Watsonia, **10**, 1–17 (1974).

Variation within *Cardamine pratensis* L. in England

A. DALE and T. T. ELKINGTON

Department of Botany, The University, Sheffield S10 2TN

ABSTRACT

Cytological and morphological studies have been made on populations of *Cardamine pratensis* L. from a wide range of habitats in England, particularly from the central and northern regions of the country. Chromosome counts have been made on 47 plants from 27 populations and all are $2n = 56$ except for one population, which has plants with $2n = 58$. Previous counts from England have the range $2n = 30$–64. Measurements of field samples show a wide variation in many vegetative and floral characters, the majority of which are correlated. Comparisons with transplant samples show that much of the variability is due to phenotypic plasticity. The habitat data indicate that most of this variation is determined by environmental factors and this was confirmed by experimentation.

The combination of morphological, cytological and ecological characteristics, which has been used to divide the species into two segregate taxa (*C. pratensis* L. *sensu stricto* and *C. palustris* (Wimmer & Grab.) Peterm.) in lowland north-western Europe, cannot be directly applied to English material, since the range of morphological variation and ecological tolerance of the $2n = 56$ cytotype in England spans that recorded for these two taxa on the Continent.

INTRODUCTION

Cardamine pratensis sensu lato is well known as a group with an exceptional range of chromosome numbers in Europe, from $2n = 16$ (diploid) to $2n = 96$ (dodecaploid) with many intermediate euploid and aneuploid numbers. In most European countries where populations have been extensively studied cytologically, e.g. Sweden and Denmark (Lövkvist 1956), Poland (Banach 1950) and the Netherlands (Berg 1967), a considerable range of numbers is present within the country and sometimes within a single population. In contrast, Hussein (1955) found only plants with $2n = 30$ and $2n = 56$ in an extensive study of British populations, although Manton (1932) had previously recorded $2n = 32$ and $2n = 64$ from Cambridge and Southport respectively, while Lövkvist (1956) found plants with $2n = 30$, 38, 48 and 56 in Devon, and $2n = 56$, 57 and 58 in Scotland.

C. pratensis s.l. encompasses substantial morphological variation and several distinct species have been recognized in arctic, central and southern Europe (see Lövkvist 1956, Jones 1964). In lowland north-western Europe several authors have suggested that morphological and cytological variation are associated and have proposed a separation into two taxa. Lövkvist (1956) and Jones (1964) recognize two species in this area: *C. pratensis* L. *sensu stricto*, with chromosome numbers below $2n = 56$, and *C. palustris* (Wimmer & Grab.) Peterm., with $2n = 56$ or above. Berg & Segal (1966), however, separate the two taxa at the subspecific level as the type subspecies of *C. pratensis* and *C. pratensis* subsp. *palustris* (Wimmer & Grab.) Janchen respectively. Banach (1950), Lövkvist (1956) and Berg & Segal (1966) all report a correlation

TABLE 1. FLORISTIC LISTS OF REPRESENTATIVE SITES OF *CARDAMINE PRATENSIS*

Site	3	4	5	7	10	11	12	13	18	20	23	24	27	29	31	32	33	36	38	39
Soil pH[1]	6·8	6·4	5·7	5·3	6·6	5·7	5·3	5·1	7·2	6·1	6·2	6·2	7·2	6·4	6·6	6·6	6·9	4·9	7·5	7·0
Equisetum arvense	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	2	–	1
E. palustre	3	–	–	1	3	1	3	–	–	–	–	–	–	–	–	2	5	–	–	–
Agrostis stolonifera	–	–	–	–	–	5	4	5	–	6	4	4	–	6	–	–	1	–	–	5
Carex acutiformis	–	4	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. flacca	–	–	–	–	6	–	–	–	–	–	–	–	5	–	7	–	–	–	3	4
C. lepidocarpa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	5
C. nigra	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–
Dactylis glomerata	–	–	–	–	–	–	–	–	4	–	–	4	–	–	1	–	–	–	–	–
Deschampsia cespitosa	–	–	–	–	–	4	2	–	–	–	–	–	–	2	–	–	–	4	–	–
Eriophorum angustifolium	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	5
Festuca ovina	–	–	–	–	–	–	–	–	1	–	–	–	–	–	5	–	–	–	8	4
F. rubra	–	–	–	–	4	–	–	5	7	–	–	5	–	–	–	–	6	4	–	–
Glyceria fluitans	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	5	–	–	–	–
Holcus lanatus	–	4	5	–	6	5	4	5	3	6	5	4	4	4	–	–	6	–	–	–
Juncus articulatus	–	–	–	–	4	–	1	–	–	–	–	–	–	6	–	–	–	–	–	4
J. effusus	–	–	4	3	4	3	2	4	–	–	–	–	–	–	4	–	–	5	–	–
Lolium perenne	–	–	–	–	–	–	2	–	–	–	5	–	–	–	–	–	–	–	–	–
Phragmites australis	7	7	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Poa trivialis	–	–	–	–	4	1	4	–	2	–	–	4	3	–	5	7	–	4	–	–
Achillea millefolium	–	–	–	–	–	–	–	–	3	–	–	–	–	2	–	–	–	–	–	–
Bellis perennis	–	–	–	–	–	–	–	–	3	–	2	–	–	–	–	–	–	–	–	–
Berula erecta	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cardamine pratensis	2	3	3	3	3	3	3	3	2	2	4	4	2	4	1	4	4	4	3	3
Calystegia sepium	–	2	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cerastium holosteoides	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	4	–
Cirsium arvense	–	–	3	3	–	–	–	3	3	1	5	4	1	–	–	–	–	–	–	–
C. palustre	–	–	–	2	–	–	–	3	1	–	–	–	–	–	2	–	–	–	–	–
C. vulgare	–	–	–	–	–	–	–	–	2	–	1	–	–	–	–	–	–	1	–	–
Epilobium palustre	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	2	2	–	–
Filipendula ulmaria	–	1	4	–	–	–	1	3	–	–	–	–	–	4	2	1	–	–	–	–
Galium palustre	–	–	1	–	–	–	1	3	–	–	–	–	–	–	–	–	–	–	–	–
Hydrocotyle vulgaris	–	3	3	4	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–

