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Intraspecific variation in Yorkshire fog
within a limited geographical region.

A thesis presented in partial fulfilment
of the requirements for the degree of
Master of Science in Botany
at Massey University

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1973.

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Abstract.

Topodemes of Yorkshire fog were sampled from within a 50 km radius of Massey University, from ecologically diverse sites, and grown under uniform environmental conditions in order to study the variation in various plant characters between them. In the first of the two experiments undertaken, topodemes were compared as spaced plants in an experimental field. Several characters related to the sexual phase of the life cycle of this perennial grass species (panicle production, seed weight and survival-vigour of plants subsequent to flowering) were not observed to vary between topodemes. For the other such character measured (date of panicle emergence) the differences between topodemes observed were considered to reflect differences in time of pollen release. Thus, where source habitats of differentiated topodemes were in such close proximity that gene flow between them was likely, they were probably effectively isolated.

In the second of the two experiments, topodemes were grown under three water treatments (waterlogged, plentifully watered and periodically dried) in 5-inch pots, one plant per pot, so that differences between topodemes and the effects of the different water treatments on the topodemes could be studied simultaneously. For different vegetative characters studied, topodemes were found to display stable and plastic response to the diverse water treatments, and to be differentiated both in mean response over all, and in pattern of response to, the water treatments. An attempt was made to determine the relationships between the responses of different characters, and between this hierarchy of plant response and environmental variability within and between source habitats. Differential topodeme responses could in some instances be considered to reflect adaptation to the

source environmental conditions. Topodemes T10 and T02, from excessively drained sand dune habitats, possessed more densely hairy leaves, and produced longer laminae under the dry treatment, than topodemes from wetter source habitats. T10 under the dry treatment was able to withstand a greater degree of internal moisture stress than other topodemes before showing signs of wilting. T02 under the dry treatment possessed fewer stomata than topodemes T01 and L02 from marsh and swamp habitats respectively, and in mean response over all water treatments possessed broader laminae than topodemes P02, P04 and L00, also from habitats in which water table level was high throughout the year. P04 and L02 from continuously waterlogged source habitats produced longer laminae under waterlogging than other topodemes, and the latter topodeme, again under waterlogging, possessed a significantly greater mean compressed diameter than other topodemes. However, the evidence for this adaptation did not involve direct experimentation, and therefore the possibility that the genetic divergence demonstrated between topodemes was due to various chance effects, rather than disruptive selection, was not considered irrelevant.

Acknowledgements

The author wishes to acknowledge the guidance and assistance of the following persons, without whose help this thesis could not have been completed :

Drs. Margot Forde[1] (Botany Department) and R.J. Clements[2] (Agronomy Department) for their stimulating joint supervision of this thesis, and Dr. J.P. Skipworth (Botany Department) for willingly taking over as official supervisor.

These three persons for assistance in the harvest of the glasshouse experiment, field planting of spaced plants (R.J.C.), harvesting of field plants during my absence overseas (M.F. and J.P.S.), and guidance in preparation of material for microscopic examination (J.P.S.).

Mr. R. Fletcher (Applied Maths Division, D.S.I.R., Palmerston North) for statistical guidance and use of computer programmes.

Dr. E.L. Breese (Welsh Plant Breeding Station, Aberystwyth) for reading the draft.

Numerous other staff members of Massey University, Plant Physiology and Grasslands Divisions of D.S.I.R., Palmerston North, and Seed Testing Station, Department of Agriculture and Fisheries, Palmerston North for helpful discussions, comments and technical assistance during the course of this thesis.

Margaret Aldrich, Margaret Brogden and Marie-France Nerdinger for the typing of the script.

My wife Linda, family and friends for their generous assistance.

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CHAPTER 1

INTRODUCTION

1.1 The present investigation

Topodemes[1] of Yorkshire fog (*Holcus lanatus* L.) were sampled from various sites within a limited geographical region, and a study made of the variation in plant characters associated with the environmental variation of the source habitats. Yorkshire fog is a perennial, cross-pollinated grass, displaying a wide ecological tolerance, growing in such diverse habitats as coastal sand dunes, peat swamps, and sub-alpine grasslands. This wide geographic and ecological distribution has been reported to be accomplished by ecotypic differentiation (Basnyat, 1957; Bocher and Larsen, 1958). Differentiation over short time-spans has been observed within numerous grass species where selection differentials are high (e.g. in *Agrostis tenuis*, Bradshaw, 1959; in *Anthoxanthum odoratum*, Davies and Snaydon, 1973; in *Avena fatua*, Allard, 1965; and in *Holcus lanatus*, Antonovics, 1971). However, for one such species (*Phalaris tuberosa*) in Australia, McWilliam et al. (1971) were not able to demonstrate ecotypic differentiation. These authors concluded that the apparent evolutionary conservatism of this species in this situation was brought about by broad adaptability of individual genotypes and inability to regenerate from seed, rather than lack of genetic variability or insufficient selection differentials.

The aim of the present investigation was to determine how adaptation of Yorkshire fog topodemes to the various water regimes of the source habitats was achieved. The approach was genecological.

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[1] The term "topodeme" is used to denote plants of the given species derived from a given topographical area. Where it is used in these chapters nothing more is implied by its use.

The collection sites were chosen within a 50 km radius of Massey University to include the range in habitat water from excessively drained to continuously waterlogged. Collection of pasture topodemes was avoided since these were not expected to reflect variation in the natural environment as closely as wild, self-sown topodemes. The sampling procedures and description of the sites are outlined in chapter 2. The study of plant variation in relation to water involved characters associated with the sexual (chapter 3) and vegetative (chapter 4) phases of the growth cycle of this perennial species.

Figure 1. Variation within a Yorkshire fog topodeme.
(see Chapter 2 and Figure 9 for meaning of symbols)

1.2 Genecology

1.2.1 Intraspecific variation and its relation to habitat.

The use of plant populations in the experimental study of evolution can be dated from the investigations of the Swedish plant ecologist Turesson. Beginning in 1916 Turesson (1922a, 1922b,

1925, 1930a) employed extensive observations of widespread plant species, collected in the wild and transplanted into a uniform garden. He was attempting to discover the effects of factors of the source habitats in the differentiation between samples. These observations led Turesson to conclude that wide-ranging heterogeneous species are broken up into clusters of hereditary variants - ecotypes - corresponding to the local habitats occupied. The phenomenon was due to the controlling effects of environmental factors. For this hitherto ignored ecological study of hereditary variation in relation to the habitat, he coined the term genecology (Turesson, 1923).

Figure 2. Variation between Yorkshire fog topodemes.
(see Chapter 2 and Figure 9 for meaning of symbols)

Subsequent authors accepted Turesson's hierarchy of hereditary types (Turesson, 1922), and used his methods to describe ecotypes at the regional (e.g. climatic ecotypes of Clausen, Keck and Hiesey, 1939, 1940, 1941, 1948; Clausen and Hiesey, 1958) and local (e.g. edaphic ecotypes of

Kruckeberg, 1951; Wooten, 1973; biotic ecotypes of Stapledon, 1928; Sinskaia, 1931) levels. However, climate, which is one of the most important habitat factors, varies continuously, and thus one should expect continuous variation in a widespread species (Langlet, 1934). This led to an often heated debate on the patterns of genecological differentation, providing material for numerous reviews of varying scope (e.g. Faegri, 1937; Gregor, 1944, 1946; Clausen, 1951; Gregor and Watson, 1961; Heslop-Harrison, 1964). Much of the debate may be attributed to the definition of ecotypes, which perhaps confers a false sense of homogeneity within, and discontinuity between, products of the species and habitat (Langlet, 1963).

Currently, there is a picture of the plant species in a very fine balance with the environment (Bradshaw, 1959); the patterns of the environmental factors determining the patterns of ecological variability (Langlet, 1963). Genecological differentiation is, then, a well documented and established phenomenon. The patterns of this differentiation are still of interest in that they provide a constant stimulus to the study of natural selection and adaptation.

1.2.2 Some problems in the study of intraspecific variation.

The essential problem of genecology is to devise techniques by which genetic divergence between topodemes arising from selection, may be distinguished and studied (Heslop-Harrison 1964). Thus, genecology has been called the experimental study of adaptation and evolution (Jones and Wilkins, 1971).

1.2.2.1 Genecological trials.

The basic technique, as used by Turesson, involves sampling from the wild, followed by comparative cultivation in a uniform garden, in order to separate genetic from non-genetic components of phenotypic variation. This is followed by the application of statistical methods

designed to distinguish potentially-adaptive from random genetic divergence. However, the methods of the orthodox genecological trial have not always been adequate in distinguishing random from non-random genetic divergence (Harberd, 1957, 1958, 1961; Wilkins, 1959).

The statistical methods have involved the partitioning of genetic variance into between-topodeme and within-topodeme components. This is followed by the comparison of these components to expose as significant those differences that may be adaptive. Such an analysis is suitable only in the ideal situation where a genetically variable species has expanded its range uniformly over an area of diverse habitats, so that the selective forces in each habitat act on the same pool of genetic variability (Heslop-Harrison, 1964). Since most cases in nature do not mirror this ideal situation, there arises the problem of "general uncertainty" of variance found within a topodeme (Wilkins, 1959).

