Population variation at the edges of the altitudinal range of two Kenyan montane plant species

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SUMMARY

The variation of populations of *Lysimachia volkensii*, *Hypericum keniense*, and *Cineraria grandiflora* has been studied along altitudinal transects. If a proposed model is correct, the central populations in an environmental gradient should have the highest variance, decreasing towards the outer ones, and marginal ones could be very uniform or very variable. *Hypericum keniense* and to some extent *Lysimachia volkensii* agree with this model and it is suggested that *Cineraria grandiflora* may not do so because it is an ecotone species. A model is proposed which would account for probabilistic rather than deterministic development of variance of ecotonal populations, but its agreement with observations must be regarded as doubtful at present.

RÉSUMÉ

L'auteur a étudié les variations de populations de *Lysimachia volkensii*, de *Hypericum keniense* et de *Cineraria grandiflora* sur des coupes altitudinales. Si le modèle proposé est correct, les populations du centre devraient être les plus variables, sur une pente avoisinante, et devenant plus uniformes vers l'extérieur, et les périphériques pourraient être, soit très uniformes, soit très variables. Le *Hypericum keniense* et, en une certaine mesure le *Lysimachia volkensii* sont conformes à ce modèle. Il est suggéré que le *Cineraria grandiflora* n'est pas conforme parce qu'il s'agit d'une espèce écotone. Un modèle est proposé qui tiendrait compte du développement probable plutôt que du développement déterminant de la variation des populations écotones, mais les concordances des observations faites jusqu'à présent ne peuvent pour le moment être prises en considération qu'avec un certain doute.

In a previous paper (Agnew, 1968) an attempt was made to examine the variation in phenotypic (and thus, it was hoped, genotypic) variation of populations throughout the range of a species. For this purpose the species *Lysimachia volkensii* Engl. was chosen because it had a distribution which was conveniently circumscribed in the region of the Ngong Hills, Kenya, so that an area of possibly 15 × 5 km from 5-8000 ft altitude enclosed all local populations. This convenient plant has other useful characteristics. It is a herb, co-dominant in the stony grassland communities in which it is found, and it is a perennial but apparently without vegetative reproduction, even by layering from the prostrate lower stems, although this is shown by the closely related *Lysimachia ruhmerana* Vatke. However, the difficulty of measuring the rather plastic features proved to be a disadvantage and the pattern of variance had many anomalies, so that it was difficult to fit any model to it. The model proposed was
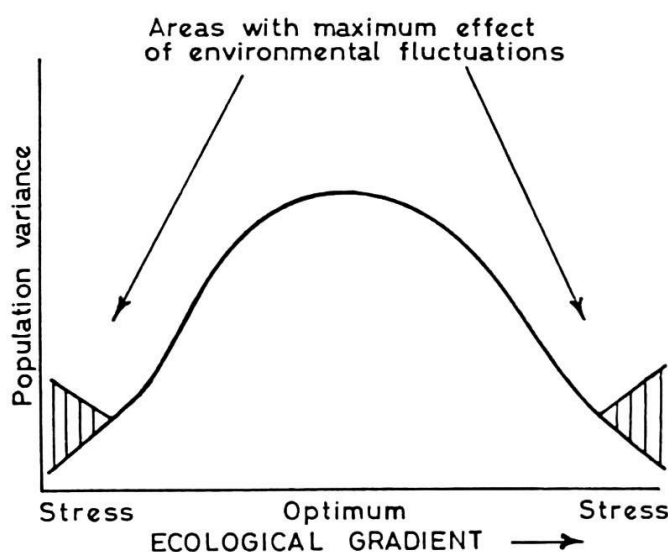
Fig. 1. — A proposed model of changes in population variance along an environmental gradient representing the ecological range of a species. Hatched areas at the upper and lower limits of the species range represent areas where variance may be very low (species retreating) or high (species advancing).

that the centre of the distributional area should be more nearly optimal ecologically than the margin, so that selection should be lower and genotypic variance greater. At the margin of the distribution selection is greater and thus the variance is lower. However, at the margins of the observed range there were extremely high as well as low variances and these can be explained by acknowledging environmental fluctuations. Thus amelioration of the environment would allow marginal invasion of new areas which would be temporarily released from environmental stress and thus have higher genotypic variance. This model is generalised in Figure 1.

