A Study of the Scottish Birch
with special reference to the
genetics and ecology of the
species.

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ProQuest Number: 10644268

ProQuest 10644268

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Introduction.

Any intensive study of one group of plants tends
to demonstrate that the degree of variability within
the group is as great as and more complex than that
between groups.   This variability, obscure in nature,
has a realness, but because of its different degree
it is difficult of description and comprehension.
Where discrete differences are present it is easy to
describe the attributes by which the types are
distinguished, and this ease of description also
tends to lead to ease of comprehension.

In wide ranging species, segregation of groups of
individuals occurs and the groups possess not only
a separate identity from, but also similarities to, the
other groups.   Such subdivisions have always troubled
the taxonomists from the earliest time, and, when a theory
of evolution based on the accumulation of small
differences was put forward (Darwin, 1859), the
importance of such small groups became very real.

Not until recently, has an enquiry into the mechanisms of the formation of these sub-units been begun, and foremost among the methods used has been that of experimental taxonomy.   The principles of this study were known to Kerner (1891) and Bonnier (1920) but it was not until Turesson (1922 et seq.) published his methods of approach that the subject really became established.

Since thenthenumber of workers here, and elsewhere, has expanded and developed the original conceptions of Turesson.

Experimental taxonomy is a branch of biology dependant on all other aspects of biology, in particular genetics and ecology; hence the alternative term genecology.   Genecology is primarily a synthetic subject and,like all synthetic sciences, subject to theorising.   However this does not detract from the study of the subject.

Since the days of Darwin selection has been cited as the causative agent of evolution, but wholly dependant on the presence of variation.   Without variation there can be no selection.   If variation

does not exist the ultimate fate of the group will
be extinction.

The agents which are selective have been determined,
anthropomorphically rather than experimentally.
This is most unfortunate, because in the minds of
purists a teleological argument is always false.
I do not think that it is permissible to discount
an argument because it is based on mental conception
rather than on a factual basis.

It may seem naive to mention that the main
selective agent is the habitat but it is necessary
to introduce this to explain the philosophical basis
of experimental taxonomy.   Experimental taxonomy
in the narrowest sense has been confined to studies
of plants because of their being easier experimental
material than animals, but the work of Dice (1934-5) on
Peromyscus is as valuable as any of the illustrations
from botanical material.   However, the zoologists
have done admirable work on the geographical
differentiation of species, and in the geographical
replacement of races, particularly the ornithologists,
Rensch, Kleinschmidt, and conchologists, Diver, etc.
With the larger, more mobile animals divergences
likely to be caused by ecological, as opposed to

topographical factors will be negligible. Again with the more highly organised animals the factor of psychological preference must be considered. Where selection pressure is very great, ecological differentiation (or ecotypic differentiation) may begin to operate.

Plants are sedentary, except the phytoplankton, and are probably differentiated by ecological factors, rather than topographical. Selection will always be on a population and never on an individual. Hence the inadvisability of studying rare plants or common plants which occur singly, or in very small groups (say less than 20 individuals).

The experimental study of variation was begun by Kerner (1891) and Bonnier (1920) who studied the reaction of plants to altitudinal conditions different from those where they had been found. Turesson (1922) studied extensively the reaction of plants from different localities when grown under the uniform conditions of the experimental garden. The results of this led Turesson to propose a theoretical conception of the species and his system is now adopted by most workers.

He proposed that the terms _ecotype_, _ecospecies_, and _coenospecies_, should be used to denote those subdivisions of a breeding unit (which may or may not be identical with a taxonomic species) having the following characteristics.

Ecotype:- Groups of individuals capable of freely exchanging genes with other similar groups but differentiated, physiologically, or morphologically (or both) into ecologically distinct categories.

Ecospecies:- Groups of individuals capable of limited exchange of genes, with other similar groups.

Coenospecies:- Groups of individuals incapable of exchanging genes, with other similar groups.

This is a useful classification, and has been modified to accomodate different types, e.g., replacing ecotype with topotype, Gregor (1938,1939).

Danser (1929) proposed a system, not universally accepted, where the criterion of affinity was the capacity of crossing of individuals. This does not take into consideration the interchange of genes, and only accounts for the degree of affinity of the individuals and not the situation as found in nature.

To have differentiation of any sort, there must

be a polymorphic assemblage of individuals. Where

a species is uniform in its morphology, immediately

obvious, or its physiology, obvious because of its

rarity (cf. the phrase 'exacting in its requirements',

which is often used) then divergence does not occur.

Differences may or may not be selected by the

environment, and in the latter case no correlation

between environment and plant will be able to be

established unless by chance.

To sum up we may say, differentiation is present

and the aim is to explain the selection of parts of

the heterogeneous mass and the dynamics of the variants.

The genus _Betula_, as are all tree genera, is very

highly polymorphic and has been of considerable

taxonomic importance. It is considered to be 'difficult'

but has been surveyed by a number of authors.

Within the genus the species _Betula alba_. L. has been

examined critically and no two authors agree with each

other on the status of the species.

Helms and Jorgenson (1925) showed that within the

species _B. alba_. L. there exist two chromosome races

corresponding to _B. verrucosa_. Erh. and _B. pubescens_. Erh.

The site which was examined also contained a plant the

chromosome number of which was intermediate between the others. The immediate conclusion was that the plant had arisen through hybridisation. Johnsson (1944) (1946) and Löve (1944b) found other specimens with the intermediate number but the former author, who has studied all natural Scandinavian plants which are known to possess this intermediate (triploid) number, came to the conclusion that it is not a hybrid but has arisen by a different process (see p. 44)

It is interesting to compare the conclusions reached by the cytogeneticist with those of the taxonomists. Morgenthaler (1915) and Gunnarson (1925) thought that all variation could be ascribed to hybridisation. Gunnarson in particular maintains that hybridisation is widespread and to the geneticist some of his proposed hybrids, erected on herbarium material only, are to say the least ill-founded.

In Betula the prime factor for studying variation is present allowing the further study of the problem of differentiation and divergence. The question arises to what other factors is this variation related ?

Since there are two distinct genetic types (the diploid B. verrucosa and the tetraploid B. pubescens), there is the possibility that the variation in the

two species, if species they be, may follow the same course, acted on by the same selective factor.

The work presented in the following pages represents the study of the variation, and the distribution of that variation in the Birch of the Central Scottish Highlands.

I wish to thank the Forestry Commission, members of the staff of the Scottish Society for Research in Plant Breeding, and members of the staff of the Botany Department of Glasgow University for their assistance.

The Sampling Area.

The material used in this study was obtained from natural populations. The question which can be asked immediately is what criteria determine whether or not the population is natural ? This decision is completely subjective but because of the infrequent planting of birch by man it can be assumed that any extensive area of birch is the result of natural seeding. Not only is this what normally happens but where planting has occurred it is natural birch which is used. The seedlings which are used in planting, mostly for amenity purposes, are usually collected in the field. Thus there has been little dilution of the native stock of genes by genes introduced in stocks obtained from outside Britain.

The sampling area is a linear belt extending across the Central Highlands of Scotland from the Moray Firth, across the Cairngorms to the Atlantic Ocean. Some idea of the climatic conditions occurring in the area can be obtained from table II. The altitudinal range of the stations is that of Betula itself, viz. 0' - 2,100' in the area studied. The individual stations vary in their altitudinal range (cf. Station I and Station 12). If altitudinal distribution can

Fig. 1.

The dotted line shows the route along which
sample stations were chosen.   The open circles
the B. nana sites and the solid dots isolated samples
of B. alba L.

replace topographical distribution in its effect

(Watson 1948) in that it alters climate in the same

way, then within the stations of wide altitudinal range,

variation of similar type to topographical variation

should be found.

Ashby (1950) showed that variation in day length

affected morphological attributes of plants, but since

the stations occur at the same latitude, and have the

sa me day length this factor need not be considered.

Ecological niches will be as prevalent and as

varied on any one site as across the main belt but if

the variation is independant of ecological factors

the wide ranging sampling zone will bring out such

differences as are present.

Stations were sampled at 5 mile intervals

along the belt shown on the map (Fig. 1.).   It was

not possible to sample at every 5 mile interval

but this arbitary rule was followed as far as conditions

permitted.   Chance played a large part in the selection

of stations and one particular station (4) is not truly

representative of the area.   Table I shows that there

is a marked uniformity of site as can be seen by the

associated flora.   This method of describing stations

is modified from Braun-Blanquet (1931).

The co-habitants will reflect the nature of the habitat as effectively as any other measure. To the competent ecologist they are probably better indicators of habitat than any physical or chemical measurement.

BETULA

Calluna vulgaris
{ Vaccinium myrtillis
  V. vitis idea. (Eastern)
Molinia caerulaea.

Eriophorum spp (St.4)

Potentilla tormentilla (always present except St. 1.)

Pteridium aquilinum
{ Oxalis acetosella
  Holcus lanatus
  Agrostis alba coll. sp.
  C. vulgaris
  Scabiosa succissa
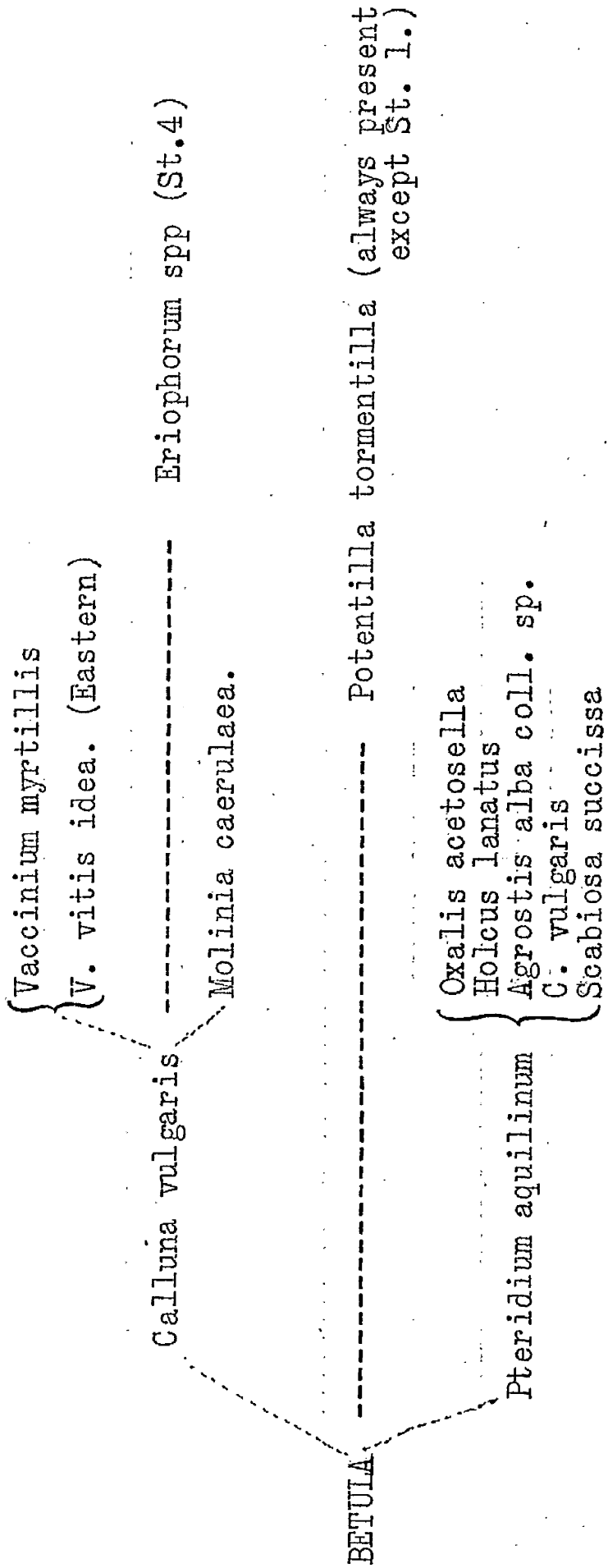
Fig. 2.

Schematic representation of the ecological structure of a birch wood. There are two major divisions within which there is a number of sub-divisions.

TABLE I.

Station	Dominant	Peculiar
1.	No real dominant	Gentiana campestris
2.	Holcus & Pteridium	Comarum palustre) Hydrocotyle vulgaris)
3.	Calluna	Galium verum
4.	Eriophorum	Orchis maculata
5.	Holcus, Pteridium	Solidago virgaurea
6.	Calluna	Juncus squarrosus
7.	Pteridium	Filipendula ulmaria
8.	Pteridium	Cnicus arvensis
9.	Pteridium	Lathyrus montanus
10.	Pteridium	Gnaphalium sylvaticum
11.	Pteridium	Juncus lamprocarpus
12.	Pteridium	
14.	Pteridium	Juncus supinus
15.	Pteridium	
16.	Pteridium	Epilobium hirsutum
17.	Agrostis alba Pteridium	Equisetum sylvaticum
18.	Pteridium & Calluna	Drosera rotundifolia
19.	Pteridium	Hypericum pulchrum
20.	Pteridium	
21.	Pteridium	Solidago virgaurea
22.	Pteridium	Scrophularia nodosa
23.	Pteridium & Calluna	Fragraria vesca
24.	Pteridium & Calluna	
25.	Pteridium	Senecio jacobea

Table I lists the stations, their dominants and the plants frequent within the station but not generally common throughout the sampling area. It can be seen that the ground flora of the birch wood is of three main types

        a) Pteridium dominant

        b) Calluna dominant

        c) Pteridium - Calluna codominant.

In only one case (station 4) this does not occur. Station 4 is rather anomalous because it is situated on a raised bog (see Photo) and the woods of the surrounding district are not of this type. Other stations are more or less similar edaphically, being either situated on glacial drift (not boulder clay), which has been podsolized or on stabilised scree (small scree derived from argillaceous rocks).

No pH's or other characteristics of soil were determined since the variation within a station could be as large as between stations. There will certainly be measurable differences of ecological factors between the stations but the difficulty of assessing the data, so gathered, does not warrant the use of such data since the main aim of the thesis is the degree of genetic differences between populations and not their ecological differences.

Fig. 2 represents what may be considered as/an idealised system for the ecological relations of the birch, particularly the phytosocial relations.   The birch woods can be divided into two:

a) with <u>Pteridium aquilinum</u> as the field layer dominant.

b) with <u>Calluna vulgaris</u> as the field layer dominant.

An intermediate stage, if it is a stage, consists of a field layer with the above species co-dominant.   This last type does not usually present a very uniform facies to the observer and its instability may be due to its not having reached equilibrium.

Certain characteristic plants are associated with a) and b) but only one plant, <u>Potentilla tormentilla</u>, has been found in all stations (except Station I, which is a very unstable, littoral population, since it is exposed to severe flooding).   The plants lists after the major subdivisions in fig.   are those found always with the dominant.   The dotted line to <u>Eriophorum</u> denotes affinity with the <u>Calluna</u> type and not a co-habitation.

Using fig. 2   in conjunction with table I gives a good general idea of the structure of the birch wood.

Plate I.

Some representative birch woods of the sampling area.

    1.& 2. show the hillside type of population.

      3. shows the raised bog population (4).

      4. is an aerial view of St.14 and shows the

        density of the individuals.

Plate I shows photographs which illustrate typical birch habitats.

Meteorological aata, obtained from the Air Ministry are presented in Table II for areas representing the Eastern and Western ends of the sampling area.

Table. II.

Monthly Average	Gordon Castle (E)			Fort William (W)		
	Rain	Temp.	Hrs.Sun	Rain	Temp	Hrs.Si
Jan.	2.02	38.9	43	8.98	39.2	14
Feb.	1.92	39.3	71	6.94	39.5	49
Mar.	2.32	40.5	112	6.20	40.7	87
Apr.	1.75	43.9	136	4.16	44.3	127
May	2.12	49.5	171	3.65	50.5	170
June	2.00	54.1	174	3.28	55.1	170
July	3.26	57. 5	149	4.53	57.4	121
Aug.	3.17	56.7	132	5.76	57.0	110
Sept.	2.50	53.0	115	5.91	53.3	95
Oct.	3.16	47.6	94	6.57	47.9	63
Nov.	2.88	41.8	54	7.60	41.7	25
Dec.	2.69	39.1	35	9.42	39.6	7
TOTAL	29.77		1305	73.00		1038

The only obvious differences between the two localitie is the distribution and amount of rainfall. One can infer

that the amount of sunshine is correlated with the above because the lowest number of hours per day occurs in the months with highest average rainfall, i.e. hours of sunshine are inversely proportional to the cloud cover.

In the East rainfall is relatively heavier in the summer months while in the West the highest monthly average occurs during Winter. However, the absolute summer rainfall is much less in the East than in the West.

Mean monthly temperatures differ but little and the main difference is in the amount of precipitation.

Other data show that this change in rainfall from East to West is progressive with local variation where some peculiar topographic influence is exerting a specific effect. For all practical purposes the gradient may be considered as being continuous from East to West.

Sampling Methods.

Populations of birch are seldom continuous, each forming an areal unit possessing some degree of distinctness. Isolated individuals may occur but rather infrequently, and, where they do, it is unlikely that they are important as genetic bridges between populations. Few plants in Britain are absolutely continuous over their whole range. Others again occur as individuals or

small groups of individuals (e.g. Sorbus) and in this case the problem of gene flow is very different.

Because of this property of the species each population can be considered as a unit. The sampling methods which are used have been developed with this property in mind.

Leaves, fruits, and bract scales were collected during the first year of study (1949) and in the second year male catkins were collected in addition to the material collected in 1949.

During 1949, observations of habit, and other characters not capable of analysis in the laboratory were studied. However, habit is such a variable character that it is difficult to assess with any degree of objectivity. Observation showed that all types of habits occur in both species, therefore, no, or little advantage, is gained by considering this character.

In 1949 one leaf, chosen from any part of the tree, was taken from each tree of the sample. Jentys-Szaferowa (1937) had carried out a preliminary biometrical analysis of the collective species B. alba. L but this paper was not brought to my notice till later. In this paper (1937) she discusses the

types of leaves which are found growing on one tree
and the amount of variability within these different
groups.   There are four types commonly encountered:

1.   Long shoot leaves,

2.   Epicormic leaves,

3.   Catkinate spur shoot leaves,

4.   Vegetative spur shoot leaves.

The leaves of group 1 & 2 occur singly while the
others are borne in small clusters of 2 & 3.   The
degree of variability is least among the leaves borne
of the vegetative spur shoots and greatest among the long
shoot leaves.   In 1950 only leaves of groups 3 & 4 were
collected.

The indiscriminate type of sampling which was used in
1949 was found, fortunately to have included very few
leaves which could be considered as having been taken
from long, or epicormic shoots. (See fig.   for a
comparison of the mean values of the 1949 and 1950
samples.)

The number of leaves in the sample from each station
varied but was always greater than 20 (except the sample
from Station I, 1949).   The size of the sample is an
indication of the size of the station, but the principle

of the method was the same for each station. A random route was selected and trees along this route were sampled. Where the station was at the same height above sea level over its whole extent the line of sampling was indiscriminately chosen. If the station covered ground where the height above sea level was changing, the sample was collected so that trees from all altitudes were represented in the sample. The usual procedure in the latter case was to collect fairly generally while ascending, then making the main part of the collection descending.

Trees bearing catkins are not as common as one would expect, especially in dense woods. Where low light intensities prevail fruiting trees are confined to the periphery of the wood, though the possibility that the other trees are capable of bearing catkins in their higher branches must not be excluded. A sample of catkins is not therefore random, because it is confined to those trees bearing catkins, bearing catkins because of their being exposed to more favourable habitat conditions. In very large populations the sample of catkins will be representative of the genotypes present in the population, but in small populations chance will play a large part in

An example of an impression (natural size) obtained
by using the method described in the text (opp).

determining what trees (hence genotypes) occupy the situations favourable for reproduction.

The quantity of catkins, that being a measure of reproductive capacity, varies from year to year, but not necessarily in the same way for each population. Table III gives the number of catkins collected in the two years and St, 17 is noticeably different from all of the others.

The leaves were not retained as such, but as impressions, since impressions are easier to handle, and less likely to be lost.   The method of making the impression is:-

      1.   Place the leaves on a hard surface, adaxial surface uppermost.

      2.   Cover with a sheet of carbon paper, copying sirface towardsone.

      3.   Place a piece of paper over the whole and rub over the position of the leaves with a pencil (the type used by joiners is excellent).

The reproduction obtained from the carbon image (see photo.) is good enough to measure such attributes as shape, size, venation, and in very

favourable cases wartiness and hairiness. Using this method it is possible to store large numbers of 'leaves' conveniently both during and after field work.

The catkins were kept separate, in seed envelopes till arrival at the laboratory, and then an image of a bract and a fruit from the middle region of the catkin was obtained using a photographic enlarger. All measurements were made on this image.

In 1950 a collection of male catkins was made in order to try to obtain some data concerning meiosis. Examination of the male catkins in 1949 showed that the pollen had been formed at the time of collecting but in 1950 meiosis was just taking place. This was surprising because the 1950 collection was taken at the same time as the 1949 the actual dates being:

     1949   August 15th - 27th

     1950   August 15th - 20th.

To overcome the difficulty of treating cytological material in the field, fixatives, in which the material could remain without injury were chosen. The two types of fixative used were Muntzing's modification

of Navashin's fluid and Allen's P.F.A. 3.

The male catkins were immersed in the fixative as soon as possible after collecting. They remained in the fixative till the completion of the trip and were treated in the normal fashion, with a considerably longer period of washing, on return to the laboratory. The long time of immersion in the fixative did not seem to have any adverse effect on the cutting qualities of the material, but the fixation image was not perfect, the chromosomes showing that condition known as 'stickiness'. This is probably caused by the fixative's not penetrating with sufficient rapidity.

The Determination and Distribution of the Chromosome

Races.

The only completely satisfactory way to establish the distribution of the chromosome races is to study the plants in their actual localities, getting the root tips from the field.   This is possible with the smaller herbaceous plants (where also it is possible to transport the plants to the experimental garden), but with the larger woody angiosperms several difficulties present themselves,

viz.   a.   It is difficult to ascertain the organic connection of the root selected with the tree selected.

b.   In the field mycorhiza is universally present.

c.   It is not possible to transport the plants to the experimental garden for further studies.

The only alternative which offers itself in such circumstances is to progeny test a certain number of selected trees and this test will establish the chromosome number of the parent.

For meiotic studies male catkins were collected and

fixed in the field, but this is hardly the best way of dealing with the small chromosomes of birch which are difficult to handle by normal techniques. Where successful, meiotic preparations are more revealing than the straight determination of the chromosome number. Preliminary studies of the chromosome number are important to be able to assess the full implications of the meiotic figures.

Fruits of birch were collected each lot being kept separate. Ten fruits from each tree were allowed to germinate on 1% plain agar. As soon as the radicle was prominent the whole seedling was fixed in Muntzing's Fluid for 24 hours.

It was found that the rate of germination could be speeded up if the fruits were subjected to cold treatment. Joseph (1929), working on American species of Betula, found that stratifying the seed enhanced the number of seedlings obtained when germinated at normal temperatures. This technique does not induce germination, merely speeding it up.

During the first year of study this procedure
was employed, but in the following year rather than
adopt this time consuming method, it was preferred
to germinate the seed at a higher temperature.
This is just as efficient, since all seeds containing
embryos, which are going to germinate, will have
germinated by 7 days.

The seeds were germinated in a mycological
incubator set at 24°C, and thus were kept in the dark.
Sarvas (1950) showed that exposure to light increases
the rate of germination, but that there is no difference
in the final numbers of seedlings obtained from treated
and untreated seed.

The fruit of Birch is a samara and it is rather
difficult to separate the true seed from the fruit,
so the fruit is used in all instances where the
seed is normally employed cf. the caryopsis of the
Gramineae.

There is no difficulty in getting fruits
containing fertile seeds to produce seedlings, but
what is surprising is the large number of seeds
which do not possess embryos.   Frequently, there
are more seeds with no embryos than with embryos.
Very occasionally both ova are fertilised and two
embryos mature, giving rise to two seedlings on
germination.

