STUDIES IN *Colobanthus quitensis* (Kunth) Bartl. AND *Deschampsia antarctica* Desv.: VII. CYCLIC CHANGES RELATED TO AGE IN *Colobanthus quitensis*

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ABSTRACT. Variation in performance, as measured by leaf size, with plant age, as estimated from cushion diameter, is demonstrated for *Colobanthus quitensis*, and its implications in terms of community structure are discussed.

MUCH of the variation in performance and vigour of a species can be attributed to differences in environmental factors within its range, but in long-lived species the age of the individual may also be important. Kershaw (1960, 1962*b*) showed that plant vigour in some perennial species increased with age, reaching an optimum at maturity and then declining as the plants aged, and he suggested later (Kershaw, 1964) that similar growth curves might exist in many other perennial species. However, because of the difficulty of ageing most herbaceous perennials, such data are available for only a few species. Rhizome morphology makes ageing possible in some pteridophytes (Watt, 1955) and monocotyledons (Kershaw, 1962*a*; Callaghan and Lewis, 1971), while counts of annual rings have been used extensively to age species which produce secondary thickening (Watt, 1955; Kershaw, 1960). For anatomical reasons neither of these techniques was feasible with *Colobanthus quitensis* but, even had this not been so, the destruction of the vegetation that they entail would have precluded their use because of the species' sparse and restricted distribution in Antarctic regions.

In communities on Signy Island, South Orkney Islands (lat. 60°43′S., long. 45°38′W.), *Colobanthus quitensis* commonly occurs as scattered individuals forming dense, discrete hemispherical cushions which are sufficiently symmetrical to enable accurate measurement of their diameters. It was considered that, with certain precautions, this non-destructive and rapid method could give a reasonable indication of the age of a plant. By restricting sampling to cushions at a small uniform site, the effects of climatic and environmental variability could be reduced and differences in the growth rates of individual plants minimized so that cushions of the same diameter could be assumed to be of approximately the same age.

For the diameter of a cushion to be related to its age, however, it is also necessary that the annual growth increment of the plant remains constant, a situation rarely, if ever, realized although possibly approached by plants growing in extreme habitats.

With these conditions in mind, an investigation was undertaken on Signy Island in December 1969 to determine whether it was possible to relate the performance of *C. quitensis*, as measured by leaf length and breadth, to the age of individual plants, as estimated from cushion diameter.

METHOD

Because both clump diameter and leaf size were variables, it was essential that large samples be taken to allow for micro-topographical differences. This extensive sampling necessitated a small uniform study area where there was a high density of uncoalesced *C. quitensis* cushions of various diameters. A suitable site, 7 m. by 7 m., was chosen at *c.* 15 m. a.s.l. on the north-facing slopes of Observation Bluff, where cushions of *C. quitensis* had not coalesced despite their abundance.

In order to determine the sample size necessary to obtain a reasonably accurate estimate of leaf length, extensive measurements were taken from two cushions of *C. quitensis* from Signy Island growing at Birmingham, prior to the collection of field samples. Standardization of leaf age was achieved by selecting one of the second pair of leaves below the apex of each culm. This enabled measurements to include the smallest culms encountered and ensured that fully developed leaves were selected. Graphs relating the mean values of leaf length to sample size (Fig. 1) indicated considerable fluctuation in estimates based on less than 18 leaves but that little

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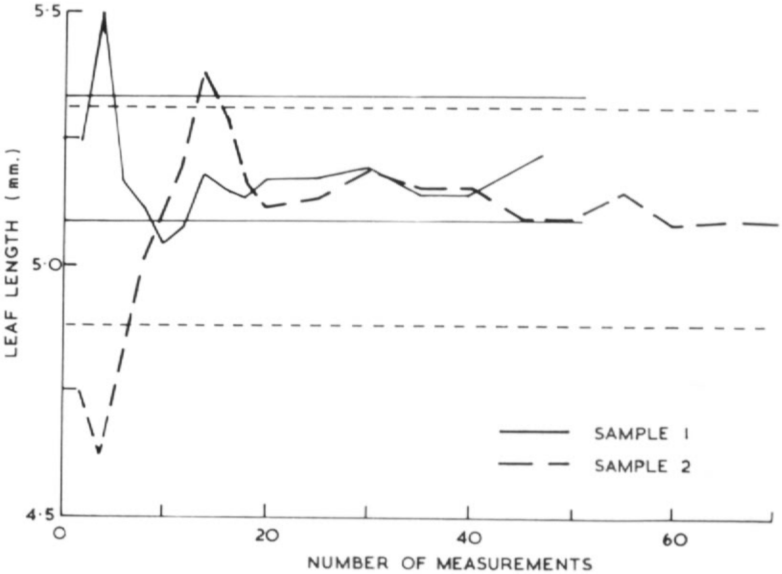