(1) Wilkins (1959) considered the situation in which an area has been colonized by an unrepresentative invasion from another, so that "adaptive" differences arising secondarily as a consequence of selection, are confused with, and cannot be separated from, the original chance differences between colonists and the original gene pool. This aspect of the general uncertainty of within-topodeme variance may be overcome by choosing habitats within the same geographical area, so that non-adaptive differences may be expected to vary at random between them (Wilkins, 1959).

(2) Harberd (1957, 1958, 1961) considered the consequences of genotype reduplication in topodeme samples that have come about due to clonal spread of a single genotype throughout a large area. He suggested that by extensive rather than intensive sampling, so that the numerous topodemes sampled may be grouped according to habitat, the emphasis of the study may be shifted to demonstration of differences

between ecologically-associated groups of topodemes (Harberd, 1961; Lewis 1969). For this, the error term in the statistical analysis will be between-topodeme within-habitat, rather than within-topodeme variance.

In a genecological trial, one must assume that the plants have settled down to the environmental conditions of the trial before character reading can commence. The characters recorded, then, are products of the genotype and test environment; they contain no component relating directly to source environment (Harberd, 1961). Where mature plants are sampled an indefinite time may be required to nullify the effects of the source environment (Gregor, 1930). Thus, cultures from seed are at an advantage in that they will have grown and developed under the test environment from the time of sowing (Gregor 1930). But by taking seeds, one is sampling potential rather than realised variation (Briggs and Walters, 1969), since whole plants are a sample of the status quo. The implications of this are most important when one is sampling from diverse habitats in such close proximity that gene exchange between them may occur (McNeilly and Bradshaw, 1968). A seed sample, then, may contain individuals poorly adapted to the environmental conditions under consideration (Bradshaw, 1959; Jones and Wilkins, 1971). In such a situation both seed and mature plant samples are valuable in that a comparison between cultures from both would reveal magnitudes of selection differentials and gene flow (McNeilly and Bradshaw, 1968). Barber (1965) has also suggested estimation of selection differentials, in his studies of natural variation in Eucalyptus, by comparisons between trees in the wild with their open-pollinated seedlings. Since environmental factors fluctuate from year to year in an otherwise stable environment, a seed sample will be a better sample of the "effective breeding unit" than a similarly sized whole-plant sample taken in only one year (Clausen, 1960). However, if the sample is to be of the status quo, a seed sample may not

be adequate (Heslop-Harrison, 1964).

The ability of plant populations to respond adaptively to a variety of habitats (e.g. Fisher, 1960) will be obscured if the plants are tested under only one set of environmental conditions. Clausen, Keck and Hiesey (1940), being aware of this situation, made clonal transplants of their experimental material into varied environments. The test environment may also invoke characteristics not expressed in natural environments (Sinskaia, 1958; Clausen and Hiesey, 1958) and where this occurs, reciprocal transplants (see section 1.2.2.3) are a means of overcoming this limitation of the transplant garden technique.

1.2.2.2 Habitat factors.

One of the most intractable problems of genecology is the identification of individual habitat factors responsible for selection of a given genetic difference between topodemes. There is always the possibility that some unsuspected factor is more important than any previously defined or measured (Wilkins and Lewis, 1969). A considerable part of this problem may be solved by accurate definition, control and knowledge of the history of the environmental conditions at the sampling sites (Snaydon, 1970). Such a situation exists at the Park Grass Experiment, Rothamstead (Warren and Johnston, 1964), where known fertilizer (since 1856) and lime (since 1903) treatments between plots have allowed the development of a mosaic of contrasting environments, with sharply-defined borders.

Yet, plants respond to the habitat as a whole (Turesson, 1922a; Wilkins, 1960). They do not respond to abstractions from it that are conveniently measured (Wilkins and Lewis, 1969). Thus, the identification of single habitat factors, for correlation with single plant characters (commonly used as evidence for adaptation), is a convenient simplification that could lead to fallacious reasoning about natural selection (Wilkins and Lewis, 1969). To circumvent this problem, one may regard the plants

themselves growing at a particular site as indicators of the environmental conditions there. The use of floristic analysis to extrapolate to the habitat conditions, as done by Wilkins and Lewis (1969), is preferable to instrumentation of single habitat factors made over short time periods, considering the length of time and consequently the diversity and complexity of the environmental conditions that the plants must have encountered during their history. The methods used by these authors involve selecting associated species, known to have a restricted ecological range, to be used as an indicator of the particular conditions. The occurrence of these species may then be correlated with genecological data (see Jones and Wilkins, 1971). However, if ecotypic differentiation is a logical explanation for the wide adaptation within a species, then the worth of a species as an indicator of particular environmental conditions is considerably reduced (Gates, Stoddart and Cook, 1956). Thus, the ecotype or local population, now considered to be more fundamental ecological units than the species (Ehrlich and Raven, 1969), should be used for this purpose (Clausen et al., 1941; Constance, 1953).

1.2.2.3 Plant characters.

The problem of which plant character(s) to study in genecological investigations has provided material for considerable controversy since Turesson. Morphological characters (Gregor, Davey and Lang, 1936; Gregor, 1938, 1939; Davey and Lang, 1939) are most easily measured (Morley, 1959), and thus were utilized almost exclusively in early genecological study. For this reason, and because of the classificatory value for both taxonomy and synecology placed on the genecological units by Turesson (1930b), classificatory (Constance, 1953) and taxonomic (Gregor, 1944, 1946b; Gregor and Watson, 1954) aspects of genecological differentiation have received most attention (Heslop-Harrison, 1964).

However, with the realisation that morphological characteristics of plants could not be used as a guide to their physiology and genetic

behaviour (Salisbury, 1940), and with the reawakening of workers to the ecological aspects of genecology (Barber, 1956), it became obvious that it was important to discover those characters chosen by natural selection (Morley 1959). Physiological (Clausen, 1951; Hiesey and Milner, 1965) and biochemical (McNaughton, 1965; Bjorkman, 1968) characters were considered fundamental to this adaptation (Morley, 1959; Wilkins, 1960; Cooper, 1963; Briggs and Walters, 1969). The visible structural features were considered significant only in that they represent, or are concomitants of, the physiological equipment (Salisbury, 1940). With the development of gel electrophoresis it is now possible to determine protein characters in organisms (e.g. isoenzyme patterns in leaf material, McWilliam, et al., 1971). Such characters are considered basic to adaptation (Gould and Johnston, 1972) in that they are directly determined by the genetic material. This technique has especial significance for the study of geographic variation in animals where previously the distinction between genetically based, and environmentally induced, variation was almost impossible (Gould and Johnston 1972).

It has often been assumed that phenotypic characters are adaptive without experimental evidence to support this view. However, where differences in plants and habitats are correlated this may be taken to indicate adaptive divergence, since the only reasonable explanation of their existence is the differential effect of selection in the various habitats (Heslop-Harrison, 1964). While such correlations suggest adaptive significance, the character involved may merely be a by-product of a more basic, biologically-significant, structure or process (Snaydon and Davies, 1972). Thus, attempts to show that a single character difference reflects adaptation to a single habitat usually reveals unexpected complexities in both plants and habitats (Jones and Wilkins 1971). Other aspects of the uncertainty involved in assumptions of adaptation have been discussed above (see section 1.2.2.1 general

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uncertainty of within-topodeme variance).

This extreme emphasis on physiological variation, due partly to the advancement of techniques allowing its study, and partly to the fact that often the more conspicuous differences in morphology may not be related to physiological variation (Jones and Wilkins, 1971), probably explains the neglect of structural features and their important physiological consequences. There have been, however, some notable exceptions, for example by Holmgren, 1968, and Lewis, 1969. Also, the ecological-physiological significance of shape and structure was considered by Bocher (1963) who, in his comparison of floras from different climatic and edaphic zones, noted similar environmentally-orientated morphological trends both at the genecological and intergeneric levels (c.f. Clausen, Keck and Hiesey, 1941). Similar trends may also be observed between plastic response and hereditary variations (Turesson, 1922b; Clausen, Keck and Hiesey, 1940; Bjorkman and Holmgren, 1963) and between species at the genecological level (Turesson, 1925, 1930; Clausen, Keck and Hiesey, 1941; McMillan, 1964, 1965). Such evolutionary parallelism at these different levels has been taken as evidence that structural differentiation is causally adaptive (Turesson 1922, 1925; Harberd, 1964; Bradshaw, 1965).

Since Raschke (1960) it has been realised that the size and shape of leaves, leaf anatomy and plant habit, have a profound influence on the physiological behaviour of plants, especially with respect to gaseous and heat exchange between plant and environment. It is now possible to calculate the physiological effects of structural features from empirical formulae (Gates, 1962), and these have been applied to physiological studies (e.g. Beardsell, 1970). The importance of this to genecology is that it is now possible to investigate experimentally the physiological significance of structural differentiation in plant populations (Lewis, 1969).