TABLE 1—*continued*

Lotus pedunculatus	–	–	–	–	3	–	–	3	–	–	–	–	–	–	–	–	–	–	–	1
Lythrum salicaria	–	1	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mentha aquatica	4	2	1	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–
Plantago lanceolata	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–
Potentilla anserina	–	–	3	–	–	–	1	–	3	–	–	–	–	–	–	–	–	–	–	–
Prunella vulgaris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	3
Ranunculus acris	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	4	–	–	–	–
R. ficaria	–	–	–	–	–	–	–	–	3	–	–	–	–	4	4	–	–	–	–	–
R. repens	–	–	5	–	4	3	6	4	3	3	4	3	2	2	4	4	–	–	–	–
Rubus fruticosus	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–
Rumex acetosa	–	–	–	2	4	–	–	3	1	4	–	3	–	3	–	4	–	–	–	–
R. crispus	–	–	3	–	–	–	2	–	–	–	3	–	–	–	–	–	–	–	–	–
R. obtusifolius	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	4	–	–	–	–
Senecio aquaticus	–	–	–	–	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–
S. jacobaea	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–
Stellaria alsine	–	–	–	1	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Taraxacum officinale	–	–	–	–	–	–	–	–	1	–	–	–	–	1	1	–	–	–	–	–
Trifolium repens	–	–	–	–	–	–	4	3	3	–	4	4	1	–	4	3	4	4	–	–
Urtica dioica	–	–	2	–	–	–	–	–	2	–	4	5	–	–	–	–	–	–	–	–
Viola palustris	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Acrocladium cuspidatum	7	4	–	–	1	–	–	1	–	–	–	–	8	–	6	–	–	1	–	–

Species present at only one site: (3) Cladium mariscus 3, Juncus subnodulosus 3, Alnus glutinosa (seedlings) 3, Apium nodiflorum 3, Eupatorium cannabinum 2, Eurhynchium confertum 1, Marchantia polymorpha 3, Peltigera canina 1. (4) Iris pseudacorus 3. (5) Glyceria maxima 4, Lotus corniculatus 3. (7) Sphagnum recurvum 4. (10) Eleocharis palustris 4. (13) Polygonum hydropiper 1, Rumex conglomeratus 3. (18) Anthoxanthum odoratum 4, Arrhenatherum elatius 4, Cynosurus cristatus 6, Galium cruciata 2, Leontodon autumnalis 3, Veronica chamaedrys 3. (20) Poa annua 5, Polygonum amphibium 4. (23) Leontodon taraxacoides 1. (27) Equisetum variegatum 4, Epilobium hirsutum 1, Viola hirta 1. (29) Lathyrus pratensis 3, Myosotis scorpioides 4. (31) Luzula campestris 7, Caltha palustris 2, Lychnis flos-cuculi 3. (32) Carex pendula 4, Phleum pratensis 4, Plantago media 1, Sanguisorba officinalis 4. (33) Carex arenaria 1, Rhinanthus minor 2, Salix repens 8. (36) Agrostis canina 3, Juncus squarrosus 3, Galium saxatile 4, Sagina procumbens 1, Bryophytes 8 (Acrocladium cuspidatum, Hylocomium splendens, Polytrichum sp., Rhytidiadelphus squarrosus, Lophocolea cuspidata, Scapania undulata). (38) Selaginella selaginoides 3, Carex capillaris 1, Minuartia verna 3, Potentilla erecta 1, Thymus drucei 5, Ctenidium molluscum 4, Preissia quadrata 1, Rhacomitrium lanuginosum 4. (39) Parnassia palustris 3, Pinguicula vulgaris 3, Ranunculus flammula 2, Sagina nodosa 2, Bryophytes 7.

[1] Soil pH was determined electrometrically on a soil/water paste at field capacity.

between habitat and chromosome number of plants, the main environmental variable being soil moisture content. Areas of relatively high soil moisture content, e.g. marshes, carr and wet grassland, contained plants with higher chromosome numbers (subsp. *palustris*), while plants from relatively dry areas of grassland and some woods had lower chromosome numbers (subsp. *pratensis*).

A study has therefore been made of English populations to investigate the relationship between their cytological and morphological variation and to compare this situation with that described from other European countries. Population samples and living plants were collected from a wide range of habitats in England, particularly from the centre and north.

CYTOLOGY

Chromosome counts were made from both mitotic and meiotic preparations. Excised root-tips were pretreated with 0·002M 8-hydroxyquinoline for 3 hrs and fixed in 3:1 absolute alcohol : glacial acetic acid. They were hydrolysed in N hydrochloric acid at 60°C for 10 minutes and stained with Feulgen Reagent. Root-tips were either squashed in propionic orcein and made permanent by the liquid CO_2 method, or squashed in 45% acetic acid, air-dried, counterstained in 1% Giemsa and air-dried again. Pollen-mother-cells were stained in propionic orcein, squashed and made permanent by the liquid CO_2 method. All preparations were mounted in Euparal.

The chromosome numbers counted are given in the Appendix. All counts were $2n = 56$, with the exception of the population on Widdybank Fell, Durham (v.c. 66), where the two plants counted were $2n = 58$. Meiosis was regular in all the pollen-mother-cells examined.

ECOLOGY

The vegetation at each site (localities given in the Appendix) was characterised by listing the species within a 0·5m square quadrat using the Domin scale. The Sørenson Coefficient of Similarity (after Poore 1953) was used to compare the floristic similarity of all sites. Selected levels of Coefficients of Similarity are shown in Fig. 1 and representative floristic lists, together with soil pH, in Table 1. Soil pH was determined on samples taken from the top 10 cm of the profile.

Inspection of the levels of the Sørenson Coefficients of Similarity (Fig. 1) shows that most of the sites can be grouped into two sets, which appear to differ primarily in soil moisture status. Sites 5–14 are all marshes or very wet grasslands with *Holcus lanatus*, *Juncus effusus* and *Cardamine pratensis* as constant species. Other common associates are *Equisetum palustre*, *Agrostis stolonifera*, *Deschampsia cespitosa*, *Poa trivialis*, *Cirsium palustre*, *Galium palustre* and *Ranunculus repens*. The pH range of these sites is 5·1–6·9 with a mean of 5·7. Sites 14–28 (with the exception of 20 & 27) are damp limestone/chalk grasslands. Site 20 is a damp grassland on the Coal Measures near their boundary with the Magnesian Limestone in Derbyshire, and site 27 is a dune-slack at Braunton Burrows, Devon, with a high calcium carbonate content (Willis *et alii* 1959). Constant species are *Agrostis stolonifera*, *Holcus lanatus*, *Cardamine pratensis*, *Ranunculus repens* and *Trifolium repens*, with *Festuca*

