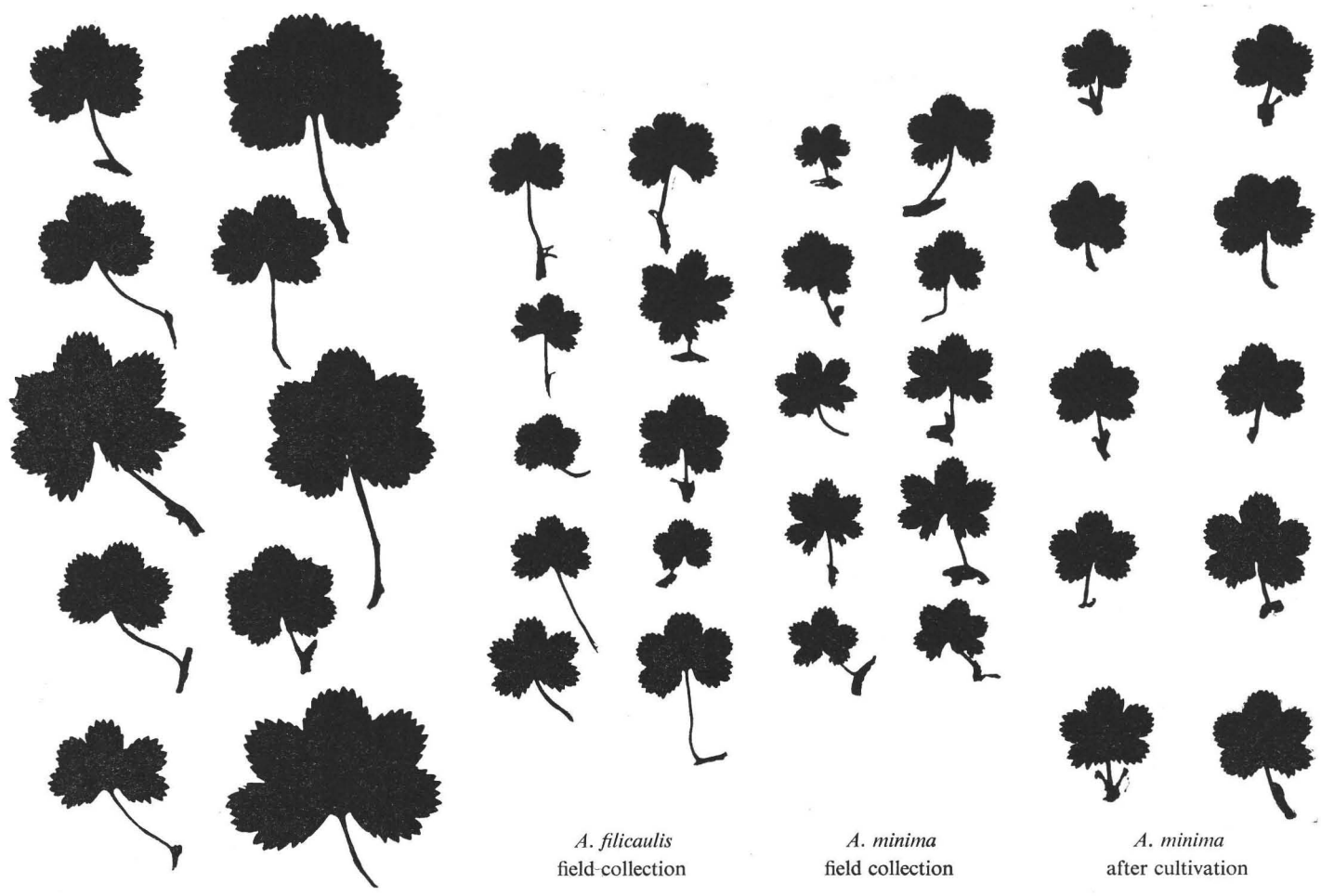


Fig. 1. Single leaves collected from twenty plants—ten of each species—before and after cultivation. The leaves are arranged in the same order in each set (× 1).

(b) *Stipules and base of the petioles*

In *A. minima* these are usually without the wine-red pigment usually found in *A. filicaulis*.

TABLE 2. Measurements of plants cultivated in boxes.