This sterility is so frequent that it presents
a problem of the first magnitude.   Is it genetic
or is it determined by external factors ?   McVean
(1952) working on the alder, Alnus glutinosa, is
studying a similar problem from the ecological aspect.
He is not decided whether this condition is caused
by unfavourable climatic conditions, t,

      a.   At the time of pollination.

   or b.   Between pollination and fertilisation.

Alder flowers much earlier than birch and the time
between pollination and fertilisation is more prolonged.
There is therefore a longer period of exposure to
inhospitable climatic conditions.

A solution of the problem as to whether this sterility
is determined by intrinsic or extrinsic factors will
only be forthcoming when controlled crossings are
performed, but the abortion of anthers and other cyto-
logical/evidence (see pp. 32 & 33) tend to make me think
that this character is determined by intrinsic factors,
in the final analysis, genetic.

TABLE . III.

	1949			1950		
St.	Fertile	Sterile	Total	Fertile	Sterile	Total
1.	6	7	13	18	4	22
2.	13	5	18	3	5	8
3.	–	–	–	2	2	4
4.	8	8	16	9	16	25
5.	6	10	16	6	13	19
6.	3	3	6	9	0	9
7.	5	8	13	7	15	22
8.	14	2	16	5	20	25
9.	8	8	16	8	9	17
10.	–	4	4	2	3	5
11.	12	4	16	9	25	34
12.	15	1	16	2	48	50
14.	11	–	11	6	36	42
15.	8	8	16	5	32	37
16.	4	3	7	11	9	20
17.	15	1	16	–	3	3
18.	14	2	16	19	6	25
19.	8	3	11	3	11	14
20.	15	1	16	13	18	31
21.	8	7	15	2	3	5
22.	5	2	7	18	3	21
23.	11	5	16	15	6	21
24.	14	2	16	13	6	19
25.	4	4	8	27	1	28
TOTAL	207	98	305	212	294	506

Table. Ⅲ. gives the total number of catkins collected, those which were sterile and those which were fertile. While the number of fertile catkins has not increased with the larger collection of 1950 the number of catkins bearing sterile seeds has tripled, but this does not seem to be a difference in the ratio of fertile to sterile but an increase in the number of catkins which developed fruits without the stimulus of fertilisation.

Flowering of one tree occurs over a period and it is likely, if climate is the deciding factor of fertile seed production, that some catkins on a tree would show the effects of inclement weather. This does not occur, and observations on the nature of the seeds from a single tree show that all are uniformly good or bad. Generally trees with many catkins are found to possess a large number of good seeds, those trees with few catkins are usually bearing fruits which contain seeds with no embryos.

It appears that the development of fruit is independant of the stimulus of fertilisation. The fruits which do develop in such cases are smaller than normal, in a few instances so small as to be obviously defective but in most instances they are quite normal in regard to their shape.

Another issue which will affect the spread of genes is whether or not birch has mast years as do other forest trees e.g. beech. If a mast year coincides with a year suitable for the establishment of seedlings, the genotypes which survive may not be the same as would have resulted under normal conditions.

(For further discussion on these points see p. 92)

To continue, after this brief parenthetical discussion, the seedlings were fixed in Muntzing's Fluid, washed, dehydrate infiltrated, and embedded in the usual way (see Darlington and La Cour p.123 1947). Sections were cut at 10μ, stained in Methyl Violet 2B (0.1% solution for 10 mins.), differentiated, and mounted in a neutral mounting medium (for further details of cytological technique see Appendix).

To obviate the tedium of section cutting, squash methods were tried but only recently with success. The standard schedules do not seem to be suitable with the material which we are studying. Differentiation is not as good as could be desired but interpretable results can be obtained using Acetic Lacmoid (Darlington and La Cour 1947).

Meiosis was studied in sections cut at 10μ and stained in Methyl violet 2B.

Table IV shows the distribution of the diploid and the tetraploid races.

TABLE IV

Station	1949 2x.	1949 4x.	1950 2x	1950 4x	TOTAL 2x	TOTAL 4x
1.	5	–	13	–	18	–
2.	5	2	3	–	8	2
3.	–	–	1	–	1	0
4.	–	5	–	3	0	8
5.	–	7	2	3	2	10
6.	1	2	4	–	5	2
7.	–	4	–	4	0	8
8.	1	9	–	3	1	12
9.	1	6	1	5	2	11
10.	–	–	–	–	0	0
11.	–	9	1(?)	3	1(?)	12
12.	–	12	–	2	0	14
14.	–	9	–	3	0	12
15.	–	6	–	4	0	10
16.	–	3	–	7	0	10
17.	1	13	–	–	1	13
18.	–	12	–	11	0	23
19.	–	8	–	1	0	9
20.	–	11	–	9	0	20
21.	–	6	–	2	0	8
22.	–	4	–	14	0	18
23.	–	11	–	11	0	22
24.	–	12	–	9	0	21
25.	–	3	–	21	0	24

The number of diploids which has been found is smaller
than one would have expected and on y one station (1) is
composed entirely of the dip oid.   One diploid has been
found west of the watershed though others no doubt occur.
According to the diagnosis afforded by morphological
characters, trees belonging to the diploid race occur
frequently to the west of the watershed.   Only two
stations east of the water hed are composed entirely of
the 𝔞𝔞𝔞𝔞𝔞𝔞 tetraploid, and as has been remarked station 4
is not characteristic of the district.   The other,
Station 7, is so placed that it is in the area of transition.
In this very fluid region there are likely to be
populations of tetraploids, and mixed populations of
tetraploids and diploids with the latter forming the main
body of the population.   There are no cytological
data for Station 10 and the particular interest which
this statio.. holds for us is that the majority of the
trees approach the diploid, as far as morphological character
are concerned, and a small number, those bearing catkins,
are more similar to the tetraploid.   'Because of the
absence of suitable mitotic figures a count of the
chromosome number of this station is not available.

The two cytological races of <u>Valeriana officinalis</u> have been shown by Skalinska (1947) to have ecological preferences. The higher octoploid is the more widespread and can tolerate more adverse conditions than the tetraploid. It seems that the tetraploid birch, which has not been proved to an autopolyploid of <u>B</u>. <u>verrucosa</u> but merely a plant with twice the chromosome number of this species, exhibiting morphological characters which are a continuation of those found in the warty birch, is also more tolerant of extreme conditions. With the valerians it seems that the two races belong to the same speciesbut diverge both ecologically and cytologically, the former probably a concommitant of the latter. Proof that that the tetraploid birch is an amphidiploid has not been obtained but the evidence which Johnson has accumulated seems to indicate that <u>B</u>. <u>pubescens</u> only contains the <u>verrucosa</u> genome twice.

In the birches there are no species with a chromo-number of 14 (i.e. a haploid number of 7) but in the related <u>Carpinus betulus</u> the haploid number is 7.

The lowest haploid number that has been found in the
birches of the north temperate zone is 14, but the
presence of the lower number in related genera, and
other evidence tends to support the hypothesis that
the basic number of the genus is actually 7.   This
argument is without absolute proof since the ancestral
14 chromosome member of the genus has not been found
and may be extinct.   This would mean that the diploids
occurring today are in reality tetraploids which because
of their long existence as plants have become so balanced
that they behave as normal diploids.   A similar
situation is seen where an amphidiploid (which is really
tetraploid in its chromosome complement) remains after
its parental types have become extinct.   This has
been used by Johnsson (1945) to explain the parentage of
B. pubescens which is thought to have had as one of its
parents B. verrucosa and some other 28 chromosome birch
which is now extinct (or so rare that it has not been
discovered).   Manton (1950) uses similar arguments
to explain the polyploid series in the Pteridophytes.

    In order that a successful amphidiploid can be p
produced it is necessary that the contributing genomes
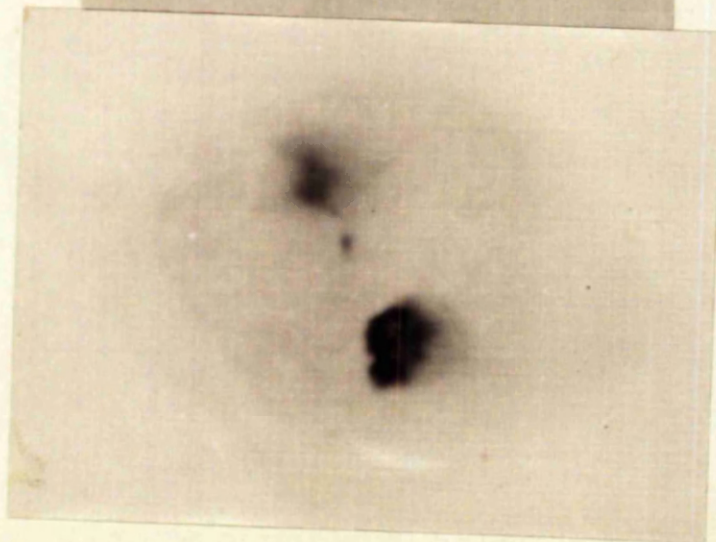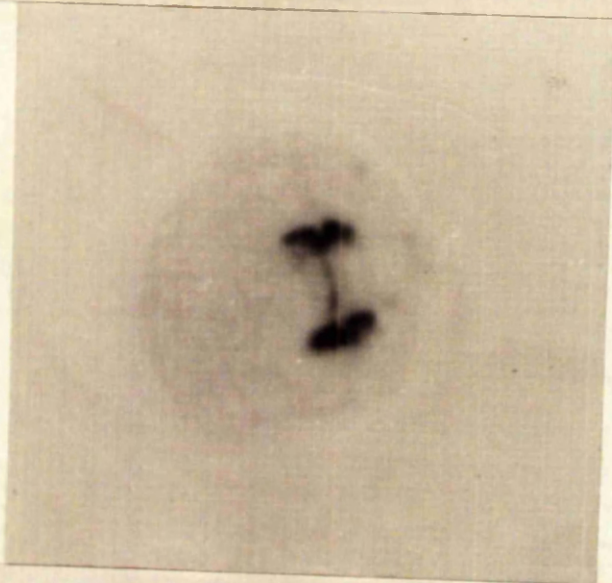
PLATE. II.

a). DIPLOID.

TETRAPLOID. b)
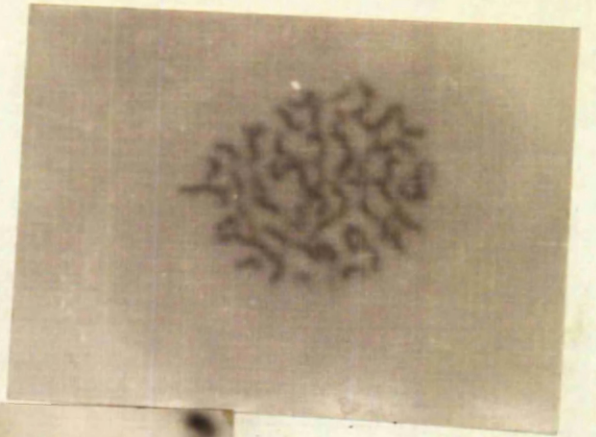
a) RINGS IN THE DIPLOID, SHOWING THAT THERE HAVE BEEN TRANSLOCATIONS.

d) & e). CHROMATIC BRIDGE & FRAGMENTS INDICATING INVERSIONS. (BOTH FROM TETRAPLOIDS).

are not only sufficiently closely related to allow
their acting as a unit but also divergent enough to
prevent the formation of aberrant figures at meiosis.
The exact relationships between the genomes has never
been determined.   There is the possibility that
genetically isolated races of the same species may be
sufficiently divergent in their genetic make up to allow
of the formation of this new type.   I think that
B. pubescens has arisen from the crossing of two
distinct genetic races of the same species rather than
as the result from the hybridisation of two species.

Within the two cytological races, genetic
differentiation, as measured by cytological evidence,
though not by morphological divergence, has been marked.
Meiotic stages (see Plate II) show that there have been
translocations, witness the formation of rings, and
inversions, proof of which is obtained by the presence
of chromatic bridges and the elimination of acentric
fragments, in both the diploid and tetraploid races.
In the diploid, quadrivalents have been seen, but in the
tetraploid no larger association than this seems to
occur, except rings.   The presence of quadrivalents
in the diploid is evidence that the sets of chromosomes

making up the genome of 14 chromosome have not become
sufficiently divergent to allow of absolute separation
of the originally homologous chromosomes. ` This is
evidence that the basis number of the genus is in
reality 7 and not 14 as has been commonly thought. As
well as the more usual aberrations of meiosis there are
present in a large number of instances other anomolous
features not normally connected with the process. There
is frequently the extrusion of large amounts of chromatic
material and always the extrusion of the nucleolus into the
cytoplasm. This latter feature is not rare and occurs
in other groups of the plant kingdom (cf. Olive (1950)).
One feature which may be of some importance is the
abortion of the anther at some stage prior to the
formation of the spore. There is no evidence
suggesting the exact time of this abortion but it probably
occurs at a pre-meiotic or very early meiotic stage. I
have quoted this (see P. 98) as evidence of the unbalance
of the diploid set of the particular individual showing
this feature, but further work on this very important

point is necessary before one can be sure of the
exact implication of the phenomenan. No unusual
associations of tetrads have been observed. It
would be expected that where there is so much
cytological aberration in the course of meiosis that
there would be the formation of micronuclei and
'tetrads' consisting of two, three and five or more
members. Such structures have not been seen.
Some obviously dead pollen grains have been seen
but they were members of a normal tetrad, at least
normal in that it contained 4 spores.

The large degree of cytological divergence which
has occurred would explain the sterility which has
been encountered in the seed of the trees. If
unsuitable haploid sets come into contact through
the pollination of a female flower by a male spore
which is highly different from the spore contained
in the ovule then sterilty would result. In
plants other than alder and birch (and the Gymnosperms)
this condition would not exist since there is almost
immediate fertilisation of the ovum from gametes
produced by the spore, since more than one pollen grain
can be a potential contributor to the zygote and alternativ

chromosome arrangements are available.   In the plants

mentioned

/there is a resting period between the time of pollination

and the fertilisation of the ovum.   The initial stages

in the development of the fruit proceed with the

stimulus of pollination, and no doubt terminate, but

fertilisation is only possible with the gametes which

are present at the base of the style.   If these

gametes are not complimentary to the female gamete there

are no others available to allow a normal fertilisation

to take place.   It would appear from the data on the

table that the formation of viable zygotes can proceed

if one of the parents is not too highly aberrant.

It is usual to find that there is either a sufficiency

of good seed or that the seed contains &#%& few

embryos (less than 10%).

Self fertilisation would provide an escape to this

difficult and biologically adverse phenomonen, but

since birch is monoecious and protandrous (but see

Jentys-Szaferowa (1938)(p.73)), the chance of self

fertilisation is slight, disregarding any genetic

system which may be present to prevent its occurring.

Woodworth (1930) showed that parthenogenesis occurred

in _Alnus rugosa_, and more recently Larsen has produced

a triploid alder which is apomictic, and it may be that

Betula is approaching a condition where one of the more
satisfactory methods of overcoming the heterogenity of
chromosome complements would be the adoption of some
apomictic method of reproduction.   But this would not
only provide a biological escape to this uncompromising
situation but also the road to an evolutionary cul-de-sac.
However if sufficient polymorphism exists within the
species at the time when this occurs, there will be enough
diversity to allow of further selection.   Once
equilibrium has been reached, evolutionary stagnation sets in.

No triploids were found in the seedlings which were
examined.   If hybridisation between B. verrucosa and
B. pubescens is a frequent occurence there should be
proof of such hybridisation in the presence of triploids
in the progeny of the trees which were sampled.
Triploid birches have been found by Helms and Jorgenson
(1925), Johnsson (1944), and Löve (1944b), and in all
cases the morphological features of the triploid were
closer to the diploid than to the expected intermediate.
In some of the cases the features were those of an
exaggerated diploid.   Johnsson is of the opinion that
the triploid has not arisen as the result of hybridisation
but by the fusion of two gametes of B. verrucosa one of

which is unreduced. This would explain the resemblance
of the triploid to <u>verrucosa</u> and the absence of any
feature which one might suppose would have resulted from
the fusion of a <u>verrucosa</u> with a <u>pubescens</u> gamete.

In the area examined,triploids, formed by hybridisa-
tion, could only be formed in the transition area between
stations 7 and 12, where there appears to be a
cohabitation of the two species.   If the method which
Johnsson describes is that which is actually operative
in the field, then the triploid will only occur in the
extreme eastern half of the sampling area.   The
stations 2, 3 and 6 form a group where the communities are
still young and are thus in an ecologically unstable
condition.   The problem here is one of ecological as
well as genetical replacement.   This ecological
replacement takes place at a rapid rate and is radically
different from the process of gene flow.   It will only
occur where there has been some change in the climate.
Such a change took place at the end of the Ice Age and
there has been a number of such changes since then.
Recently Seifett. (1948) claims that there is an
amelioration of the climate of Europe taking place at

the present.   This would account for the migration

of species, as species in the countries of Europe are

doing at the present time; birch will be no exception

to this.

Ecological replacement will always be directional,

and can never, even under theoretical conditions, be

random and normal.   Gene dispersal is theoretically

normal but selection is superimposed on this system.

This selection will appear to be directed because of the

gene coferring on the bearer some selective advantage

(if the gene confers on the bearer a negative selective

value, it will not survive) and will therefore follow

some ecological (external) factor.   This selection will
n
not be the same as ecological replacement.

Schmucher (1942) shows B. verrucosa and B. pebescens

as having a very similar range of distribution with the

latter being the more widely distributed.   The

interesting feature about Schmucher's maps is that the

whole of Britain is included in the distributional

area of both species.   My own

observations show that the diploid is rare in the West

Scottish Highlands.   This is in accord with the

general inference which can be drawn from the maps, i.e.

B. verrucosa is the less hardy and is not so wide

ranging as the tetraploid.   Hagerup (1933) showed

that within Vaccinium there are two cytological races,

the one of higher polyploidy being the hardier.

Löve (1944a) in his studies of Rumex subgenus acetosella

came to the conclusion that polyploidy alters the

physiology to as great an extent as the morphology and

with Rumex the octoploid was the slowest growing, and

hardiest.   This general rule, is not without exception.

Numerous instances are known where the reverse is the

case, i.e. the diploid is the hardiest.

It has been shown, rather by inference than experiment,

that crosses within the members of the same cytological

races are not universally successful.   What evidence is

there to suggest that crosses between the two distinct

races will be successful ?

Morgenthaler (1917), and Gunnarson (1925), have been

foremost among those who claim that the polymorphism

within the collective species B. alba L. is due to

hybridisation between the subspecies (or species) of the species. There is a continuous morphological gradient from that supposedly representing the type B. verrucosa to that of B. pubescens and beyond e.g. to B. tortusa Led. and B. carpatica Wald. & Kit.

Are there two types which have given rise to this heterogenous assemblage by crossing and back crossing or is the variation the result of some other process ? Helms and Jorgenson were of the opinion that the triploid which they had found was the result of a cross pubescens X verrucosa. Because of its inability to produce seed it could not maintain itself as a triploid but though possessing seed sterility it did not possess pollen (hence gametic) sterility. They did not find any tree with a chromosome number intermediate between n 14 - 21 but they did find some (5) with a chromosome number between n 21 - 28. The conclusion they reached was that the pollen, n 21, could pollinate and fertilise B. pubescens. The resulting back-crosses are almost indistinguishable from B. pubescens except on cytological examination. The peculiar aspect of this is that the original hybrid would have been assigned to B. verrucosa

by a competent taxonomist though the backcrosses do
not possess any character which could have come from
the B. verrucosa. This seems to confirm the
contention of Johnsson that the triploid is not hybrid
in its origin.

Jentys-Szaferowa (1938) attempted to prove the
impossibility of indiscri\ mi /ate hybridisation by an
analysis of the types of pollen which were being
released each day during the period of anthesis of the
birch. She was not trying to show that there was a
physiological or genetical barrier to crossing/ ,but merely
the physical separation of the species by their
flowering at different times in the spring. Size
is not a good criterion to use in determining the
association of a separable plant organ with some
known type of plant, for, unless the ranges of size
are disjunct they will form a continuous series. The
pollen of birch falls into this latter category.
Some qualitative character, if available, is a much
more reliable indicator of origin. The frequency
distributions which she obtained from pollen

collections were divided subjectively, into two constituent normal curves, with their means of samples of known types. To overcome some of the shortcomings of this method large numbers (over 100) of grains were used. Where approximately 100 did not occur the separation of the curve into its constituent parts was not effected. The reasoning behind taking the large numbers is that there is less chance of the distribution obtained experimentally, differing from that which would be obtained from the combined data of two theoretically normal curves.

The conclusion reached was that B. pubescens flowered about 12 days later than B. verrucosa and since pollen of B. pubescens was not available to pollinate the stigmas of B. verrucosa the hybrid was formed from the cross pubescens X verrucosa. This is because the time of flowering of B. verrucosa extends into the time when the other species has started to flower. From her calculations she came to the conclusion that the Forest of Wola is composed of 56%, 40% and 4% verrucosa, pubescens, and hybrid

respectively.

She uses her conclusions to explain the situation at Maglemose where the first known hybrid birch was found. The hybrid tends, and this is an assumption of hers, to approach B. pubescens in its time of flowering, so the hybrid pollen is available to pollinate the later flowering species. The back cross will have a chromosome constitution somewhere between 21 and 28 (in the haploid state). This is approaching the condition of introgression (Anderson (1949)).

Another important observation of Jentys-Szaferowa is that the time of flowering is the same more or less for the individuals of the one species in different parts of its range. I cannot confirm or deny this, but there is a considerable difference in the time of flowering of individuals of the same species which are situated close by each other. The separation in the times is as much as 4 or 5 days.

Can the conclusions of the above authors be applied to the Scottish birches ?

No triploids have been found in nature or in the
progeny tests. This is an indication of the purity
of the two cytological races. If genes of one can
be introduced into the other the process must be
something other than that normally associated with
hybridisation. If diploid gametes of B.verrucosa
are formed there is the possibility of their
fertilising the tetraploid's gametes. The resulting
zygote will have the same chromosome number as a
zygote which has been formed from the fusion of two
normal pubescens gametes. Here is one way in which
introgression can proceed. Unfortunately it cannot
be detected by any method, and if Johnsson's presumed
parentage of the 56 chromosome type is correct the
progeny of such an hypothetical cross as that outlined
above will have three verrucosa gemomes in its make up.
Johnsson (1945) tried to produce the hybrid experiment-
-ally but was remarkably unsuccessful. I have not
had sufficient time to attempt controlled crossings
or manipulation of the genomes to use the conclusive
evidence of such experiments in an understanding of
the structure of the local birch populations, but
work is in hand to remedy this very serious omission.

In the Central Highlands of Scotland the cytological races of the birch are not only separated genetically but also spatially. There is only a small area of overlap, probably less than it appears from the results. This is due to the abnormal stations 2 and 4, particularly the latter. The diploid is confined to those areas where there is a specific evaporation/precipitation ratio. The principal factor determining this ratio is the amount of rainfall. Superimposed on this major factor there are local edaphic factors which will alter the main sequence of the trend. Station 4 is the best example of this, since it is in an area of internal drainage and this has resulted in the formation of a raised bog in an area where the evaporation/precipitation ratio does not normally permit the formation of such communities. Station 2 is also fairly wet, as can be seen by the associated types which are present in this station (e.g. Comarum palustre).

The diploid is confined to those areas where the water balance is low. If the contention of Seifert is correct the diploid should be expanding at the expense of the tetraploid but there is a fuller discussion on this question on p. 102 et seq.

Biometrical Studies of the Leaves.

Leaves have always been used as indices of specific relatiohship and though they are subject to the influence of external agents they are usually taken as being characteristic of the plant. Unfortunately, taxonomic descriptions of leaves do not lend themselves to treatment by statistical methods. It is difficult to find a single measurement which can be used to classify leaves, but if such could be found it would enable leaves to be compared with much greater ease.

Length, breadth, and point of maximum breadth and ratios of these have been used in the cataloguing of the leaves of birch. Some of the above measurements relate to size and others to shape. It has been shown that size and shape are independent of each other, and it is therefore admissible to treat each separately, but exception to this is seen in the smallest leaves of the fertile spur shoots. Shape is an attribute of the leaf which is less likely to be affected by any variation of the external factors than

size, so most of the findings have been obtained from
the shape of the leaf rather than variations which have
been observed in the size.

