

REGIONAL VARIATION OF *ALNUS GLUTINOSA* (L.) GAERTN. IN BRITAIN

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MORPHOLOGICAL VARIATION

In its external morphology *Alnus glutinosa* is a rather variable species and it is possible that a similar physiological variability exists. The most obvious differences are in habit, leaf size and shape, and catkin size.

Generally, the alders in the north and west of Britain are shorter and more gnarled than those to the south and east, but this may well be a habitat modification, brought about by exposure to strong winds and growth in less suitable soils, and not genotypic. The multiple-stemmed bush habit is most frequent on waterlogged soils but may be induced by damage to the sapling.

Leaf outline varies from orbicular through cuneate to ovate or obovate. The apex may be strongly emarginate, rounded or even acutely pointed as in *Alnus incana*. The leaf outline is fairly constant for each tree, although the shape of the apex may vary. The margin may be undulate with one or two pronounced sets of teeth, or smoothly curving and with only tiny serrations.

The hairiness of lamina surface, vein angles and petioles is also variable.

Asymmetric leaves are frequent, and differences between long and short shoot leaves do not appear to be as pronounced as in *Betula*.

Pistillate catkins may be globular or elongated, and the free points of the fused scales may or may not be visible.

Size of seeds (fruits) also varies considerably, and roughly proportionately with catkin size. The range of variation illustrated by Kujala (1924) for Scandinavia is less than that now recognized in Britain (Plate 2).

Catkins less than 10 mm. long have very tiny seeds (1.5×1.0 mm.) which in turn give rise to small, weak seedlings.

Leaf and catkin sizes were selected for statistical examination in 1949. Leaves were collected at random from spur shoots and from near the apex of long shoots, avoiding immature or obviously deformed specimens. Length was measured from the insertion of the petiole to the distal end of the mid-vein, and breadth at the broadest point at right angles to this line.

Pistillate catkins could not always be measured at the green-ripe stage, but it was found possible to utilise old catkins provided length was measured from the insertion of the stalk to the tip of the centre scale, ignoring the extra length given by any reflexed basal scales.

Twenty leaves and twenty catkins from each of five or ten trees per population were measured, and two or three adjacent populations in each district were sampled where possible. This method was used in preference to the collection of one leaf per tree since populations were often small.

Mean dimensions of leaves and catkins for any one tree in the Arran and Chippenham populations were found to be constant from year to year.

Data from the eighteen populations sampled are summarised in Tables 1 and 2. The location of the populations is shown in Figure 1. The same data have also been presented graphically elsewhere (McVean 1953).

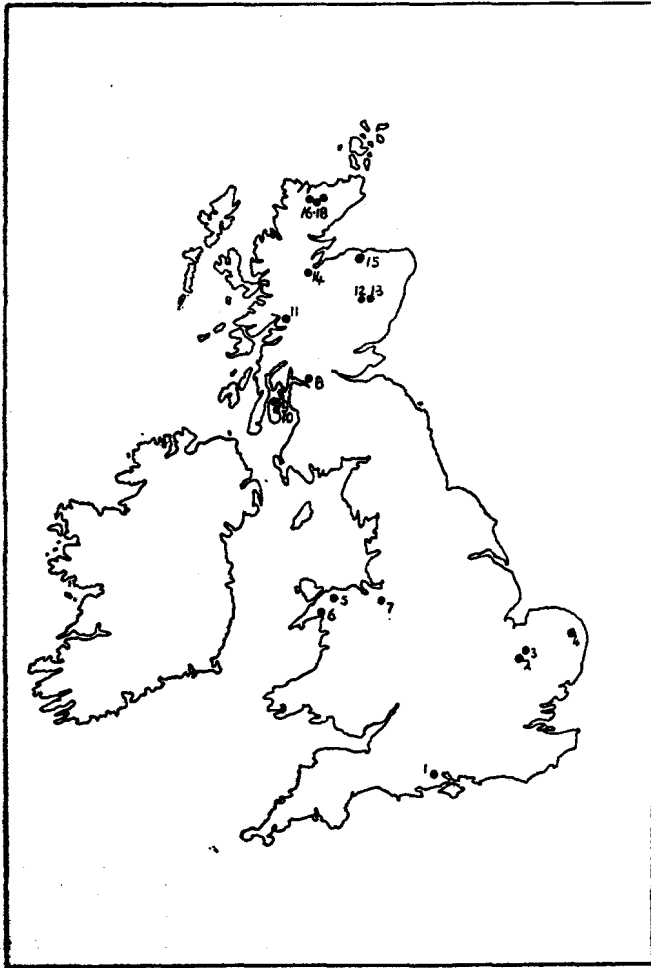


Fig. 1. Location of populations shown in Tables 1 and 2.