Just as plants respond to the habitat as a whole (section 1.2.2.2), so plant response is a holistic or multidimensional process. This process involves a variety of interdependent plant factors (Sokal and Rinkel, 1963). Thus, as many characters as possible should be considered similtaneously (Harberd, 1964; Gould and Johnston, 1972) followed by use of one or more of the many methods of analysis of character variation available (Crovello, 1970). However, any experiment which ignores competition cannot be used to predict what will be found in the wild (Jones and Wilkins, 1971). Thus, an alternative approach is to measure response of the whole plant to the whole environment, by testing survival of the plant in a given habitat. It is this response that is of adaptive significance; all other evidence is circumstantial (Wilkins, 1960). The reciprocal transplant method as used by Snaydon and Davies (1972, for reference) measures this response, by measuring survival half-life of topodemes in their source and other habitats. Competition methods have been used extensively in the past, but they usually involved measurement of individual plant characters (e.g. Charles, 1964 and McWilliam et al., 1971).

1.2.3 Adaptation to heterogeneous environments.

The techniques of genecology discussed above are designed to show that habitat-correlated plant variation is genetically based and so subject to selection (Heslop-Harrison, 1964). However, in any given investigation the variation observed may be explicable in terms of (1) Hybridization between taxa whereby the parent taxa are completely swamped by hybrids, presenting a situation having the characteristics of selection (Harberd, 1961), (2) Genecological differentiation (Heslop-Harrison, 1964), (3) Direct effect of the source environment upon plant phenotype (Bradshaw, 1965) or (4) Action of natural selection upon environmentally-induced transmissable variation (see section 1.2.4.4). Thus, where intraspecific spatial variation is observed, one must distinguish between these four

possibilities.

(1) If within one geographical region most taxa could be shown to display parallel differentiation or if it could be shown that different characters respond differently to different environmental influences, then it is unlikely that the situation could have arisen by hybridization (Harberd, 1961).

(2) Differentiation is most likely to occur where environmental factors vary in space, but are relatively stable with time (Levins, 1962, 1963; Maynard-Smith, 1966). Soil factors have this type of variability, and differentiation in response to this factor has been demonstrated frequently, even in situations where gene flow is considerable (for examples, see previous sections). Genetic adaptation to heterogeneous environments may also occur under conditions where the environment fluctuates in a regular way. Such periodicity is an essential feature of the environment of all living organisms. Organisms have often been demonstrated to exhibit similar rhythms in their physiological and chemical activities (Sweeney, 1963; Wilkins 1969), and consequently have the ability to perform given activities at given environmental times; that is, times of day, phases of tide and seasons (Enright, 1970). The structural, physiological and behavioural characteristics allowing organisms to do this are almost certainly not directly attributable to the environment, since it may be shown that in the absence of entraining environmental rhythms, biological periodicity continues (see Wilkins, 1969, for examples).

(3) Irregular, unpredictable fluctuations are also a feature of the environment and plants are seen to respond to these by possession of broad adaptability of individual genotypes (Bradshaw, 1965; Cook and Johnson, 1968; McWilliam et al., 1971), allowing direct modification of the phenotype. Plasticity displayed by higher plants is made possible by their mode of growth by apical meristems (Heslop-Harrison, 1964). As in the genetic situations above, plasticity must not be considered

unconditionally as being adaptive, but direct supporting evidence is required (e.g. Whitehead and Luti, 1962; Whitehead, 1962, 1963; who show that anatomical and morphological changes induced by wind were advantageous to the overall water economy of their experimental plants). And now that the physiological consequences of structural features of plants can be calculated from empirical formula (Gates, 1962), many more such definitive studies on the adaptive significance of plasticity may be carried out (e.g. Cook and Johnson, 1968). The remarkable property of some plant characters to remain relatively invariable in the face of environmental change (e.g. seed size, Puckeridge and Donald, 1967), while other characters show high plasticity, is considered a homeostasis affecting the characters most important for maintaining a continuity between generations (Allard and Bradshaw, 1964). The adaptive significance of this homeostasis can be seen in the repercussions of change in these "constant" characters (Harper, Lovell and Moore, 1970). The ability to respond phenotypically to various habitats must itself be genetically controlled and so subject to selection (Bradshaw, 1964). Such genecological divergence in plasticity has been demonstrated in morphological (Mooney and Billings, 1961; Cook and Johnson, 1968) and physiological (Bjorkman and Holmgren, 1963) characters.

1.2.4 The genetic system and intraspecific variation.

The powerful all-pervading effect of the environment in determining the extent and pattern of genecological differentiation (Bradshaw, 1959) was first stressed by Turesson (1925): "Ecotypes do not originate through sporadic variation preserved by chance isolation; they are on the contrary to be considered as products arising through the sorting and controlling effects of the habitat factors upon the heterogeneous species population". Since then our understanding of genetic variation, its generation, recombination, exposure, conservation, concealment and loss (Darlington, 1939; Mather, 1943), and its interaction with the habitat

factors in producing intraspecific variability has increased and expanded (Bradshaw, 1959; Snaydon, 1962; Snaydon and Davies, 1972). Thus, the genetic system, and the factors impinging upon it, govern the flow of genetic variability in a population, so affecting the potentialities for response to selection (Heslop-Harrison, 1964). Numerous review articles (Heslop-Harrison, 1964; Gould and Johnston, 1972) and chapters in books on biosystematics (Davis and Heywood, 1963; Solbrig, 1970; Jones and Wilkins, 1971) discuss this aspect of natural variation. Thus, only the more interesting or recent studies will be discussed here as they impinge upon adequate design and execution of a genecological investigation.

1.2.4.1 Availability of adaptive variation.

Without genes of adaptive value, a population cannot evolve under the influence of natural selection (Bradshaw, 1959). Populations of *Festuca ovina* (Wilkins, 1957) and *Agrostis tenuis* (Bradshaw, 1953) display tolerance of heavy metal contamination. Other species growing immediately adjacent to contaminated soils do not show this tolerance; an observation explicable in terms of the absence of adaptive variation allowing these plants to tolerate these conditions (Bradshaw, 1959).

1.2.4.2 Discontinuous or continuous variation?

Most variation observed in nature is so subtle that quantification is required to discover its patterns of distribution (Gould and Johnston, 1972). Further, characters considered to be components of fitness are quantitative (Sokal, 1962) in that they vary continuously, and are thus considered to be under polygenic control (Mather, 1943). As such, these characters tend to be responsive to even minor environmental changes, responding rapidly and vigorously (Bennett, 1964). Direct assessment of the genetic basis of intraspecific variation, that in the past involved complex breeding routines (Clausen and Hiesey, 1958), or in special circumstances gross chromosomal differences of major

Mendelian genes (Dobzhansky, 1970), is now possible using the techniques of gel electrophoresis (for examples, see section 1.2.2.3).

1.2.4.3 The reproductive system.

A proper analysis of the selective forces within any habitat requires a knowledge of the "free path of a gene per generation" (Barber, 1965), which requires a knowledge of the size of the breeding units. In obligate self-pollinating plants, each plant forms the entire breeding unit. Thus, by preventing recombination, such a situation must be considered an "evolutionary cul-de-sac" (Darlington, 1939). However, there are probably few or no species, or species complexes, that do not retain the ability of recombination, even in apomictic species (de Wet and Harlan, 1970). In cross-pollinating species, the size of the breeding unit (free path of a gene per generation) is determined by the spatial pattern of plant distribution, which is influenced by many factors (Heslop-Harrison, 1964). For example, discontinuities within the geographical range of a species, whatever its cause, will allow evolution of distinct populations by preventing gene flow (Bradshaw, 1959). Spatial discontinuity observed in Potentilla glandulosa in Southern California (Clausen et al., 1939) probably accounts for discontinuity between coastal subspecies typica and inland subspecies reflexa (Briggs and Walters, 1969).

Another factor influencing the spatial pattern of plant distribution is the mode of pollen and propagule dispersal. For example, the free path of seed in Eucalyptus is about equal to half the size of the tree (Barber, 1965). Where dispersal vectors involve animals, birds or wind, these distances will be much greater, so reducing the isolating effect of local edaphic discontinuities, even where the distribution pattern is fragmented, as in coastal Plantago maritima (Gregor, 1946). Where insect and bird pollination occurs, the ecological limitations and behavioural patterns of the vectors (Levin, 1970; Macior, 1973) might effectively exclude gene exchange between concentrations of plants within

close proximity (Free, 1966, on pollination ecology). In wind pollinated species, the effective pollen range may be quite small (table I), since the chance of fusion between gametes of remote origin is determined by proportions of local and foreign pollen in the atmosphere (Heslop-Harrison, 1964). Despite these often small effective

Table I: Effective pollen range.