The rhomboidal shape of the birch leaf is best
measured by considering the position of the widest part
of the leaf blade.   The index which has been used
has been derived from the ratio of the position of the
widest part of the leaf blade to the length of the
leaf measured along the midrib.   After considering
the ratio of the length to breadth it was decided that
this was not a true measure of the shape of the leaf.
it does not need complex mathematics to show that two
leaves each of length a and breadth b can differ from
each other yet be classified in the same group e.g.
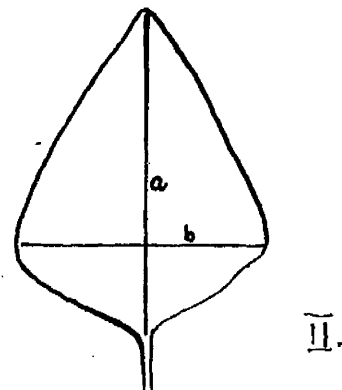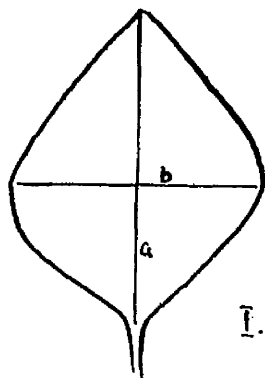
Obviously I differs from II.

Another feature of this ratio is that many shapes
and sizes can be represented in the same class.
Leaves possessing the measurements 12/6, 10/5 and
6.5/3.25 are all graded together though it is possible
that they belong to vastly different natural groups.
To try to make the categories more exclusive by
multiplying by another measure of the leaf only leads
to still more multiplication of indices.

The ratio x/y in the diagram below is a ratio
which is not capable of falsifying the classes of
shape, and since size and shape are independent similar
values can be grouped in the same class.
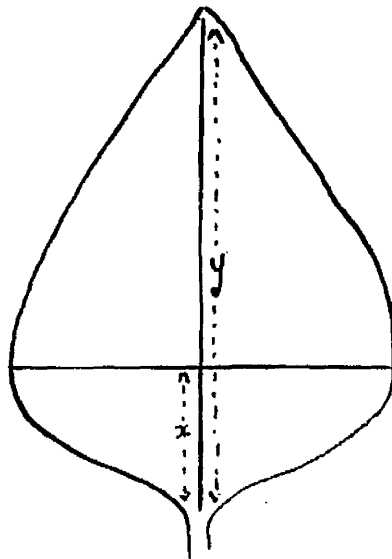
Other features of the leaf which might be capable
of classification were found to be incapable of
objective measurement and were discarded in favour of
the more real classes obtained from measured leaves.
Such characters as hairiness, wartiness, venation, and
the marginal dentation vary considerably in the populations
of Scottish birch but the amount of variation is so
great within a population that it is inadvisable to
study such characters till the inheritance of them is
known.

Morphogenetic studies on the form and size of
leaves have shown that leaf shape is controlled by
internal and external agencies (Ashby 1950), (Ashby
and Wangerman 1950).   Goebel (1898) described the
development of leaves as being heteroblastic, if the
leaf form changed as the plant aged.   He implied
that the shape of the leaf was a function of the age
of the plant.   If no such changes took place the
development was termed homoblastic.

In the tree species heteroblastic development is
to be expected and a study of the leaves of the long

shoots, epicormic shoots, and prolectic shoots indicates
that these leaves follow a course of development
similar to this.   The leaves of the dwarf shoots
do not, as would be naturally assumed, follow this type
of development.   The dwarf shoot is a perennial organ
and the leaves are borne in clustersof two and three,
clusters which arise at the same level on the dwarf shoot,
The leaves of the sterile and fertile dwarf shoots
differ, but the difference is caused by the variation in
the size of the two types of leaf, the smaller, on the
fertile dwarf shoots, being relatively longer than broad,
and having a point of maximum breadth nearer the centre.
The development of leaves on the fertile dwarf shoots
seems to be either normal or very abnormal, the larger
leaves being almost the same shape as those of the sterile
dwarf shoots.   Jentys Szaferowa (1937) advanced
the theory that the presence of the catkin in some way
affected the nutritional balance of the dwarf shoot
so that the leaves whichd evelope are not normal.
Since the larger leaves of the fertile dwarf shoot are
normal it seems that the factor which is preventing
the normal growth of the leaves is the shortage of water

to the developing leaves, (compare this with the
experimental findings of Ashby).

Among the external factors which are thought to
influence the shape of leaves there are:-

a. The water relations of the plant and the habitat.

b. The length of day.

Since the collections were taken at the same latitude
the day length is the same for all the samples which
were collected. This factor can be disregarded as
causing any of the differences of shape which is found
between the stations. There are marked differences
between the water relations of the stations if only the
rainfall is considered, but, as we have seen, there are
other factors which can contribute to this very nicely
adjusted system.

The morphogenetic responses of leaves seem to be
large and easily observed whereas the genetic
differences controlling leaf shape are of small order
(except such cases similar to the mutation OKRA in
Gossypium hirsutum Hutchinson (1934).).
Laciniated types of leaves are found within the genus
Betula and a study of the forms with this type of leaf

has been made by Saarnijoki (1946), who examined

B. dalecarlica and B. urticifolia, the latter

belonging to the 56 chromosome group and the former

to the 28 chromosome group. In addition to examining

B. dalecarlica Saarnijoki looked at others which are

included in the B. verrucosa complex. Though the

appearance of these types in any population is rather

spasmodic they are fairly common in the Scandinavian

countries and one can expect them to occur in Britain.

None has been found in the populations which have been

examined by me, and I have seen no reference to their

being present in the British Isles. The expression

of this character is not very absolute, the range of

variation which is found in the one tree agreeing with

the taxonomic description of many of the so called

species. It is possible that those types of leaves

are controlled by factors which operate in a similar

fashion to the Okra series of genes in Gossypium.

The assessment of leaf shape was carried out with

the idea in mind that the shape of the leaf is less

liable to the disturbing influences of the external

environment.   It is necessary to try to get a character
of this nature since the study of the variation was not
undertaken in the same way as that practised by the
others interested in the field of experimental taxonomy.
Many factors must be considered in the studying of the
variation in a species and with the trees there is the
overriding problem of time. ' Time taken to complete a
generation, time taken to become established in the
experimental garden, and time taken to reach the stable
stage after the initial seedling period.   Other
attributes of the leaf are certainly worthy of further
study but until it is possible to get the various
population established in a plot where the conditions
of the environment are the same for all, the measurements
which are taken will be of little value.

Leaf size is such a factor.   It is easily measured
and it is obvious that there is considerable difference
in the stations which were chosen for examination.
However there is marked difference within each population
but trends can be seen, noticeably the effect of extreme
moisture.   Station 4 has a mean length and breadth
much lower than that of the others.

Size can be measured by taking the product of the
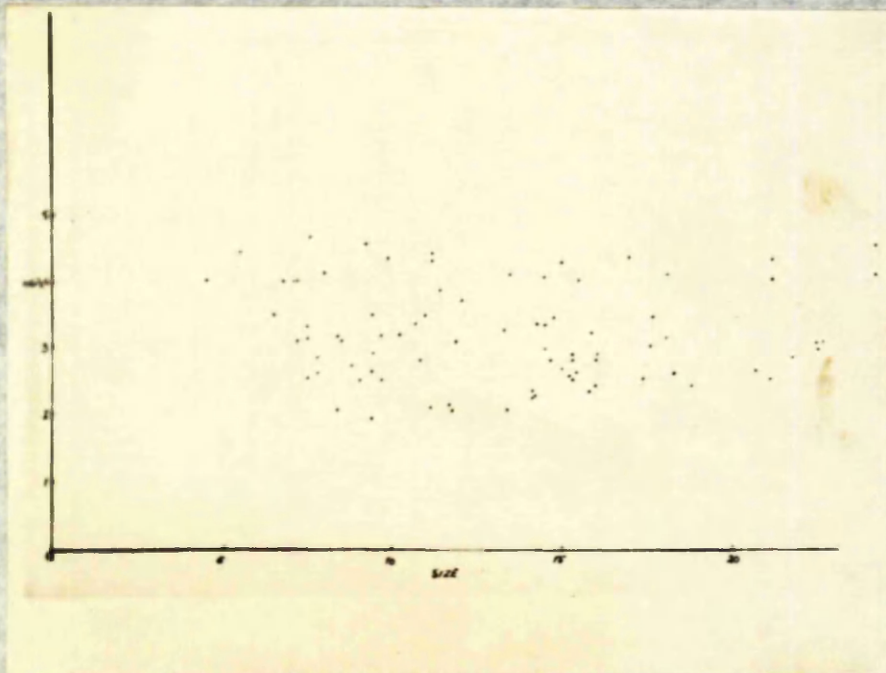
Fig. 3.

Scatter diagram of leaf size plotted against leaf shape.   Note the lack of correlation.

length and breadth, and dividing by two. The diagram
below illustrates this much better than any description.
The small descrepancies introduced by the outlines of
the leaf not being straight can be disregarded.
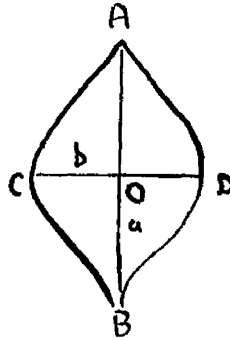
$\Delta\ ACB\ =\ \frac{1}{2}\ AB.CO$

$\Delta\ ADB\ =\ \frac{1}{2}\ AB.OD.$

$\therefore\ \Delta ACB + \Delta ADB = \frac{1}{2}AB(CO+OD)$

$ie.\ ACBD = \frac{1}{2}AB.CD = \frac{ab}{2}$

$= area\ of\ leaf.$

Fig. 3 shows the scatter diagram of leaf size
plotted against leaf shape for some of leaves. From
the manner in which the points are distributed it is
obvious that there is no need to complete the diagram
by taking all the values that have been obtained. It
can also be seen that there is no necessity of finding
the statistic r it being obvious that there is no
correlation.

TABLE. IV.

| St. | 1949 | | | 1950 | | | |
---	L.	B.	R.	L^s	B^s	L^f	B^f
1.	46.4	37.9	1.225	38.2	33.9	33.1	27.0
2.	35.8	29.7	1.207	35.9	31.6	36.3	26.0
3.	36.8	30.8	1.191	34.8	28.6	31.0	22.0
4.	32.2	28.1	1.152	25.9	22.2	22.2	17.8
5.	29.9	24.5	1.239	27.3	24.0	26.2	20.8
6.	35.0	31.6	1.111	31.8	28.1	27.0	21.5
7.	33.9	28.3	1.206	30.8	26.1	26.2	19.2
8.	31.1	26.3	1.201	27.4	26.8	26.0	18.4
9.	29.1	25.0	1.175	30.7	25.8	25.6	19.1
10.	33.8	28.9	1.193	32.1	27.8	21.0	15.4
11.	31.2	25.8	1.223	29.1	25.6	25.4	18.9
12.	32.9	25.7	1.305	29.8	24.1	26.7	19.5
14.	32.8	26.5	1.247	33.8	26.4	25.3	17.9
15.	36.5	30.4	1.208	37.0	28.8	28.3	23.7
16.	29.9	25.7	1.168	35.5	28.1	33.5	25.7
17.	34.8	26.7	1.321	35.9	27.9	32.3	20.7
18.	35.9	28.9	1.247	36.4	26.8	30.4	21.4
19.	37.2	30.6	1.246	35.3	28.4	31.6	22.6
20.	35.9	27.2	1.280	36.0	27.0	28.0	19.6
21.	38.3	31.1	1.236	38.5	30.6	33.0	26.2
22.	37.7	29.2	1.302	39.0	30.0	34.6	23.5
23.	34.8	28.0	1.265	35.9	28.7	29.9	22.4
24.	36.2	29.8	1.223	38.8	31.1	29.7	21.1
25.	37.1	32.3	1.155	38.2	30.7	32.7	24.7

Fig. 4.   Distribution of leaf size.

length steril
leaves

length fertil
leaves

breadth steri
leave

breadth ferti
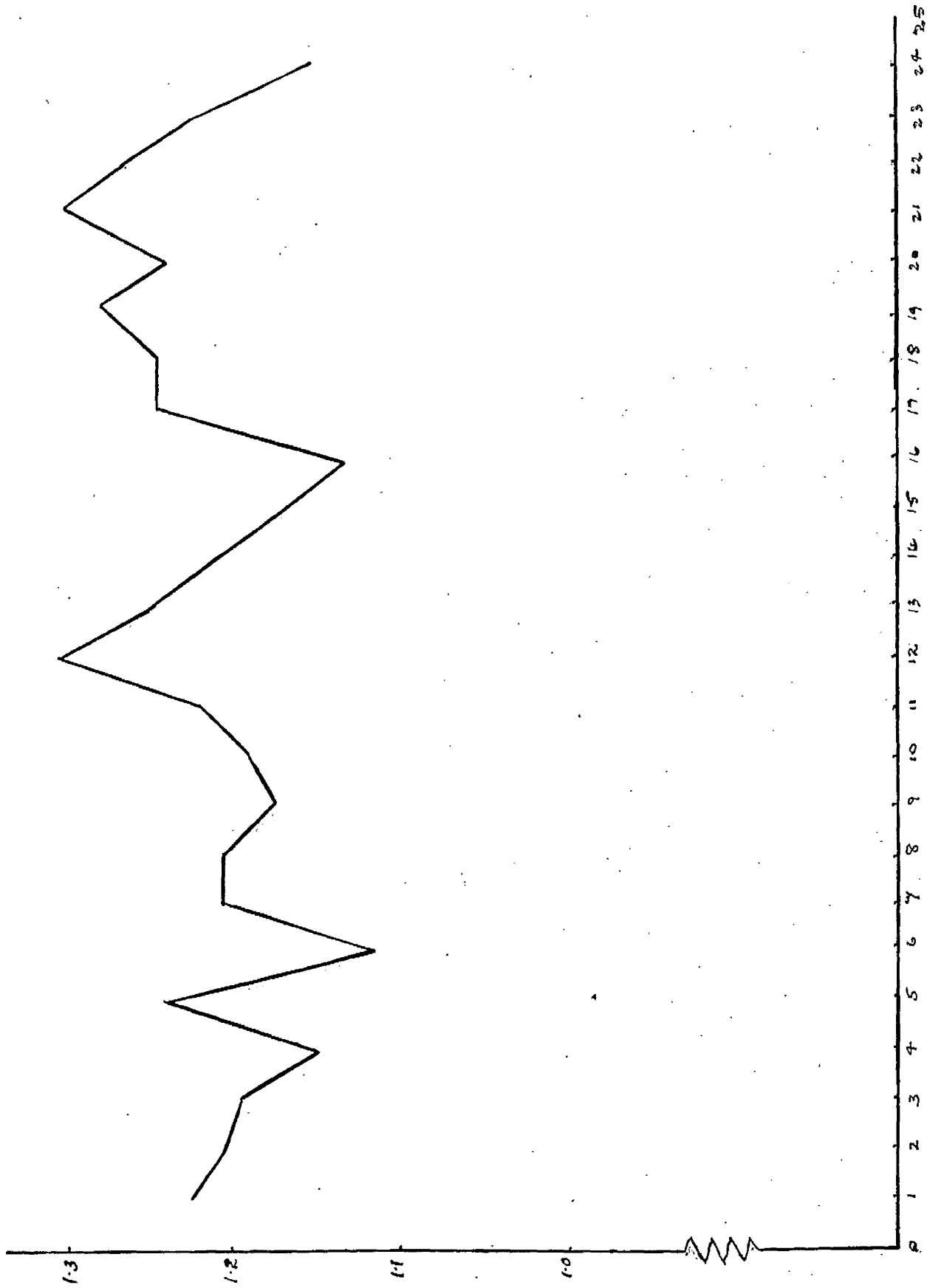leave
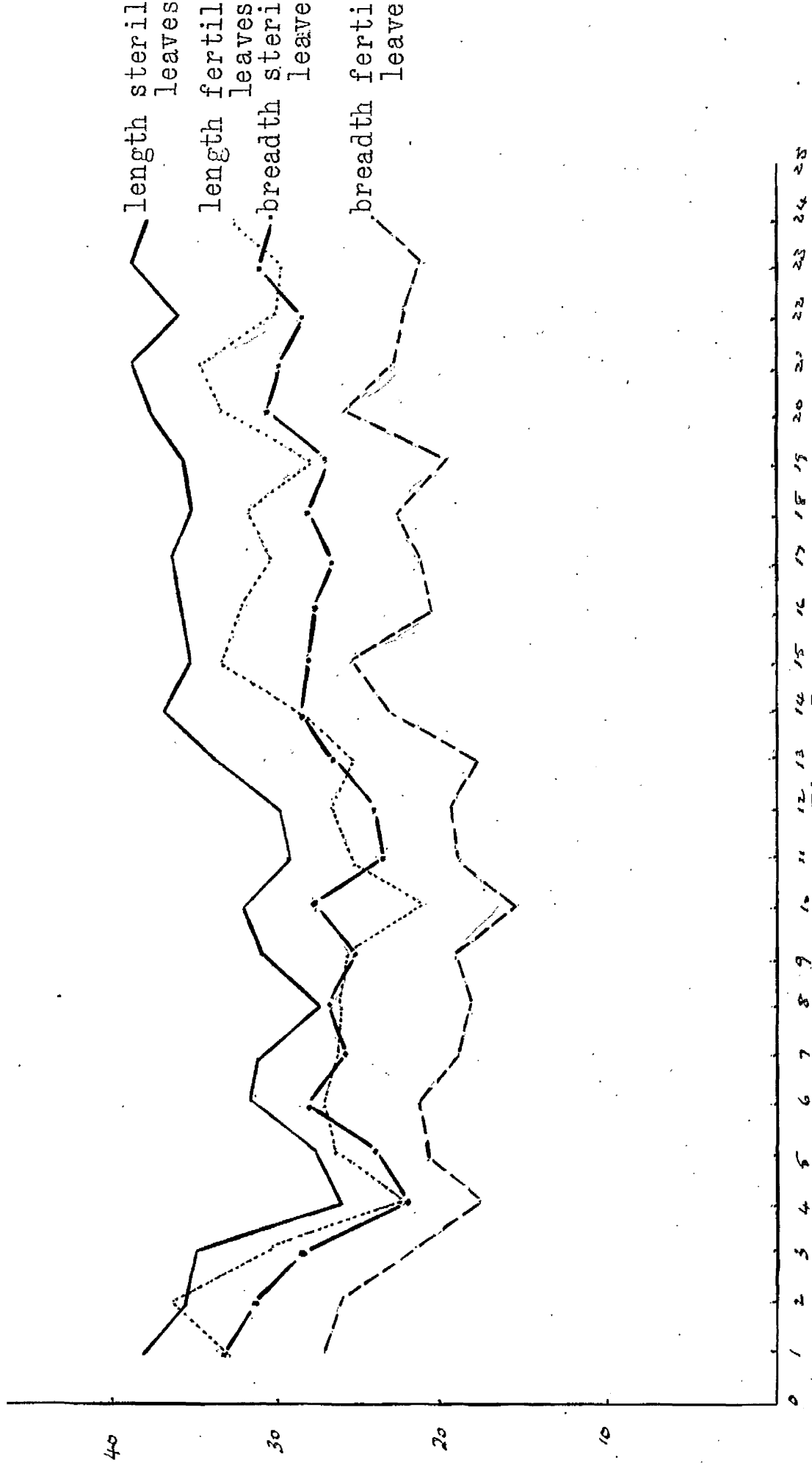
Fig. 5.
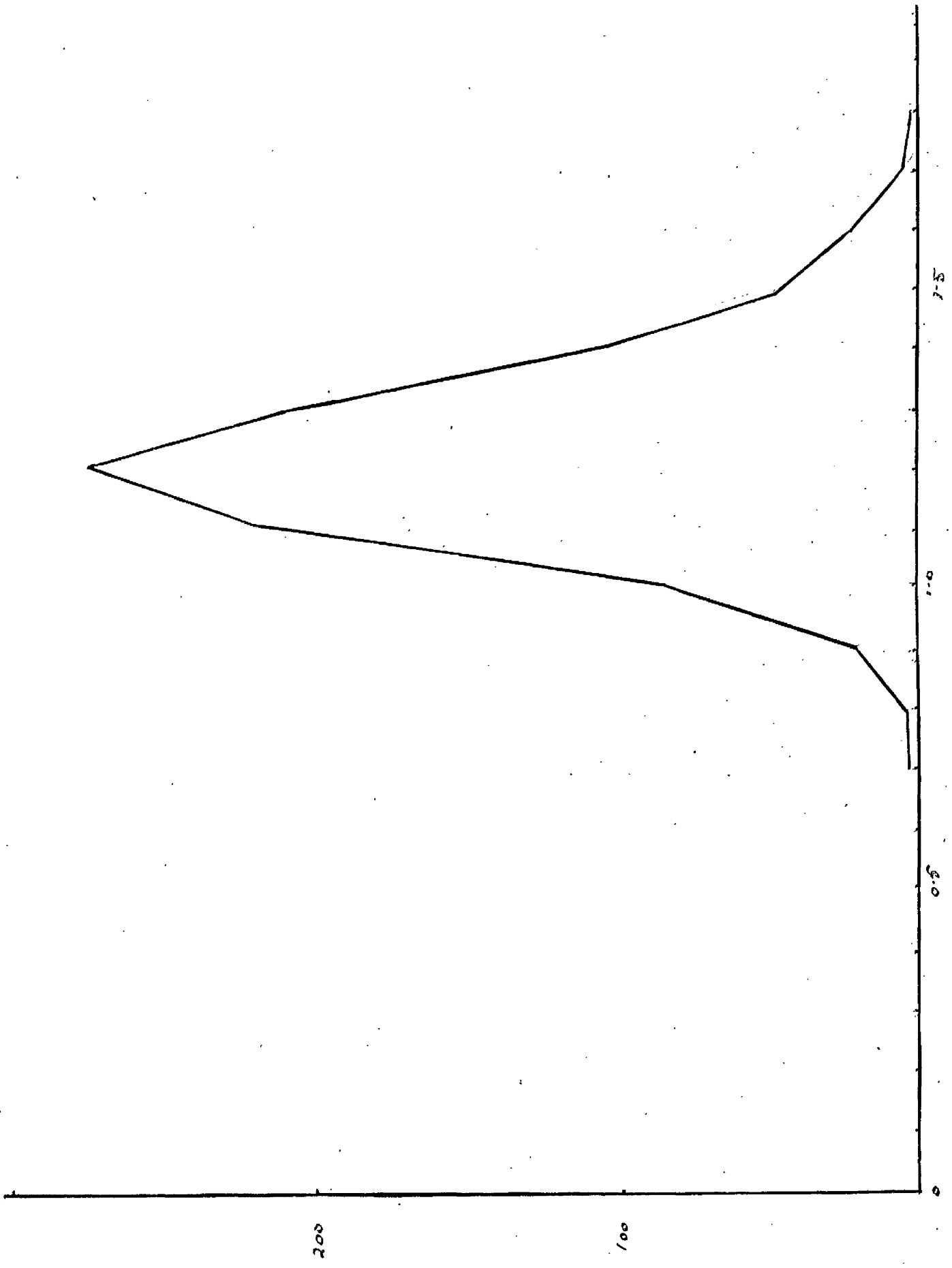
Fig. 6.   Frequeny polygon of the values assumed by the leaf size.

Figs. 4 and 5 show the distribution of length
and breadth and the ratio length ; breadth in the
stations which were sampled. This 'graph' is only
an idealised pictorial representation of the
numerical data presented in table   because the
stations are not situated such that they form an
arithmetic series, however it enables us to
comprehend the trends, at a glance.   All graphs
where the stations form the scale of the abscissa are
of this type and represent no more than an easy way
of summarising the data.   Even though the graph
is not mathematically correct we can see that the
absolute measurements of length and breadth, and the
ratio length ; breadth will not be of use in
correlating leaf characters with the cytological
race.