Fig. 1. Reduction in the variation of mean leaf length with increase in sample size for two samples of *Colobanthus quitensis* from Signy Island. Horizontal lines indicate a 0·25 standard deviation either side of the final mean.

increase in accuracy resulted from additional sampling above this number. It was, therefore, considered adequate to measure 20 leaves from each cushion or, where this was not possible due to the small size of the plant, one leaf from every culm present in the cushion. Samples were selected to give the widest possible range of plant size, leaf length and breadth being measured to the nearest 0·1 mm. using a binocular microscope, while the maximum diameter of each cushion was measured horizontally across the plants to the nearest millimetre. The degree of correlation between leaf and cushion size was established by subjecting the results to various regression analyses.

Results and Discussion

When mean leaf length and breadth are plotted against cushion diameter (Figs. 2 and 3), there appears to be a tendency for the smallest and largest cushions to bear smaller leaves than intermediate-sized plants. However, the scatter of points was great, indicating a considerable variability in the performance of plants of approximately the same age, due partly to local environmental effects resulting from micro-topography.

Quadratic regressions of the form $Y = a + bx - cx^2$ were highly significant ($>0 \cdot 1$ per cent) when fitted to both the mean leaf-length and mean leaf-breadth data and accounted for 21 and 18 per cent of the variation, respectively. The cubic regression of leaf length with cushion size (Fig. 2) was also significant at the 5 per cent level, while both cubic and quartic regressions were significant at the $>0 \cdot 1$ per cent level with the leaf-breadth measurements (Fig. 3) but none was an improvement on the fit of the quadratic regression to the data. Thus the phasic development which Kershaw (1964) suggested as being widespread in perennials can be seen to occur in *Colobanthus quitensis* which reaches a mature phase when the cushion is between 40 and 70 mm. in diameter.

It is, unfortunately, not possible to age cushions of these sizes accurately. Measurements of *C. quitensis* seedlings on Signy Island indicate that they rarely grow larger than 5 mm. in diameter in their first year and that many small plants 15–20 mm. in diameter were *c.* 5 years old, having probably grown from seeds formed in the 1964–65 season when weather conditions were favourable for seed development (Edwards, 1974). However, plants larger than this were of unknown age, and failed to show any measurable increase in diameter during the growing season.

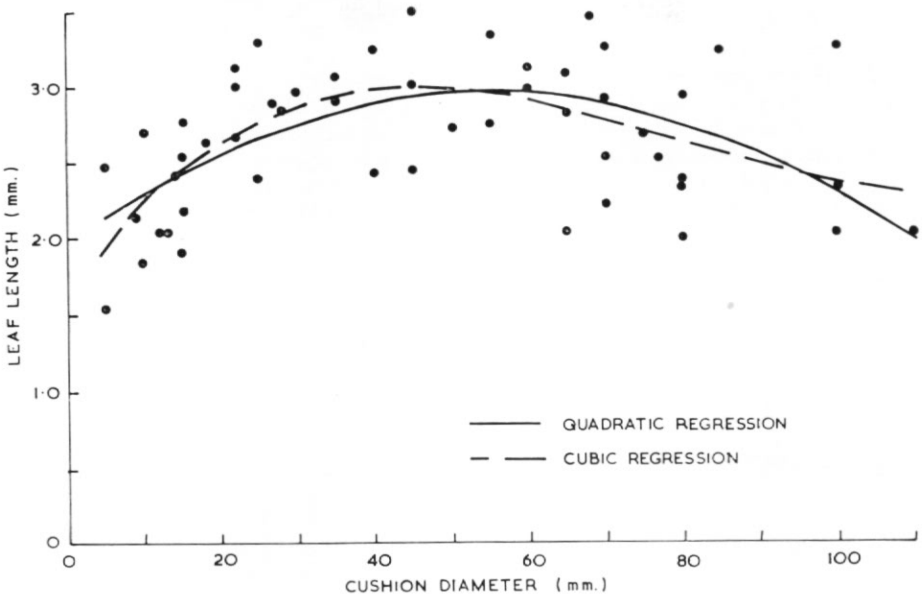

Fig. 2. Relationship of leaf length to cushion diameter in *Colobanthus quitensis* on Signy Island. Each symbol represents a mean value of 20 measurements.