Species	Distance	Gene flow	Source
Zea mays	18 metres	1%	Bateman (1947)
Lolium perenne	2 metres	15%	Griffiths (1950)
Agrostis tenuis	16 metres	4%	McNeilly and Bradshaw (1968)

pollen ranges, pathways do exist for gene flow in continuously-dispersed wind-pollinated species, and thus discontinuities are unlikely to arise (Mayr, 1963), or where they do arise in close proximity (McNeilly and Bradshaw, 1968; Snaydon, 1970), gene flow can be expected to slow the process of differentiation (McNeilly and Antonovics, 1968).

Ehrlich and Raven (1969) cite examples of both plants and animals where spatial differentiation has occurred in the absence of extrinsic barriers to gene flow (see also Thoday's experiments on reproductive isolation induced by selection in *Drosophila melanogaster* and Antonovics, 1971). They conclude that gene flow is considerably more localised than previously thought. The debate on the relative importance of gene flow and selection in differentiation (and consequently on speciation) continues (e.g. Endler, 1973).

1.2.4.4 Environmentally-induced heritable variation.

Heritable variation in some instances has been recently shown to be induced by the environment. Such environmental effects may be transmitted vegetatively (Breese, Hayward and Thomas, 1965) or via the seed, either cytoplasmically (Hayward and Breese, 1966) or perhaps in

the nucleus (Durrant, 1962; Evans, 1968a, 1968b; Hill and Perkins, 1969). These environmentally-induced differences, being transmissible, and so subject to selection, may increase adaptation of populations to particular environments. However, nuclear effects have only been induced in a few characters in inbred lines of Linum and Nicotiana (Hill, 1967); and vegetatively and seed-transmitted "plasmon" differences in Lolium (Hayward and Breese, 1966; Hayward, 1967) have been recorded only for a few characters in long lived perennials with little sexual reproduction. The mode of inheritance may, then, be seen to affect the patterns of genecological differentiation especially where selection differentials are low. Snaydon and Davies (1972) consider an example where a large maternal component of inheritance, being less subject to recombination and gene flow, may increase the rate of differentiation, since the seed would be shed into an environment to which it was well adapted.

1.3 Previous investigation of Yorkshire fog.

1.3.1 General description.

This species is a perennial, fibrous-rooted, tufted, diploid (2n=14) grass, completely covered with hairs, although a wide range of pubescence within the species has been observed (e.g. Basnyat, 1957). Sheaths are split, slightly keeled, green with distinct purple veins, although anthocyanin-free plants are common. The leaf blade widens slightly beyond the ligule, is flat or rolled, 5-10mm wide, pubescent on both surfaces, and keeled until near the tip. Stomata occur on both adaxial and abaxial surfaces, arranged in parallel rows, two to three files wide, immediately adjacent to the primary veins, and usually only one file wide adjacent to the secondary veins. Spikelets are usually two-flowered, both flowers possessing anthers, but usually only the lower one hermaphrodite. A number of variants have been described, including dark green rosette dwarfs and chlorophyll-deficients, both

probably due to mutation. For a more full description of this species, the reader is referred to Beddows (1961a), Metcalfe (1960) and Hubbard (1958).

1.3.2 Geographic distribution.

Yorkshire fog is found in temperate pastoral grasslands throughout the world. Its centre of origin is probably the Iberian peninsula, but it has spread throughout Europe and North West Africa (Beddows 1961a) and has been introduced into Asia, Australasia, the Americas and South Africa. In New Zealand, probably because of its prolific and efficient means of seed dispersal, and its tolerance of a wide range of habitats, it has spread throughout both main islands and the more remote Chatham and Auckland Islands. Its colonization limits probably exceed those observed in the British Isles (Munro, 1961) where the species is ubiquitous over a wide altitudinal range (Beddows, 1961a).

1.3.3 Ecological distribution.

Intraspecific variation in a number of characters of Yorkshire fog in Western Europe (Bocher and Larsen, 1958), is seen to reflect recurrence of certain climatic, edaphic and biotic sequences. Each plant character is closely associated with length of the active growing period, which is related to temperature regime and incidence of seasonal moisture stress (McMillan, 1959), exposure to wind, and influence of the grazing animal (Stapledon, 1928). Differentiation within this grass species has also been observed in many characters in New Zealand (Basnyat, 1957). The differentiation has been attributed to natural selection (Munro, 1961) acting over the relatively short period since the initial introductions of Yorkshire fog into this country 100-150 years ago. These introductions were thought to be from a limited supply of English seed (Munro, 1961) although no evidence for this could be found in the literature. Whether the differentiation has come about by the release

of variation through recombination, and the interaction of this variation with the local habitats (as suggested by Munro, 1961), or by fixation of chance genetic divergence (the "founder effect", Mayr, 1942), or by some combination of the two, New Zealand is now a centre of diversity for Yorkshire fog (see 1970-1971 Yorkshire fog collection of Clements, Agronomy Department, Massey University).

1.3.3.1 Climatic factors.

The length of the growing period is considered to be under climatic control and may be equated with the period of time for which evapotranspiration is greater than 25.4mm (Munro, 1961, fig 4a). Thus, during the wet months, temperature is probably the limiting factor, whereas in the warmer summer months, moisture probably determines the length of this period (Munro, 1961, fig 4b,c). Numerous regions of diverse growth periods may, then, be described in New Zealand. In this country, Yorkshire fog exhibits a wide range of tolerance of temperature regimes, as do most other western European pasture grasses (Mitchell, 1956; Mitchell and Lucanus, 1960). This adaptation is considered to result from genetic divergence between plants of these regions, although much of the variation observed is found within regions (Munro, 1961, see fig 4d). Temperature tolerance of this grass is considered by Mitchell (1959) to be between that of *Lolium perenne* and *Dactylis glomerata*. In controlled environment studies, this worker showed that the growth rate of foliage on an individual tiller (considered an estimate of production under sward conditions) remained high between 13-30 degrees C with an optimum at 16.7 degrees C. The study of seasonal growth rhythms in this and other species, shows Yorkshire fog to be relatively constant in production (Lynch, 1949; Suckling, 1960). Production is considerably reduced by a lowering in temperature, and, to a lesser extent, by a lowering in light, yet growth and new tiller production continue during the winter.

1.3.3.2 Edaphic factors.

Yorkshire fog is exceptional for its almost complete lack of edaphic specialisation (Levy, 1955; Beddows, 1961a), growing on areas of varying soil moisture, waterlogged to average, and varying fertility, high to low (Levy, 1955), with little apparent effect on growth (Munro, 1961). Although its optimum pH range is 5.0-7.5, it is a colonist on soils of much higher acidity, for example, on wet, poorly-drained peat and rush-dominant flats (Davies, 1944). It has also been reported to form a "first class meadow grass" on soils of almost pure sand (Spillman, 1920); that is, soils characterised by low fertility and rapid water drainage.

Another example of the edaphic tolerance of this species was provided by Antonovics (1971, see table 1). He indicated the relative selective advantage of contrasting types of Yorkshire fog found in natural populations growing on and around a lead/zinc mine. The selection pressure for heavy-metal tolerance on this mine soil was found to be intense (estimate of coefficient of selection, by comparison of seed and adult plants, was 0.46). Thus, in this situation, populations of Yorkshire fog were seen to differentiate, in spite of gene flow between them.

The basis for these wide tolerances are not known, although several factors have been suggested that might be of importance in the supply of nutrient requirements under seemingly adverse conditions.
(1) Anatomy of the root incorporates a radial cortex with many small, irregular air spaces; structures which may increase efficiency of nutrient uptake when soil water level is high and aeration restricted (Soper, 1959).
(2) The root system appears adapted for absorption of nutrients from the surface layers of the soil (Boggie, Hunter and Knight, 1958). The fine network of roots and hairs may appear above the surface under

water logged conditions.

(3) Cation-exchange capacity of root systems (Mouatt, 1959; Jackman, 1959), suggest that Yorkshire fog has high competitive ability for phosphate, nitrogen and potash where their deficiency may limit growth. Even when soils are estimated to be extremely low in calcium and phosphorus, it shows normal amounts of these nutrients (Davies, 1952).

(4) In some soils, the roots of this species may become extensively infected with endotrophic mycorrhiza (Nicolson, 1960). This symbiosis may be of ecological significance in allowing fixation of small critical amounts of atmospheric nitrogen (Stevenson, 1959).

1.3.3.3 Biotic factors.

Yorkshire fog persists under a wide range of pasture management regimes, although its growth-habit and vegetative reproduction are most suited to a defoliation system maintaining some herbage cover (Levy, 1955; Beddows, 1961a). In association with other species, the results of severe defoliation may depend upon the chief companion species; with *Dactylis glomerata* such grazing will eliminate *Dactylis* allowing Yorkshire fog to increase; with *Agrostis tenuis*, fog will be eliminated (Beddows, 1961a). An explanation of this observation may be found in the controlled environment study of Mitchell (1956). Under sward conditions, growth of Yorkshire fog involves leaf expansion on a moderate number of large tillers, whereas in *A.tenuis* it is on a large number of small tillers.