Fig.6shows the distribution of the size classes
of length : breadth ratios for the year 1949.
There is no obvious departure from normal and the
slight skewness which is present could easily be
attributed to the class intervals which were
selected.   If the above is compared with fig.7

where the distribution of the leaf index is shown,
it can be seen that the latter is measuring a
population which consists of two types differing
from each other by possessing different mean
values for the one character which forms a
continuous sequence when all the individuals are
considered.   We know that two such types exist.

It is rather a fortunate accident that the
diploid does not occur in a frequency greater than
that in which it is actually present, for it is
possible that the distribution, if the proportions
were in the region of 50 : 50, would more nearly
approach normal, so masking the compound nature
of the population, if the other fact were not present,
viz. the data obtained from the cytological
examination.   As it is we know that the population
is composed of two types and the morphological
evidence supports this (see also figs. 8 and pp.66&71)

In the above measurements there is no need to
distinguish between leaves obtained from catkinate
and non-catkinate shoots since the series is
continuous.   There is a tendency for the 'fertile'

leaves to be relatively longer than the 'sterile'
leaves when they are compared with their breadths,
i.e. the ratio length : breadth is larger.   They
also tend to smaller than the 'sterile' leaves.

How far is the index which has been used in
the measurement of shape a true indication of the
shape ?   Other characters of the leaf are also
varying along with the alteration of the position
of the widest part of the leaf blade.   Most
noticeable among those other characters are the
basal and apical angles.   It is futile to measure
these angles since they are determined by the
position of the widest part of the leaf.   The only
other attribute of the leaf which can affect these
angles is the absolute breadth.   I can see no way
of including this into the one measure which could be
easily handled.   The diagram below shows the way
in which the movement of the line AB (line of
maximum breadth) can effect change in the apical and
basal angles.   As the line AB moves towards X,
the apical angle increases and the basal angle

decreases. On moving towards Y the opposite happens. Changes in the absolute breadth modify the rate at which this takes place.
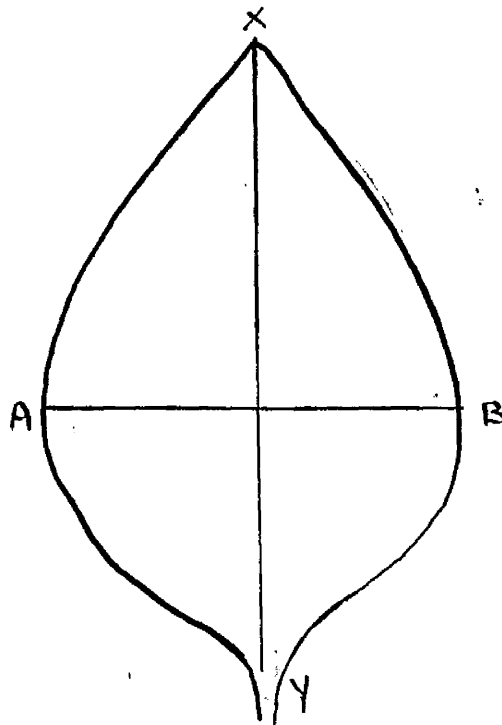
There is the tendency that as AB approaches Y its length increases, so increasing the basal angle at a greater rate than if the breadth remained constant.

With this premise we can take it that the ratio length : point of maximum breadth is the best measure of the shape of the birch leaf.

It is necessary to show that the measure that we have chosen is capable of discriminating between the
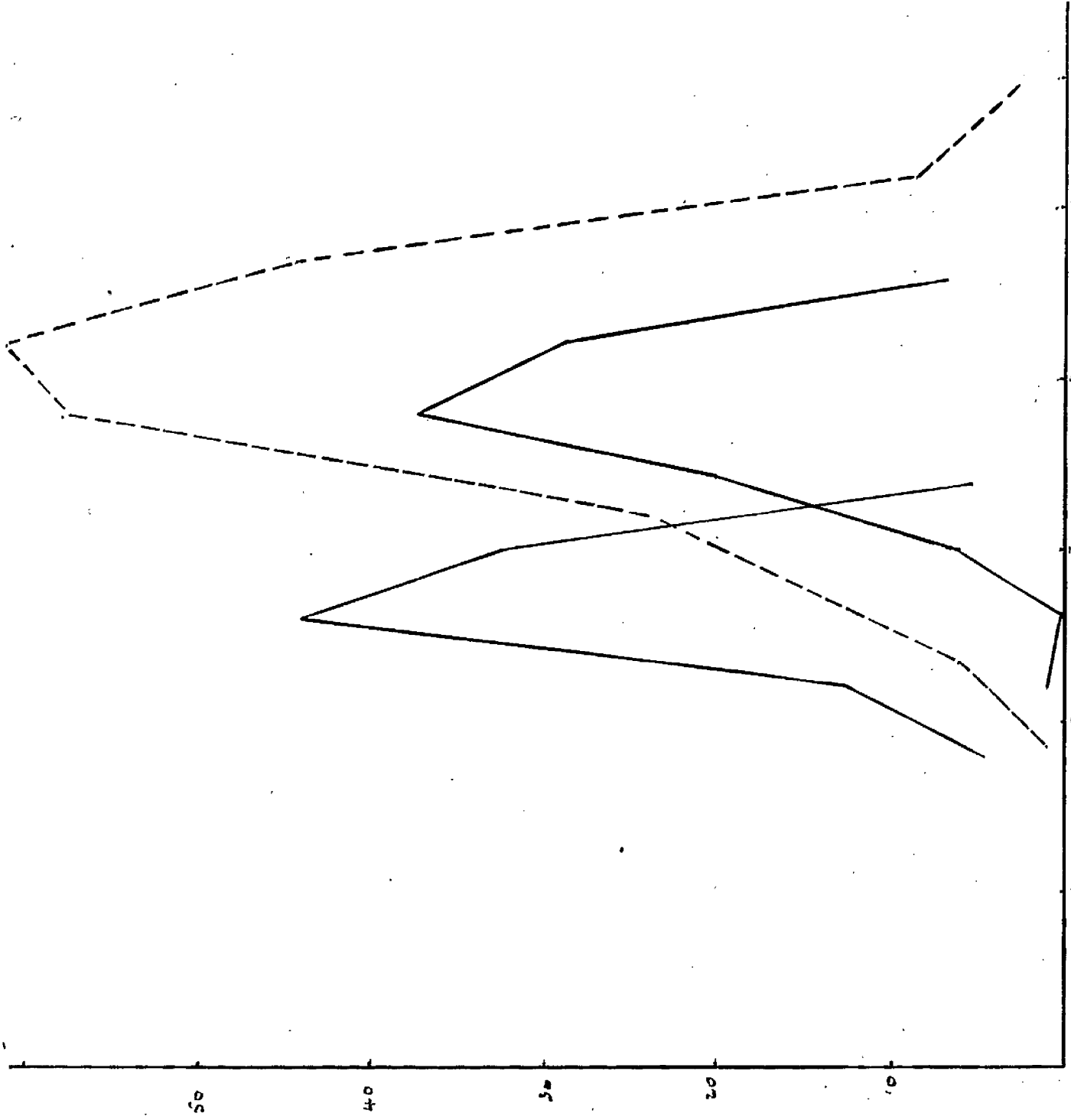
Fig. 7. Frequency distribution of the leaf index
Solid curves: left hand one, diploid; right hand one, tetraploid
Dotted curve: total number of observations from the sampling area

two cytological races, knowing that the individuals chosen belong to the different races. 100 leaves from a diploid and 100 leaves from a tetraploid (the diploid was obtained from Corstorphine and the tetraploid from Pollokshaws) were measured and the difference in the means tested for significance. The difference is significant at the 0.01 level. Fig. 7 shows the distribution of the values obtained. The difference is marked but to only consider interspecific variability, without assessing the amount of variation within the species, would subject to doubt the conclusions drawn from the main body of data. Intraspecific variation was tested and it was found that if certain types of diploid were selected it is possible to arrange the members in a graded series with the members of the tetraploid. There is no significance between the values of the means of adjacent members in this continuous series. This much can be learnt from the above; any division which is made is wholly subjective and careful manipulation of the data will allow this division to be substantiated by statistical
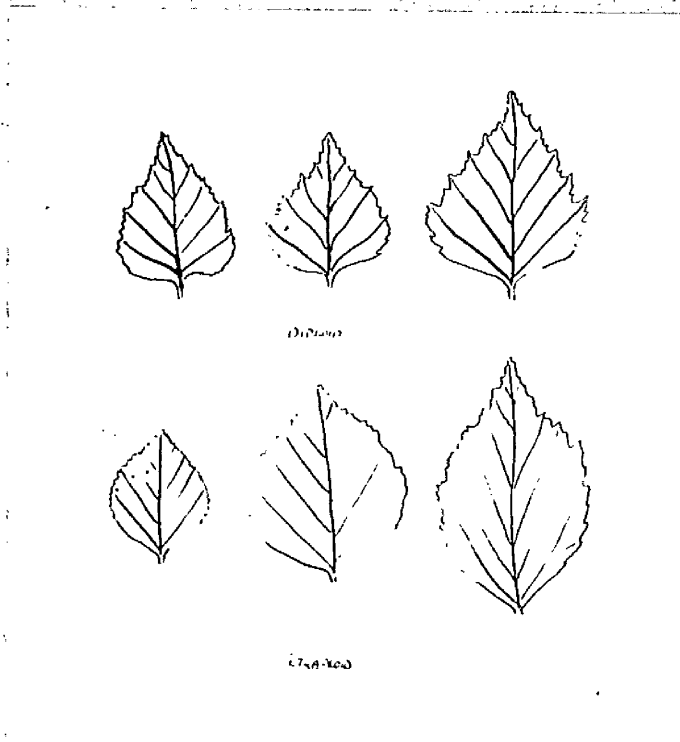
Fig. 8. Leaf shapes of the two cytological races, diploids on the upper row, tetraploids on the lower.

TABLE. V

Station.   Leaf Index.

	1949	1950	1950(sterile)	1950(fertile)
1.	3.12	3.49	2.97 * *	3.74
2.	3.44	3.21	3.14	3.54
3.	3.34	3.38	3.32	3.82
4.	3.76	4.01	3.61 * *	4.53
5.	4.30	4.34	4.39	4.30
6.	3.52	3.40	3.54	3.79
7.	4.21	4.18	4.06 * *	4.39
8.	4.12	4.21	3.85 * *	4.65
9.	3.83	4.01	3.82 *	4.37
10.	2.96 * 3.37		3.09 * *	4.57
11.	4.34	4.20	4.17	4.21
12.	4.31	4.40	4.06	4.53
14.	4.17 * * 4.40		4.32	4.44
15.	4.31	4.22	4.19	4.24
16.	4.14	3.98	3.71 * *	4.37
17.	4.42 * * 3.89		3.85 * *	4.67
18.	4.36	4.49	4.04	4.57
19.	4.05	4.12	4.06 *	4.36
20.	4.29	4.42	4.41	4.43
21.	4.09	4.20	4.21	4.16
22.	4.09	4.27	4.19	4.39
23.	4.16	4.22	4.06 *	4.39
24.	4.19 * * 4.52		4.30 * *	4.83
25.	4.34	4.28	4.16	4.42

* * Significant at the 0.01 level.

* Significant at the 0.05 level.

techniques. The only statistical method which was

regularly employed was the test of significance

between sets of figures from two distinct groups.

Other techniques cannot be employed without there being

wrongfully applied, since the amount of variation in

the external factors of the stations does not permit

of the use of any of the principles of the analysis

of variance.

Table V shows the mean values for the leaf index

for 1949 and 1950 and also the values of the index

for the sterile and fertile leaves of the 1950

collection. The 1949 and 1950 figures are derived

from the total number of leaves irrespective of

whether they were taken from sterile or fertile

dwarf shoots. The separation of the two types of

leaf was made because of the suspected difference

between them, but this difference is not a general

feature being present in 50% of the stations.

An analysis of the leaves of the spur shoots

(about 75 leaves from each type of dwarf shoot) was

carried out to determine the effect of position on
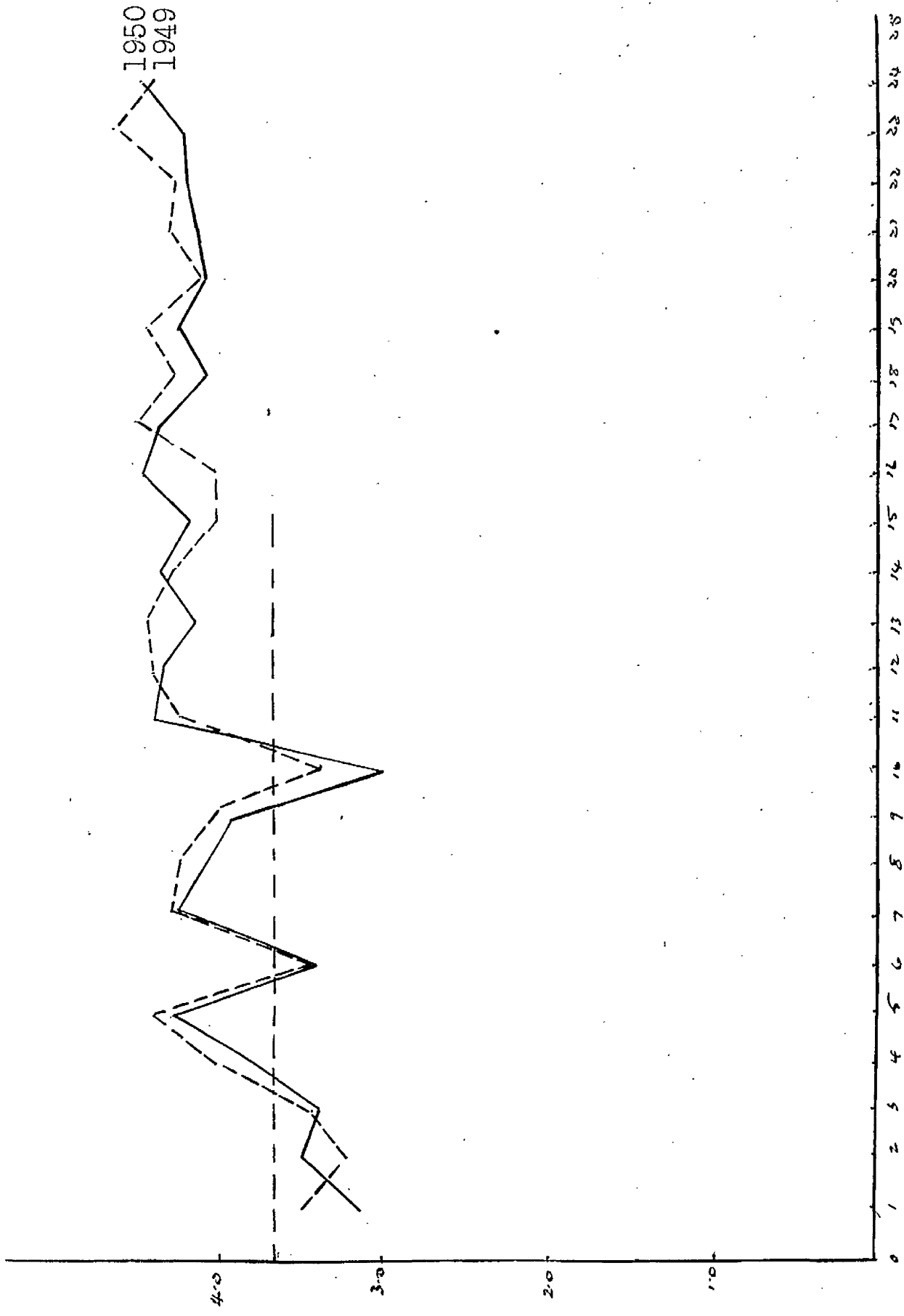
Fig. 9.   Distribution of the leaf index for 1949 and 1950.

the same genotype.   The difference in means is
most significant, being well in excess of that
required for a probability of 0.01.

What is the reason for the relative homogeneity
of the population means ?   The reason lies, I
think, in the unconscious selection of fertile
dwarf shoot leaves which are nearer the shape of
the sterile dwarf shoot leaves, and also the smaller
number in the samples.   The totals for the two
years do not show a great degree of difference
and those which deviate from the others can be
explained by the differences in the proportions
of the sterile and fertile leaves in the two
collections.   This is certainly the case with
stations 10 and 17.   The reason for the
significant difference in the means of stations
14 and 24 is unknown but it may be due to a
seasonal difference rather than to any other
factor, e.g. errors in the sampling.

The major trends are not masked by these
results.   From fig. 9, those stations which have
low mean values are seen to be those which are
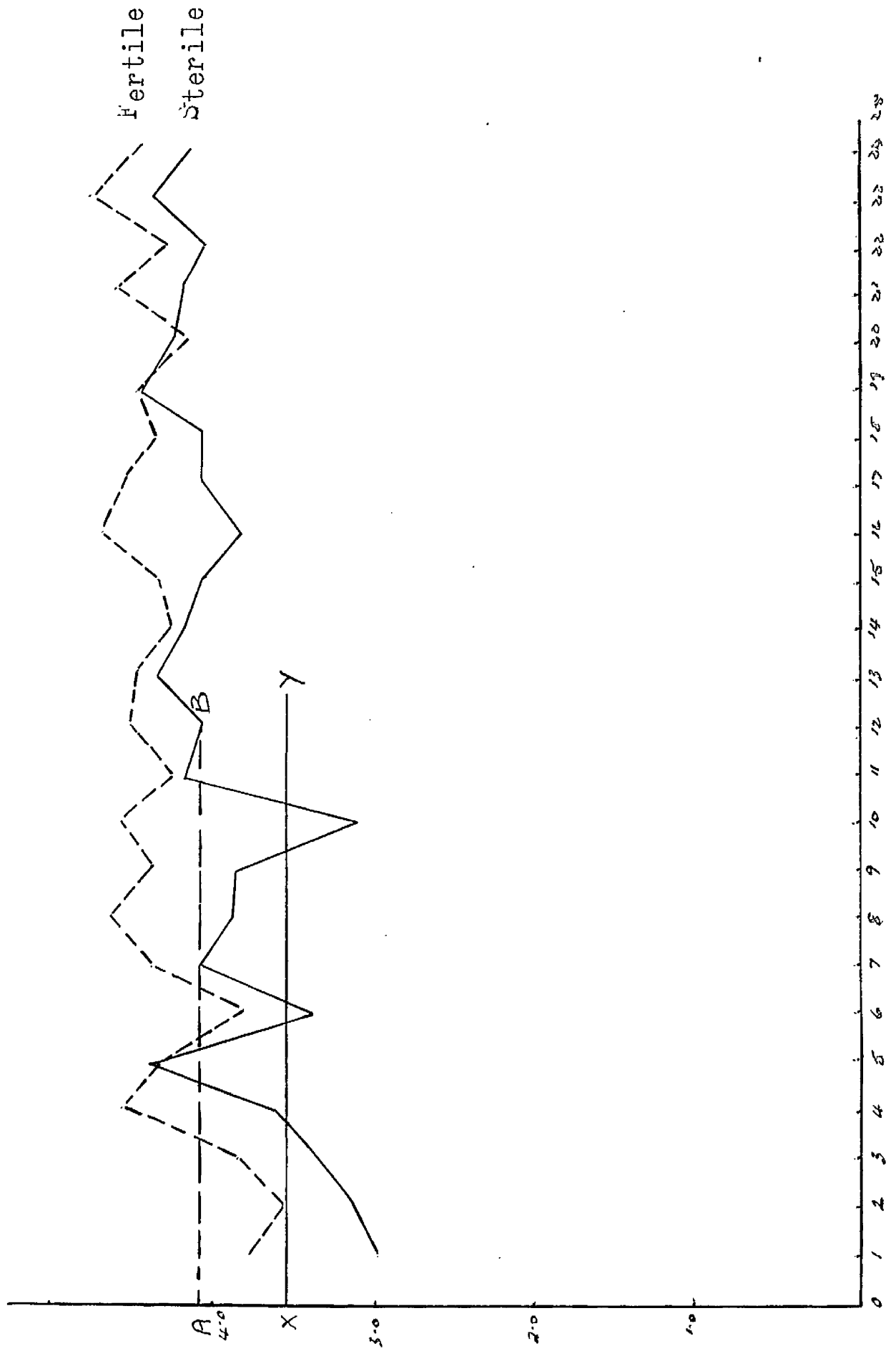
Fig. 10. Distribution of the leaf idices of the fertile and sterile dwarf shoot leaves.

mainly diploid; lying below the dotted line.
One station which is classified as a diploid on this
basis is Station 10 and this is still cytologically
unknown to us.   This station when we look at fig.
is the only one with a marked difference in the
values of the means of the fertile and sterile leaves;
stations 8 and 17 show this feature to a less marked
degree.   In stations 8 and 17 diploids have been
found but the main breeding population is tetraploid
(station 9 also possess this character).   The
fertile leaves have come from that part of the
population which is contributing to the evolutionary
potential while the sterile leaves may or may not be
drawn from that part of the population which is
static with reference to its being selected.
Station 10 shows this in its most exaggerated form,
no diploids being actually collected but most of the
individuals conforming to what could be classed as
the diploid.

Even the fertile leaves follow the same course
but with a slightly higher mean value (cf. the lines
AB and XY in fig. 10 all mean values of fertile

leaves below AB and sterile leaves below XY coming from diploids).

From the data we can gather that here there is a cline in leaf index, as measured by the population mean, running from east to west with definite gradation from the east to the watershed (except where a pure population is encountered) and then levelling out where the one type, the tetraploid is dominant. This variation could be considered as clinal because the mean values represent not so much a change in the character but a change in the ratio of the diploid : tetraploid. This is a dimorph cline in the original conception of the cline, but is the concept of the cline valid where the contributing members do not interbreed ? With subspecific differentiation (whatever this loose term implies) divergence has not proceeded to such a stage that the separate entities, subspecies if you will, are incapable of limited exchange of genes. One very important qualific--ation which should be added to the concept of the cline, if it is to be applicable to all biological

systems, is the determination and inclusion in the concept, of the factor operative in preventing absolute freedom of recombination of characters between those groups which are potentially (or have been in the past) capable of unlimited gene exchange. The zoologist considers, probably correctly, that geographical isolation is the prime factor allowing divergence to proceed, and this is in no way connected with the organic divergence, which eventually arises. In the plant kingdom, as effective and probably more effective agencies are capable of bringing about the initial isolation.

With birch in Britain there is no geographical isolation nor is there ecological (since the birch-wood appears to colonize very similar sites, but the change in rainfall from east to west may be factor which tends to separate the two races), and it seems that isolation has arisen by the development of genetic races within the cytological races, which have remained pure within themselves.

If we only consider B. alba. L., or as part of it has been called Betula series verrucosæ Sukacz. geographical differentiation has proceeded to a marked extent if taxonomic differentiation is taken as a

reflection of this separation.   However, genetic
divergence has not proceeded to the extent that
the taxonomic units are incapable of breeding
together.

Biometrical Analysis of the Catkin Scale.

The catkin scale, or bract, as it is sometimes called, is one of the most variable characters of birch and as such it is used to distinguish the various taxonomic divisions. The shape of the scale does not lend itself to easy measurement which can allow one figure to represent the whole shape. The most satisfactory index, indicating the shape, is trigonometric and not arithmetic but the figures still allow comparisons to be made.

A bract was selected from the central third of the female catkin under examination, placed in the negative carrier of a photographic enlarger and the projected image (the magnification was kept constant for all examinations) was outlined using a hard pencil to trace the outline of the image. No other attributes of the bract was recorded but there are important variations in the degree of hairiness. The density and distribution of the hairs vary both within and between the two races. In the present analysis a measure of the hairiness is not required but if definite crosses are to be performed some method of detailing the character would be necessary. It is impossible to study characters such as hairiness which may be controlled by oligogenes until proved to be in fact controlled by

controlled by such systems. The laws concerning
the fixation of genes in these systems are well known
and have been thoroughly examined by a number of
workers e.g. Sewall Wright (1943), and others. In
these observations the main object is real y the
study of the competitive action of the various allelo-
morphs, and though of great importance in the study
of populations, our main interest is in the inheritance
of quantitative characters.