TABLE 1
Alder leaf measurements

Population	Mean Length (mm.)	Regional mean	Mean Breadth (mm.)	No. of trees measured
1. Matley Bog, Hants.	54.8 ± 6.1	(54.8)	53.8 ± 6.9	10
2. Chippenham Fen, Cambs.	71.7 ± 13.5		59.3 ± 11.7	10
3. Santon Downham, Norfolk	65.2 ± 8.2	66.7	59.0 ± 11.5	5
4. Ranworth Broad, Norfolk	63.3 ± 6.7		57.1 ± 7.2	10
5. Conway Valley, N. Wales	59.8 ± 8.5		54.1 ± 9.9	10
6. Portmadoc, N. Wales	57.2 ± 7.9	61.9	54.1 ± 8.0	10
7. Chester	68.9 ± 6.5		56.9 ± 8.3	10
9. North Arran	58.6 ± 7.1	(58.6)	52.7 ± 7.4	20
11. Glen Nevis	59.8 ± 9.8		55.5 ± 8.0	10
12. Ballater, Deeside	47.4 ± 6.0	53.2	40.6 ± 5.0	5
13. Kinord, Deeside	45.4 ± 5.5		46.0 ± 8.6	5
15. Garmouth, Spey Bay	60.2 ± 6.3		52.5 ± 6.3	10
16. Sutherland i	52.1 ± 6.5		52.0 ± 7.2	10
17. Sutherland ii	49.8 ± 7.4	52.3	45.3 ± 5.5	10
18. Sutherland iii	55.0 ± 6.1		48.0 ± 5.1	10

TABLE 2
Alder pistillate catkin measurements

	Population	Mean Length (mm.)	Regional mean	Mean Breadth (mm.)	No. of trees measured
1.	Matley Bog	10.8 ± 2.1	11.0	7.6 ± 1.6	10
	Holmesley Bog	11.2 ± 2.0		7.7 ± 1.1	5
2.	Chippenham Fen	15.0 ± 3.6		10.4 ± 1.8	10
3.	Santon Downham	13.7 ± 2.9	13.9	10.0 ± 1.8	5
4.	Ranworth Broad	13.1 ± 2.5		9.1 ± 1.0	10
5.	Conway Valley	12.9 ± 2.3		9.1 ± 1.5	10
6.	Portmadoc	11.4 ± 2.0	11.9	7.7 ± 1.0	10
7.	Chester	11.5 ± 2.1		8.4 ± 1.0	10
8.	Mugdock, S.W. Stirling	10.8 ± 2.2		8.0 ± 1.8	10
9.	N. Arran i	10.8 ± 2.9	11.2	8.0 ± 1.3	20
10.	N. Arran ii	11.0 ± 2.4		8.1 ± 1.5	10
11.	Glen Nevis	10.1 ± 2.5		7.7 ± 1.7	10
12.	Ballater	11.9 ± 1.8		7.7 ± 1.4	5
13.	Kinord	9.3 ± 1.1	10.7	6.6 ± 0.9	5
14.	E. Loch Ness	11.1 ± 1.9		8.2 ± 1.4	10
15.	Garmouth	11.3 ± 2.2		8.1 ± 1.0	10
16.	Sutherland i	10.5 ± 2.5		8.2 ± 1.3	10
17.	Sutherland ii	8.5 ± 1.5	9.2	7.4 ± 1.2	10
18.	Sutherland iii	8.6 ± 1.9		7.1 ± 1.4	10

Moss (1914) recognised three varieties of *Alnus glutinosa* in Britain on the basis of leaf and catkin sizes.

Var. *macrocarpa* Loudon. Laminae about as long as broad (7.8 cm.) and with larger and coarser serrations. Pistillate catkins about 3 cm. long at maturity.

Var. *typica* Moss. Laminae intermediate in shape and size (5.6 × 4.5 cm.). Pistillate catkins 1.7-2.0 × 1.0-1.4 cm. "Believed to be the common south and lowland form and not yet known for Wales, Scotland or Ireland."