1.3.4 Reproduction and longevity.

1.3.4.1 Vegetative reproduction.

Yorkshire fog, which is generally accepted as a perennial, may under some conditions behave otherwise (Bocher and Larsen, 1958). In dense natural vegetation and under grazing, competition will check growth and formation of flowering tillers; thus, the species remains perennial. Under more lenient competitive conditions (spaced plants in an experimental

garden) plants will die after a few years, particularly after luxuriant flowering (Bocher and Larsen, 1958). Under conditions that prevent flowering, regeneration occurs by production of near-prostrate rosette shoots (Tansley, 1934) or, more generally, by development of new shoots and roots from the nodes of runners. The blanketing effect of such development accounts for the species' aggressive smother habit (Beddows, 1961a).

1.3.4.2 Sexual reproduction.

Flowering behaviour and compatibility in Yorkshire fog has been studied by Beddows (1961b). The self compatibility of this species follows that in other wind-pollinated grasses, with the exception that plants of high self-fertility have not been observed. From his observations, Beddows concluded that this grass is highly self-sterile and that selection against self-fertility must have been strong.

The geographic distribution of some flowering characteristics in this species have been studied by Bocher and Larsen (1958) in Europe; and Jacques, Schwass and Basnyat (see Munro, 1961) in New Zealand. Cultures from seeds of southern European and northern New Zealand origin may flower in the year the seeds are sown. This tendency decreases northwards in Europe and southwards in New Zealand, so that cultures from British seed (Beddows, 1961b), and southern South Island, New Zealand seed (Schwass, 1954), will not develop inflorescences until their second year. In both instances, the proportion of first year flowering plants is highly correlated with mean temperature of the coldest month, suggestive of the photoperiodic and temperature requirements in flowering in the species. Plants of southern European origin, possessing this tendency to flower without especial temperature or photoperiodic requirements, were found by Bocher and Larsen (1958) to be short-lived "pauciennials", or annuals. Such types have been observed in New Zealand,

and appear to be those having a high proportion of flowering to vegetative tillers. They tend to be from the arable areas of the South Island (Munro, 1961); that is at latitudes where the species is likely to possess low temperature and photoperiodic requirements in flowering.

Seed production is generally limited to the lower of the two florets in each spikelet, but even so, the species is a nortoriously prolific seed-producer. The seeds are extremely light, and with the relatively large surface area provided by the spikelets, seeds are easily distributed by the wind, although there appears to be no evidence as to how far they may be carried (Beddows, 1961a).

For notes on viability of seeds, germination and seedling morphology, the reader is referred to Beddows (1961a).

1.3.5 Chemical composition.

Yorkshire fog has the capacity to maintain average mineral content similar to that of other species, even under a wide range of soil moisture and fertility conditions (see section 1.3.3.2). A similar lack of discrepancy between this and other species is shown in relation to the proportion of nitrogenous compounds, sugars, ash, fructosans and organic acids (Bathurst and Mitchell, 1958).

In their studies of the chemical composition of swards, Fagan and Milton (1931) observed that growth-stage was more important than species in determining nutritive value. Floral emergence was found in all species to be associated with a decline in crude protein and a rise in fibre content of dry matter. Low relative palatability associated with onset of heading (Davies, 1925), may be accounted for by the low nutritive value, characteristic of most grasses at this time, although in this species this is probably more pronounced because of the velvet-like pubescence covering the foliage (Cowlishaw and Alder, 1960).

However, if grazed alone, and not allowed to become rank, there is little difficulty in herbage being consumed throughout most of the year (Watkin, 1960). The relationship between palatability and prolific heading during the flowering period, infection by Puccinia coronata, and growth habit in spaced plants, has been examined by Basnyat (1957).

An anatomical examination of indigestible herbage fractions of Yorkshire fog and other species, shows a relatively low proportion of either sclerenchymatous or collateral vascular bundles (Regal, 1960).

1.3.6 Pathogens and parasites.

An extensive list of the pathogens and parasites that are associated with, and infect Yorkshire fog, is included in Beddows (1961a). Of particular interest is the rust Puccinia coronata, which may cause extreme reduction in palatability in this grass species (Basnyat, 1957); and Pythomyces chartarum, the causal organism of facial eczema, which may grow in the medium of dead basal tissue associated with this grass (Barclay and Wong, 1961).

Chapter 2

YORKSHIRE FOG TOPODEMES

2.1 Sampling procedures.

During February and March, 1972, Yorkshire fog topodemes, from a wide range of habitats, were sampled within a limited geographical region. All collection areas were within a 50km radius of Massey University (see figure 3). The areas were selected to encompass a range of environmental water regimes, and included excessively drained sand dunes and continuously waterlogged swamps and marshes. Each area was large (100-200m across), and so probably included a diverse range of micro-environments for growth of Yorkshire fog. The presence of this species, the accessibility of the area and the possibility of gene flow, in the form of both pollen and seeds, from adjacent, contrasting habitats, determined the exact locale sampled within each area.

A seed sample of the topodeme of each area was collected; one panicle per plant. Two metres was the minimum distance between successive plants sampled, and within each area, at least 20 plants were sampled. The seed for all plants of each topodeme was bulked, and stored in paper envelopes, over silica-gel, to prevent both germination and deterioration.

2.2 Source habitats.

The location, elevation and description of the natural environment of each collection area is given below. The number in parentheses following each topodeme name refers to the grid reference on the New Zealand topographical map series N.Z.M.S.1, sheets N148 Tangimoana, N149 Palmerston North, or N152 Levin. The date on which each of the samples was collected is also given in parentheses, following the elevation data for each topodeme.

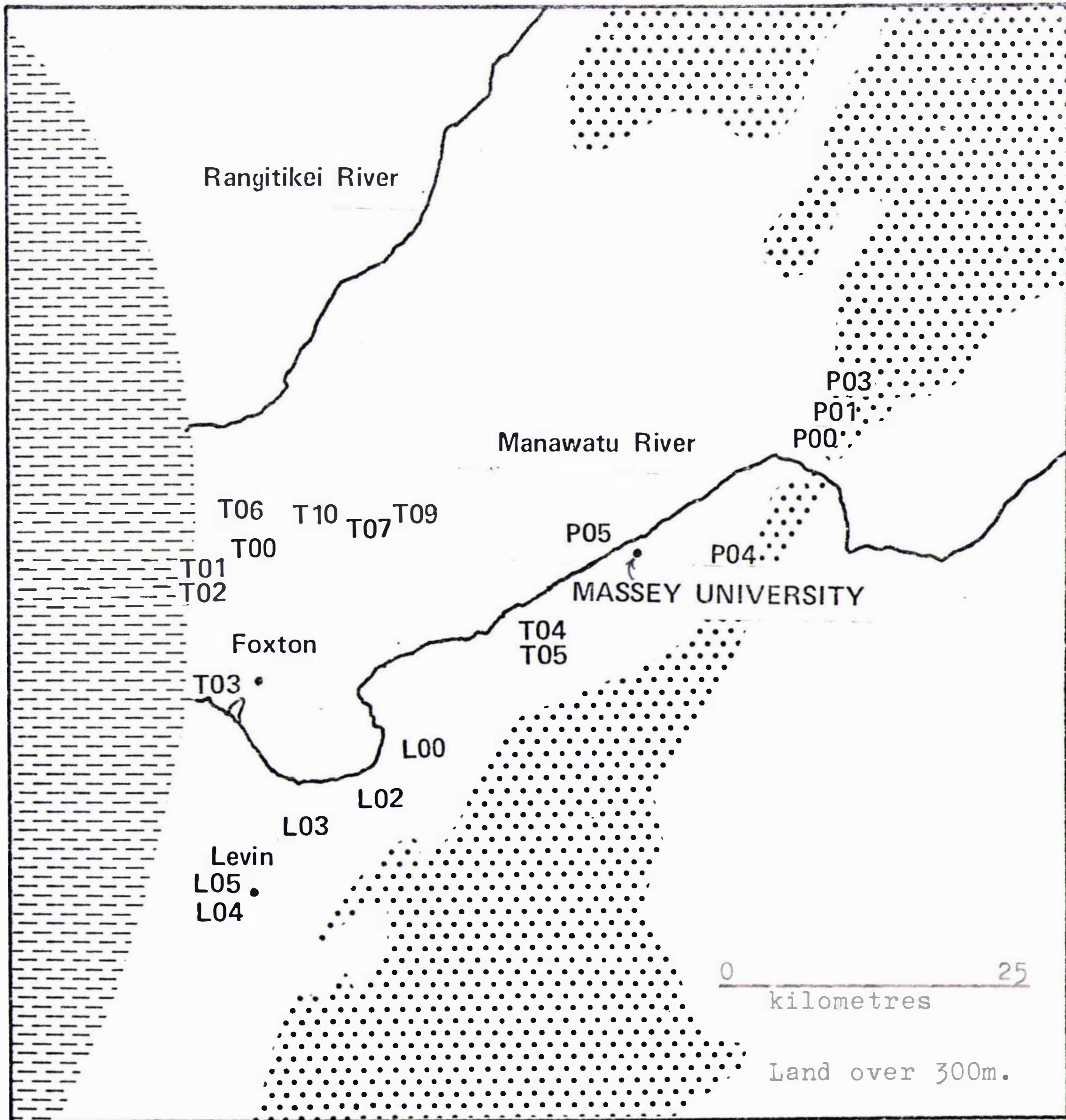


figure 3 The collection sites

TOO Lake Kaikokopu, Himatangi. (N148 785 327), elevation less than 30m (25.2.72).