The successful establishment and propagation
of those genotypes which are fixed in the population
is determined more by the rate of development than
by possession of the character. If the shape
of an organ measures the rate changes associated
with growth then it is possible that its mode of
inheritance is polygenic. Changes in shape can
also be effected by single genes, but their effect
is usually of an all or nothing nature e.g. dumpy in
Drosophila. In contrast to this absolute effect
polygenic systems control the character in a continuous
manner and are probably without effect per se on the
survival of the individual. Single gene factors
controlling shape usually have adverse effects on the
survival of the carrier. Multiple allelomorph
series may at first sight appear to be
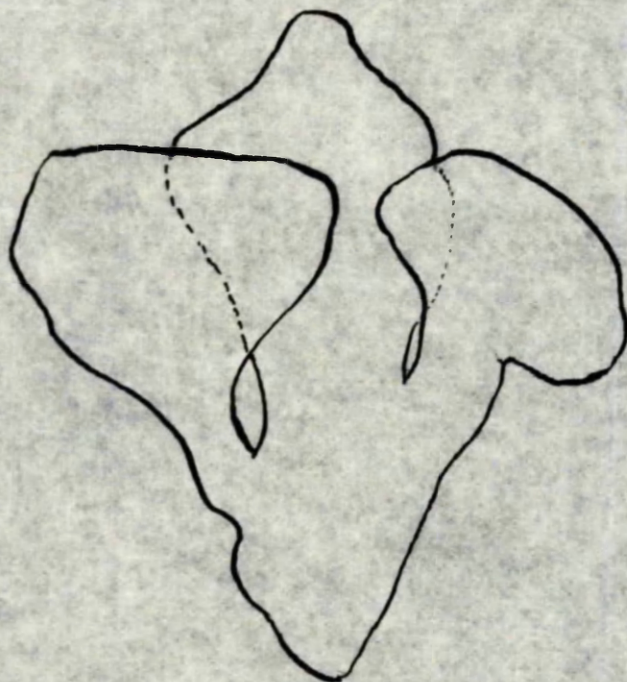
Fig. 11.

Bract in which the three primordia have developed individually (x12).
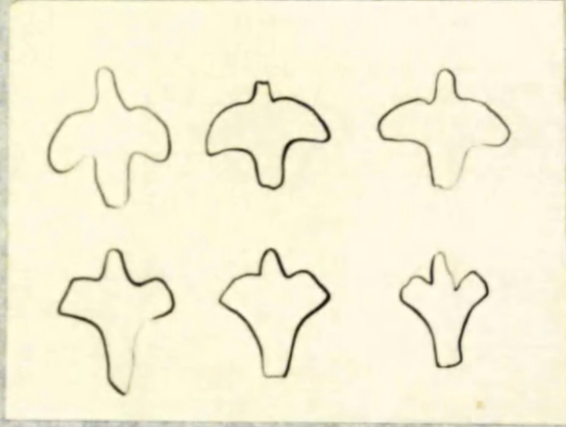
Fig. 12.   Variation in the shape of the bracts (diplo
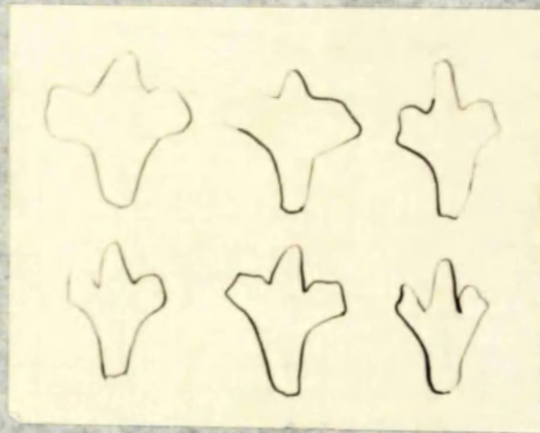
Fig. 13,   Variation in the shape of the bracts (tetra
ploid).
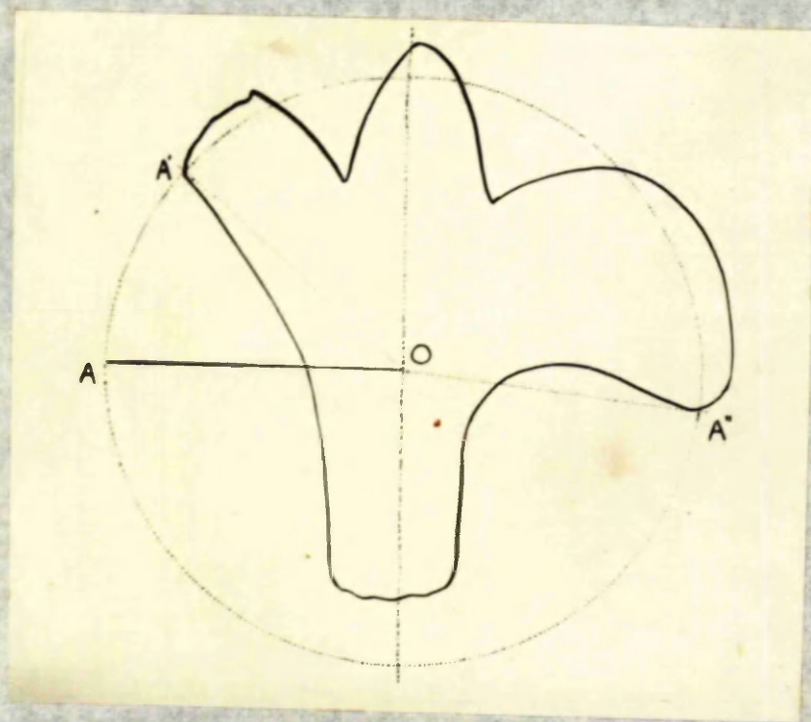
Fig. 14.

Diagrammatic representation of the mathematical
relationships of the bract. The point O can be considered
as an origin about which the line OA rotates. If OA
is of constant length then the hypothetical shapes of the
bravts can be traced out. However OA only rotates
through a small angle the extremes being OA' and OA"
which give the extreme types of bracts which are found.
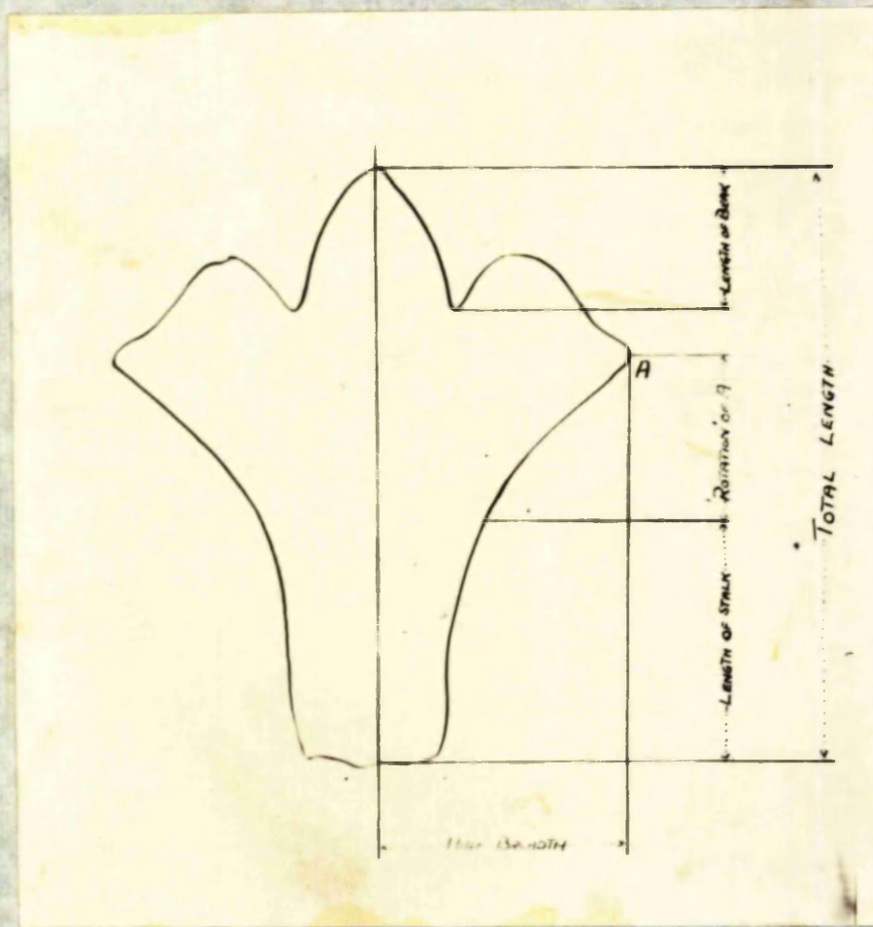
Fig. 14a.

Measurements employed in assessing the bracts.

the same in their effect as a polygenic system but in reality the variation is discontinuous.

The catkin scale which separates from the ripe catkin is not a unit in itself but a structure derived from three separate primordia. Willis (1922) states that the three initials are carried up on a stalk which is a later development. Others (Abbe, 1935) suggest that the stalk is also compound being derived from the same three initials. Evidence to support the second view is afforded by the presence of bracts which are tripartite to the base (see fig.11). Whichever is correct it seems that the stalk is a later development than the lobes of the bract and as such it can be compared with the petiole of a leaf.

Figs. 12 & 13 illustrate the extreme types of bract that are found in the most geographically distinct populations (Stations 1 & 25) and though each tends to a certain type it can be seen that there is an insensible gradation from the one to the other (note all shown from St. 1 are diploid and those from St.25 are tetraploid.).

The index used to describe the bract is obtained by considering the degree of rotation of the edges of the side lobes (points A' and A" in the diagram). (fig 14)

TABLE. VI.

Station	Bract Index.
1.	4°
2.	14°
3.	7°
4.	20°
5.	13°
6.	9°
7.	18°
8.	16°
9.	12°
10.	23°
11.	21°
12.	25°
14.	26°
15.	22°
16.	23°
17.	27°
18.	26°
19.	24°
20.	23°
21.	19°
22.	25°
23.	25°
24.	33°
25.	23°

Fig. 15.   Distribution of the bract index.

LENGTH OF ATTRIBUTE

Stalk

Beak
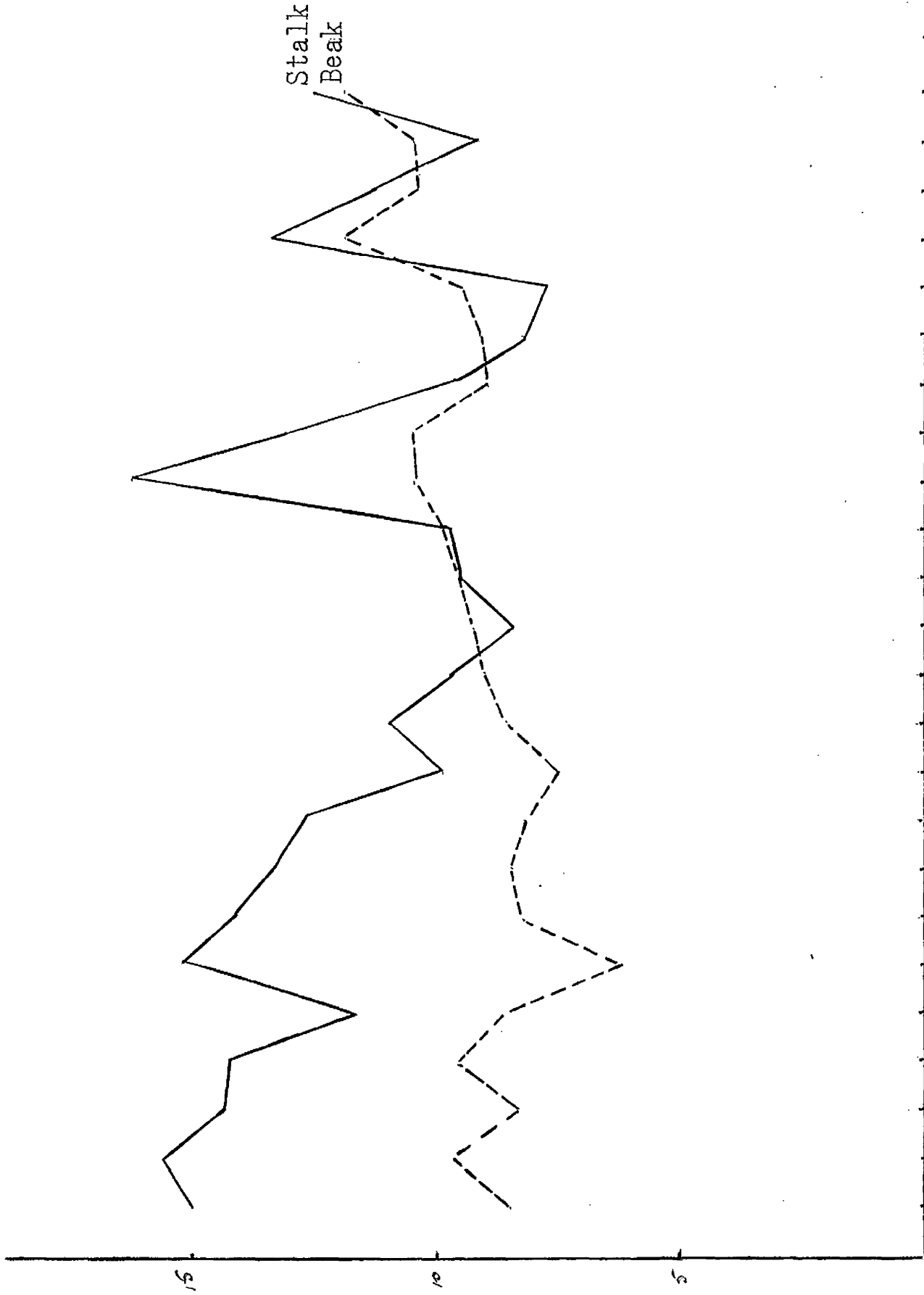
Fig. 16.

Table $\overline{VI}$ gives the mean values of the bract index

for the stations and Fig. 15 shows those points plotted

against their geographical location. The graph is very

similar to that of the leaf index, confirming the

gradual change in the mean values of the index as the

watershed is approached from the east. The values of

the mean level out beyond St. 10 and the values, though

increasing from St. 1 to St.10, fluctuate rather markedly.

The reason for this fluctuation is the presence of pure

populations of tetraploid in the transition area. This

is most noticeable with St. 4.

The arguments used in the discussion of the distribu-

tion of leaf shape are valid here and these data serve

to substantiate those derived from the study of the

leaves.

Other characters of the bract which were measured in

addition to the bract index were

    a). Length of stalk.
    b). Length of beak.
    c). Point of maximum breadth.

Fig. 16 shows the course which the values of <u>a</u> and <u>b</u>

take. <u>c</u> will be considered in a later section.

Trends' can be seen in the graph, trends similar to

those shown by the leaf index and bract index but in
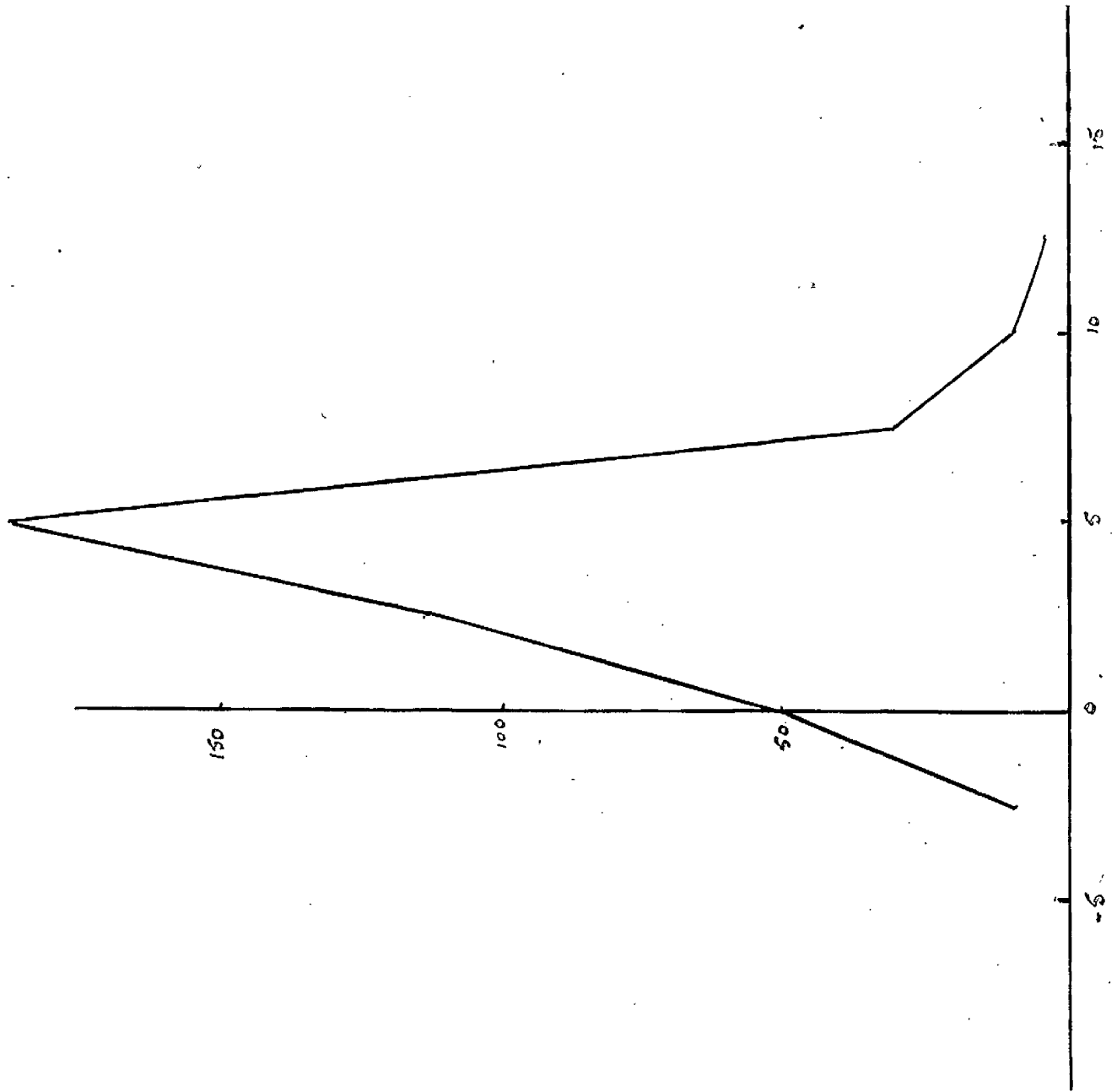
Fig. 17. Frequency polygon of the values taken by the bract index.

the stalk the fluctuations of the value are great.
This fluctuation of the value may be caused by there being
no selection for the length of the stalk and such fixation
and expression of the character as occurs, is determined
by chance.   The greatest amount of variation is
found in the western populations.   The interpretation
of this variation can only be undertaken when the external
conditions of the environment are constant, i.e. in
the experimental garden.   However the very presence
of such a large amount of variation does lead to some
speculation concerning its fixation in such a small
area.

The curve of the frequency distribution of the
bract index (fig.17) is almost normal, though there is
a slight deviation towards the lower limits.
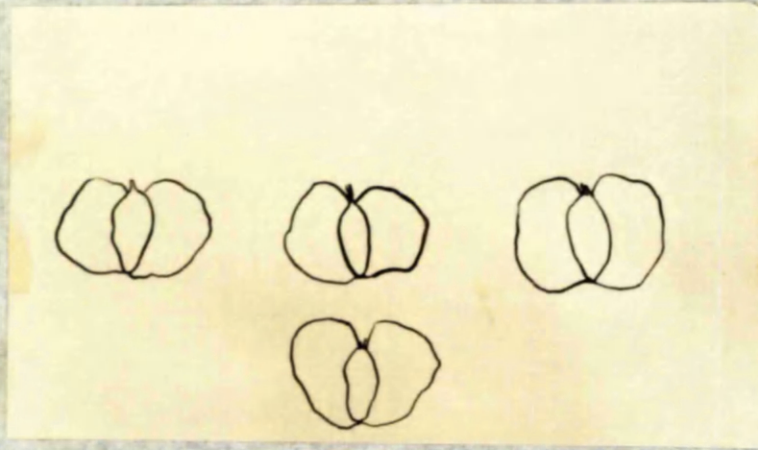
Fig. 18. Samaras from the two most widely
separated populations. The upper from
St. 1 (all diploid), the lower from St. 25
(all tetraploid).

Biometrical Analysis of the Samaras.

The samara of birch varies principally in the size of the wing. Morgenthaler used this 'fruchtflugelbreit' as one of his main characters in the determination of the affinity of the individuals which he chose to call hybrids.

The diploid possesses the larger wings and the tetraploid can have a fruit which is almost wingless. B. nana fruits are also without any extensive wing. Along with the variation in the size of the wing there are changes in the form of the wing (see fig.18). The larger broader wings are so shaped that the stigmas do not protrude beyond the wing: in the smaller wings the membrane comes away from the central body at an angle further removed from the perpendicular, than those of the broad winged type. Such differences in shape are quite constant and there is no need to take separate note of such.

The central portion of the samara (that portion containing the embryo) does not vary in width between and within the cytological races, except where there has been the development of small shrivelled sterile fruits. Though measured this has not been used in the

TABLE. VII

Station.	Samara Wing Breadth.
1.	13.92
2.	11.75
3.	10.38
4.	10.36
5.	8.82
6.	11.94
7.	8.64
8.	8.56
9.	8.32
10.	7.40
11.	7.06
12.	7.06
14.	6.88
15.	8.12
16.	9.22
17.	8.66
18.	8.88
19.	7.21
20.	6.00
21.	6.18
22.	8.69
23.	7.10
24.	7.58
25.	8.60
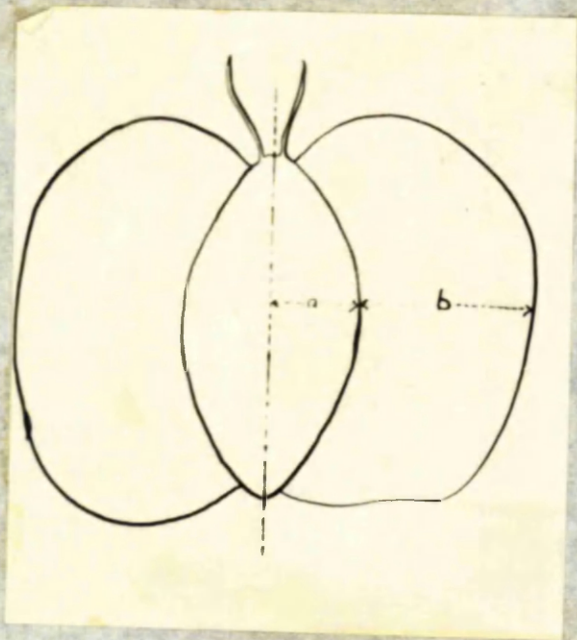
Fig. 19.

Measurements employed in assessing the smaras.
    a. Half breadth of kernel.
    b. Half breadth of the total wing breadth.