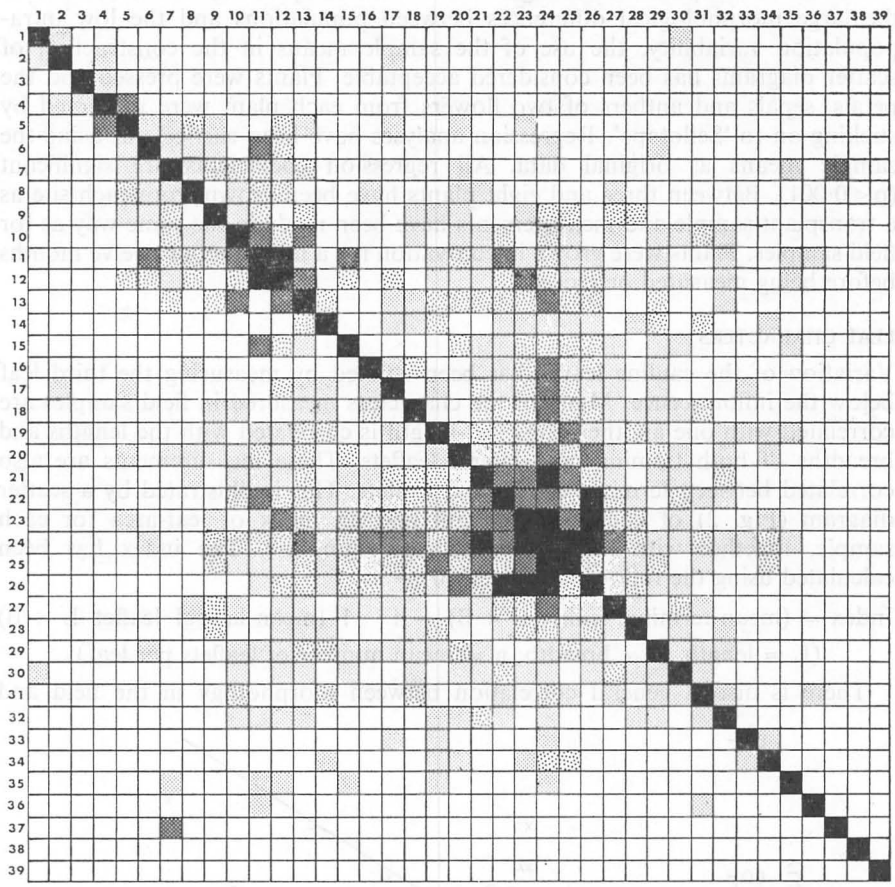

FIGURE 1. Selected levels of the Sørenson Coefficient of Similarity for all sites; levels depicted are: 60% and above ■, 50%–59% ▩, 40%–49% ▒ and 30%–39% ▒.

rubra, *Poa trivialis*, *Bellis perennis*, *Cirsium arvense*, *Rumex acetosa* and *Urtica dioica* as common associates. Soil pH ranges from 5·4–7·6 with a mean of 6·8.

Of the remaining sites, 29–34 are marshes and wet grasslands, and 35 is a dune-slack; all possess some affinities to the two previous groups. Site 1 is a base-rich marsh similar to the *Phragmites* fens (sites 2–5). These have *Phragmites australis*, *Cardamine pratensis* and *Acrocladium cuspidatum* as constant species with *Filipendula ulmaria*, *Mentha aquatica* and *Equisetum palustre* as common species. Finally, site 36 is a wet mountain pasture, 37 is a base-rich *Sphagnum* flush draining into a peat bog, whilst both 38 and 39 are base-rich flushes immediately below limestone outcrops.

MORPHOLOGY

METHODS

Field samples and transplants have been collected from a wide geographical and ecological range of sites (see Appendix). The size of field samples varies

from two to ten plants. Although some of the samples are small, because of the large morphological differences between populations and the low intra-population variability, the use of the sample means in the construction of scatter diagrams has been considered acceptable. Plants were pressed and the petals, sepals and anthers of two flowers from each plant were preserved by sticking on to 'Sellotape'. Regression analyses have been carried out using the sample means as original data. All regression coefficients are significant ($p < 0{\cdot}001$). Between three and eight plants have been grown from each site as a transplant sample and measurements have been made in the same way as for field samples. Plants were grown in cultivation for a minimum of twelve months before being measured or scored.

LEAF CHARACTERS

Variation of the cauline leaves has been studied by measuring the third leaf below the inflorescence. Many of the characters measured in field samples are correlated with one another, thus leaf-length is correlated with the lengths and breadths of both terminal and lateral leaflets. These measurements are also correlated between terminal and lateral leaflets. This is illustrated by a scatter diagram (Fig. 2) of cauline leaf-length and an index of leaf-area for each sample, together with the calculated regression line. The index has been calculated using the following expression:—

Index = (mean terminal leaflet L × B) + n − 1 (mean lateral leaflet L × B)

(L = length, B = breadth, n = mean number of leaflets per leaf)

There is also a general correlation between morphology in the field and

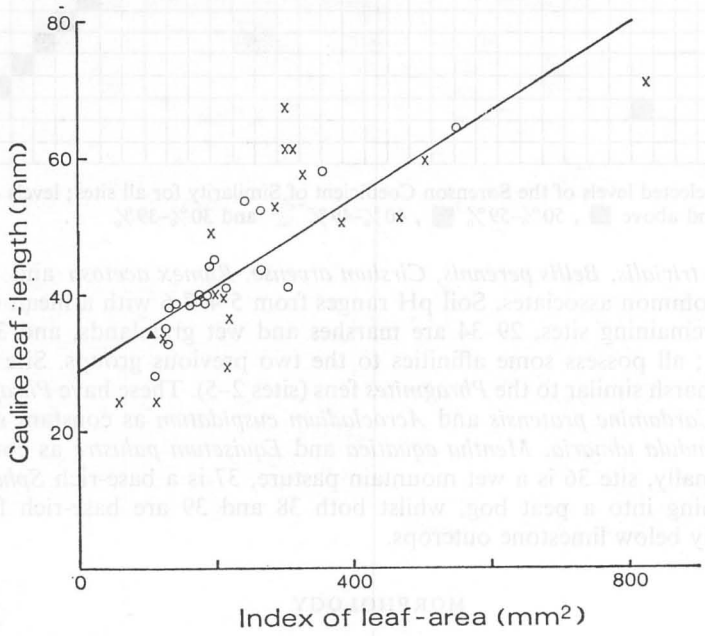

FIGURE 2. Scatter diagram and regression line of index of leaf-area and mean leaf-length of cauline leaves for field samples. Chromosome number: ○ $2n = 56$; ▲ $2n = 58$; X not determined.