Var. *microcarpa* Rouy. Laminae 4.5 × 3.5-4.0 cm. and with smaller and finer serrations. Pistillate catkins 1.5 × 1.0 cm. "Common form in hilly and northern localities though it also occurs to some extent in the south of England down to Somerset and Suffolk."

The variation is actually continuous so that the above varieties merely cover arbitrary ranges on the gradient. Furthermore, though correlation coefficients have not been calculated, it is apparent in the field that the largest catkins do not necessarily grow on the trees with the largest leaves, and the same applies to the small forms. Neither are the large-cone trees more robust in growth and with more coarsely toothed leaves as Moss suggests.

The largest catkins obtainable during 1949-52 at Chippenham Fen, Cambs., the *locus classicus* of var. *macrocarpa*, have been 27 and 28 mm. long (Plate 3). The mean dimensions for twenty randomly gathered catkins from this tree were found to be 19 × 12 mm.

Catkins of *typica* size have been collected in Arran and Glen Nevis though mean dimensions for each tree were below the *typica* limit.

It is apparent from the data that there is a decrease from south to north and from east to west in both leaf and catkin size. The gradient is not a smooth one unless populations are grouped regionally, as for leaf and catkin length in Tables 1 and 2. The decrease in catkin length amounts to over 5 per cent per degree and leaf length to almost 4 per cent per degree of longitude.

In Figures 2 and 3 the size distribution of 200 catkins from each region studied is

presented in histogram form. Catkin and length breadth have been multiplied together to give simple numbers which express size more adequately than either linear dimension. It can be seen from histogram Σ 1-7 that catkin size forms a unimodal curve slightly skewed towards the smaller sizes.

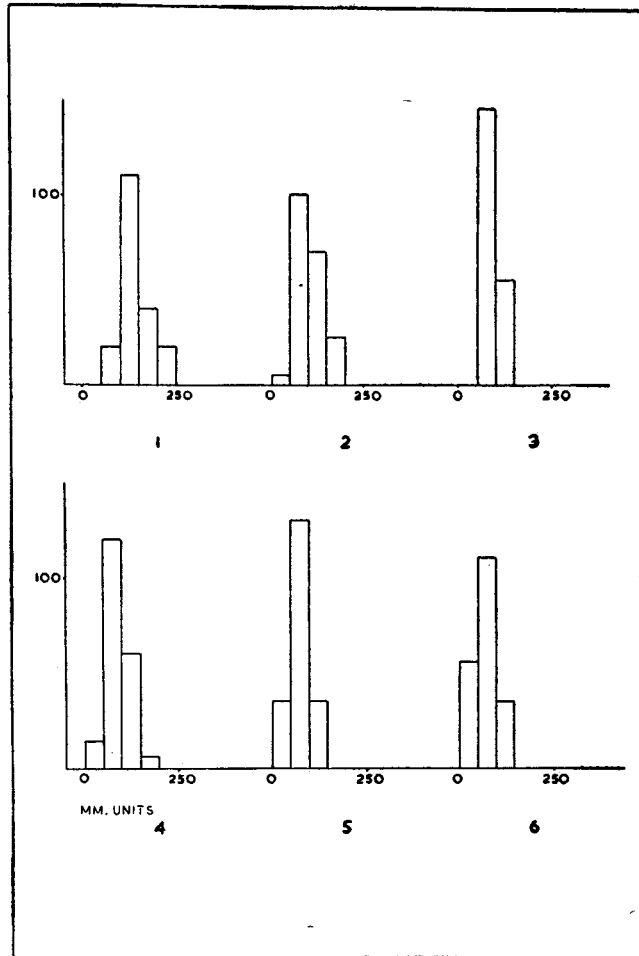


Fig. 2. Size distribution of alder catkins in each district studied. Catkin length \times catkin breadth is expressed as "mm. units" on the abscissa, and the ordinate gives number of catkins measured.

- | | | |
|----------------------------|----------------|-----------------|
| 1. East Anglia | 2. North Wales | 3. Mid Scotland |
| 4. N.E. Scotland | 5. Deeside | 6. Glen Nevis |
| 7. Sutherland (see Fig. 3) | | |

Since the method of sampling has resulted in the variation studied being non-homogeneous (compounded of that "within a tree" and "between trees") only differences in means of at least three times the standard error have been regarded as significant (i.e. a level of significance of 0.27 per cent).

It has been found that each population is not significantly different from its near neighbours but that significance increases with distance. Thus Santon Downham, Chippenham Fen and Ranworth Broad populations are not significantly different nor are those of Sutherland, but any one of the first group is significantly different from any of the second.