Samara Wing Breadth
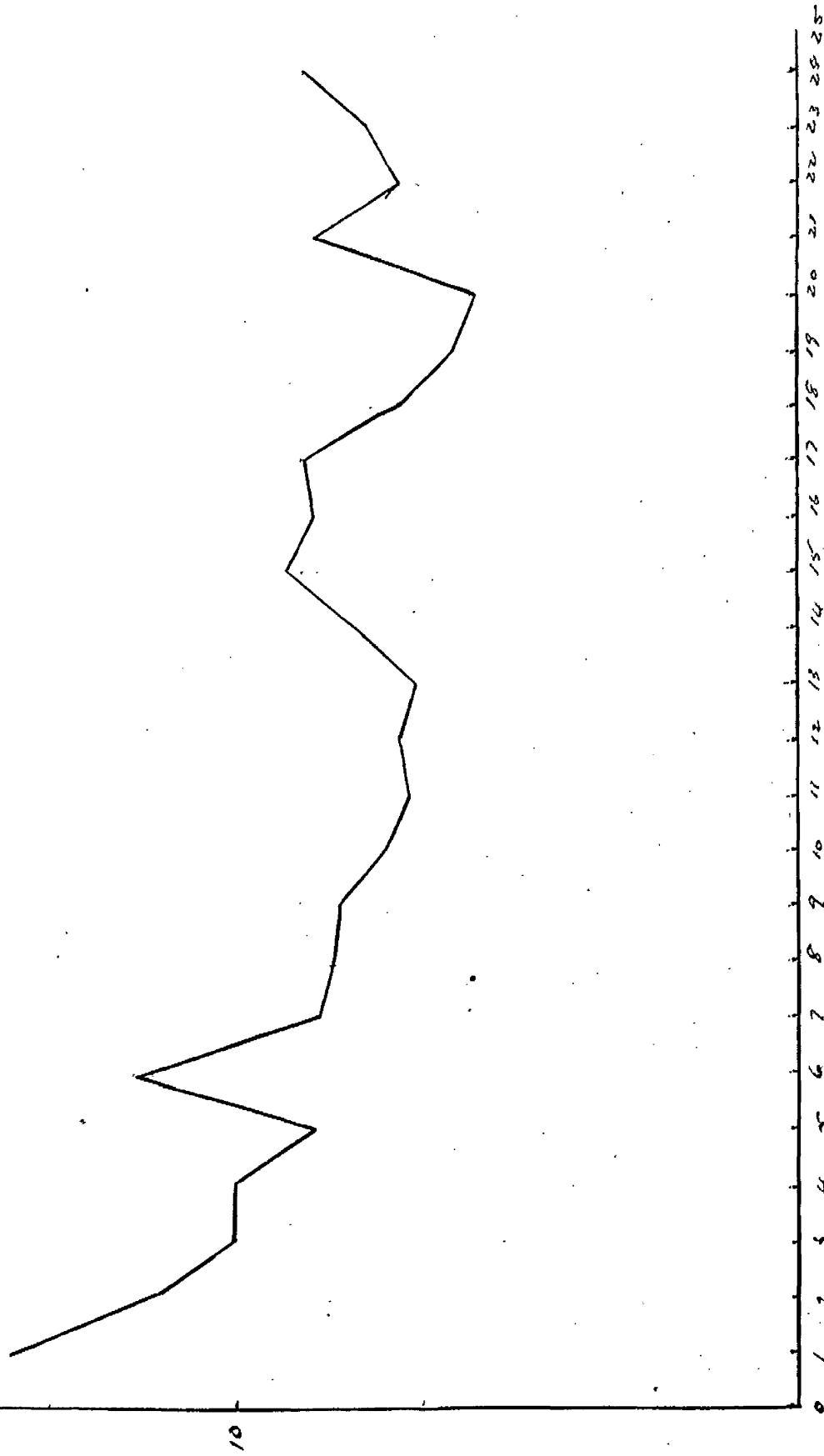
Fig. 20.   Distribution of the samara wing breadth.
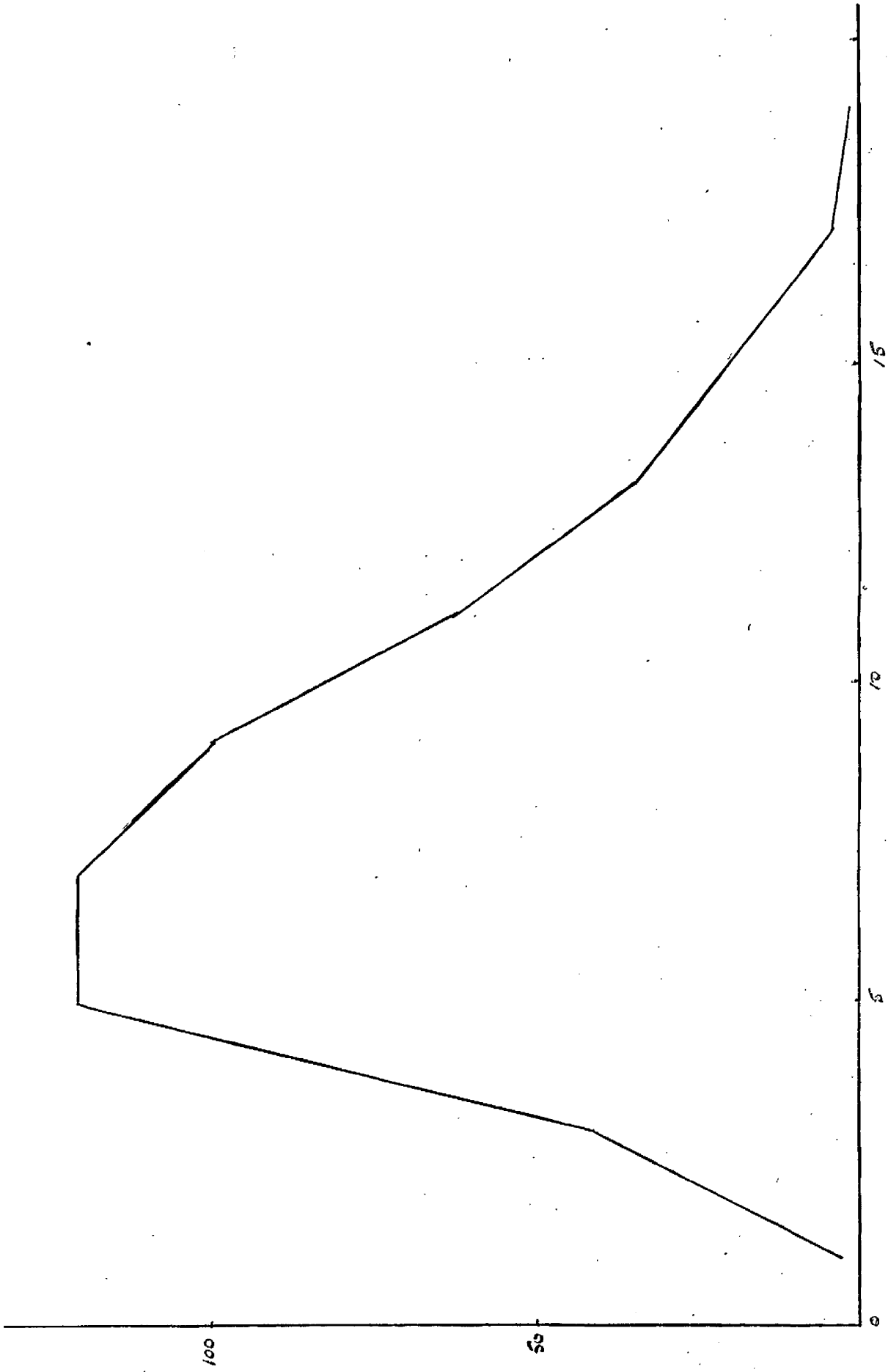
Fig. 20a.   Frequency polygon of the samara wing breadth values.

analysis.

A samara obtained from the same portion of the catkin as the scale, was enlarged by the same method and at the same time as the bract and the image measured by means of a squared grid scaled in arbitary units. This same grid was used to measure the bracts. The measurements taken were the width of one wing of the samara and half the breadth of the central region (see fig.19). As explained the former is sufficient to discriminate between the shapes found in the samara.

Table VII and fig.20 show the mean values and the relationship of those mean values between the stations. The trend is once again the same but because of the different measure there is first a decrease and then an increase in the value then this lower value remains fluctuating about a mean which does not alter significantly from a linear function parallel to the X-axis. This should be compared with the leaf and bract index where the values first increased then steadied and oscillated about their own mean.

This could be compared with the mathematical relation-ships

a). $f(x) = cx \pm k_1$

b). $f(x) = a \pm k_2$

Where $f(x)$ is the value of the attribute, c and a are

constants, k_1 and k_2 are limited variables.   The formula in

<u>a</u> represents what is happening where there is a graded

linear change, as is occurring from St. 1 to St. 10 and the

relationship in <u>b</u> that where a certain mean A varies within

the limits $A + k_2$ and $A - k_2$.   This last condition is

that present in the western half of the country.

Again there is no need to comment on these results, the

arguments used in the previous instances holding in this

case.

Further evidence concerning the nature of the populations

can be gathered from this and the previous sections.

Where germination of the seed was successful the

chromosome number of the particular individual from which the

sample was taken is **kh**own.   Unfortunately the one very

interesting population (St.10) still remains cytologically

unknown but the evidence first from the fertile spur shoot

leaves and now from the bracts and samaras completely

confirms the conclusions which were based on the leaf meas-

urement data.   Station 10 is morphologically diploid but

effectively tetraploid as a reproducing unit.   Similar

trends can be seen in all of the graphs.   Thus St. 6 is

diploid in all its characters (proved cytologically) and

that St. 2 possess high mean values for most of the characters which have been studied. Other features of this type are seen from the graphs and tables.

The measures dealt with in the last two sections are more diagnostic than the leaf index, not because they are more distinctive but because of the different range of values taken by the attribute. For taxonomic purposes the bract index and the samara wing breadth afford the best diagnosis where one is willing to accept a subjective assessment rather than an actual measurement. The ease with which the leaf index can be found makes it suitable to use in an exhaustive enquiry into the structure of any area of birch, providing that the chromosome count is taken at the same time.

Supplementary Consideration arising out of the
study of the bracts and leaves.

In considering satisfactory indices for use in
classifying the characters of plants one is struck
by the probability that the measurements, though
taken on different organs are in reality measuring
the system of genes, or the expression of one
system, of genes on the different organs of the plant.
When account is taken of the homologies of the various
organs it becomes essential to distinguish between
true affinity of attributes and independence of the
values obtained.   Anderson and De Winton (1935)
studied the effect of different genes on the leaves,
calyx, and corolla of Primula sinensis and though
noting the results they did not actually state
whether the effect was the same on each.   They did
state that the genes had an effect on all the organs
studied and it appeared that the effect was of major
proportions.   Secondary effects on each organ could
be produced by other genes not having such a fundament-
al function.   These secondary effects were inherited
independently of the others.
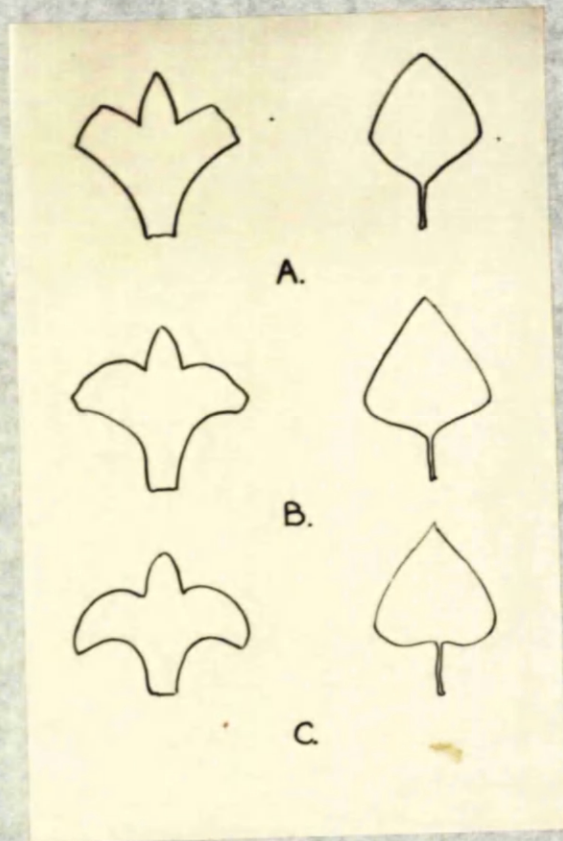
Fig. 21.   Some of the supposed homologies between
the leaf and the bract.

Leaf Index

Bract
(pt. of maximum
breadth)
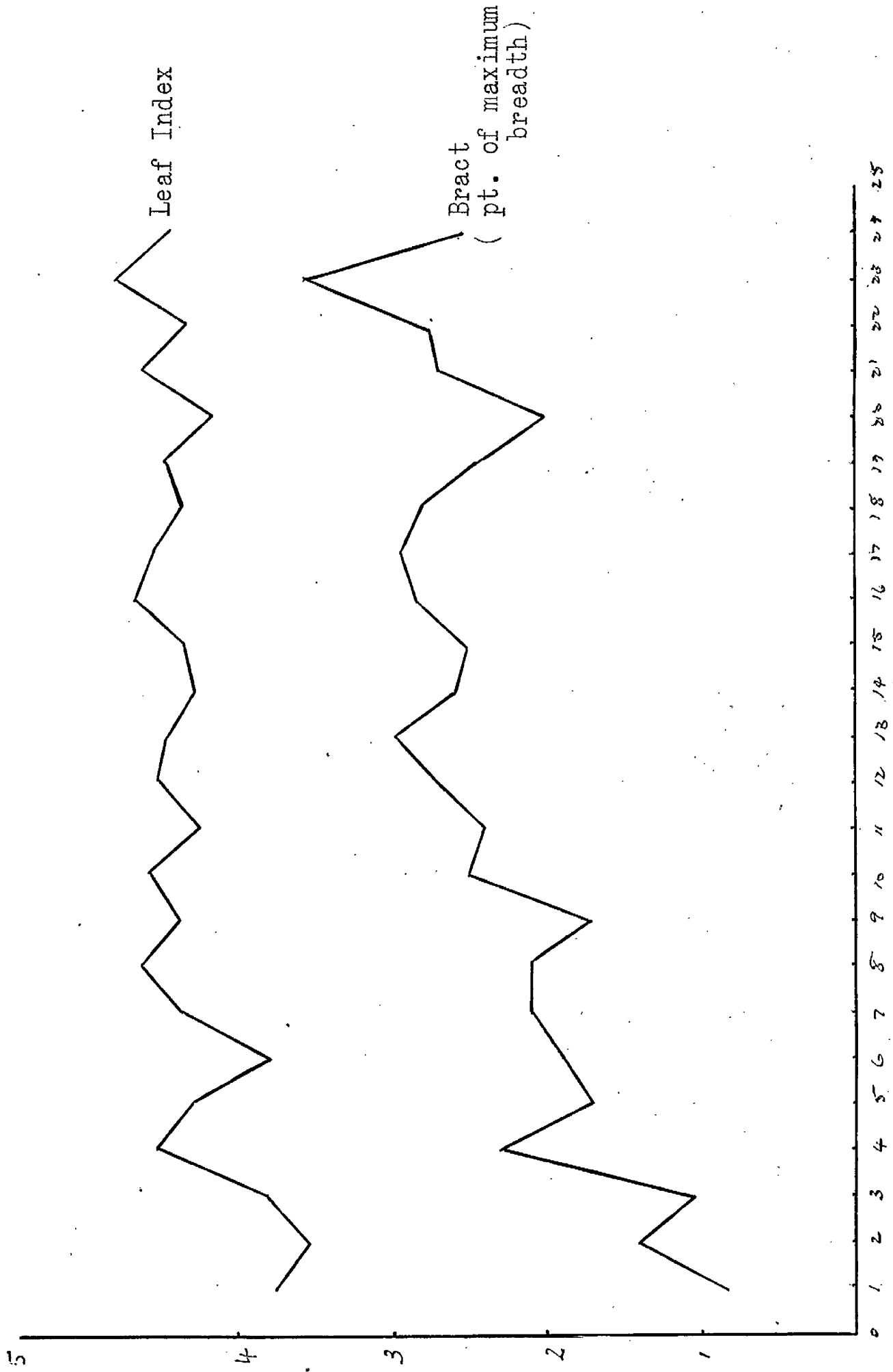
Fig. 22.

Comparison of the values of the leaf index and the

equivalent value for the bract.
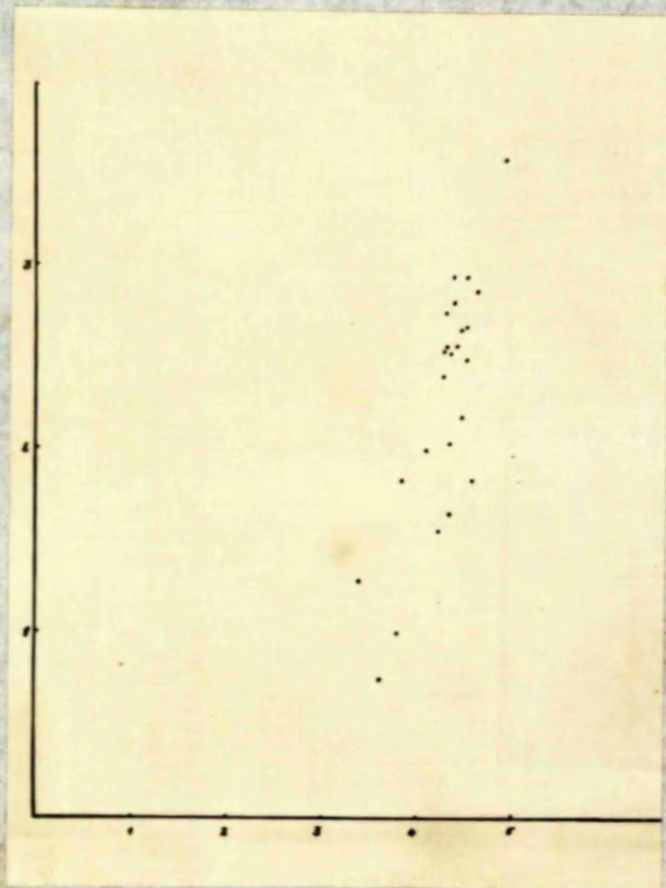
Fig. 23.

Scatter diagram of the mean values of the leaf index and the mean value of the point of maximum breadth of the bract.

Since the bract is probably foliar in origin,
we may suppose that the genes controlling such a
prime feature as shape, would affect the leaves and
bracts int the same way.

It is unfortunate that no record was kept of
petiole length because this would have helped to
have made the hypothesis more valid, since the bract
may be considered as leaf blade and petiole.

Fig. 21 shows some of the supposed homologies
in diagrammatic form. The three types shown are
the extremes with an intermediate. Type C is not
common among leaves, being confined to the epicormic
and long shoot leaves, though it is not infrequent among
the bracts. Fig. 22 shows the graphs of the leaf
index and the comparable measure for the bract, the
point of maximum breadth, for all the stations. The
values are seen to vary in the same direction and the
two curves follow each other quite closely. The
scatter diagram of the mean values of the bract measure-
ment and the leaf index is shown in fig. 23. The
correlation coefficient is significant (0.01 level)

all values

were tested and not just the means of the stations).

The bract, however/is not a single structure but composite (Abbe, 1935), formed during the development of three primordia. If the growth of each primordium is controlled by the same set of genes which control the growth of the leaf primordia, even though the final structure is composite it will reflect the processes operating on eabh primordium.

The similarities of shape in the bract and the leaf are the result of the expression of the same set of genes on the same basic unit (the primordium).

This system which does not seem to have been mentioned in the literature, though Anderson's data (1950) indicates that the petals and sepals of _Iris_ vary in the same direction (the actual measurement taken was length).   The more complex attribute of shape is controlled in the same way as the more simple measure of shape.

If a basic set of genes does control such fundamental but essential processes, modifying genes may control the smaller differences that are found between the types rather than a mutation in the set.   Such a change in the basic set should not be considered as not occurring, for large changes may be due to an altering of the basic equilibriu e.g. laciniation of the leaves of _Gossypium_, as in the mutation Okra.

These modifying genes will probably act in time because
of the type of differentiation that is present in plants.
In the morphogenesis of animals (which have a more simple
embryology but a more complex organisation) genes having an
effect in time will not possess the same type of expression
as the 'time' genes in plants.

One example of this is seen in the genes controlling
the distribution of the anthocyanin in the Old World cottons
(Hutchinson 1932).

The genes are:-

R ----- pigment the whole plant

R^1 ----- pigments only the leaves and calyx

R^c ----- pigments only the calyx

R^s ----- pigments the stem and the base of the petals

r^o ----- no spot on the petals and pigment only on the
hypocotyl

r^g ----- no anthocyanin and only a white spot on the
petals

$r^o \cdot g$ ----- red spot on petals with white margin,
hypocotyl red.

This series forms a set of multiple allelomorphs but
the reaction is not the same as the series which gives rise
to the grades of eye colour which are found in Drosophila.
The above set is ааааааа tempoarl: the dominants R, R^1, R^c, and

R^s act in time, the first three having their effects in that order, i.e. in the presence of R pigment production starts at the beginning of the development of the individual. If any of the others is present, production begins at a successively later stage in the growth of the individual. The recessives i.e. the absence of any of the dominants have entirely different results .

Since this physiological process has been shown to be controlled by a series of genes then it is not unlikely that other basic physiological processes e.g. the determination of leaf shape and bract shape, are under the control of genes which have a modifying complex acting in time.

Tentatively the following scheme is drawn up:-

1.   There is a fundamental set of genes controlling the expression of basic characters.

2.   Rate genes acting on this set of genes effect quantitative changes in the expression of the basic set.

3.   'Time' genes controlling physiological reactions e.g. pigment production, control the distribution of the metabolites.

4.   Mutation of genes in the basic set have a major effect on the fundamental processes associated with the

original set.

    5. Independent mutations can arise outside of
this scheme.

The Hybrid Swarm on Ben Loyal.

Though hybridisation between the two common species has not been observed in the field an area, in which crossings between B. nana and B. pubescens had occurred was examined. Dovaston (1949) expressed the opinion that there had been crossing of the species and backcrossing of the resulting hybrids to each of the parental types. On my examining the population in June 1950, the extensive inter\[m\]ngling, which Dovaston suggested was present, could not be found. Reports of crosses between B nana and other members of the Betulaceae are numerous cf. Lindquist (1947) and Blytt (1906), and indeed it seems to hybridise more readily with species of the B. alba complex than some of those species do among themselves.

All the chromosome counts which have been made on B. nana have shown that the species is diploid with 2n = 28. I have not been fortunate enough to obtain a figure for the population on Ben Loyal but the peculiar aspect of this population is that it is hybridising with a tetraploid. Till the exact chromosome complement of the members of the Ben Loyal population is known no conclusions of any consequence can be drawn.

PLATE. III

Hybrid.

B. pubescens.

B. nana.

Fig. 24.

Leaf shapes of the parental types and the putative
hybrid.

B. nana is a small arctic plant found only in Britain at the higher altitudes and latitudes of Scotland, and even there it is rather rare.   In the tundras of the extreme north it forms one of the main elements of the flora but in the Scottish Highlands it is present in patches which, though often dense, are small in area and widely separate. Most often it occurs far from other birches but on Ben Loyal (Sutherland) B. pubescens ascends the gorges of the burns eventually reaching the area occupied by B. nana. The arborescent birch does not extend beyond the edge of the gorges, apparently because the severe winds sweeping over the coll prevent its growing satisfactorily, though it survives as seedlings and depauperate specimens where shelter is afforded by Calluna and other ground vegetation. The dwarf birch is only present on the exposed ground.

The suspected hybrid was found where the two types meet viz. along the edge of the gorge.   This hybrid was determined purely by morphological criteria and cannot be safely assigned to the product of a cross between the two species.

Plate three shows the area, and photographs of the hybrid and its two parents.   Fig.24 shows the leaves of the three types.

It is interesting to look at this hybridisation in the
light of the hypothesis that Anderson (1949) has suggested.
The hybrid occupies an ecological niche which is intermed-
iate between that of its parents.   If this hybrid is
fertile the large number of recombinants which arise in the
second generation should occupy all the intermediate types
of habitat.   There has been no 'hybridisation' of the
habitat at this site as was happening in the Missouri
valley when Anderson examined the Irises of the flood
plains.

Discussion.

In the analysis of the distribution of the Scottish birch, two alternative bases are offered on which to build any theory.

1. That the birch population of Scotland is one unit.

2. That the birch population is more than one unit.

We shall consider both.

The evidence, though circumstantial, indicates that the diploid and tetraploid races tend to remain pure, though, and this has not been shown to occur in Britain, there is the infrequent chance of transfer of genes from the one stock to the other. Actual transfer of genes has not beenddemonstrated but because of the nature of the variation present in the whole population, there seems to have been, and might easily still be, a mingling of the characters of the two races (I hesitate to call them species).
Ways in which this can be effected have been discussed on p. 36 et seq.

With this evidence, support can be given to either alternative.

a. Consideration of the first possibility.