The sample area was found to leeward of a row of willow trees which line the eastern shores of the lake, on a raised, narrow, walkway bounded by the lake on one side and a drain on the other. The drain was filled with water in the summer when the collection was made. The soil is Hokio sand, which is raw sand with a thin alkaline A1 horizon. The soil water table level is high in both winter and spring and the soil dries out only marginally in summer. Rank Yorkshire fog was found, with Lupinus arboreus, along the walkway. Smaller plants were also found on much wetter ground on the sides of the walkway in association with Ranunculus parviflorus, Cerastium vulgatum, Geranium molle, Nasturtium officinale, Rumex crispus and Juncus bufonius.

TO1 Himatangi Beach. (N148 755 325), sea level (5.3.72).

The sample area was found about 400 metres inland from the foredunes, where a "sand hollow" had formed. An upwelling of seaward seeping water had resulted in the formation of a marsh, in which the soil remained moist throughout the year, with standing water in the winter. The major species present were Leptocarpus simplex, Scirpus nodosus and Juncus pauciflorus. Trifolium glomeratum, Melilotus alba and M.officinalis could also be found.

TO2 Himatangi Beach. (N148 755 325), elevation less than 30m (5.3.72).

Yorkshire fog was also collected from high sand dunes (Waitarere sand with an A1 horizon) immediately adjacent to TO1. Here, the sand dries out excessively, especially in summer when surface temperatures can become very high. Strong westerly winds are an important characteristic of this situation. In this relatively extreme environment, plants, for example, Ammophila arenaria, Desmoschoenus spiralis, Cassinia leptophylla, Pimelea arenaria and Lupinus arboreus, possess striking

adaptations to facilitate their life here. Such adaptations include rolled, hairy, reduced, small and thick leaves. In the comparative shelter of the three latter species, Sonchus oleraceus, Melilotus alba and Hypochaeris radicata can be found in association with Yorkshire fog.

T03 Manawatu River, Foxton. (N148 765 202), sea level (3.3.72).

The collection site was along the tidal river edge, upriver from the Foxton boathouse. This very exposed site included a Meanee-soil saline flat which remains moist throughout the year, due to the high water table level. This area is occasionally flooded by brackish water. Plant species found here include Spinifex hirsutus, Coprosma acerosa, Plantago coronopus, Salicornia australis, Mesembryantheum edule, Leptocarpus simplex, Phormium tenax, Lupinus arboreus and Juncus maritimus. Yorkshire fog was also collected from the windward side of a man-made stop-bank which lines the river further inland from the saline flat.

T04 Ashlea Road, Tokomaru. (N148 967 225), elevation less than 30m (1.3.72).

Yorkshire fog was collected from a drain which ran across an open field of Lolium perenne and Trifolium repens. The field was situated immediately adjacent to Ashlea Road, 1.2km from the intersection of Ashlea Road and Makerua Rangitane Road. The soil, made up from alluvium and peat, does not dry out in the summer; in the winter the water table is high. Other species found in the drain included the rush Juncus pauciflorus and Ranunculus parviflorus. A line of poplar trees on the opposite road-side provided some shelter from the prevailing westerly winds.

T05 Ashlea Road, Tokomaru. (N148 967 225), elevation less than 30m (1.3.72)

Yorkshire fog was also sampled from the roadside immediately

adjacent to TO4. The soil characteristics of this area were probably similar to that of TO4. The luxuriant growth of Calystegia, Ranunculus parviflorus and Cyperus ustulatus provided a well sheltered, high humidity micro-environment for growth of Yorkshire fog and other pasture grasses.

TO6 Lake Pukepuke. (N148 785 367), elevation less than 30m (5.3.72).

The area sampled, on the eastern shore of Lake Pukepuke, had a similar soil to that at Lake Kaikokopu, where the water table level remained high throughout most of the year. Unlike that site, however, Yorkshire fog was found growing amongst the raupo (Typha orientalis) right up to the lake edge.

TO7 Taikorea-Pyke Road Intersection. (N148 919 336), elevation less than 30m (5.3.72).

The grazed pasture from which Yorkshire fog was collected, extended over the small hill at the intersection of Taikorea and Pyke Roads. The soil was Foxton black sand which dries out for three to four months over the summer. The few species found growing on the hill-side were Daucus carota, Hypochaeris radicata and the grasses, Dactylis glomerata and Yorkshire fog. In depressions on the hill-top, in association with cow dung, lush growth of these grasses, suckling clover and Geranium molle was found.

TO9 The Flat, Taikorea-Pyke Road Intersection. (N148 920 336), elevation less than 30m (5.3.72).

This area lay immediately below and to the east of TO7. The soil is an Omanaku peaty silt loam with a high water table that does not dry out in summer. The area sampled was that most distant from TO7, so that the probability of gene flow from TO7 into TO9 was low. Yorkshire fog, Poa trivialis and Anthoxanthum odoratum were the dominant pasture grasses. Other species were Juncus effusus, Ranunculus acris, Rumex

obtusifolius, Hypochaeris radicata, Bellis perennis, Cirsium arvense, Taraxacum officinale and Polygonum hydropiper.

T10 Taikorea Road. (N148 860 355), elevation 50m (5.3.72).

The sample area was found on stable sand dunes on the south side of Taikorea Road, 4.7 km west of Taikorea School. The soil here was a Waitarere sand which dries out excessively in the summer (c.f. habitat of T02). Pinus radiata and Lupinus arboreus were the dominant species present. Lycium ferocissimum, Ammophila arenaria, Urtica urens and Muehlenbeckia australis were also present over much of the area.

P00 Saddle Road, Ashhurst. (N149 275 433), elevation 300m (28.2.72).

The exact site was a 45 - 60° north-facing slope on the roadside, 1.9 km towards Ashhurst from the Saddle-Cook Road intersection. The area is sheltered from the prevailing westerly wind, but not from the east winds. The soil, Tokeawa steep land soil, is relatively shallow. It dries out in the summer but remains moist during the rest of the year. Animal tracks followed the contours of the slope, providing flat areas which remained moist well into the summer. Yorkshire fog, Dactylis glomerata, various clovers and Hypochaeris radicata cover most of the slope. Yorkshire fog was also found amongst bracken fern (Pteridium esculentum) on near-vertical face at the top of the slope.

P01 Wharite Road. (N149 315 456), elevation 490m (28.2.72).

The area sampled was a narrow strip of roadside, about 400m past the Wharite Peak road turnoff. The area was bounded on the north side by a bush-covered valley, and on the other by the road-way. The bush close to the road, mainly Rangiora (Brachyglottis repanda), provided shelter from the wind and rain. The soil was of very low fertility and remained moist throughout most of the year. Other species included Dactylis glomerata, Agrostis tenuis and a species of Ranunculus.

PO2 Wharite Peak Road. (N149 325 462), elevation 760m (28.2.72).

A slip, probably due to water seepage, had occurred in a man-made cutting just above this newly-formed roadway, 3km from Wharite Road. The bush and the road completely surrounded the area, which faced south, and so was sheltered from the sun and from most winds. The very low fertility Ruahine steep land soil was almost entirely composed of large greywacke chips. This soil remains very wet throughout the year. Yorkshire fog and Anthoxanthum odoratum were the only pasture grasses present. Mosses and lichens covered most of the area which was scattered with seedlings from the woody species of the surrounding bush (e.g. Griselinea littoralis, Carpodetus serratus, Aristotelia serrata, Brachyglottis repanda and Rubus cissoides). Other plants found were a species of Carex, Blechnum fluviatile, Blechnum procerum, Uncinia uncinata, Acaena novezealandiae, Lotus pedunculatus and Digitalis purpurea.

PO3 Wharite Peak. (N149 332 473), elevation 900m (28.2.72).

The sample area was situated on the roadside just below the T.V. transmitter station at Wharite Peak. This was an open area, with no trees growing except as seedlings (e.g. Pseudowintera colorata). Consequently, the area was very exposed. The soil, Rinata silt loam, is of extremely low fertility and remains moist throughout the year. Two species with a spreading growth habit, Agrostis stolonifera and Acaena anserinifolia, covered most of the area. Other species found were Juncus pallidus, Juncus lampocarpus, Blechnum filiforme, Hydrocotyle moschata, Polystichum vestitum, Olearia colensoi and Astelia solandri. Mosses, Hypochaeris radicata and Cirsium palustre were found with Yorkshire fog in moist depressions where the spreading habit plants tended to be absent.

P04 Browns Flat, Tiritea Catchment. (N149 125 230), elevation 440m (5.2.72).