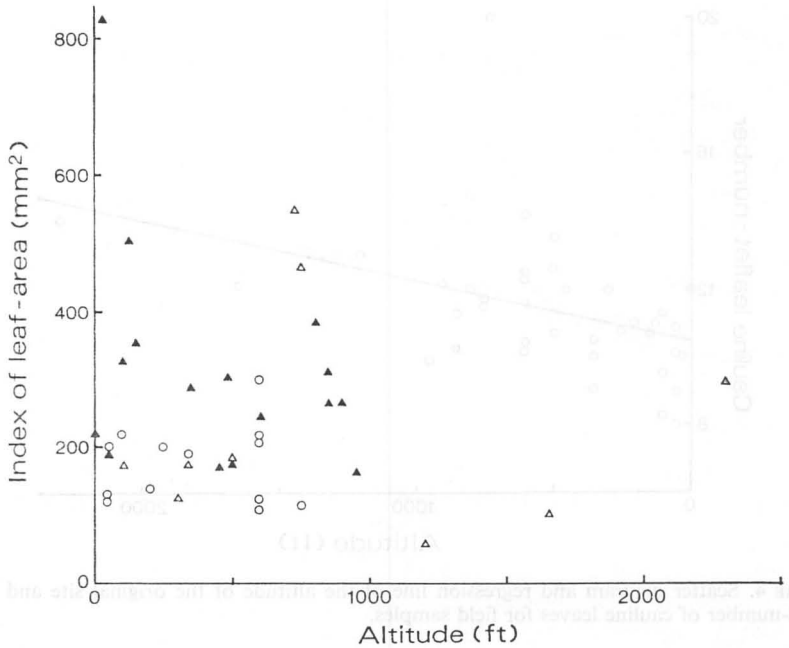

FIGURE 3. Scatter diagram of the altitude of the original site and index of leaf-area for field samples. Habitat: ▲ wet sites with tall vegetation; △ wet sites with short vegetation; ○ dry sites with short vegetation.

habitat. This is illustrated in Fig. 3, where a scatter diagram is given of the index of leaf-area and altitude of each locality, together with an indication of which samples originate from habitats characterised by relatively high or low soil moisture and by short or tall vegetation (shorter or taller than 0·5 m at the time of sampling). Plants growing in sites with low soil moisture (mainly grasslands) and short vegetation have a low index of leaf-area (and therefore from Fig. 2 short leaves) and are confined to altitudes below 800 m. Above this altitude *C. pratensis* is restricted to wet marshes and grasslands where it occurs as plants with a low index of leaf-area. At lower altitudes there is a wide variation in the index of leaf-area of samples from sites with high soil moisture. The highest index is from a site with tall marsh vegetation dominated by *Phragmites australis* (site 4) and it seems reasonable to suggest that this is a response to shading. The variation in altitude is also closely correlated with annual rainfall.

The mean number of leaflets per cauline leaf of field samples is not correlated with any of the other leaf characters measured. Variation in mean number of leaflets is, however, correlated with the altitude of the locality as shown in Fig. 4, together with the regression line.

Much of the variation in these characters is due to phenotypic plasticity. This is shown by the comparison of means of field samples and transplant measurements for the length of leaves and terminal leaflets (Fig. 5). Almost all the transplant samples have a lower standard error than the field samples from the same localities.

Rosette leaves and particularly their lateral leaflets have often senesced by

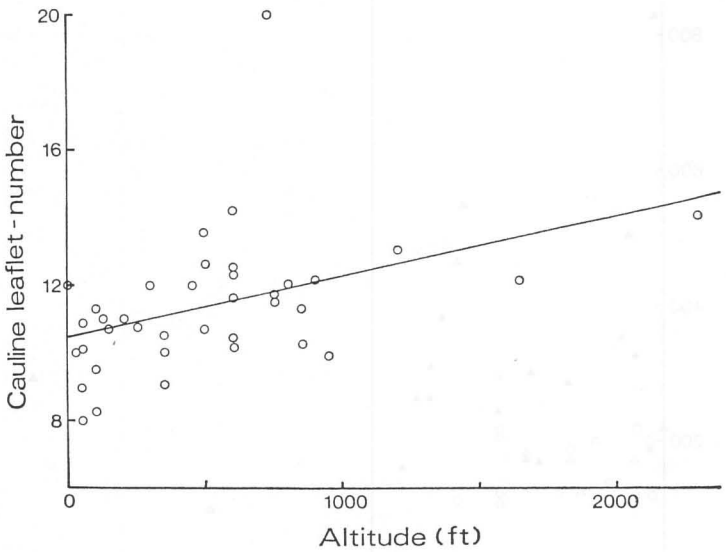

FIGURE 4. Scatter diagram and regression line of the altitude of the original site and mean leaflet-number of cauline leaves for field samples.

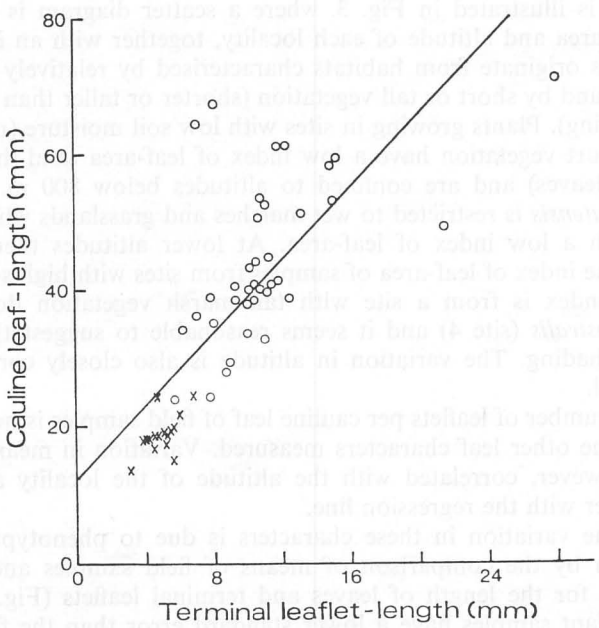

FIGURE 5. Scatter diagram and regression line of the mean length of terminal leaflets and mean length of cauline leaves for field samples (○) and transplants (X).

flowering time and measurements were therefore restricted to the terminal leaflet of one leaf from each plant. Measurements of cauline leaves have shown, however, that the variation in the size of terminal leaflets is correlated with that of the lateral leaflets and overall leaf-length. The length of terminal leaflets from rosette leaves is correlated with their breadth and with the corresponding measurements of cauline leaves. There is a high correlation between the length/breadth ratios of terminal and lateral leaflets from cauline leaves and a lower but significant one between the length of the terminal leaflet and its length/breadth ratio.