Characters	*A. minima* (*10 plants*)	*A. filicaulis dwarf ecogenodeme* (*3 × 10 plants*)
1. No. of shoots	4·7 ± 0·45	5·7 ± 0·45
		7·3 ± 0·44
		6·4 ± 0·67
2. Length of petiole (cm)	1·9 ± 0·17	10·0 ± 0·40
		8·7 ± 0·40
		9·2 ± 0·39
3. Breadth of leaf (cm)	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

(c) *Leaf lamina*

In *A. minima* the leaves are usually blue-green, and the lamina of mature leaves tends to be recurved and rather stiff with lobes which are V-shaped in cross section. *A. filicaulis* is less blue, often pure green, and the lobes are more open and the lamina flatter and not stiff. These differences can be seen in Fig. 2. The leaves of *A. minima* are much smaller with five full lobes, while in *A. filicaulis* another pair of basal lobes is more frequently well developed. The longer lobes of *A. minima* have 9(11) teeth on the median lobe while *A. filicaulis* has 11(13).

(d) *Indumentum*

The indumentum of the upper and lower surfaces of the leaf lamina were scored separately in five classes, one being almost glabrous, five very hairy. The flower-stems were scored in seven grades, six being least hairy and 0 most hairy (Bradshaw 1963a, p. 306). The hair characters of *A. filicaulis* have been considered in the first paper of this series. Dwarf ecogenodemes of subsp. *filicaulis* and subsp. *vestita* are known, and some of the former were almost glabrous when collected in the field. The leaves of *A. minima* were almost all class I on the upper surface and in only one case were the leaves more hairy (classes 3 and 4 respectively). An analysis of the hairiness of the flower-stem comparable with that of *A. filicaulis* was difficult because of the smaller number of internodes in *A. minima*, four or five against six or more. The flower-stems of 25 plants of *A. minima* were examined. In all cases the first internode was glabrous (this is often so in *A. filicaulis*) and frequently the second also. The whole flower-stem in ten plants was grade 6, the same as subsp. *filicaulis*; those of the other plants were hairy throughout, 12 were placed in grades 0–3, and three in grades 4–5. Clearly there is variation in the indumentum similar to that in *A. filicaulis*.

CHROMOSOME NUMBERS

Chromosome counts were obtained of pollen-mother-cells of two plants of *A. minima* from different localities on Ingleborough (*c.* 34/750747). These were as follows: $2n = c.\ 105$ and *c.* 108 for one plant, and for the other $2n = c.\ 103$, *c.* 98 and *c.* 99 (the last two values

TABLE 3. Associates of *Alchemilla minima*.

The figures indicate cover/abundance on the Domin scale in quadrats 25 cm × 25 cm in area. × = present in the same community near the quadrat. + = present in the quadrat.

Localities

1 Ingleborough, 34/714733, 950 ft, W aspect
2–7 Ingleborough, *c.* 34/721753, 800 ft, NNW aspect
8–9 Whernside, *c.* 34/734798, *c.* 1,600 ft, SE aspect
10–14 Ingleborough, *c.* 34/737745, *c.* 2,000 ft, S and W aspect

Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Alchemilla glabra	–	–	1	–	1	–	–	1	–	–	–	–	x	–
A. minima	+	2	1	1	1	1	3	2	1	+	3	3	3	3
A. xanthochlora	–	–	x	1	–	–	–	–	–	–	–	–	–	–
Achillea millefolium	–	–	1	–	–	–	1	–	2	+	2	2	1	2
Bellis perennis	+	2	1	–	1	–	–	2	2	+	–	4	4	2
Cardamine pratensis	–	–	–	–	–	–	–	1	–	–	–	2	2	1
Carex caryophyllea	+	–	–	–	–	1	–	–	3	–	3	3	3	–
C. panicea	+	5	5	5	7	2	–	–	2	–	–	–	–	–
Campanula rotundifolia	–	–	–	–	–	1	–	–	–	+	–	2	1	2
Cerastium holosteoides	–	–	1	–	1	–	–	1	1	+	2	2	2	3
Erophila verna	–	–	–	–	–	–	–	–	–	+	1	–	–	–
Euphrasia officinalis	+	1	–	–	1	1	1	2	1	+	1	2	1	2
Galium sterneri	–	–	–	–	–	–	–	–	–	+	1	2	1	3
G. verum	–	1	–	–	1	1	–	–	–	–	–	–	–	–
Leontodon autumnalis	+	2	2	1	2	2	2	2	3	–	–	–	–	–
Lotus corniculatus	+	–	–	–	–	1	–	–	–	–	–	–	2	–
Luzula campestris	–	–	1	–	–	1	1	1	1	+	4	–	–	1
Plantago lanceolata	+	–	2	1	2	2	2	3	4	–	–	1	2	–
Potentilla erecta	+	–	1	1	–	2	–	–	–	+	–	–	–	–
P. sterilis	–	–	–	1	–	–	–	–	1	+	2	2	1	–
Poterium sanguisorba	+	–	–	–	–	x	x	–	–	–	–	–	–	–
Prunella vulgaris	+	2	2	1	2	2	2	3	2	–	–	3	2	–
Ranunculus acris	+	1	–	–	–	–	–	1	–	+	–	2	2	2
R. bulbosus	–	–	–	–	–	–	1	–	–	–	2	–	3	2
R. repens	–	–	2	1	–	1	–	–	–	–	–	–	–	–
Rumex acetosa	–	–	–	–	–	–	–	–	–	–	2	–	–	3
Sagina procumbens	–	–	1	–	–	–	1	–	–	+	2	2	2	1
S. nodosa	–	1	1	–	1	–	–	–	–	–	–	–	–	–
Taraxacum spp.	–	1	–	1	1	1	–	–	–	–	–	–	–	–
Thymus drucei	+	–	–	1	–	–	–	2	–	+	3	3	3	4
Trifolium repens	+	1	2	1	1	–	2	2	–	+	2	2	3	3
Veronica chamaedrys	–	–	–	–	–	–	–	–	–	+	–	–	–	1
Viola riviniana	–	–	–	–	1	–	–	1	–	–	1	–	–	2
Agrostis tenuis	4	3	–	3	3	4	7	4	4	–	4	5	5	–
Anthoxanthum odoratum	–	–	–	–	–	–	3	3	3	–	–	–	2	–
Briza media	3	2	1	2	1	2	–	–	–	–	–	4	–	–
Cynosurus cristatus	3	1	2	2	–	2	5	4	4	–	x	–	3	2
Deschampsia cespitosa	3	–	2	1	3	2	–	–	–	4	1	–	4	3
Festuca ovina	5	5	5	8	7	8	7	7	7	8	9	7	8	9
Helictotrichon pratense	–	–	–	–	–	–	–	–	–	5	–	–	–	3
Koeleria cristata	–	2	–	–	–	2	–	–	–	+	–	–	–	4

Additional species occurring in one quadrat only: *Alchemilla glaucescens* (5), *A. filicaulis* subsp. *vestita* (1), *Hypochaeris radicata* (1). *Juncus effusus* (14). *Leontodon hispidus* (1), *Veronica officinalis* (6), *V. serpyllifolia* (14), *Holcus lanatus* (7), *Nardus stricta* (4), *Sieglingia decumbens* (3).

are probably too low). These are within the range for *A. filicaulis* ($2n = 101–110$) and near the values obtained for a dwarf montane subsp. *vestita* plant from Mickle Fell (35/809244), which were $2n = c.$ 105 and *c.* 109 (Bradshaw, 1963b, p. 323).

Distribution

So far *A, minima* has been recorded from two mountains only, Ingleborough and Whernside (34/77 and 78) in the Craven area. All the dwarf plants collected from other montane pasture areas became larger in cultivation and belong to *A. filicaulis* (Bradshaw 1963a, p. 316). Walters (1949) first recorded *A. minima* from the east side of Ingleborough at about 1,000 ft (310 m) altitude, and around the 2,000 ft contour on Simon Fell. Now, *A. minima* has been found in suitable habitats down to 750 ft (230 m) on the north west slopes of Ingleborough. Recently, more plants were found on Whernside at 700 ft (220 m) and 1,000 ft and between 1,600 ft (500 m) and 1,800 ft (560 m). In all the localities *A. minima* plants were plentiful.