Brown's Flat is an extensive flat area at the head of the Tiritea Stream in the northern Tararua ranges, to the east of Palmerston North. The area has been cleared of bush and extensively drained; however, much of it was swamp when the Yorkshire fog collection was made. The soil, Ramiha mottled silt loam, is of low fertility and high water table level. Standing water remains throughout the year on the lower, swampy areas. Species found included *Cyperus ustulatus*, *Juncus bufonius* and *J. pallidus*, *Glyceria fluitans*, a species of *Epilobium*, mosses, *Cirsium palustre* and *Hypochaeris radicata*. Yorkshire fog was the dominant species on the drained ground, and was also found growing in the swamp.

P05 Cloverlea Road, Kairanga. (N149 060 348), elevation 30m (6.3.72).

The sample area was on the railway embankment on the south side of the crossing at Cloverlea Road, The "soil" of the embankment possibly did not reflect the characteristics of the surrounding Te Arakura sandy loam which has a moderately high water table in winter and dries out in summer. It is likely that the embankment soil was more extensively-drained than this. The plant species growing here included *Lupinus arboreus*, *Helminthia echioides*, *Sonchus asper*, *Achillea millefolium*, *Senecio vulgaris*, *Conium maculatum*, *Galium aparine*, *Hordeum vulgare*, *Dactylis glomerata* and *Bromus mollis*.

L00 Makerua-Rangitane Road. (N152 955 162), elevation 30m (1.3.72).

The collection site was along a fence line on the sheltered side of the main drain stop bank where the Makerua-Rangitane Road crossed the main drain. A small drain from which Yorkshire fog was collected ran parallel to the fence. The soil was a Kairanga type, a heavy clay with poor drainage, in which the water table level remains high, especially in

winter. Cattle have contributed to pugging of the soil near the fence. Other species present included mosses, Lotus major, Hypochaeris radicata, Ranunculus repens, Rumex conglomeratus and Juncus pallidus.

LO2 Buckley Road, Shannon. (N152 895 102), elevation 40m (1.3.72).

Yorkshire fog was collected from a peat swamp situated adjacent to the roadside 1.1km from the Buckley Road-State Highway 57 intersection. The soil, Makerua peaty loam, remains wet throughout the year. A grass species provided a mat-like covering over the whole area, across which isolated clumps of Scirpus lacustris, Juncus effusus and J.lampocarpus were growing. Other species found were Lotus major, Rumex conglomeratus and Ranunculus repens.

LO3 Webbs Swamp, Koputaroa. (N152 854 087), elevation 40m (1.3.72).

This swampy area, situated to the west of the railway line about 200m north of the Kiputaroa store, was surrounded by rolling farm land. The soil was an Opiki complex of mixed peat and alluvium which remains wet throughout the year. Yorkshire fog was found throughout the area which was covered by luxuriant growth of Typha orientalis, Phormium tenax, Ulex europaeus and Pteridium esculentum. Mosses, a species of Ranunculus, Hypochaeris radicata, Bellis perennis and Blechnum minus were also found. Yorkshire fog was even seen growing from the bole of Carex secta.

LO4 Muaopuku Park, Lake Horowhenua. (N152 781 043), elevation 30m (1.3.72).

Yorkshire fog was collected from the shore zone where rough pastures to the west of the boathouse came to the edge of the lake. A seasonal fluctuating lake level is a characteristic of this shore zone in which the soil remains wet throughout the year. The rush, Juncus pallidus and a species of Mentha were dominant in the shore zone. Other species, Cyperus ustulatis, a species of Ranunculus and Glyceria fluitans,

along with Yorkshire fog, were also present.

LO5 Grazed field, Lake Horowhenua. (N152 785 046), elevation 30m (1.3.72).

Yorkshire fog was also collected from a grazed field adjacent to the lake, immediately north of Muaopuku Park. The actual site was similar to LO4, but a little further from the shore. Consequently, the soil was not as saturated as that at LO4, especially in the summer. Mosses and Juncus pallidus, the dominant species near the lake, gave way to clovers (e.g. Trifolium repens) and other legumes (e.g. Lotus major), flatweeds (e.g. Hypochaeris radicata), the occasional dock (Rumex conglomeratus), a species of Ranunculus and pasture grasses (e.g. Dactylis glomerata) further from the shore. Yorkshire fog was ubiquitous over the whole area.

2.3 Seed characters.

The characteristics of a given plant, growing in a given environment, are the resultant of the interaction between the plant's genotype and the particular environmental conditions. Thus, where phenotypic differences between plants are observed, there must exist some doubt as to whether these differences are mainly due to genetic divergence, or to the direct result of environmental differences, or to some combination of the two. For example, measurements made on material collected from the wild must be seen to reflect this doubt. Such was the case for measurements of weight and viability of the seeds of each of the topodeme samples.

Seed was removed from the panicles collected, bulked for each topodeme, then cleaned. Care was taken to keep the seed dry, by storing it over silica gel in a desiccator. The following seed characters were measured on each topodeme:-

(1) Seed weight. Four 100 seed lots were weighed in grams.

(2) Percentage germination. Counts of germinating seeds on moist filter paper, after 6 and 14 days, were made so that percentage germination could be determined. Two hundred seeds were used for the determination of percentage germination.

From these data, the significance of differences between topodemes was calculated by means of an analysis of variance for one criterion of classification (seed weight), and a Chi-square test (percentage germination).

Seed weight. Table II, mean seed weight for topodemes, indicates those topodemes for which mean seed weight differed significantly, at the 1% level. Those topodeme means that can be considered equal have been bracketed by a line. Thus, differences between those topodemes which

Table II: Seed weight (wild material)

Topodeme	Topodeme mean 100 seed weight (x 10^{-3} grams)
L04	35.50
T07	34.50
P01	34.50
L02	34.25
L00	34.00
T10	33.75
T00	32.75
T05	32.50
T04	30.50
P04	30.25
T09	30.00
L05	28.50
P02	28.00
T06	27.50
T02	26.50
P05	26.25
L03	24.25
T03	22.75
T01	20.25
P03	14.75

d.01 = 5.05

are not bracketed are considered highly significant. For example, the mean seed weight for topodeme L04 is greater than that for P04, T09, L05, P02, T06, T02, P05, L03, T03, T01 and P03; and P03 has a lower mean seed weight than that for all other topodemes.

Percentage germination. Table III, mean percentage seed germination for topodemes, summarises the data for seed germination. Those topodemes found to differ significantly from the overall mean percentage germination (all topodemes, see appendix II), were P05, P03 and L05.

Table III: Percentage germination (wild material)

Topodeme	Percentage germination	Topodeme	Percentage germination
T01	66	T04	78
T02	82	T05	75
T09	65	T06	72
T10	82	T07	77
P01	90	L03	62
P02	83	L04	90
P04	91	L05	57
L00	74	P00	63
L02	92	P03	41
T00	83	P05	54
T03	58		

For those topodemes in which the percentage germination was low, the seedlings selected might not have been a representative or random sample of the surviving topodeme. Therefore, results obtained with mature plants from topodemes in which percentage germination was low (chapter 3), might have been meaningless. For this reason, topodemes P05, P03, L05, P00, L03 and T03 were not considered for the glasshouse experiment (chapter 4).

CHAPTER 3.

THE FIELD EXPERIMENT: COMPARATIVE CULTIVATION

3.1 Introduction.

Yorkshire fog presents an extensive array of differentiated climatic types, from those winter-growing, of low latitudes, to those almost winter-dormant, of higher latitudes (Basnyat, 1957; Bocher and Larsen, 1958). In the temperate pasture grasses, the requirement by high latitude types, unlike those of low latitudes, for an inductive cold period and, or, short days for flowering (Larsen 1947; Ketellaper, 1960; Cooper, 1960; Parker, 1972), forms the basis of the perennial habit (Breese, 1966). It ensures that the tillers formed in one season will not flower until the next, so providing for a vegetative overlap from one season to the next. As a consequence, low latitude plants are often short-lived, and, in extreme cases, function as annuals or 'pauciennials' (Bocher and Larsen, 1958), so escaping summer drought in the form of seeds. In such plants, the ratio of flowering tillers to vegetative tillers tends to be large. Also, the ability of these low latitude types to grow in winter, can be highly correlated with frost susceptibility (as found in *Lolium perenne*, Cooper, 1963).

Yorkshire fog, like other temperate pasture grasses, also displays a notable range of differentiation to pasture management and soil type (Beddows, 1961a; Munro, 1961). For example, the influence of various grazing intensities results in profound modifications to growth habit and flowering time (e.g. Breese, 1966). Flowering time (date of floral emergence) in any year also depends upon the response of each genotype to its local climate (Beddows, 1961b). The effects of flowering on the root system of grasses have been discussed numerously (e.g. Soper, 1958, for ryegrass). Heavily flowering plants

show considerable sloughing of the root cortex, and a subsequent decline in efficiency of water and nutrient uptake. This is of major ecological importance in the survival of the plant over subsequent dry periods. These aspects of the biology of Yorkshire fog provide the basis for this field study.

The aim of this experiment was to discover whether variation existed among samples of Yorkshire fog topodemes in response to a uniform environment, and to relate this pattern of response to the environments of the source habitats.