FLORAL CHARACTERS

Character means were calculated from two measurements per flower and from two flowers per plant. Lengths of all parts measured, i.e. sepals, petals, long and short filaments of stamens, are correlated. This is illustrated in Fig. 6, which is a scatter diagram of mean lengths of petals and long filaments, together with the calculated regression line for both field and transplant samples. The diagram also shows that these characters are influenced by habitat conditions in the same way as leaf-length and index of leaf-area. Thus, large-flowered plants are predominantly found in tall vegetation with a high

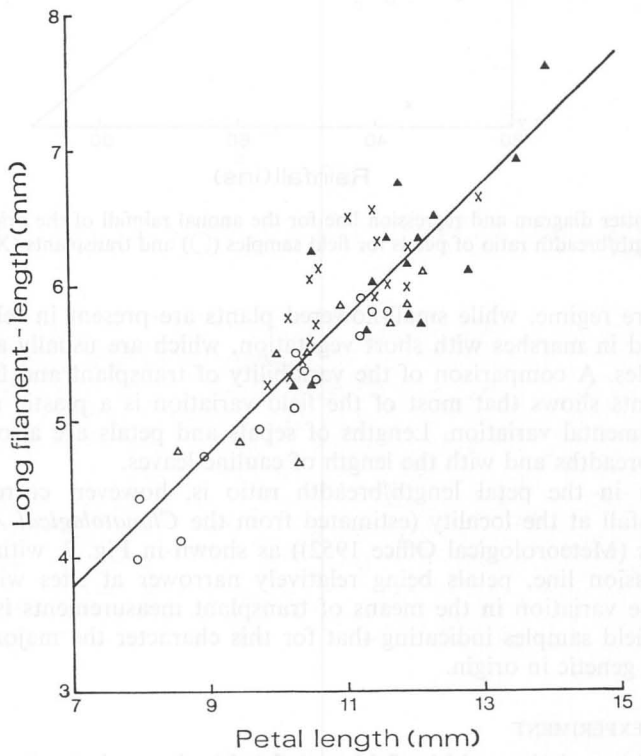

FIGURE 6. Scatter diagram and regression line of mean length of petals and mean length of long filaments of stamens for field samples and transplants (X). Habitat of field samples: ▲ wet sites with tall vegetation; △ wet sites with short vegetation; ○ dry sites with short vegetation.

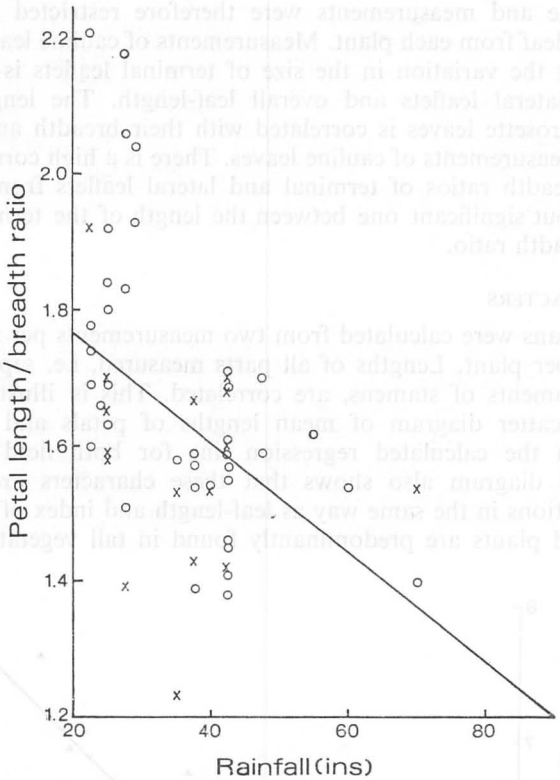

FIGURE 7. Scatter diagram and regression line for the annual rainfall of the original site and the mean length/breadth ratio of petals for field samples (○) and transplants (X).

soil moisture regime, while small-flowered plants are present in relatively dry habitats and in marshes with short vegetation, which are usually at relatively high altitudes. A comparison of the variability of transplant and field sample measurements shows that most of the field variation is a plastic response to the environmental variation. Lengths of sepals and petals are also correlated with their breadths and with the length of cauline leaves.

Variation in the petal length/breadth ratio is, however, correlated with annual rainfall at the locality (estimated from the *Climatological Atlas of the British Isles* (Meteorological Office 1952)) as shown in Fig. 7, with the calculated regression line, petals being relatively narrower at sites with a lower rainfall. The variation in the means of transplant measurements is similar to that from field samples indicating that for this character the majority of field variation is genetic in origin.

PLASTICITY EXPERIMENT

Much of the variation within field samples has been shown to be due to phenotypic plasticity and an experiment was therefore carried out to investigate the plasticity within several clones subjected to a number of treatments. Plants from Blo Norton (Site 3), Wicken Fen (4), Burbage Brook (7), Repton (12)

and Cressbrook (21) were cloned from individual leaflets grown on wet sand (Lövkvist 1956). Five plants from each site were then grown in pots set out in a randomised arrangement under each of the following treatments:

Treatment

A mist propagator in a heated greenhouse
B bench in same greenhouse
C outdoors, in a tray of water
D outdoors, sunk into ash beds and watered regularly

After *c.* six months growth, one rosette leaf from each plant was removed and measured. Measurements of terminal leaflet thickness, however, were made on two leaflets per plant. The site means for all measurements are given in Table 2. Silhouettes of representative leaves of plants from Wicken Fen (4) and Burbage Brook (7) at the end of this experiment and from field samples are shown in Fig. 8. Analyses of Variance were made on site and treatment means and where these were significant a Duncan's Multiple Range Test (Duncan 1955) was carried out (Table 3).