Because the analysis of *Lysimachia volkensii* did not disprove or confirm the model, other species were examined, for Kenya has a great altitudinal range of undisturbed habitats and species can be found which are available in natural populations both at the upper and the lower margins of their range. The following is an account of investigations into two of these species, the tree *Hypericum keniense* Schweinf. and the herb *Cineraria grandiflora* Vatke, along a transect through the forest on the western slope of Mt Kenya.

Material and methods

Populations were analysed in the field, all measurements being made on fresh material. The control procedure of cultivation under uniform conditions was not followed. In the investigation of *Lysimachia volkensii*, populations were brought into cultivation and it was shown that the relative variance of characters from these populations changed not at all after cultivation. Naturally the expression of characters changed, most plants becoming larger-fruited, for instance, under cultivation, but since the interest of this investigation is in the variance of the character, not its mean, this does not matter. Whether this would have been the case with the *Hypericum* or the *Cineraria* remains open to doubt, but there seems no special reason to believe either of them more plastic in any respect than the *Lysimachia;* in fact the characters measured included more flower and fruit expressions which appeared much less variable than in the latter species. In any case the long life history of the *Hypericum* precluded cultivation in the rather short time available although other control methods were possible such as cross grafting.
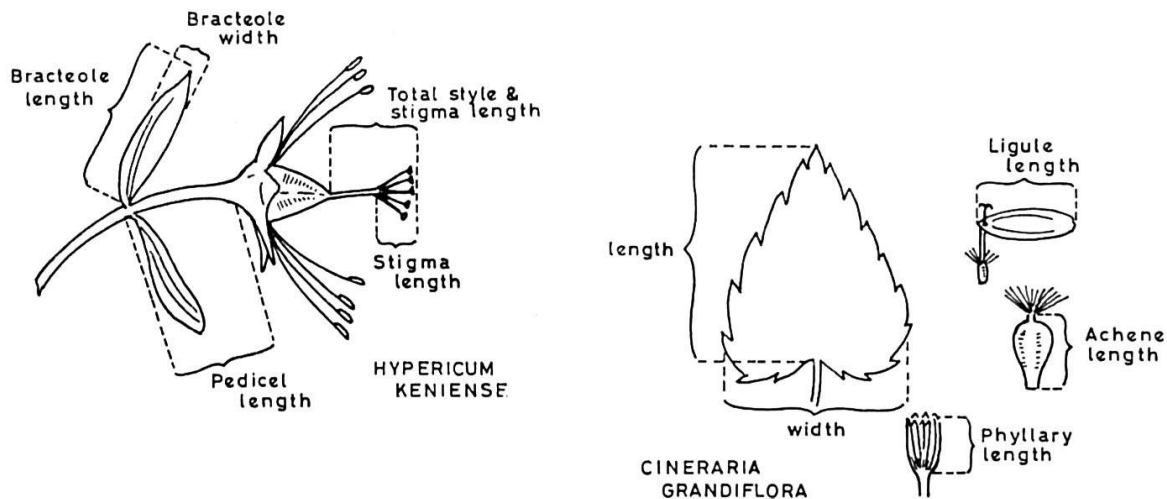
Fig. 2. — Diagrams to show measurements made on *Cineraria grandiflora* (right) and *Hypericum keniense* (left) populations.

A population was taken as a group of plants more than 200 m from another analysed population. This is always a weak definition in such situations where the extent of genetic interchange between populations is unknown, but here I was attempting to sample populations along an altitudinal gradient and most were, of necessity, more than 500 m apart.

Measurements were made of numerous characters from a series of individuals before a choice was made of those to appear in the final analysis. Naturally those characters most easily measured and with the least within-individual variation (phenotypic plasticity) and with the greatest value in distinguishing individuals were used. Measurements were made as is diagrammatically represented in Figure 2 and the mean expression of these characters over the altitudinal range of both species can be seen from Figures 3 and 4. As an example *Hypericum keniense* had little individual variation in its leaves and it was impossible to distinguish individuals unless over 10 leaves were measured from each plant, and so this character was abandoned. As expected, floral and fruit characters were the best, despite normally high correlation between the size measures of the parts of a flower. In any case this high correlation is removed from the final expression of variance by the analytical method of presenting the *generalised variance* as a figure representing the overall variance of each population. This method was suggested by Wilks (1932) who showed that the generalised variance of a population is given by the determinant of the variance/covariance matrix of character measurements.

The technique yields figures which rank in the same way as the variances of individual character measurements in the main, that is they are intuitively sensible, as well as providing a summary of variation which is particularly relevant to this investigation.