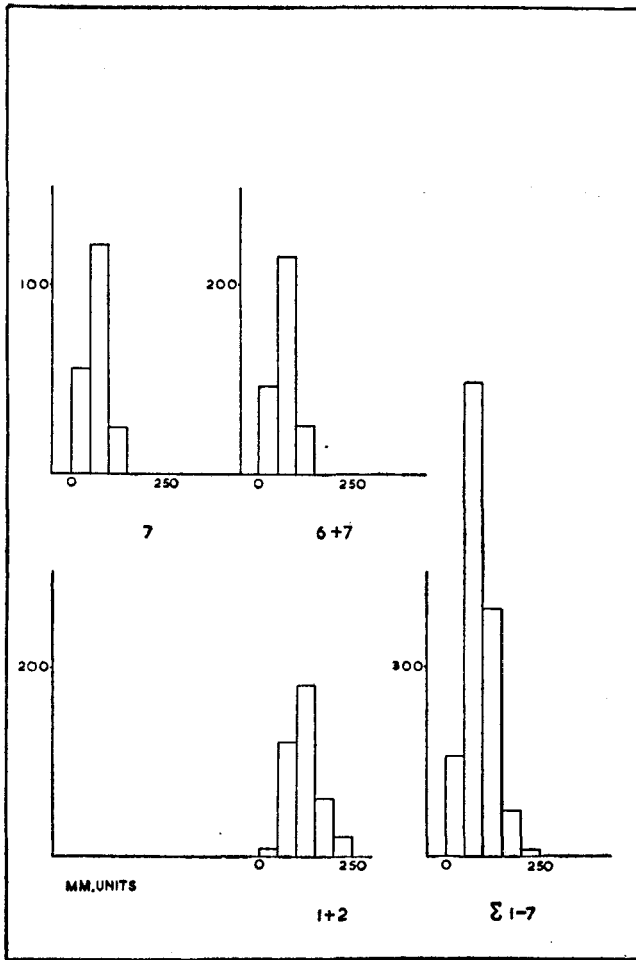


Fig. 3. Histograms 6 + 7 and 1 + 2 show the different size distributions in north and south respectively, and $\Sigma 1-7$ is a summation of all populations.

The Sutherland populations are also significantly less variable than those of S.E. England.

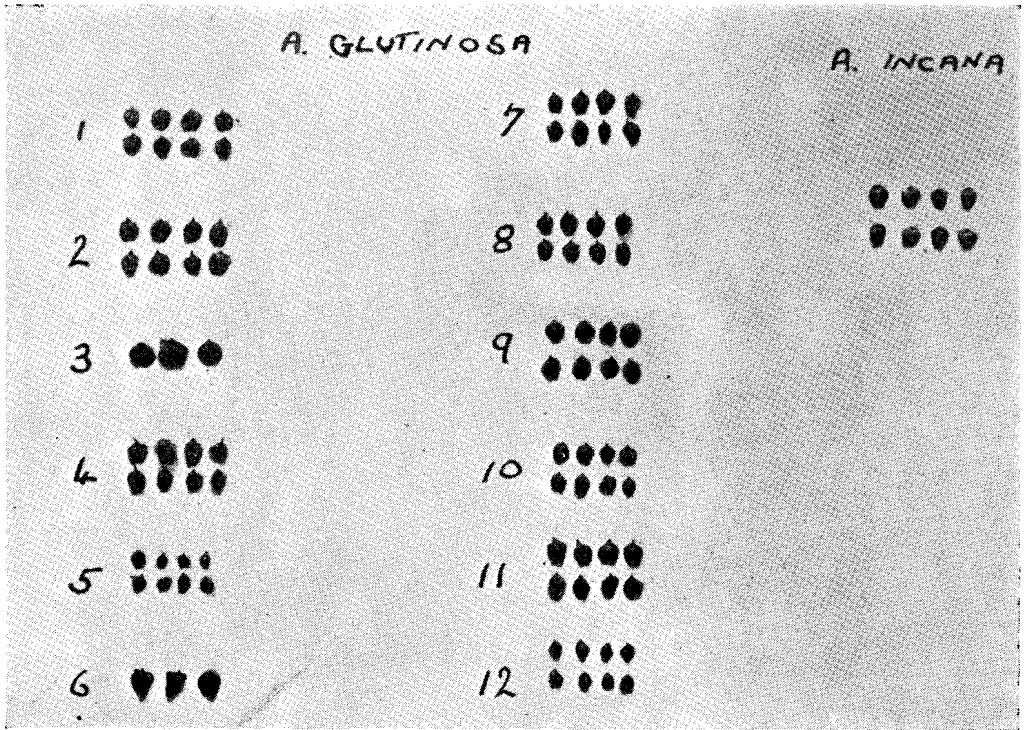
The New Forest populations of Matley and Holmesley Bogs are anomalous (see discussion).