The results show that for the rosette leaf characters of length, terminal leaflet-length, and length/breadth ratio only the differences between treatments are significant. Thus for all these characters there is a high degree of phenotypic plasticity.

For terminal leaflet thickness and the numbers of leaflets per leaf, both the site and treatment variation is significant. The drier treatments B and D produce significantly thicker leaves than the wetter treatments A and C and

TABLE 2. MEAN MEASUREMENTS (MM) OF CLONED PLANTS FROM FIVE POPULATIONS FOR ROSETTE-LEAF CHARACTERS UNDER FOUR TREATMENTS IN THE PLASTICITY EXPERIMENT

Site	Treatment	Leaf-length	Terminal leaflet characters				No. of leaflets
			Length	Breadth	L/B	Thickness	
Blo Norton	A	88·8	9·4	11·1	0·85	0·186	4·6
(3)	B	71·4	6·6	7·1	0·93	0·204	10·0
	C	35·6	4·8	6·6	0·73	0·194	5·8
	D	40·8	5·6	7·8	0·72	0·205	5·4
Wicken Fen	A	97·6	17·4	19·7	0·88	0·194	6·6
(4)	B	43·1	10·1	12·5	0·81	0·210	7·0
	C	21·2	5·6	8·2	0·68	0·183	5·0
	D	23·2	6·7	8·8	0·76	0·215	6·4
Burbage Brook	A	133·6	12·8	15·1	0·85	0·198	7·8
(7)	B	63·4	6·6	8·4	0·79	0·227	11·4
	C	37·2	4·2	6·0	0·70	0·209	10·6
	D	31·8	4·8	5·8	0·83	0·214	10·2
Repton	A	112·0	10·6	13·1	0·81	0·180	7·0
(12)	B	57·8	8·1	11·5	0·70	0·194	10·0
	C	25·0	5·1	7·1	0·72	0·174	5·4
	D	31·8	5·8	8·6	0·67	0·167	7·8
Cressbrook	A	126·2	16·2	18·2	0·89	0·193	7·4
(21)	B	40·4	6·3	7·6	0·83	0·199	9·0
	C	27·2	4·1	5·5	0·75	0·182	9·4
	D	23·4	4·3	5·3	0·81	0·235	9·0

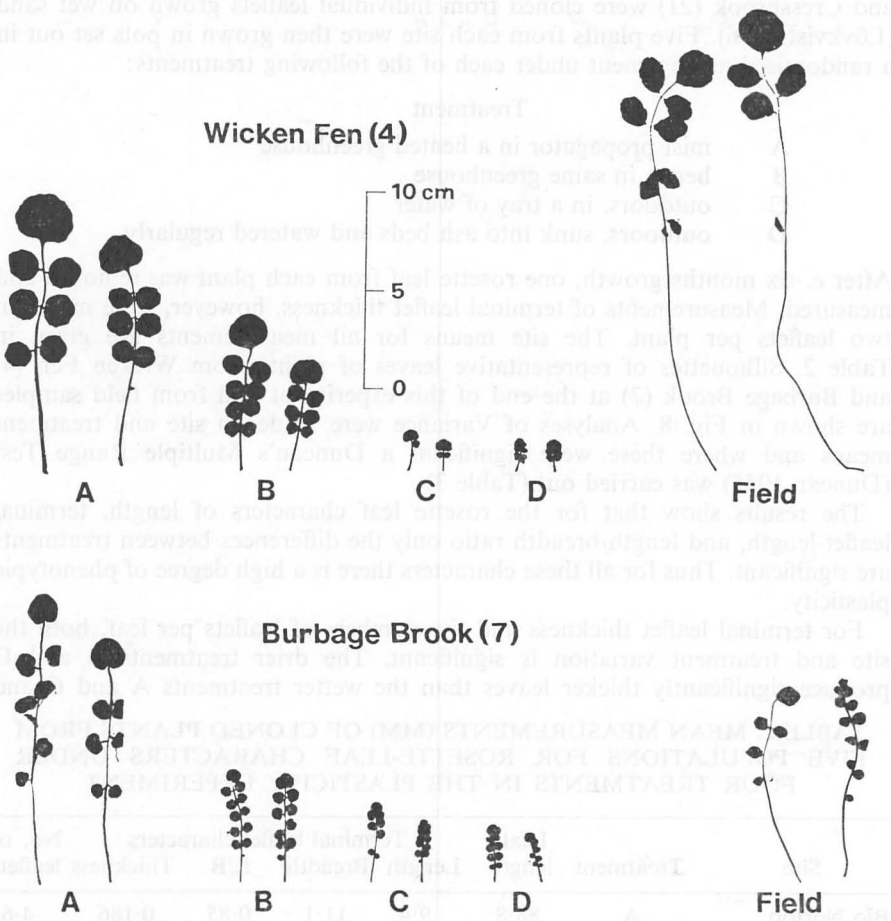

FIGURE 8. Silhouettes of selected leaves from plants originally from Wicken Fen (4) and Burbage Brook (7) grown in the different treatments of the plasticity experiment and from field samples.

they also produce more leaflets. This indicates that plants in drier habitats might have leaves with more and thicker leaflets than those from wetter habitats. However, a 't' test comparing mean leaflet numbers for field samples from wet and dry habitats does not show any significant difference. Inspection of the variation between sites shows that the mean number of leaflets increases with altitude, the sites being at 40, 100, 150, 600 and 950 ft. The relationship between altitude and number of leaflets appears, therefore, to have a partial genotypic basis.

The mean length, breadth, length/breadth ratio and stalk length of lateral leaflets were measured for Burbage Brook (site 7) only. The length, breadth and length/breadth ratio followed the terminal leaflet trends closely. Stalk length was greatest in treatment A becoming shorter in the order A, B, C, D.

This experiment shows that characters of the rosette leaves are extremely plastic and that soil moisture, air temperature and humidity influence this

TABLE 3. STATISTICAL ANALYSES FOR ROSETTE-LEAF CHARACTERS FROM THE PLASTICITY EXPERIMENT

For Duncan's Multiple Range Test, sites and treatments are ranked in decreasing order of magnitude with square brackets indicating those differences which are not significant ($p > 0{\cdot}05$).