Now the variance of a character is frequently correlated with its mean so that in this analysis the greatest generalised variance would naturally be expected from that population with the largest character means. Where means follow altitude as for instance "pedicel length" and "total style and stigma length" do in *Hypericum keniense* (Figure 3) or as "phyllary length" does in the *Cineraria* (Figure 4) this will naturally impose constraints on the pattern of generalised variances found. For this reason all measurements have been transformed logarithmically, and the generalised variances computed from these transformed values. Generalised variances are given in Figures 5, 6 and 7 plotted against population altitude.

Hypericum keniense Schweinf.

This tree is one of the endemic woody East African Hypericums which appear to have evolved along the mountain masses. The tree is single-stemmed without suckers or apparent vegetative reproduction and grows to 15 m tall in the uppermost woodland zone of the Aberdares, Mt Elgon and especially the western side of Mt Kenya. Here

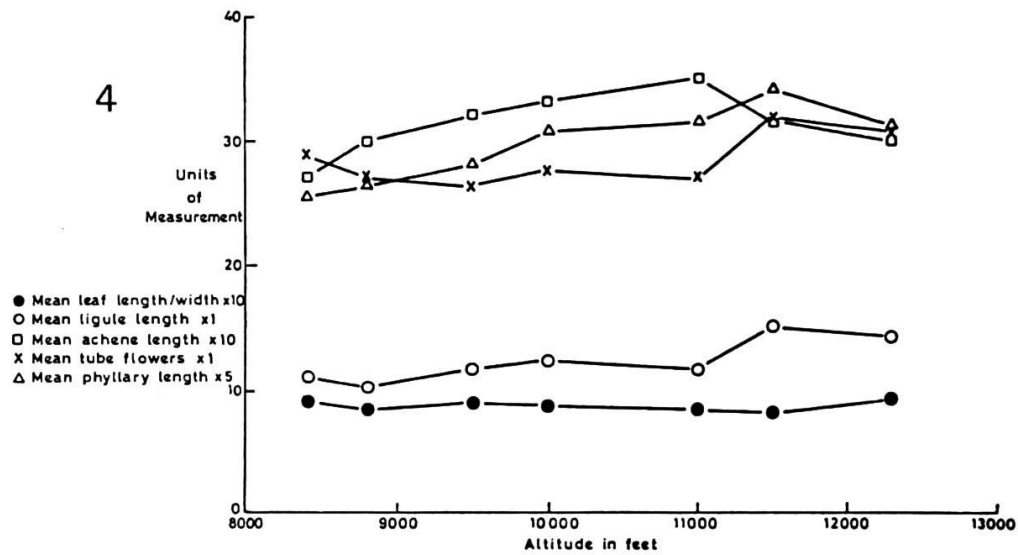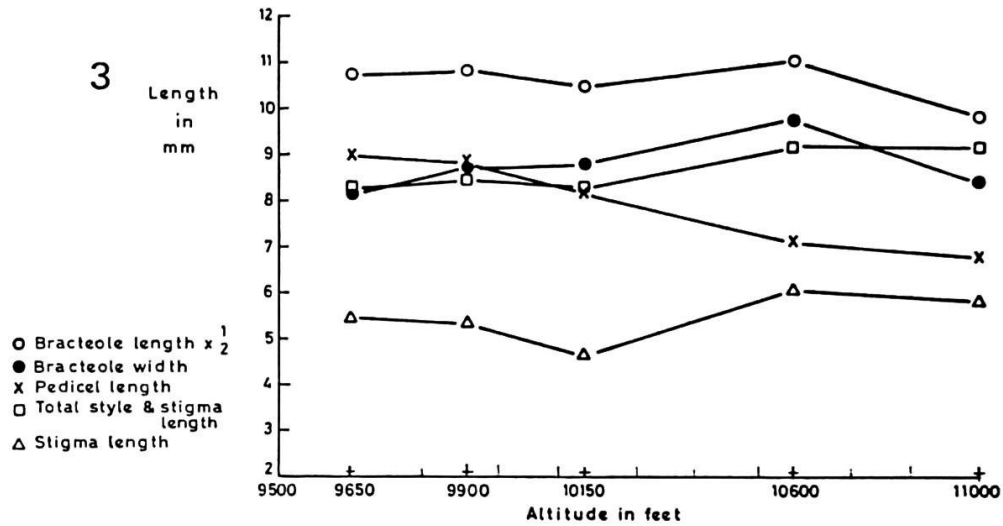Fig. 3. — Means of 5 characters of *Hypericum keniense* populations along its altitudinal range by the Naro Moru Track, Mt Kenya.