Leaf and catkin measurements were also made over an altitudinal range of 1300 ft. (397 m.) in W. Inverness-shire (Table 3), but no variation with altitude was detected.

TABLE 3
Altitudinal variation in leaf and catkin size

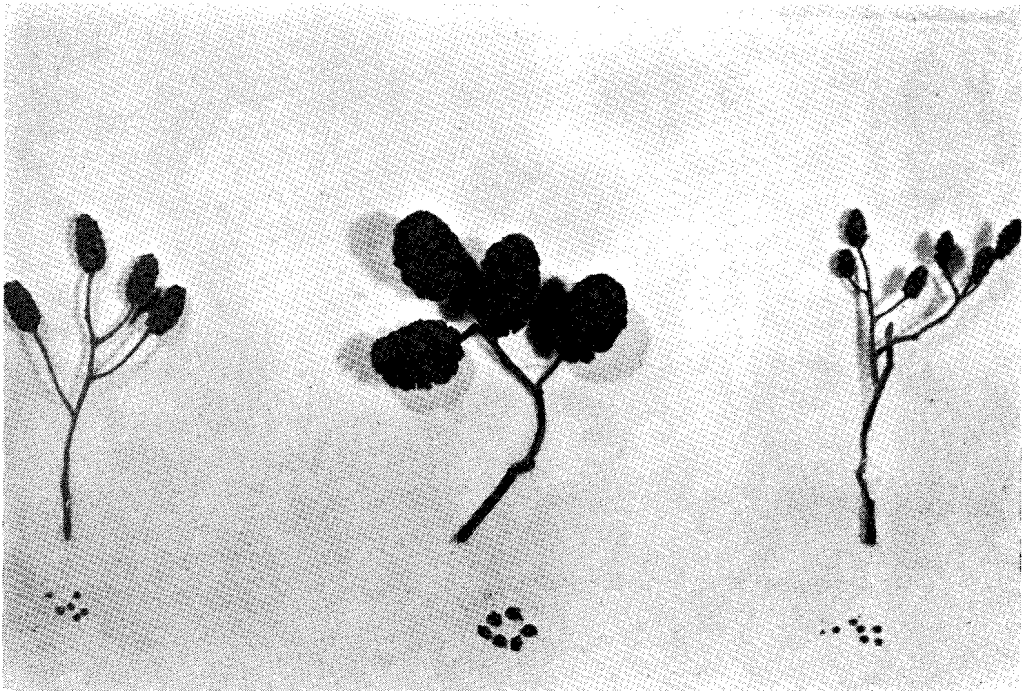
Locality	Altitude (m. O.D.)	Mean Leaf size (mm.)	Mean Catkin size (mm.)
Loch Treig	260	52.5 × 46.3	8.5 × 8.0
Loch Treig	351	51.4 × 51.9	7.9 × 7.9
Loch Treig	460	58.6 × 52.4	8.9 × 8.1
Glen Nevis	61	59.8 × 55.5	10.1 × 7.7
Glen Nevis	275	66.9 × 65.2	9.3 × 7.9

PLATE 2.



(c. nat. size). Alder fruits from different British populations. 3 and 6 are abnormal (galled).

PLATE 3.



($\times \frac{1}{2}$) Pistillate alder catkins. Left to right : "microcarpa," Woodwalton Fen, Hunts.; "macrocarpa," Chippenham Fen, Cambs.; "microcarpa," N. Arran.

CYTOLOGY

Chromosome counts, in seedling root tips, of "macrocarpa," "microcarpa" and "typica" material from Chippenham and the West of Scotland all gave $2n = 28$, the diploid number. Larsen has reported the occurrence of tetraploid alders in Denmark (Ording 1939), and Johnsson (1950) has described colchicine-induced chimaeras, with diploid and tetraploid layers, as being stunted in growth, with large, irregularly lobate, deeply toothed leaves which are often asymmetric, while wholly triploid plants had more robust growth than diploids and strikingly large leaves.