Characters	Analysis of Variance: Variation	Significance (p)	Duncan's Multiple Range Test
Leaf-length	Sites	N.S.	—
	Treatments	< 0·001	A B | D C |
Terminal leaflet-length	Sites	N.S.	—
	Treatments	< 0·001	A B D C
Length/breadth ratio of terminal leaflets	Sites	N.S.	—
	Treatments	< 0·01	A B D C
Thickness of terminal leaflet	Sites	0·025	7 | 21 4 3 | 12
	Treatments	< 0·05	| D B | | A C |
Number of leaflets	Sites	< 0·01	7 21 | 12 | 3 | 4 |
	Treatments	< 0·01	B D C A

plasticity. It also demonstrates that there is genotypic variation in the number of leaflets and in the thickness of the terminal leaflet.

In order to examine flowering characters the experiment was continued the following year after the plants had overwintered outside in the ash beds. Only a few plants produced flowering stems and flowers, but the results suggested that the length of the flowering stems and cauline leaves, and the length and breadth of the cauline leaflets, all varied in a similar way to those for the rosette leaves.

DISCUSSION

The results show that in England the $2n = 56$ cytotype is widespread over most of the country. This is a similar situation to that found by Hussein (1955), although in our survey plants with $2n = 30$ were not found, no doubt because sampling in southern England, reputedly the major area of this cytotype, was more restricted than in the Midlands and northern England. Plants with $2n = 58$ were found at one locality, this cytotype having been previously recorded in Britain by Lövkvist (1956). This comparative uniformity of chromosome number in England is to be contrasted with the situation on the Continent where most populations have a range of chromosome numbers.

The habitat data show that the $2n = 56$ cytotype has a wide ecological range, from lowland marshes, fens and grassland to upland marshes above 2000 ft. Thus the situation most Continental authors have recorded, where cytotypes are restricted in their ecological tolerance, does not occur in England, the $2n = 56$ cytotype being apparently able to occupy the whole range of habitats available to the species.

Morphological studies of this cytotype have indicated that most of the variation in both vegetative and floral characters is due to phenotypic plasticity and this is confirmed by the experiment where a number of clones were subjected to varying environmental conditions. The correlations between morphology in the field and physical factors such as soil moisture and altitude also indicate that the morphological variation is largely controlled by environmental factors. The variation of a few characters, e.g. petal length/breadth ratio, appears to be genotypic and the correlation of this character with annual rainfall suggests that it may be genecologically based.

The taxonomic position of the $2n = 56$ populations has been investigated by comparing their variation with the differences given by Lövkvist (1956) and Berg & Segal (1966) for the two segregate taxa which they distinguish. The main vegetative character which has been used is whether the cauline leaflets are stalked (subsp. *palustris*) or not (subsp. *pratensis*). In the $2n = 56$ populations sampled, plants with and without stalks are present. Examination of the rosette leaves produced in the experiment on phenotypic plasticity (see Fig. 8) indicates that the development of the stalk is influenced by environmental conditions, the best-developed stalks being on leaves produced from plants grown under high humidity in a mist propagator. These leaves resemble most closely those found on plants in tall marsh vegetation. Comments on other vegetative characters vary; thus Berg & Segal (1966) state that subsp. *pratensis* has smaller leaves than subsp. *palustris*, while Lövkvist (1956) does not mention this character. The present investigation has shown that leaf-size is highly variable. The variation in floral characters are compared, using polygonal graphs (Fig. 9), with the limits given by Berg & Segal (1966). It is evident that the variation recorded in the $2n = 56$ cytotype in England spans the complete range described for the two segregate taxa. The morphology of

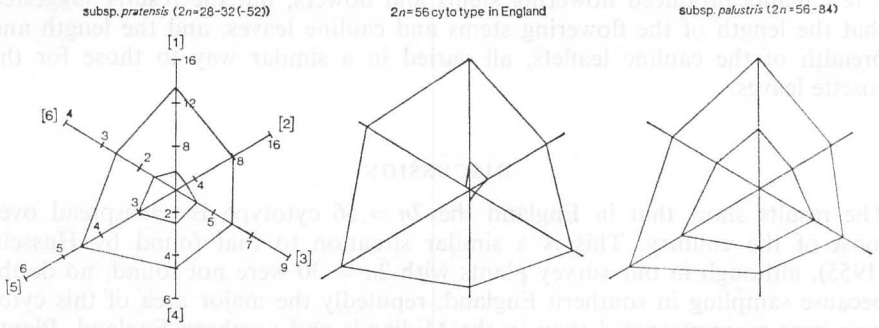

FIGURE 9. Polygonal graphs of floral characters for the $2n = 56$ cytotype in England and for subsp. *palustris* and subsp. *pratensis* (data from Berg & Segal 1966). Maximum and minimum measurements (mm) of individuals are plotted on separate polygons for (1) petal-length, (2) petal-breadth, (3) length of long filaments of stamens, (4) length of short filaments of stamens, (5) sepal-length and (6) sepal-breadth.

the $2n = 58$ cytotype shows no distinctive features when compared with the $2n = 56$ populations.

The combination of morphological, cytological and ecological characteristics used by several Continental authors to divide *C. pratensis* in lowland north-western Europe into two taxa cannot, therefore, be directly applied to English material, since the range of morphological variation and ecological tolerance shown by the $2n = 56$ cytotype in England spans that recorded for the species as a whole on the Continent. Furthermore, since it has been demonstrated that the major part of the morphological variation in England is due to phenotypic plasticity, a reassessment, using experimental techniques, of the characters used to distinguish cytotypes on the Continent would seem to be necessary.

ACKNOWLEDGMENTS

We wish to thank Miss J. E. Lowery, whose B.Sc. thesis on *Cardamine pratensis* formed the foundation of our study, and Miss D. Wright for her valuable technical assistance.

REFERENCES

BANACH, E. (1950). Studies in karyological differentiation of *Cardamine pratensis* in connection with ecology. *Bull. Acad. pol. Sci., Cl. II, Sér. Sci. biol.*, **1**: 197–211.

BERG, C. C. (1967). Cytotaxonomic studies in *Cardamine pratensis* in the Netherlands. *Acta bot. neerl.*, **15**: 683–689.

BERG, C. C. & SEGAL, S. (1966). De Pinksterbloem in Nederland. *Gorteria*, **3**: 77–86.

DUNCAN, D. B. (1955). Multiple range and multiple F-tests. *Biometrics*, **11**: 1–42.

HUSSEIN, F. (1955). Chromosome races in *Cardamine pratensis* in the British Isles. *Watsonia*, **3**: 170–174.