If the birch population of Scotland is to be considered
as potentially panmictic the differentiation which has
arisen between the races must have done so by the operation
of non-genetic processes.   Prime among these is spatial
isolation.   Since we have dealt with characters which
are non-adaptive (or better non-selected), the/of the accumulation
genes which control the expression of these characters
wil proceed accirding to the laws of chance.   Has this
variation proceeded at random ?

The significance of the direction of the change
in the mean values o. the characters studied has been
noted (p. 63) and the meaning of it discussed.   Since it
is associateu with a change in the proportions of the two
genetic racws, and also with a change in the climate,
particularly the rainfall, it appears that the characters
are not of this non-selected type.

If the graphs of the mean values are examineu in
greater detail the variation of the means shows some inter-
esting features.   Once the population consists entirely
of tetraploids the variation shows no tendency to become
associate. with a factor intrinsic to the tree.   What

happens is that each population has a particular value

which falls between certain limits disposed about a

general mean.   In the transition zone the variation

is of this type but because of the complicating factor

of proportions of types present in the populations

there is the tendency for the values of the means to

arrange themselves in an ordered series.   No

extensive area of diploids has been found in the north

of Scotland but where such an area exists it will show

that the diploid varies as much as the tetraploid.   The

Scandinavian workers consider that the diploid

B. verrucosa is a uniform species and that the tetraploid

is the one which varies to the greatest extent.   Till

conclusive evidence proves this we shall take it that

the one is as variable as the other.   It is not

necessarily true that since one possess/twice the genetic

material (as observed and not actually determined

quantitatively), it also possess twice the number of genes

and hence twice the variation potential of the other.

From this, there are two factors responsible for the

pattern which the variation takes.

1.   The directive influence of climate and ecology.

2.   The random differentiation caused by mechanical

separation of each population.   .

The significance of the climate and ecology in determining the pattern of variation has been discussed elsewhere and we shall return to this aspect of the problem in another part of this section.

The random variation which is present in all populations has been the subject of much discussion and the theoreticians have contributed the most valuable material to this discussion, particularly Sewall Wright (1921, 1931, 1943 and 1946).

In any local population the numbers of individuals which differ from each other will be a function of the number of genotypes which are capable of giving rise to different phenotypes regardless of the effect of the modifying influences of the environment.   Where phenotypes are similar, the cause may be either the expression of similar genotypes, or moulding of different plastic genotypes by the modifying influences of external conditions.   With species which are not plastic, i.e. where the genotype is rigid in its requirements and conservative in its expression, a uniform facies will be presented to the observer.   In a theoretical consideration the expression

of characters which are not selected,and which are not
subject to change by extrinsic factors,will be as determin-
ed by the genotype and solely by this intrinsic complex.
The variation which we are studying is of this type.

Within any one station there is a certain amount
of variation.   How does the range of this variation
compare with that found in the whole population ?
The only valid measurement is the mean value of the
character studied but the sets which contribute to this
mean will not be the same in each population.   Any
division into sets will be purely arbitary and, though
an assessment of the numbers in each group would be
useful, it would lead to conclusions based of false
fundamentals.   In measuring the proportions of
genotypes determined by two alleles in a pupulation it
is not only useful but necessary to divide the population
into groups.   Where multi-factorial systems are operat-
ing, similar groups can be erected but the number will be
large.   If, as has been assumed, the effect of the
indiᵥiduals genes in such systems is additive, then if $\underline{x}$
                 present
dominants are/ the effect will be kx - p (p is the effect of
recessives if such effects are subtractive; where the
recessives have no effect p = 0.   k is a variable which

can be made equal to 1 by suitable choice of values

viz. each dominant gene contributing the same amount

to the system). It has never been proved that each

gene of a polygenic system, when present as a dominant,

contributes the same amount to the phenotypic expression,

so that genotypes possessing the same number of dominants,

say x, may not have the same phenotype. Where the

expression of a character is determined by as few as

four genes the number of genotypes which is formed by

various combinations of dominants and recessives is

large and the variation is almost continuous. Mather

(1943) gives a resumé of the implication of polygenic

inheritance in mendelian populations. We have no

other alternative but to consider that the inheritance

of shape (leaf, bract, and fruit) is under the control

of polygenic systems.

Let us now consider the factors which can effect

the fixation of variants within the populations :-

1. Size of the population.
2. Type of mating system.
3. Number of generations passed since the
   establishment of 2.

Sewall Wright emphasised the importance of the

size of the breeding population in the fixation of

characters. He showed that where the breeding
population is small there tends to be the fixation of
non-adaptive or even deleterious characters. This
effect called drift can operate in any group of
individuals constituting a distinct unit and in
subsequent papers he showed that the most rapidly
evolving system is one composed of units separated in
space; the so called 'island model'. This allows of
interpopulation differentiation and, with migration of
the different types which have arisen in each distinct
population permits of the maximum operation of selection
on an optimum system, since the migrants may be more
successful than the indigenous type.

Such a system operates in birch.

The breeding population is small. In considering
the structure of a population we have:-

1. The total number of individuals.
2. The number of reproducing individuals.
3. The number of males reproducing.
4. The number of females reproducing.
5. The non reproductive part.

Observations show that the number of functionally
female trees is small. Birch is monoecious so an

individual is potentially hermaphrodite but in actual
fact individuals are functionally neuter, male or
hermaphrodite.   Since the population number, N, is
nearest the lowest number of one reproducing group,
in this case it approximates to the number of
functionally female trees.   No counts of the number
of trees which actively contribute to the female
population have been made but the number in the seed
samples reflects this number.   It is much smaller
than supposed.

Essentially we are dealing with small populations.
What other factors can lead to the establishment of
nonadaptive characters ?   One dealt with by
Salisbury (1930) is the fixation of characters in the
seedling stage which in no way enable the adult to be
at an advantage over others in the population.   This
happens with many organisms.   Another factor is
the long reproductive life of the birch (and other
trees).   With the capacity of contributing to the
gametic and zygotic population for a number of years
there is the chance of survival of genetic material
from a disadvantageous genotype or of non-adaptive
characters.   Where selection depends on a whole or

nothing basis a more uniform population will result.
With directed breeding long discontinuous breeding
cycles do not produce the same effect as random
breeding does on the same system.

Birch is monoecious. Sewall Wright (1921)
showed that a population of monoecious individuals
could be considered as similar to a population of the
same size but made up of equal numbers of males and
females. The approach of homozygosity is 1/2N
(in 1943 he gives the figure $(\frac{1-1/2N}{2N})$ per generation.
If each local population is indeed a separate unit,
each should present a certain degree of homozygosity,
quantitatively similar but qualitatively distinct
i.e. as was pointed out by Sewall Wright the homozy-
gotes which are fixed are done so on the basis of
pure chance. Where·selection is operating, the
homozygotes which are fixed will be similar if the
direction of selection is the same in all the
populations. If this system were in operation,
i.e. closed breeding units under the influence of
selection, each population should present a certain
degree of uniformity. This is not the case. Two
factors may be responsible for this non uniformity:-

1.   Migration of genes.

2.   The non-operation of selection.

Migration of genes in plants can only take place
by the passive mobility possessed by gametophytes
and dissemules (seeds, or cuttings etc.).   The
fruit of birch is adapted for wind dispersal but the
distances covered by them   are small. Exception-
ally, a few seeds may be transported over,large
distance by some abnormal mechanism.   The pollen
on the other hand is capable of wide dissemination
by wind and hence may be responsible for the
distribution of genes.   It is difficult to measure
the exact distance which pollen can travel and still
                          be
remain alive and so/able to contribute to the breed-
ing population of the area in which it finally
arrives.   The distances travelled will vary from
day to day and from year to year,depending on the
wind strength, barometric pressure, humidity, and
temperature to mention just a few of the external
factors which determine the range of the pollen's
dispersal.   The indication is that migration of
genes does not take place to any great extent by
the movement of pollen.   The establishment of

seedlings (not necessarily many, say 0.01%) from adjacent populations is the factor which contributes most to the effects of migration of genes on the uniformity of a population. With the small number of migrant gametes contributing to the actual production of zygotes, the effects of competition are great and the probability of one acting as a partner in a successful fertilisation is small. Where the migrant zygote becomes established in a population it is likely to/phenologically similar to the others in the population and with its production of genes (as gametophytes) the number of migrant genes in the population is large. Because of the infrequency of this latter occurrence, migration plays a small but important part in contributing to the variation which is present in the populations.

The other factor, absence of selection, may be of greater importance but it must always be kept in mind that the measurements were made on characters which were thought to be unaffected by the effects of selection. Because of this, absence of selection cannot be considered as a factor determining the variation, just as we cannot use selection as a factor

to explain that variation which is directed (in this case
that small area where the proportions of the two cytological
races are changing).

We are left with the number of generations which have
been passed through since the establishment of the breeding
system 2 as an explanation of the variation.   This
is the number of generations passed through by a local popula-
ion on the same site, or in an area which can be shown to
have had breeding continuity for a considerable time,
and not the number of generations since the establishment of
the species.   The life of natural birch can be put
at say, 100 years though it is probably less.   All the
stations which were examined were from 20-70 years old
but one (St 10) may have been older and another (St 6)
younger.   There is no evidence proving that they are
occupying sites which have been permanently occupied by
birch.   The uppermost limit of colonization is since
the end of the Ice Age, but because of the temperature
changes no one tree genus has been able to survive on the
same site as a dominant.   If the stations which have
examined have not been interfered with by man, and

this is unlikely, they have been probably occupied by
burch f r not more than 1,000 years.   This means that
say 20, generations have been passed through since the
establishment of the stations.   The approach to
homozygosity has hardly begun.

b. Discussion of the second possibility.

Can the population be sud divided ?   Let us
consider factors which may be able to cause sub-division
of the population: they are all genetic.

We have dealt quite fully with the aspect of different-
iation, in the case of the two cytological races
(diploid and tetraploid) being considered as the one
unit, and since we have introduced subdivision we are
now considering the second alternative.   Points
made with regard to local populations are still valid
in the present arguments if the local population consists
of the one race.

Genetic factors potentially capable of causing isola-
tion are :-

1. Alteration of the chromosome number by the
   process of polyploidy.

2. Changes in the basic chromosome complex by the
   production of translocations and inversions.

3. Differentiation due to mutations affecting the
   physiology of reproduction e.g. sterility factors.

All three may be in operation at the same time.

There are two polyploid races within the Scottish population of Betula and the evidence which we have indicates that each tends to remain pure. There is little transfer of genes from the one to the other and such transfer as does occur is rare and the product of a very abnormal biological occurrence (see p.63). It is permissible to say that the Scottish birch is divided at the level which we have erected as the basis for separation 1.

Can the chromosomal aberrations present in the populations act as effective isolating mechanisms ? We have discussed the presence and the probable consequences of translocations and inversions but we have still to consider them as isolating agents.

There are present in the populations the types of cytological abnormalities which have been mentioned in the previous paragraph and from the work of Dobzhansky and Tan (1936) on Drosophila pseudo-obscura and miranda we can safely assume that they are able to cause separation of the bearers. Their work was instrumental in showing the genetic homologies and differences of the

two species.   It is almost impossible to decide whether
class 2 or 3 is responsible for the initial separation.
When we consider the large number of unsuccessful
pollinations which occur in birch it appears likely that
there is some factor operating to prevent the free union
of gametes.   The peculiar pollination-fertilisation
cycle of birch does not permit of alternatives.   If
an unsuitable male gamete is present as the result of
pollination,no viable zygote is formed since fertilisation
is impossible.   Some chromosome arrangements will be
capable of accepting the vast majority of other arrange-
ments and it is only the occasional zygote which does
not survive.   On the other hand where the female parent
is of a highly aberrant nature it will only be the odd
fertilisation which produces a viable zygote.   Inter-
mediate types of chromosome arrangements can occur, but
the intermediate fecundities which are present are probably
the result of inclement weather conditions at the time
of pollination or fertilisation, and are not a reflection
of the intermediate aberrations.   This can be an isol-
ating mechanism.   Within a population there are those
types which possess aberrant chromosome arrangements,
so we have isolation within the two cytological races.

Blakeslee (1929) and Blakeslee et al. (1937) showed that there exists within <u>Datura stramonium</u> a number of chromosome races which are regionally separated. These prime types as they were called, could be crossed and the translocations found with certainty. The prime types are homozygous for such translocations and therefore unable to be distinguished from each other unless crossings are made. In birch, individuals are heterozygous for translocation within any one region or population i.e. the chromosome types have not been selected for homozygosity. This may be another result of the long generation time of birch.

The forces selecting for homozygosity of chromosome arrangements are much more powerful than those operating on allelic series (whether multi- or other-wise). We see that it is possible for non adaptive characters to become fixed under such circumstances and even, in some few instances, there may be the fixation of <u>deleterious genotypes</u>. With the presence of such aberrations in the population, the number of breeding individuals is much reduced. The approach to homozygosity, genic or chromosomal will be much more rapid. This would be so

if birch were a quick breeder.   It is not.

Individual genes which may act as isolating agents
have not been sought &&&, principally because of the
difficulty of detecting them with such intractable
material, but their absence should not be precluded.
Important as they are in any genetic system they can
never enable a species to become separated into
homozygous groups.

Though the facts which have been presented in
support of the hypothesis that the genus Betula and
in particular the collective species B. alba is
composed of separable units I think, intuitively more
than by any logical process of reasoning, that the
collective species should be considered as the one
unit.   (Note: I have deliberately refrained from
qualifying this unit, and it is quite valid to
consider that B. alba consists of a number of
taxonomic units).

Du Rietz (1930) and Stebbins (1950) are of the
opinion that the genus is the more natural unit
than the species in the Betulaceae and the Salicaceae.
Du Rietz does not categorically state this, but it is

implied in his using the term syngameon. His
hypothesis that there are two systems causative
of the polymorphy found in the families mentioned
above is very attractive and it is well to consider
them here.

1. A system in which a number of taxonomically
separable units have become established and subse-
quent hybridisation between the units has produced
a polymorphic aggregation of individuals, cf. the
Salicaceae.

2. A polymorphic group of individuals from which
there is arising a number of units (not necessarily
taxonomic) cf. the Betulaceae.

In this I agree with Du Rietz.

During the period of maximum glaciation it is
unlikely that any arborescent species survived on
the ice free areas present in the ice sheet (the
nunataks). It has been claimed that these nunataks
afforded refuge to the hardier plants which subsequent-
ly migrated from these nunataks to the uncolonized
areas exposed on the retreat of the ice. There is
little vegetation on such nunataks as exist in

Greenland and Antartica, and thepresent, in all

probability reflects the past.   I see no reason for

claiming that the nunataks were a reservoir of plants.

Assuming that the nunataks were not refuges of

birch this species must have been forced into an area

somewher in Central Asia.   The present distribution

of Betula does not suggest a forced migration south-

wards (ther is only one colony of birch south of Europe

and that is very local , Lindquist, 1947), but a

migration to the east.   The colonization of the

areas exposed by the retreat of the ice was made by

individuals descended from this central stock.

Probably the stock was finally fairly uniform and the

migrants reflected this parent scource rather accur-

ately.   With the migration, which would at first

proceed at random (i.e. radially and uniformally),

there arose the possibility of differentiation

effected by isolation in space, as has happened in

Betula series verrucosæ , and also the variation

which can arise by genetic isolation.   The initial stages

of this genetic isolation may have been present in the

glacial remnant and it has been the separation

afforded by migration which brought it into greater
prominence.   Huxley (1942) considers genetic factors
as isolating mechanisms and comes to the conclusion
that they may operate in plants as a prime mover of
speciation, but it is unlikely that they are solely
responsible for the process in animals, it being
necessary to have in addition geographical isolation.

Lindquist's hypothesis concerning the migration
of B. verrucosa var. saxatilis and B. verrucosa var
lapponica supports the contention that the glacial
remnant of the Betulas was centred in Central Asia.
These varieties of B. alba arose separately at some
stage in the migration, one, the former moving along
the North European Plain, the other, reaching the
western regions of Europe via Northern Russia, Finland
and the Swedish Norrland.   They have met in Northern
Sweden, there being a zone of intergradation in the
area of overlap.   They seem to be remaining pure.
An analysis of the situation over the whole of
Sweden show that the two varieties make a dimorph
cline running from south to north; saxatilis -
lapponica.   Var. lapponica does not occur in
Britain.

One big problem without solution is the time of origin
of the tetraploid. It may have been that Betula
had become separated, previous to the glaciation, into
a number of species, all of which were forced into the
central retreat and two of these crossed and by
amphidiploidy gave rise to the tetraploid. This
allopolyploid could only be stable if the constituent
genomes were not closely related. It seems that I
have contradicted myself about the structure of this
refugee nidus but the resulting panmixia brought about
before the migration started would entail:-

1. The production of allopolyploids, if possible.

2. Approach to homozygosity within types of the
   same chromosome number.

3. Because of the extreme selection pressure the
   types which would survive would be remarkably
   uniform.

The immediate pre-migration population would consist
of polyploid series each of which was remarkably uniform.

If we compare this withthe Salicaceae, we can see
that if the process is cyclical, and the same syatem

operates in the willows. then the willows are at
a stage which birch passed previous to migration.

Contrary to what is most

commonly held, I believe that ecological migration is a rapid phenomenon (cf. Skallam, 1951) depending on accident rather than obeying any set of laws. Initial colonization will proceed with the type which is present at the time when the colony arises. Selection will only operate whenever intraspecific competition comes into being i.e. no matter how badly an individual may be adapted to the particular station, if it is the only one which is present it and its descendants will survive till something better is introduced, either from outside or by recombination and mutation.

The same thing, on a smaller scale is happening in Britain.

Equilibrium has not been reached and genetic races (which may or may not be ecological or geographical races) are still being crystallised from the mass of individuals constituting the genus Betula.

How can this variation be classified and comprehended ?

The concept of the Ecotype was proposed by
Turesson (1922) and has been developed by Gregor (1944),
Turrill (1946), and Clausen, Keck and Heisey (1939) as
a taxonomic unit applicable to subdivisions of the
species.   Turessons work was of an observational
character but the fundamental ideas behind the
hypothesis are sound.   The subsequent work of the
authors mentioned above helped to establish the ecotype
as a working hypothesis and also the importance of this
unit in the understanding of the dynamics of the species.
Slight differences are attached to the interpretations
of the term by different authors/particularly bet-
and such differences exist
ween the school of experimental taxonomists of the New
World and those of the Old.   The difficulties are
more imaginary than real, for the ranges of the plants
in the areas worked by the American authors are much
larger than that of the European (Gregor in discussion).

A significant advance was made in the subject of
classification of the variation found in a species when
Huxley (1938) introduced the term cline as an auxiliary
taxonomic unit.   A solution of the difficulties
confronting the student of evolution in small groups of
species is being approached by the use of those two

concepts.   Gregor (1946) in particular considers that
the synthetic methods introduced by using these concepts
will do much towards supplying the answer to interpreting
the variation found in the widespread and biologically important
ant.. species.

Huxley's interpretation of the geographical replace-
ment of races is based on his knowledge of the animal
kingdom and though there is much in common between plants
and animals, some features of the plant do not permit of
their being studied in quite the same fashion.

The cline concept depends on the replacement of one
race of a species by another differing from the first in
some small quantitative character (either a single charac-
ter or a small change in the total organization of the
individual e.g. size), or in the gradual change of propor-
tions of types present in the populations of the species
as one proceeds in some definite direction.   An example
of the second case, quoted by Huxley, is the cline in the
guillemots (Uria aalge) where the percentage of individuals
possessing the character 'ringed' increases in the northern
populations of the guillemot.   Such a cline as this is
spoken of as a dimorph cline.

In my opinion the concept of the cline should be confined to replacememt of races either geographically of ecologically, and a further condition is that the members of a c.ine should be capable of interbreeding with each other. This prevents our considering the situation found in the birches as a dimorph cline of the two chromosome races. It also precludes the use of such terms as taxo-cline and chronocline (Huxley, 1939). There is no great loss in not having a term to denot continuous variation of taxonomic characters but the loss of a term denoting continuity of variation in temporal direction is quite serious, though the proposal on p. 114 for this type of continuous variation may be used as a suitable alternative.

If there is any correlation between the external environment and the variation of the plant, then the variation will always be clinal. All such characters which are selected by the habitat will show this feature of being clinally distributed. Some other characters which do not seem to have any relation with the survival of the individual may in some way be assoc- iated with other more important attributes of the individua by being so closely linked to other characters that they

segregate as a unit or by the genes controlling the character having a pleiotropic action.   It is impossible to prove that the possession of a character confers on the bearer any advantage over the other individuals of the same species, and the only evidence available, is the interference that to live successfully is a function of the attributes of the organism that is living.   The separation of two types of variation is permissible, but for discussion on this aspect of variation see Mayr (1942) and recent papers by Cain (1951) and Carter (1951).

To me it is inconceivable that leaf shape conveys survival value to an individual if the leaf is independent of the external environment.   In the forest trees the shape of the leaf seems to be of little value in conveying advantage to the/bearer but in such plants as the plantains (Gregor, 1939),differences in the shape of the leaf are of prime importance in determining the survival of the individual. With the plantains and herbaceous plants possessing linear leaves, survival of the plant in closed communities is dependent on the leaves receiving sufficient light to carry on the photosynthesis.   In denser stands the individual with longer leaves is more likely to survive than the remainder.

In the flower, shape, except in those very special-
ised orders, will confer little advantage to the bearer
though some of the secondary effects of shape, e.g.
development of the anthers and ovaries may be hindered
by shape of the petals and sepals,and can be of negat-
ive survival value.   The   physiological differences
present in strains will be operative to a greater extent
in the selection of types eventually forming geograph-
ical and ecological races.   This can explain the
morphological similarity of widely disjunct races or the
dissimilarity of races growing in close proximity to
each other.   The degree of morphological different-
iation will depend on the capacity of the species to
          morphological
produce/mutations.   Where the species does not possess
this capacity,morphological differences will be few and
the number of physiological races may or may not be as
high as in other groups possessing the ability to vary
morphologically.   One does not need to consider differ-
ent species of the angio sperms to realise the truth of
this since the illustration provided by the fungi is
quite conclusive.   In this group of plants the degree
of morphological variation in any one species is severe-
ly limited by the nature of the plant.   Physiological

strains are common in the fungi not because of their greater prevalence but because genetical studies are dependant on variation and it is easier to observe the physiological variants in this group than the morphological.

The apparent selective value of any morphological character should not be used as proof that the character itself is the reason of this superiority. It is more probable that the fundamental physiological processes controlling the expression of the character are the real reason for the superiority. Exception to this has been noted in the case cited above.

Though the cline is a useful adjunct to the studying of continuous variation it only describes variation which is capable of being classified in a linear fashion. A much more useful system of classification would be one which included the whole distributional area of the species which is being studied. This would increase the number of dimensions considered to two. There is still another dimension of very great importance in evolving groups, and that is time. This last dimension is the most important and has been studied by the palaeontologists of the present and past but it

has not been incorporated into a system which includes description of the variation existing at ~~the~~ any one level in the time scale.

The present is the only satisfactory instant in which to study the degree of variation present in a species, though in some cases it is possible, where there are sufficient remains, to study the potential and actual variation of the species at some other time.

Simpson, and others have split evolution into two types, complementary and not mutually exclusive. These are 'horizontal' and 'vertical', so termed because of their position on a geneological tree. This does no more than emphasise that there are two systems of evolution, and extant system and the homologous but extinct counterpart. There is no evidence to suggest that a different process is in operation from that of the past. Each is complementary to the other; the advantages of one are not present in the other e.g. wealth of variation in the present but lack of numbers of generations. The opposite conditions hold when studying palaeontological material.

It may seem to most that an additional system which supposedly clarifies the theoretical conception

of evolution creates more problems that it solves.   The
units which make up the evolutionary categories have been
named afresh by each author, who, placing some new
condition on record, uses this as an excuse for creating
a new category.   (I make no excuse for the terms which
I will propose, but I would like to justify my doing so.)
The units which have been proposed have almost always
been connected with those alreafy in existence and
contain in them some part of the prthodox taxonomic system.
On the other hand the terms which are proposed/here are
an attempt to divorce the evolutionary unit from the
classificatory unit, and may have an objective reality.