RACE DIFFERENTIATION

There are some references in the literature to the occurrence of races of different provenance in *Alnus glutinosa* and to growth disturbances following the cultivation of certain races in alien territory.

Larsen (Ording, 1939) cites the losses suffered by Danish forestry through importation of a type of alder, of more southern European origin, apparently not suited to the northern climate. At Frijsenborg the local race of *A. glutinosa* develops much better than offspring of even extremely fine trees at Meilgaard where the mother trees were even supposed to be of the Frijsenborg race.

Rubner (1934) refers to the poor growth of southern stock at Memel, Germany. The plants grew very quickly and produced fruit prematurely. They were attacked by the fungus *Valsa oxystoma* and died at the early age of 12-20 years.

In the present work the only indication of this phenomenon, apart from the morphological differences described above, has been given by the different photoperiodic responses obtained from populations from different latitudes.

In 1950, seedlings, which had been raised in the greenhouse and hardened off in the cold frame, were transferred to side-shaded plots at the Cambridge Botanic Garden on April 27th. In the transfers some groups were subjected to greater temperature changes than others, with the result that the different growth rates and final sizes attained could not be attributed to racial differentiation.

Difference in the time of leaf fall in November 1950 was, however, independent of the initial differences in treatment. On October 31st the leaves of the Arran seedlings had begun to brown while those of the Chippenham and North Wales plants were still green. A background of fallen chestnut leaves made a useful, though primitive, colour comparator, and on November 7th the Scottish seedlings were not visible against the carpet while the remainder were. The colour difference was hardly visible after mid-November, but the Scottish seedlings had by then shed more of their leaves.

The difference in time of loss of leaf function was estimated at 2-3 weeks for four degrees of latitude. About 75 seedlings were under observation.

A smaller number of Arran and Chippenham seedlings were also grown together in a plot near Glasgow where the different responses were even more marked than at Cambridge, the native seedlings browning and losing their leaves about three weeks before the others.

In 1951 seedlings from West Inverness, Arran, Lancashire, North Wales and East Anglia were grown in pots out of doors for one season. Significant differences in growth rates could not be detected but differences in time of leaf fall were again apparent, the leaves browning in the above order.

The 1950 plants, now 1-3 ft. high, again showed three weeks' difference in time of leaf fall between the Arran and southern groups. In the spring of 1952 the saplings of southern origin were markedly earlier in flushing.

Wareing (1948) summarises present knowledge of photoperiodic phenomena in

trees. He notes that northern races of pine grown in southern regions show reduced height and needle length, and first-year seedlings respond to shorter days by hastened dormancy, as compared with the home region. After the first year of growth, duration of extension-growth is unaffected by day length.

In the *Annual Report of the Swedish Association for Forestry and Tree Breeding*, 1942, variation in photoperiodism is reported for both two-year and one-year *A. glutinosa* seedlings. The Västerbotten long-day type showed marked differences in increment, in time of leaf fall and in lignification of the annual shoots compared with central and southern Swedish races.

DISCUSSION

There seems little doubt that in Britain the alder exhibits clinal variation in some features of its morphology and physiology, and that these variations tend to take place along the main climatic gradient S.E.-N.W. This would seem to belong to the large scale, geographical character gradients designated topoelines by Gregor (1938-39). (Morphological variation has not yet been demonstrated on the plants grown under uniform conditions in the experimental garden.)

There may be a continual selection for small leaves and catkins in the north-west by some factors, possibly climatic, or the situation may have arisen in the selective elimination of genes during post-glacial migration north-westward across the country. The smaller variability of the northern type indicates that some gene elimination has taken place.

The failure to establish similar morphological gradients altitudinally strengthens the belief that the differences are genotypic, since there are no barriers to gene flow over the short distances here involved. The morphological gradients exist as an alteration in the mean values of leaf and catkin size ranges rather than as a polymorph-ratio cline involving the three varieties cited above (p. 28).

Habitat preferences in the species encourage the formation of isolated local colonies which tend to intra-breed rather than inter-breed. This, along with some past planting by man, may account for the occurrence of populations of small-catkin types in an otherwise large-catkin region and *vice versa*.

It should perhaps be noted that the most serious discrepancy occurs in the New Forest populations, which lie south of the maximum extent of the Pleistocene glaciation.

ACKNOWLEDGMENTS

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