Fig. 4. — Means of 5 characters of *Cineraria grandiflora* populations along its altitudinal range by the Naro Moru Track, Mt Kenya.

Fig. 5. — Generalised variances of 5 populations of *Hypericum keniense* at increasing altitudes along the Naro Moru Track, Mt Kenya.

it is the dominant tree in the mist woodland on the upper reaches of the track from Naro Moru up to the moorlands; its altitudinal range is from 8500 ft to 11 000 ft (2591-3353 m), and its branches are often abundantly covered with *Usnea* spp.

In August, 1965, almost all trees in this strip of woodland flowered and it was possible to obtain representative twigs and flowers relatively easily.

Altitude in feet (in metres)	9650 (2941)	9900 (3018)	10.150 (3094)	10.600 (3231)	11.000 (3353)
Number	30	38	45	21	18

Table 1. — Numbers of individuals of *Hypericum keniense* found with flowers at different altitudes along the Naro Moru Track, Mt Kenya, August 1965.

Table 1 gives the numbers of individuals gathered at different altitudes and illustrates the increased performance of this species at the middle of its altitudinal range. Although repeated visits were made to the same area in the following three years we never found such abundant flowering again, and thus this analysis could not be repeated.

In *Hypericum keniense* flower characters show extremely low within-individual variance, and bracteole length and width, pedicel length, and style and stigma length were all measured (Figure 2). The means of these characters are plotted in Figure 3, and their generalised variances in Figure 5.

The problem of the significance of differences between generalised variances has not been overcome, but ratios of the individual character variances can be tested and these are presented in a summation in Table 2. There are more significant differences between the populations with the highest generalised variance (the central ones) and those at the margins of the range.

		Population altitude (ft)			
Total variance ratios between populations at these altitudes		9900	10.150	10.600	11.000
	9650	0	3	2	1
		9900	0	0	1
			10.150	1	1
				10.600	0

Table 2. — The number of significant (p < 5 %) variance ratios found for 5 populations of *Hypericum keniense* using variances of 5 characters.

The distribution of the generalised variances confirms the model given in Figure 1 but the marginal populations do not show the extremely high or low variances postulated. These 5 populations are not the only ones along this altitudinal transect. There was one at 11 000 ft (3353 m) and another at 8300 ft (2530 m) both of which consisted of very few individuals, which were not flowering at the time of the survey, or on subsequent visits. Even with these the transect may be a little short to allow the marginal populations to display great fluctuations, especially since the large showy flowers of this long-lived species may be pollinated by wide-ranging insects.

Cineraria grandiflora Vatke

Cineraria is closely related to *Senecio* but has flattened achenes, and this species is found along pathsides and forest edges from 5300 ft to 13 000 ft (1600-4300 m) above sea level in Kenya (Hedberg, 1957). It is widespread in Eastern and Southern Africa, and this great range is accompanied by much variation. Thus Hedberg *(op. c.)* sinks 6 former species into *C. grandiflora* after a careful investigation into specific limits.

A number of characters were used: leaf length/width ratio, phyllary length, number of tube florets/head, ray length and achene length, and because of the high within-individual variation, flowering shoots were taken, where possible, from each plant and the mean of five measurements taken as the individual characterisation. Compromises had to be made in this sampling programme particularly in the lowermost populations but it was always possible to measure five leaves and heads. After some analyses of this species from other parts of Kenya which are not reported here, it was decided to repeat the altitudinal transect used for *Hypericum keniense* along the Naro Moru Track on the western side of Mt Kenya, where populations are found along the roadside from 8000 ft (2438 m) to 11 500 ft (3505 m). The road has been in existence for a number of decades and the populations along it should have reached equilibrium. Table 3 gives details of altitudes, numbers of individuals found, and sterility for the seven populations analysed, and again the effect of decreased performance at the edges of the altitudinal range can be seen.

Altitude in feet (in metres)	12.300 (3750)	11.500 (3505)	11.000 (3353)	10.000 (3048)	9500 (2896)	8800 (2682)	8400 (2560)
Number of individuals in each population	12	15	> 100	> 100	> 100	c. 50	8
Number of individuals analysed	12	15	24	26	24	24	7
Percent heads with fertilized achenes	87	81	100	96	98	73	53

Table 3. — Numbers of individuals in each population of *Cineraria grandiflora* and the fertility of the individuals analysed along an altitudinal transect along the Naro Moru track, Mt Kenya, in July 1968.