JONES, B. M. G. (1964). *Cardamine*, in TUTIN, T. G., *et alii*, eds. *Flora Europaea*, **1**: 285–289. Cambridge.

LÖVKVIST, B. (1956). The *Cardamine pratensis* complex. Outlines of its cytogenetics and taxonomy. *Symb. bot. upsal.*, **14** (2): 5–131.

MANTON, I. (1932). Introduction to the general cytology of the Cruciferae. *Ann. Bot.*, **46**: 509–556.

METEOROLOGICAL OFFICE (1952). *Climatological atlas of the British Isles*. London.

POORE, M. E. D. (1955). The use of phytosociological methods in ecological investigations. III. Practical applications. *J. Ecol.*, **43**: 606–651.

WILLIS, A. J., FOLKES, B. F., HOPE-SIMPSON, J. F. & YEMM, E. W. (1959). Braunton Burrows: The dune system and its vegetation. I. *J. Ecol.*, **47**: 1–23.

(*Accepted April* 1973)

APPENDIX

Site details and chromosome counts

Site no.	Locality	Vice-county	Grid reference	Altitude (ft)	Geology[1]	Habitat[2]	Chromosome counts		No. of plants counted
							Meiotic	Mitotic	
1	Pebley Pond	Derby (v.c. 57)	43/491.785	350	M.L.	ws		56	2
2	Eshton Tarn	Mid-W. Yorks. (v.c. 64)	34/918.576	490	C.L.	wt			
3	Blo Norton	W. Norfolk (v.c. 28)	62/024.790	100	Peat on Chalk	—			
4	Wicken Fen	Cambs. (v.c. 29)	52/560.708	40	Peat on Greensand	wt			
5	Wroxham Broad	E. Norfolk (v.c. 27)	63/310.168	50	Peat on Norwich Clays	wt			
6	Wardlow Mires	Derby (v.c. 57)	43/183.757	800	C.L.	wt			
7	Burbage Brook, nr. Hathersage	,,	43/259.802	950	M.G.	wt	28		1
8	Hardwick Hall	,,	43/457.637	350	C.M.	wt			
9	Torne Bridge	S.W. Yorks. (v.c. 63)	44/677.035	50	Bunter S.S.	ds			
10	New Clipstone	Notts. (v.c. 56)	43/580.623	300	Bunter S.S.	—		56	1
11	Wardlow Mires	Derby (v.c. 57)	43/188.757	850	C.L.	wt	28	56	3
12	Repton	,,	43/272.301	150	Alluvium on Keuper S.S.	wt		56	3
13	Arlington	N. Devon (v.c. 4)	21/604.404	450	Upper O.R.S.	wt	28		1
14	Monsal Dale	Derby (v.c. 57)	43/172.708	600	C.L.	ds			
15	Quidenham	W. Norfolk (v.c. 28)	62/025.877	100	Chalk	ds			
16	Monsal Dale	Derby (v.c. 57)	43/167.712	600	C.L.	ds	28	56	2
17	Cressbrookdale	,,	43/175.746	750	C.L.	ws			
18	Cressbrookdale	,,	43/173.748	750	C.L.	ds			
19	Icklingham	W. Suffolk (v.c. 26)	52/763.726	50	Chalk	ds		56	1
20	Pebley Pond	Derby (v.c. 57)	43/485.791	350	C.M.	ds		56	2
21	Cressbrook	,,	43/173.726	600	C.L.	ds	28	56	3
22	Dovedale	,,	43/147.510	500	C.L.	—			
23	Milldale	,,	43/139.546	600	C.L.	ds	28		1
24	Milldale	,,	43/145.554	600	C.L.	ds	28		2
25	Biggindale	,,	43/143.574	700	C.L.	—			

26	Eshton Tarn	Mid-W. Yorks. (v.c. 64)	34/915.574	500	C.L.	—		56	2
27	Braunton Burrows	N. Devon (v.c. 4)	21/464.347	0	M.G.	—	28		2
28	Hopton	W. Suffolk (v.c. 26)	52/987.794	100	Chalk	wt			
29	Ashford	Derby (v.c. 57)	43/178.700	500	C.L.	wt	28		1
30	Bamford	,,	43/193.828	500	Alluvium on Edale Shales	ws		56	2
31	Monsal Dale	,,	43/171.708	600	C.L.	wt	28		1
32	Marton	N. Lincs. (v.c. 54)	43/831.825	50	Keuper Marl	ds		56	1
33	Clumber Park	Notts. (v.c. 56)	43/636.754	120	Bunter S.S.	wt			
34	Barrow-on-Soar	Leicester (v.c. 55)	43/568.177	200	Lower Lias	ds		56	1
35	Ainsdale	S. Lancs. (v.c. 59)	34/297.123	0	Keuper Marl	ws			
36	Great Dun Fell, Teesdale	Westmorland (v.c. 69)	35/703.317	2300	Yoredale Shales	ws			
37	Stanage	Derby (v.c. 57)	43/255.833	1350	M.G.	—		56	2
38	Cronkley Fell, Teesdale	N.W. Yorks. (v.c. 65)	35/839.282	1700	Dolerite	—		56	4
39	Gordale	Mid-W. Yorks. (v.c. 64)	34/911.657	1200	C.L.	ws			
40	Bretton Clough	Derby (v.c. 57)	43/210.790	850	M.G.	wt			
41	Barber Booth, Edale	,,	43/107.847	900	M.G.	wt		56	3
42	Malham Cove	Mid-W. Yorks. (v.c. 64)	34/897.638	720	C.L.	ws		56	2
43	Widdybank Fell, Teesdale	Durham (v.c. 66)	35/814.300	1650	C.L.	ws	29	58	2
44	Forest-in-Teesdale	,,	35/863.294	1200	Dolerite	—		56	1
45	Chenies	Bucks. (v.c. 24)	51/025.989	250	Chalk	ds			
46	Water End	Herts. (v.c. 20)	52/044.103	300	Alluvium on Chalk	ws		56	1
47	Spade Oak	Bucks. (v.c. 24)	41/882.873	100	Alluvium on Chalk	ws		56	1

[1] Geological abbreviations are as follows:
C.L. Carboniferous Limestone C.M. Coal Measures M.G. Millstone Grit
M.L. Magnesian Limestone O.R.S. Old Red Sandstone S.S. Sandstone

[2] Habitat abbreviations are as follows:
wt wet sites with tall vegetation (above 0·5m at time of sampling)
ws wet sites with short vegetation
ds dry sites with short vegetation