    The terms are:-

        A.   THE TEMPERON.

        B.   THE KUKLION.

        C.   THE FLUXION.

        D.   THE CLINE. (as used by Huxley)

        E.   THE DEME. (as used by Gilmour and Gregor)

    The temperon is the major unit in this system
of evolution.

    It is the mass of individuals which make up the complex

of species, species groups, or even genera, having a
relationship with each other in time.   At the present
time we can only observe a facies of the temperon but it
is possible to observe the whole of the temperon if the
fossil record is at all complete.   The most complete
temperon is probably the lineage of the horses through
the last 60,000,000 years with the various types which
have been developed from the primaeval Eohippus.   The
living horses re resent the temperon at the instant
in time at which we are actually able to observe it,
but the remains of other less successful types indicate
that the temperon was at a more complex stage at some
previous era.

The temperon may be made as large as one wishes,
to allow the maximum amount of freedom to the interpretation,
though a limit should be put on the term by prefixing, e.g.
if the variation is obviously correlated with changes
in ecological conditions the term Eco-temperon could be
used.   This allows a greater freedom to the concept
but a more precise meaning to the term.

To illustrate what is meant by allowing the term
have such scope, we may think of the following examples

    a.   the Osmundaceae.

    b.   the Angiosperms.

    c.   the Lycopodiales

Each ofthe above examples represent tempera which go back in time to different extents. The last is the oldest and the least complex at the present time, though it was very complex during the Carboniferous.

The ultimate aim is, of course,to consider all living organisms as belonging to the same temperon, but is this not equivalent to the so-called natural classification ?

The four remaing terms of the system refer to the living members of the temperon and are capable of being examined in greater detail by using experimental methods in the analysis. The terms are not original in anything but name, and similarity will be found between the implications of the terms and what has been implied by other terms used by other authors.

What is different is that there is no qualifying statement attached to the definitions, as has been the case with the majority of previous definitions. The concept is purely theoretical and the philosophy behind it is that the evolutionary units have an objective reality. Another important idea behind the concept is that the unit is itself evolving and has a structure which is capable of definition. This idea

is not new for Willis (1922) suggested a similar concept,
though he read more into it than is proposed here.
Another author who suggests that the construction of the
unit differs, (but in this instance no suggestion that
the unit is evolving is advanced), is Du Rietz (1931).
The particular instance which he uses is of interest to us
since he compares the Betulaceae with the Salicaceae and
puts forward the view that the system in each is radically
different (see p.102).

The decision as to what constitutes a kuklion, as
the major unit of the extant members of the temperon
is called, will rest with the specialist working on
the group.   A kuklion consists of the living
members of a temperon, and constitutes those which possess
fairly close breeding affinities forming the one complex.

Groups of individuals which are recognisable as being
closely related are placed in categories supposedly
denoting the degree of affinity of the groups.   When
separation has proceeded to the stage where the groups
are incapable of breeding with each other, the species
level is supposed to have been reached..   In recent
years it has been shown that more and more groups of

inaividuals are

associated even if through another.   If three groups

of individuals A,B, and C are considered, A breeding freely

with B, but not with C, and C is capable of forming

fertile hybrids with C, does one consider A,B, & C as

belonging to the same species or only B&C @ or A&B,

for if B did not exist A & C would most certainly

be considered as separate species.

It is unwise to delimit species on purely genetical

criteria since some established cases of hybridisation,

with the production of fertile hybrids, between

obviously dissimilar groups, have been observed.

The particular example which shows this condition

is that of the tribe Triticinae of the Gramineae where

intergeneric hybrids have been formed and the offspring

were fertile.   It may be that the group has diverged

more in its morphology than it has in its genetical

make up, thus leading to the separation of easily defined

groups which are less discret than they appear.

This and other cases e.g. Phleum pratense and

P. alpinum (Gregor and Sansome, 1930) and Galeopsis

tetrahit (Muntzing, 1932) led me to believe that some term

which could be used to describe all of these and any

other cases which could be found in nature would be of

distinct advantage in the

description of relationships between groups of individuals.

The kuklion is such a theoretical term which can
be used to denote relationship.   It implies no more than
that.

The kuklion can be represented as a circle containing
the groups of individuals which are related to one another
and it is possible to show the exact nature of the relation-
ship by the manner in which the groups are disposed about
the inside of the circle.   This idea is not new but
no term has been used to denote such a system.

The other units of the system are all units which
exist in nature and are capable of being found by
experiment.

The fluxion is the mass of individuals which makeup a
group, determined by the biologist, having a certain degree
of association and homogeneity allowing the mass to possess
an identity separate from other similar groups.   In the
vast majority of cases this will coincide with the taxonomic
species or with the coenospecies.   It will have a geograph-
ical distribution and will itself be made up of smaller
units.   The smaller unit is the fundamental one so far
as the experimental aspect of the system is concerned, just
as the temperon is the basic one on which the whole
hypothesis rests.   This unit is the local population

but I prefer the term deme to the phrase because we can only have one local population (i.e the population has a reality) whereas the deme will allow of comparison, as does the local population,, and of cataloguing, which cannot be done if the local population is used as the unit. There is no need to develope the original concept of the deme, but it is well to describe the concept in order to give this system a completeness which it would otherwise lack.

The deme is that body of individuals, belonging to a specifically separable group, in which there is the potential for free gene flow.   The realisation of this ideal will depend on the size of the groups.   Sewall Wright realised this.   Also Gilmour and Gregor make the comment -----" the tendency is for individuals in close proximity to interbreed more frequently with each other than with individuals at a distance, and thus small more or less isolated intrabreeding colonies are set up." (italics mine). The proposal is made that these small isolated colonies should be designated as gamodemes, but surely every unit (deme) is a potential gamodeme and the term is superfluous. The other terms, ecodeme, and topodeme are very useful as they do not replace any of the terms of orthodox or experimental taxonomy, and do not have ecological significance

We have considered the implications of the units of
the concept which are capable of individual description
and analysis. There is always present the need for a
succinct term to convey the properties of correlated and
comparable characters to the readers of any account of
variation within a species. The cline is such a term.
It allows the consideration of the replacement of types
by others belonging to the same continuous series, which
may or may not be distributed in the same way in the sub-
jective arrangement and in the area which the species
actually inhabits. Where the continuous gradient of
morphological change is correlated with the continuous
gradient of change of the extrinsic factor the cline is
a very useful adjunct to the descriptive terms used in
taxonomy, but if the cline is purely subjective, it
ceases to be of any importance in the comprehension of
variation within a species. The taxocline belongs to
this latter type. Another serious defect of the cline
is that it can only describe variation which is linear,
though in many instances the linear form is derived from
the aggregating of many minor morphological attributes
e.g. size is a function of many physiological and morph-
ological processes, and then deriving a mean from this
total. If the concept of the cline could be extended
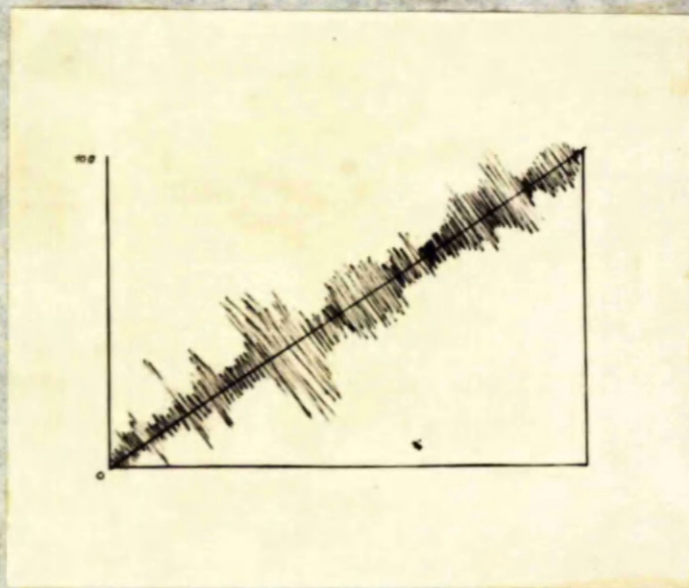
Fig. 25.   Diagrammatic scheme of the modified cline.

to include variation in two planes, one definite, the other varying, very much like the field of an electron in the theory of Quantum Mechanics, then the almost perfect system for describing the dynamic equilibria,(as the species and the local population have been called), would be in existence. Fig 25 illustrates this concept graphically. In subsequent discussion this modified concept of the cline will be used.

The fluxion will consist of a large number of clines, obvious morphological ones, and the less obvious but more important physiological. Where these clines intersect, demes will be formed and these demes will possess features which are the random combination of the characters of the cline. It is unlikely that there will only be one population at the intersection of the clines and the number of populations which is present may not appear to be arranged in any sequence. Those areas where the clines intersect will possess a number of populations (demes) and the whole area may present a facies which is without apparent order. Have we to consider that the area should be designated by some term or is the concept clear enough to permit of lucid interpretation ? The definition which I proposed for the deme stated that the potential for unlimited gene
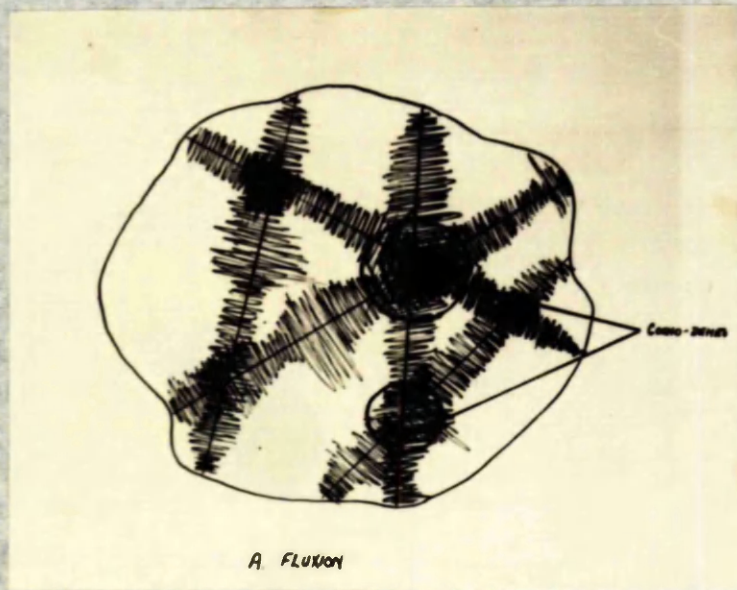
A. FLUXION

Fig. 26.   The fluxion as an areal unit composed of a numb
of clines intersecting to form coenodemes in the regions of
intersection.

Fig. 27.   A diagrammatic representation of a tempero
This has divided into a number of Kuklia, showing differ
degrees of complexity.   Some of these, in particular t
large one third from the left, have split into a system
fluxia.

flow is present and did not include any qualification
concerning continuity of cohabitation.   If this latter
must be considered, then the deme has an absolute reality -
hence the use of the plural in the description of the
complex occurring at the intersection of clines. Perhaps
a term such as the Coenodeme could be used to describe
this complex.   The individual demes of the coenodeme
would not necessarily be similar, there being so many
types of ecodemes and topodemes within the complex.

The size of the coenodeme will be variable depending
on the ecological tolerance of the species (plasticity
of genotype or variability of genotype) and the biology
of the species e.g. whether solitary, gregarious, or in
plants, rare or dominant etc.

Such a system as the above can only relate to cross
breeding species.   Where self fertilisation takes
place or where an asexual method of reproduction replaces
the sexual method, the organisation of the species will be
altogether different.   The constitution will be that of
so many pure lines.   Where the number of pure lines is
large there is the possibility of a system arising which
will copy that outlined above.   If replacement occurs
in these latter instances it will be ecological not
genetic.

We can use the experimental material of this thesis to exemplify the system.

The temperon consists of the preglacial deployment of birches which we assume to have existed, the glacial refuge, and the post glacial secondary deployment which is now in progress.

The kuklion is the genus Betula within which there are the separable groups such as:

Betula series verrucosaea

Betula pubescens complex (probably all the tetraploids)

Members of the sub section nanae.

Etc.

Each one of these constitutes a fluxion. Where two of the groups are sympatric as B. pubescens and B. verrucosa a super fluxion could be erected. Character gradients exist,and there is one in the Scottish Highlands,but my previous objections to calling it a cline still hold. Demes are universally present, and in the area surveyed the coeno deme is not so much the area disposed about the intersection of clines but the area in which two members (fluxia) of the super fluxion meet.

With modification like that above,the system

could be used to interpret and describe the variation
found in most groups of organisms.

Summary.

1.   A cytological examination of the birch population of the Central Scottish Highlands showed the existence of two polyploid races, a diploid and a tetraploid (2n = 28 & 56 respectively).

2.   The races have been claimed to belong to the taxonomic groupings specified as B. verrucosa Arh. and B. pubescens Erh.   The diagnostic characters used to specify these are valid only if the extremes are considered but, because of the presence of intermediate types, it is inadvisable to consider these groups as real evolutionary units.

3.   The polymorphy in birch has been ascribed to hybridisation of the two species, but the cytological results showed that if this hybridisation occurs it must do so at infrequent intervals.   In all the slides examined no evidence was found to substantiate this hypothesis.

4.   Analysis of the morphological characters showed that, though the change of variation is continuous, the eastern populations can be related to a scheme of character gradients.   This change of value is

associated not with a change in the character but with a change in the numbers contributing to the mean.

5.   The biometrical study confirms that the distribution, obtained by direct means in the cytological study, of the chromosome races is diploid towards/the east, tetraploids to the west.

6.   Correlation between this distribution and external factors was sought and the conclusion reached was that the tetraploid is more tolerant of excessive water than the diploid.   This water relationship should be measured in toto as a precipitation evaporation ratio because of the interaction of edaphic and climatic factors. (cf. particularly St. 4.).

7.   The suggestion that the control of homologous organs is effected by the same set of genes is advanced and its implications discussed.

8.   A hybrid swarm (?), situated on Ben Loyal between B. nana and B. pubescens is described.

9.   The causes of the high degree of variability in birch are discussed and the conclusions reached are:-

(a)   That population size associated with the mating system, and

(b)   The long generation time of birch and,

(c).   The post glacial history

have al. contributed to the peventing of the fixation

of definite types.

10.   Selection for an obviously recognisable type has

been slight and such selection as has occurred has

been for physiological rather than morphological

races.

11.   The terms of genecology are discussed and alternative

offered to allow of the recognition and comprehension

of an evolutionary unit rather than a taxonomic one

operating in birch.

12.   The genus Betula is used as an example of this

system.

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Appendix II.

Topographical details of the populations.

Station.	Height above sea level (with range)	O.S. map reference.
1.	40	341627 (sheet 29)
2.	140	317562 (" 29)
3.	650-670	239435 (" 39)
4.	400	218438 (" 39)
5.	640	397178 (" 39)
6.	500-820	116350 (" 38)
7.	770-970	025286 (" 38)
8.	790-960	968226 (" 38)
9.	760-1040	897145 (" 43)
10.	760-1040	863057 (" 43)
11.	830-990	774994 (" 43)
12.	840-1640	677962 (" 42)
13.		:
14.*	840-1550	565913 (" 42)
15.†	1440-1800	465888 (" 48)
16.	560-700	323810 (" 48)
17.	240-580	225810 (" 48)
18.	130-700	174873 (" 47)
19.	100-450	121799 (" 47)
20.	700	016789 (" 47)
21.	100	941796 (" 47)
22.	100-500	835823 (" 46)
23.	100-400	742829 (" 46)
24.	200-400-S.L.	706846 (" 46)
25.	S.L.-200	656852 (" 46)

* Stations 13 and 14 are continuous and because of the omission of St.13 from the floristic analysis it is omitted from all considerations.

† Station 15 in 1950 was drawn from a group of trees lower on the hill, but belonging to the same deme.

Cytological Techniques.

Sectioned material.

a. Methyl Violet.

Modifications on the standard technique were as follows :-

1.   If the cytoplasm showed a tendency to retain the stain after differentiation, apreliminary hydrolysis in N/10 HCl was found to help in the subsequent staining. The time of this hydrolysis must not exceed 5 mins., and it was later found that a more satisfactory method of obtaing this result was to immerse the sections in SO_2 water for 30 mins prior to stainĝng.

2.   Utilization of a weaker staining solution, 0.1% solution was normally used.

3.   Prolonged washing in running water before and after staining. (anything up to 30 mins).

4.   The inclusion of a rinse in Carbol-Xylol between clove oil and xylol I of the normal schedule.

b. Feulgen.

Not a very successful stain and only so after fixation in P.F.A. 3.

c. Heidenhain's haematoxylin.

Very poor results were obtained with this stain

Due probably to the material.

Squash Methods

Aceto-carmine (standard schedule)	Unsuccessful
Acetic-lacmoid " "	Moderate
Acetic-orcein " "	Poor
‡ Nigrosine (see von Rosen)	Erratic
Feulgen	Poor

The above methods were tried and the result of each is shown opposite the stain used.

‡von Rosen,G. 1947. The rapid nigrosine method for chromosome counts applicable to all the growing tissues of plants. Hereditas 33. 567-569.

Statistical methods employed in the biometrical studies
exemplified by reference to Population 4.

1. Leaves.

1949			1950					
A	B	C	A'	B'	C'	A"	B"	C"
25	8	3.20	16	5	3.13	13	6	4.62
25	5	2.18	19	8	4.24	17	7	4.13
19	7	3.68	17	7	4.13	14	7	5.00
20	10	5.00	17	7	4.13	17	7	4.13
18	7	3.88	15	5	3.33	11	5	4.54
22	10	4.55	15	3	2.00	19	7	3.71
21	10	4.76	18	7	3.89	17	7	4.13
18	9	5.00	19	5	2.65	15	7	4.67
22	7	3.18	13	5	3.85	17	7	4.13
28	6	2.24	17	6	3.54	12	7	5.83
16	9	5.63	16	8	5.00	14	6	4.23
24	7	2.92	20	6	3.00	15	6	4.00
19	8	4.22	17	8	4.72	13	6	4.62
23	10	4.35	16	7	4.37	15	7	4.67
23	7	3.04	18	6	3.33	18	8	4.44
25	8	3.20	19	8	4.24	17	8	4.72
16	9	5.63	19	5	2.65	13	6	4.62
28	8	2.84	20	7	3.50	13	6	4.62
28	7	2.50	17	7	4.13	24	10	4.17
27	7	2.54	22	8	3.64	12	6	5.00
22	8	3.64	10	5	5.00	20	8	4.00
21	8	3.82	11	3	2.73	11	6	5.45
19	7	3.68	17	5	2.95	17	8	4.72
24	10	4.17	25	6	2.40	17	8	4.72
28	8	2.84	26	6	2.31			
22	11	5.00	21	6	2.88			
23	8	3.48	20	6	3.00			
19	7	3.68	15	7	4.67			
21	9	4.38	22	10	4.54			
20	8	4.00	18	6	3.33			
26	10	3.85	15	7	4.67			
33	8	2.42	22	8	3.64			
23	11	4.80						
16	5	3.12						
29	8	2.76						
21	10	4.76						
23	9	3.92						
19	5	2.63						
30	7	2.33						
27	11	4.08						
18	8	4.45						
18	9	5.00						
20	9	4.50						

Column A refers to lenght measured in arbitary units

Column B refers to the point of maximum breadth measured in
the same units.

Column C is the ratio $B/A \times 10$.

A', B', and C' are the same measures of the sterile leaves of
the 1950 collection, and A", B", and C" of the fertile leaves.

Let n n' n" be the number of observations of C C' and C" respectively, and t t' and t" the totals of the sums of the values of C C' and C" respectively.

Then $m = \dfrac{t}{n}$, $m' = \dfrac{t'}{n'}$, and $m" = \dfrac{t"}{n"}$

The variance $(\sigma^2) = \dfrac{1}{n-1} \left(\sum (c^2) - \dfrac{\left(\sum (c) \right)^2}{n} \right)$ ---(1

For the 1949 figures this is

$$\dfrac{1}{42} \left(646.7949 - \dfrac{26195.4225}{43} \right) = 0.90612$$

For the 1950 figures $\sigma^2 = 0.68025$ and 0.22866 for the sterile and fertile leaves respectively.

The difference between two means is tested for significance by means of a 't-test'.   This is done as follows:-

1. Obtain the value of the expression contained within the brackets of (1). i.e. (n-1) for each set of figures.

2. Add these values and divide by two less than the total number of observations (call this g).

3. Find t^2 using the following formula.

(we shall compare the sterile and fetile leaves of the 1950 collection).

$$t^2 = \dfrac{(m' - m") \cdot n' \cdot n"}{g \cdot (n' + n")}$$

4. Test the significance of t. (by tables).

For this population g = 0.487907 and hence $t^2 = 23.798$. The value of t is significant at the 0.01 level, in other words the probability that those two sets of figures belong to the same statistical population is < 0.01.

2. Bracts.

A	B	C	D	E	(B-A)	$F(\frac{B-A}{E})$	F (in degrees)
15	19	34	44	20	4	0.200	11
20	20	34	45	22	0	0.000	0
17	16	29	38	19	-1	-0.051	-3
14	21	25	33	14	7	0.500	27
16	20	28	38	16	4	0.250	14
10	16	21	29	15	6	0.400	22
23	31	43	55	15	8	0.533	28
13	18	26	38	17	5	0.294	16
12	16	20	29	13	4	0.308	18
15	20	28	36	15	5	0.333	18
12	17	24	31	13	5	0.384	21
9	14	17	25	12	5	0.416	23
11	16	23	31	14	5	0.357	20
23	33	39	52	16	10	0.626	32
22	31	34	44	19	9	0.526	28
11	12	25	32	16	1	0.063	3
14	19	25	33	18	5	0.278	16
12	16	24	27	16	4	0.250	14
14	22	27	36	12	8	0.667	34
7	12	19	28	12	5	0.417	23
17	15	24	40	19	-2	-0.105	-6
17	22	29	36	14	5	0.357	20
9	16	20	32	14	7	0.500	27
14	21	26	35	14	7	0.500	27
12	13	26	28	18	1	0.557	29

Column A. Length from base to point of inflexion (length of

stalk).

B. Length from base to point of lobe.

C. Length from base to beginning of beak.

D. Total length.

E. Half-breadth at point of maximum breadth, i.e.

across the bract at the tips of the lobes.

F. Tangent of the angle of reflection.

The only statistic employed in the biometrical analysis

of the bracts is the mean of the angles of reflection.

The dotted line shows the route along which
sample stations were chosen.   The open circles
the B. nana sites and the solid dots isolated samples
of B. alba L.

Schematic representation of the ecological structure
of a birch wood.   There are two major divisions within
which there is a number of sub-divisions.

An example of an impression (natural size) obtained
by using the method described in the text (opp).

Scatter diagram of leaf size plotted against leaf
shape.   Note the lack of correlation.

Bract in which the three primordia have developed
individually (x12).

Diagrammatic representation of the mathematical
relationships of the bract.   The point O can be considered
as an origin about which the line OA rotates.   If OA
is of constant length then the hypothetical shapes of the
bracts can be traced out.   However OA only rotates
through a small angle the extremes being OA' and OA"
which give the extreme types of bracts which are found.

Measurements employed in assessing the bracts.

Measurements employed in assessing the samaras.
     a. Half breadth of kernel.
     b. Half breadth of the total wing breadth.

Comparison of the values of the leaf index and the
equivalent value for the bract.

Scatter diagram of the mean values of the leaf index
and the mean value of the point of maximum breadth of the
bract.

Leaf shapes of the parental types and the putative
hybrid.

Statistical methods employed in the biometrical studies exemplified by reference to population 4.

1. Leaves.

1949 A	B	C	1950 A'	B'	C'	A"	B"	C"
25	8	3.20	16	5	3.13	13	6	4.62
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16	20	28	38	16	4	0.250	14
10	16	21	29	15	6	0.400	22
23	31	43	55	15	8	0.533	28
13	18	26	38	17	5	0.294	16
12	16	20	29	13	4	0.308	18
15	20	28	36	15	5	0.333	18
12	17	24	31	13	5	0.384	21
9	14	17	25	12	5	0.416	23
11	16	23	31	14	5	0.357	20
23	33	39	52	16	10	0.626	32
22	31	34	44	19	9	0.526	28
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