All these populations grew along the roadside in the forest edge except the two top ones which were above the tree line and were in the shelter of small cliff faces. Means of these populations are given in Figure 4 and the differences between these two topmost populations and the rest can be clearly seen. Since ripe achenes were not always present it was not possible to obtain a variance/covariance matrix for all five characters for all populations unless unacceptably small samples were used for the lowest population. Thus two analyses were performed, using four characters for seven populations (Figure 6) and five characters for six populations (Figure 7). The generalised variances of the two top populations are of quite a different order from those of the lower five populations. Moreover the lower populations show quite different patterns of variation depending on whether four or five characters have been analysed, ant it seems clear that this species does not, on this site, fit the expected model of variation given in Figure 1.
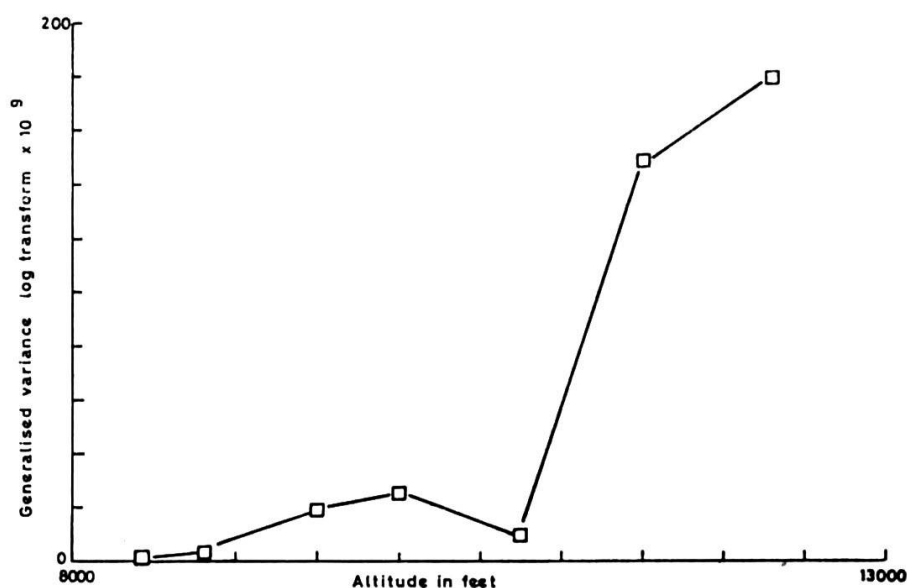
Fig. 6. — Generalised variances of 7 populations of *Cineraria grandiflora* computed from 4 characters' measurements at increasing altitudes along the Naro Moru Track, Mt Kenya.

Fig. 7. — Generalised variances of 6 populations of *Cineraria grandiflora* computed from 5 characters' measurements (with the addition of achene length compared with Figure 6) at different altitudes along the Naro Moru Track, Mt Kenya.

Table 4 gives the matrix of total numbers of significant variance ratios found for all characters except achene length. Again here the picture is very indefinite except for the clear distinction between the topmost two populations and the first forest population (at 11 000 ft) but in any case there is no indication that the slight increase in the generalised variance at 10 000 ft is meaningful.

		Population altitude (ft)					
		11.500	11.000	10.000	9500	8800	8400
Total variance ratios between populations at these altitudes	12.300	0	0	3	1	1	1
	11.500		0	2	1	1	1
	11.000			0	0	1	1
	10.000				1	2	0
	9500					2	1
	8800						1

Table 4. — The number of significant (p < 5%) variance ratios found for 7 populations of *Cineraria grandiflora* using variances of 4 characters.

Discussion

While the initial success in relating the variation of *Hypericum keniense* to the model provided the stimulus for the examination of first the *Lysimachia volkensii* and then *Cineraria grandiflora*, the undoubtedly poor fit of the latter species was very disappointing. However, there is a possible hypothesis to account for the pattern (or lack of it) observed.

The two species which show some sort of fit with the model are *Hypericum keniense* and *Lysimachia volkensii*. Both these species are dominants or codominants of their communities, which themselves form extensive areas of more or less uniform vegetation. The species whose variance bears no apparent relation to the model is found in woodland edges or similar habitats. Could this be significant?