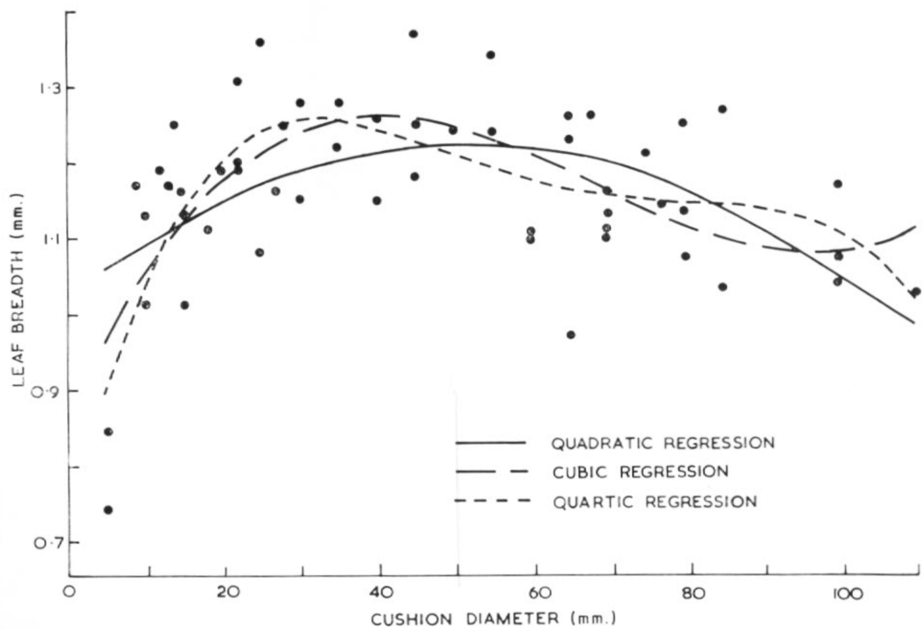

Fig. 3. Relationship of leaf breadth to cushion diameter in *Colobanthus quitensis* on Signy Island. Each symbol represents a mean value of 20 measurements.

Extrapolation from the younger plants suggests an annual increment of 2–4 mm. in the diameter of cushions, with plants 40 mm. wide having an age of between 10 and 15 years and individuals 70 mm. in diameter being *c*. 18 to 28 years old. In 1947 G. de Q. Robin noted on the label of a herbarium specimen that vascular plants on the west coast of Signy Island occurred at only a few sites which were small in extent, whereas in 1970 both species were locally abundant in several areas. It was the impression of the author, borne out by the data in Fig. 4, that *C. quitensis* cushions *c*. 70 mm. in diameter were relatively frequent on Signy Island and from the relationship outlined previously, it is possible to predict a minimum age of *c*. 18 years for these plants. Since 1947 there have been only a few summers which, from climatic data, appear to have been exceptionally favourable for the species' growth and reproduction, in particular those of 1950–51 and 1954–55. As seedlings from these years would have been 20 and 16 years of age respectively in 1969–70, some credibility can be given to the predicted age/diameter relationship.

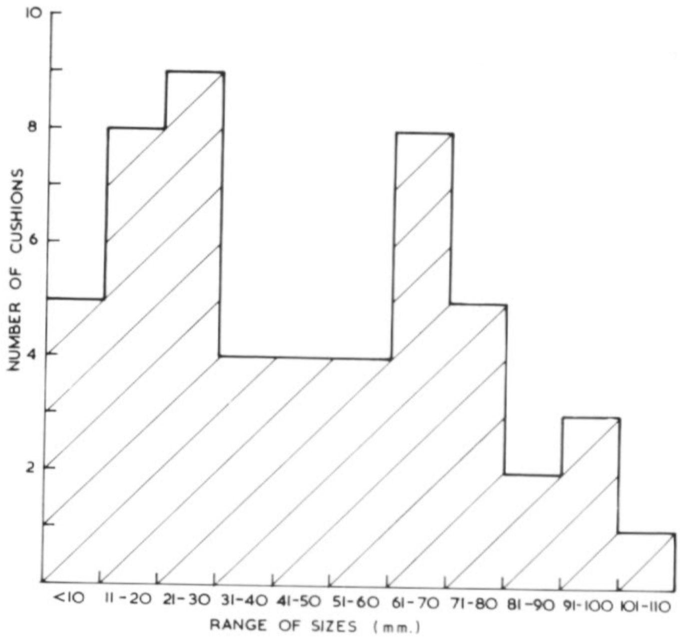

Fig. 4. Range of *Colobanthus quitensis* cushion size at Observation Bluff, Signy Island, December 1969.

The decline in performance which occurs in plants exceeding a cushion size of *c*. 60 mm. seems likely to be the result of ageing, although it could also reflect a reduced nutrient supply from the soil, impoverished by the demands of a long-lived perennial. However, nutrient limitation must be considered unlikely on Signy Island, in view of the large input from sea spray, the weathering of rocks, the down-washing of leachates from surrounding communities and bird droppings (Holdgate and others, 1967; Edwards, 1972).