Ecology

A. minima appears to be confined to the intensively grazed *Festuca-Agrostis* grassland areas on or just below the limestone strata of the Carboniferous Limestone Series of the Ingleborough district. All habitats were characterized by the high moisture content of the soil. At the lower altitudes (700 ft–*c.* 1,400 ft) this is maintained by seepage from flushes below the limestone; above this (*c.* 2,000 ft) presumably the higher humidity and rainfall are sufficient since *A. minima* grows amongst the limestone boulders where surface water is absent.

In all cases the soil was a moist, slightly sticky, dark-brown peaty loam. the lower and wetter habitats were less acidic (pH 6·5–7·3) than those at *c.* 2,000 ft (pH 5·2–6·1). No doubt, this is due to the more base-rich flushing by water from the limestone.

The associated species are listed in Table 3. *Festuca ovina* was present in all the sample areas and *Agrostis tenuis*, *Cynosurus cristatus*, *Trifolium repens*, *Prunella vulgaris*, *Plantago lanceolata* and *Euphrasia officinalis* agg. were present in most. The characteristic blue-green appearance of the lower habitats is caused by the high frequency of *Carex panicea*; *Leontodon autumnalis* is a constant species and the only records of *Poterium sanguisorba* are at these lower altitudes. *Carex panicea* is absent from the higher altitudes but several other species are more common there: these are *Achillea millefolium*, *Bellis perennis*, *Cerastium holosteoides*, *Sagina procumbens* and *Thymus drucei.*

Conclusions

This work fully supports Walters' (1949) original treatment of *A. minima* as a distinct species. The cultivation experiments have emphasized the diagnostic characters which he described, and revealed some other contrasts with the dwarf plants of *A. filicaulis*; these are set out in Table 4. Although typical plants can be identified with a fairly high degree of confidence, plants are found which are less distinct (cf. Fig. 1) and can be determined with certainty only after cultivation.

Details of the ecological preferences and associated species of *A. minima* have been given. Apparently suitable habitats in closely grazed *Festuca-Agrostis* grassland are abundant in the Pennines and may be found elsewhere. Only a relatively small number of these have been examined, and the recent discoveries of *A. minima* some miles from the early localities on Ingleborough suggests that it may be more widespread, at least in the Craven district. Some similar habitats in the north Pennines are occupied by the dwarf ecogenodeme of *A. filicaulis*. Curiously, no plants of *A. filicaulis* were collected from the populations on Ingleborough although *A. filicaulis* does occur in other habitats in the area. This raises interesting points about the evolution and history of these two species. These will be considered in relation to other members of the *A. vulgaris* aggregate in the fourth paper of this series.

TABLE 4

Character	*A. minima*	dwarf *A. filicaulis*
Rhizome	long and slender, little branched, internodes long	short and thicker, often much branched, internodes short
Base of plant and stipules	not wine-red	wine-red, sometimes rather faint
Petioles	usually about length of leaf lamina	longer than leaf lamina
Lamina	usually blue-green; lamina pleated and recurved (lobes half open, V-shaped in cross section)	not so blue, usually pure green; whole lamina flat
Lobes	usually 5, ½ radius of lamina, deep incision between lobes	usually 7, less than ½ radius of lamina, shallow incision be-between lobes
Teeth on median lobe	usually 9	usually 11
Flower-stems	several, very slender, usually with 5 internodes	few, less slender, usually with 6 internodes
Indumentum of whole plant	variable, usually less hairy than *A. filicaulis* subsp. *vestita*	variable, subsp. *filicaulis*, subsp. *vestita* and intermediate states

REFERENCES

BRADSHAW, M. E. (1963*a*). Studies on *Alchemilla filicaulis* Bus., sensu lato, and *A. minima* Walters. I. Morphological variation in *A. filicaulis*, sensu lato. *Watsonia* **5**, 304–320.

BRADSHAW, M. E. (1963*b*). Studies on *Alchemilla filicaulis* Bus., sensu lato, and *A. minima* Walters. II. Cytology of *A. filicaulis*, sensu lato. *Watsonia* **5**, 321–326.

WALTERS, S. M. (1949). *Alchemilla vulgaris* L. agg. in Britain. *Watsonia* **1**, 6–18.