A species may occupy part of any environmental gradient. If this gradient is gentle with respect to spatial distance, then the species will form populations each of which spreads out and adjusts to its immediate selective forces. If the gradient becomes more abrupt, the populations would be brought closer together so that it would be difficult for them to maintain their genotypic distinctions. Now a very abrupt gradient is just what is present in an ecotone, and *Cineraria grandiflora* is an ecotonal species. I suggest a model of this situation as in Figure 8, which shows the steepening of the environmental gradient eventually leading to the merging of the marginal zones of the species range. Here there are both very low and very high genotypic variances as the environment ameliorates to allow population establishment or becomes unfavourable and squeezes out the population. In this zone the variance of a population is determined by the very local environmental trend as it affects the ecotonal species. This trend may be brought about by "background noise" or random fluctuations in the environment, so that this model allows both high and low local variances within a population of a species occupying an ecotone. And as long as the environmental gradient of the ecotone has a greater selective importance than the environmental gradient along which ecotonal populations are sampled then the random fluctuations in these populations may be so great as to mask the trends in population variance along the longer environmental axis.

Whether the population variances of the plant investigated here are explainable in the terms of this model cannot be confirmed until more of the biology of the species is known. What environmental parameters are of greatest importance in determining the distribution of *Cineraria grandiflora*? Is the environmental gradient between woodland and grassland (the forest edge ecotone) that the species occupies of greater

Series of increasing gradients of environmental change
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(1) A continuously varying environment   (2) Intermediate   (3) Ecotone

Hatched area represents populations with unstable variances

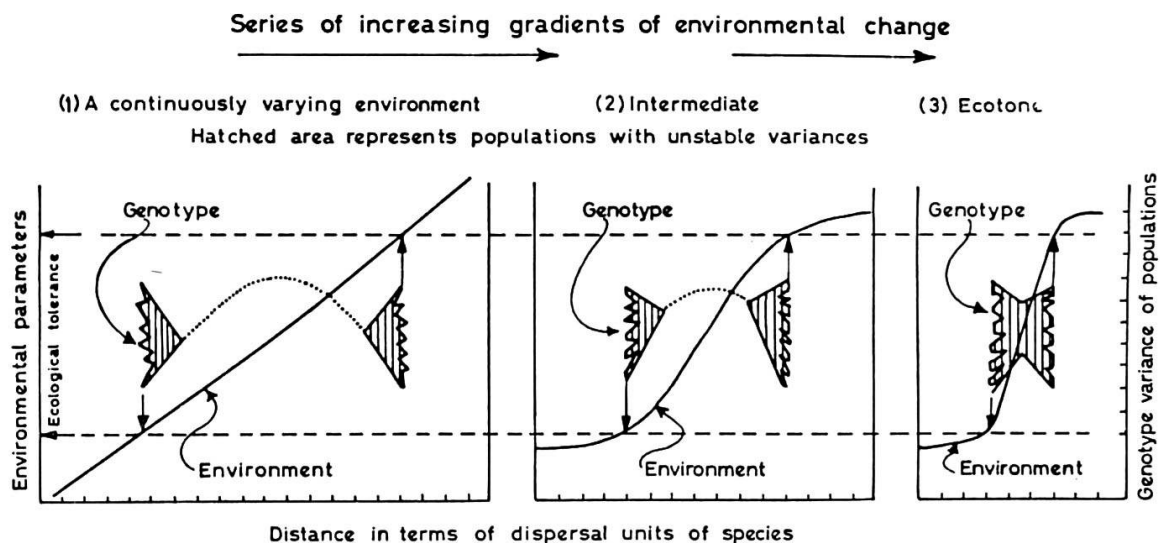Distance in terms of dispersal units of species

Fig. 8. — An attempt to model the variance condition of populations when the environmental range of the species becomes condensed from a gradual continuous environmental gradient (1) to a sharply disjunct ecological situation as in (3). The two variable "wings" of the species at the edge of its ecological range are represented by hatched areas, while the main series of more stable populations is represented by a dotted line. The line arrowed as "environment" is a diagrammatic profile of environmental change along the distance (x axis) which must be defined in terms of the dispersal potential of the species.

importance than the altitudinal environmental gradient? The lack of consistent fruit-setting in the lowest-altitude populations of the *Cineraria* seems to indicate that at least at this point the altitudinal gradient was of greater importance than the ecotonal gradient. It is difficult to see how some of these questions can be answered.

Acknowledgements

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LITERATURE CITED

Agnew, A. D. Q. (1968) Variation and selection in an isolated series of populations of Lysimachia volkensii Engl. *Evolution* 22: 228-236.

Hedberg, O. (1957) Afroalpine vascular plants. *Symb. Bot. Upsal.* 15.

Wilks, S. S. (1932) Certain generalisations in the analysis of variance. *Biometrika* 24: 471-495.