Variation in performance with age seems certain to be one of the factors which would affect the ability of a plant to compete with other vegetation in its niche. Watt (1947) showed that the intensity of shoot development in *Pteridium aquilinum* was related to the age of the rhizome system and that the stages of growth, maturity and senescence could be distinguished by the age of the individual. He also demonstrated similar cyclical changes in *Calluna vulgaris* (Watt, 1955) and indicated that an inverse relationship existed in the distribution of the two species, so that when one was in its building or mature phase, the other was at minimum density and vice versa.

A similar relationship possibly exists with *C. quitensis* and various bryophyte species in the Antarctic. Shoots of various moss species or, less commonly, of liverworts were occasionally intermixed with the shoots of *C. quitensis* in the cushions, and subjective observations suggested that the degree of invasion increased as the cushions became larger. This may be due to a decline in the competitive ability of the pearlwort resulting directly from ageing or due to an increase in the number of protected micro-habitats for the growth of moss shoots in the larger cushions, which result indirectly as the leaves become smaller.

Another effect of variation in vigour of *C. quitensis* with age may be a modification of the patterns which develop within the vegetation. Distribution patterns resulting from the morphology of a species have been widely reported in the literature (Phillips, 1954; Grieg-Smith, 1957; Kershaw, 1964) and the scale of such patterns in time and space will depend, to some extent, on the longevity and vigour of the individuals, which have been shown to be partly modified by age. It appears that *Colobanthus quitensis* exhibits a clearly contagious distribution at most of the sites on Signy Island (Fig. 5) and analysis of a contiguous grid of quadrats

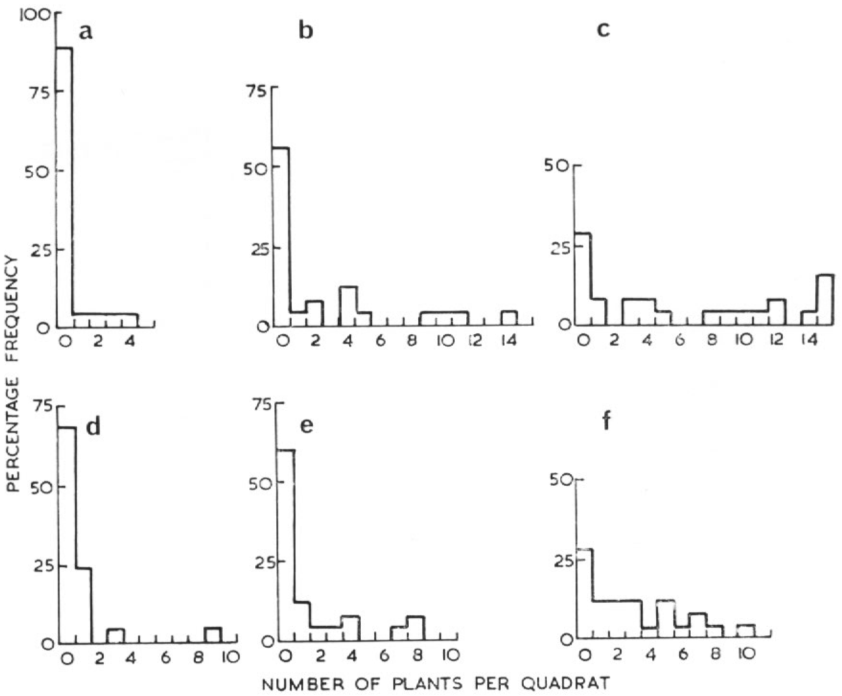

Fig. 5. Histograms of *Colobanthus quitensis* density at several sites on Signy Island, showing the clumped distribution of the species. The size of quadrat used was 40 cm.^{2}.
a. South-west of North Point; b. Shingle Cove; c. Observation Bluff; d. West of Robin Peak; e. North of Spindrift Rocks; f. Thulla Point.

indicates that individuals are clumped into areas *c.* 20 cm. by 20 cm. This results partly from the restricted dispersal of seed which appears to be mainly dependent on splash ejection from the capsules by raindrops. However, it would be unlikely that this causal factor of pattern would change greatly with age. It was also noted in some of the larger cushions that the central, presumably oldest, portion was more moribund than the outer culms and that in a few instances a group of smaller cushions appeared to have arisen as a result of the fragmentation of a larger cushion. It is likely that this contagion was brought about through the ageing of the central part of the cushion, although the possibility of it arising through the greater exposure of this part of the cushion to wind and driven ice particles cannot be ruled out.

Although many of the consequences arising from the ageing of *C. quitensis* cushions are difficult to establish, it is important that the implications of a relationship between vigour and age be considered in any study of plant distribution within a community or of vegetative and reproductive performance.

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