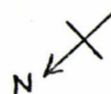
3.2 Experimental procedures.

3.2.1 Experimental design and statistical procedures.

The experiment was designed to distinguish genetic differences between topodeme samples from the effects of soil differences within the experimental area. To allow for these differences,

T00	P00	L00	T01	T06	L03	T09	T04	P02	L05	P01	P03	T07	T03	P05	L04	T02	T05	P04	T10	L02	BLOCK IV
T10	L04	L00	P04	T04	T06	L02	T05	T03	T09	P05	L05	T02	P01	P03	T07	T00	L03	P02	P00	T01	BLOCK III
P00	T10	T04	T05	T00	P02	P05	L05	T09	L03	L02	T03	T07	P01	T02	P03	L04	P04	T06	T01	L00	BLOCK II
T02	L00	P05	P00	T04	L05	T01	P04	T07	T05	T00	T03	T10	P01	P03	T06	L03	T09	P02	L04	L02	BLOCK I

Figure 4. Layout of experimental area. Planting plan.



the 21 topodemes were compared in four blocks, in a randomised complete-block design. The topodemes were, then, allocated at random to the 21 plots within each block (figure 4). Each plot was represented by 10 plants, and therefore an interaction, topodemes with blocks, could be defined. The 10 plants per plot were planted in two rows of five plants per row; with all plants at 0.77m (2.5 ft) spacing.

An analysis of variance for a randomised complete-block design, with interaction, was employed for the demonstration of topodeme differences. Where the interaction term was significant, it was used in determining the significance of topodeme differences. In every plot in the experiment, there were five plants for which the characters survival-vigour, date of panicle emergence and panicle production (see section 3.2.3), were measured. A correlation coefficient for each pair of these three characters was determined. The problems of drawing precise conclusions from these correlation coefficients are discussed in appendix VI.

3.2.2 Maintenance of the experimental area.

The test plants were grown from seed, which was germinated on filter paper, then transferred to 30 x 42 cm flats, in a sand-peat mixture with adequate fertilizer (see appendix I). The plants were kept in an unheated glasshouse for four weeks, until June 5, 1972, when they were moved outside. After a period judged suitable for acclimatization to outdoor conditions, individual seedlings were removed from the flats, and planted into the field according to the experimental design, on June 14 - 15, 1972. Periodic handweeding immediately around the plants, and rotary-hoeing between the plants, were necessary to keep the area free of weeds. Plants were thus maintained until the conclusion of the field experiment, in May 1973.

3.2.3 Characters measured.

(1) Date of panicle emergence. During December, 1972, and January, 1973, all plants were observed every two days for flowering. When four panicles had elongated so that the peduncles were visible opposite the ligule of the flag leaf, the date was recorded. In the subsequent analysis, the number of days to flowering after November 30, 1972, was used.

On February 2 - 9, 1973, all panicles on five plants per plot were harvested, placed into appropriately labelled paper bags and set aside for subsequent study.

(2) Panicle number per plant. The number of panicles for each plant (in each bag) was counted.

(3) Seed weight. Seed was collected in the bottom of each paper bag, bulked for each plot, cleaned, then weighed in four 100 seed lots.

(4) Survival-vigour. On May 7, 1973, all plants were scored 0, 1, 2 or 3 for vigour: 0 = dead; 1 = weakly growing with one or few tillers; 2 = healthy but small so might not be expected to survive competition in the wild; 3 = large, healthy and vigorous.

3.3 Results.

Analysis of variance tables and a summary of results can be found in appendix V. Where the analysis of variance has indicated differences between various means, a table of these means has been included in this section. Differences observed between topodeme means for seed weight, for panicle

number, and for survival-vigour, were not significant. Table V indicates those topodemes for which the mean date of panicle emergence was significantly different from those for other topodemes; any two topodemes not bracketed by a line (on the right-hand side of the table) can be considered different.

Table IV: Panicle production, block means

Block	Number of panicles per plant.
I	125.24
II	117.11
III	148.30
IV	147.23

(Blocks I and II are bracketed by one line; blocks III and IV by another.)

d.05 = 15.60

Table IV shows that the mean panicle number for blocks I and II can be considered significantly different from the means for blocks III and IV. The differences between the four block means for each of the remaining three plant characters measured were not significant.

Table VI, the correlation matrix, indicates no significant correlation (for definition of significant correlation, see appendix VI) between survival-vigour, and either the number of panicles, or the date of panicle emergence. There was a significant correlation between the date of panicle emergence and the number of panicles. However, the percentage variation in panicle emergence due to the linear relationship between this character and the number of panicles (i.e. coefficient of determination x 100), was only 1.15%.

Table V: Panicle emergence, topodeme means

Topodeme	Days to panicle emergence after November 30, 1972.
T09	21.36
P01	20.89
T05	20.64
T00	20.39
L00	20.39
P05	19.83
T02	18.89
P00	18.67
T01	18.61
T04	18.58
P04	18.33
L04	17.83
P02	17.33
P03	17.03
T06	16.94
T03	16.78
L03	16.08
L05	16.00
T10	15.86
T07	15.25
L02	15.17

d.05 = 2.01 days

Table VI: Correlation coefficient matrix. I.

		PP	PE	SV
Panicle production	PP	1.000		
Panicle emergence	PE	-0.107*	1.000	
Survival-vigour	SV	0.000 NS	0.086 NS	1.000

Degrees of freedom = 417; * = significant at 5% level;

NS = not significant.

3.4 Discussion.

The aim of the experiment outlined in this chapter was to expose genetic divergence between topodemes, where such divergence existed. The technique involved growing all plants under uniform environmental conditions; thus, differences that remained between topodemes could be said to have a genetic basis. So that such conclusions drawn were valid, the technique employed had to allow for inevitable soil differences within the experimental area. The significant topodeme x block interaction (for all characters), evidence of these soil differences, could be indicative of real biological interaction, whereby topodemes were responding differentially to soil differences between blocks. It could also be indicative of direct effects of soil differences within blocks. It is unlikely that the distinction between these would have been achieved by an alternative experimental design, such as a latin-square, since it is unlikely that the soil differences resulted from orderly gradients along and between blocks. Topodeme differences not due to these block (soil) effects were of interest in this study. Such differences were found for date of panicle emergence (table V), but not for any of the other three characters measured.

Panicle emergence in Yorkshire fog has been shown, to be directly modified by the environment, differences in one population between years, and to be differentiated, differences in one year between

populations (Beddows, 1961b). The differentiation in this character can, in some instances, be related to macro-climatic differences (e.g. Bocher and Larsen, 1958, regional differentiation of Yorkshire fog in Europe), although not in others (e.g. Knight, 1973, altitudinal variation in cocksfoot grass in southern France). Since all source habitats in this investigation were from a limited geographical region, such climatic differentiation was not expected. The only instances in which this could have occurred (i.e. between high altitude topodemes, P00, P01, P02, P03 and P04, and those from near sea level), the differentiation could not be related to the altitudinal differences.

The differentiation in date of panicle emergence possibly reflects a more basic differentiation, that in time of pollen release. In cross-pollinating species this could allow the effective isolation of populations in close proximity. This would be important where neighbouring habitats were ecologically diverse. Such an explanation could account for differences in date of panicle emergence between T07 and T09, and between T04 and T05. The only other topodemes for which pollen flow between them could have occurred in the wild were T01 and T02. No differentiation between these topodemes was found. The pattern of genetic variation in this character could not be related to the pattern of variation in habitat-water for which the source habitats were selected, but must have been due to other microclimatic or biotic factors.

The possibility remains that the genetic divergence was random with respect to the environment. Random genetic divergence can come about by an area being colonized by a non-representative invasion from another. Thus, differences that might subsequently arise by selection would be confused with, and could not be separated from the original chance differences between the derived and the parent populations (Heslop-Harrison, 1964). The choice of a limited geographical region from which to sample the experimental material was aimed at overcoming this uncertainty of genetic divergence.

Differences between topodemes, for seed weight, were observed for seed collected from the wild (table II, section 2.3). Yet, no such differences were observed for seed weight in the field experiment. Yorkshire fog has been reported to be highly self-sterile (Beddows, 1961b), and so seed produced in the field experiment was likely to have arisen by cross fertilization. Thus, seed produced by one topodeme could have arisen from pollen from another. However, seed weight for various grasses and cereals has been reported to be almost exclusively a maternal characteristic, little influenced by the pollen parent (e.g. Latter, 1965 for Phalaris tuberosa in Australia). If this was true for Yorkshire fog in this investigation, then the seed weight of topodemes observed in the field experiment was directly comparable with those values for seed weight of wild material. Therefore, it can be concluded that topodeme differences in seed weight, observed for seed collected in the wild, were due to direct effects of the

source environments, and were not due to genetic variation for this character. It is evident from figure 5 that plasticity in seed weight is accompanied by plasticity in viability of seeds (percentage germination). Such plasticity could have mortal consequences for the species in unfavourable growth conditions. However, where plants are perennial as in Yorkshire fog, survival from year to year probably does not rely solely upon successful germination and seedling growth.

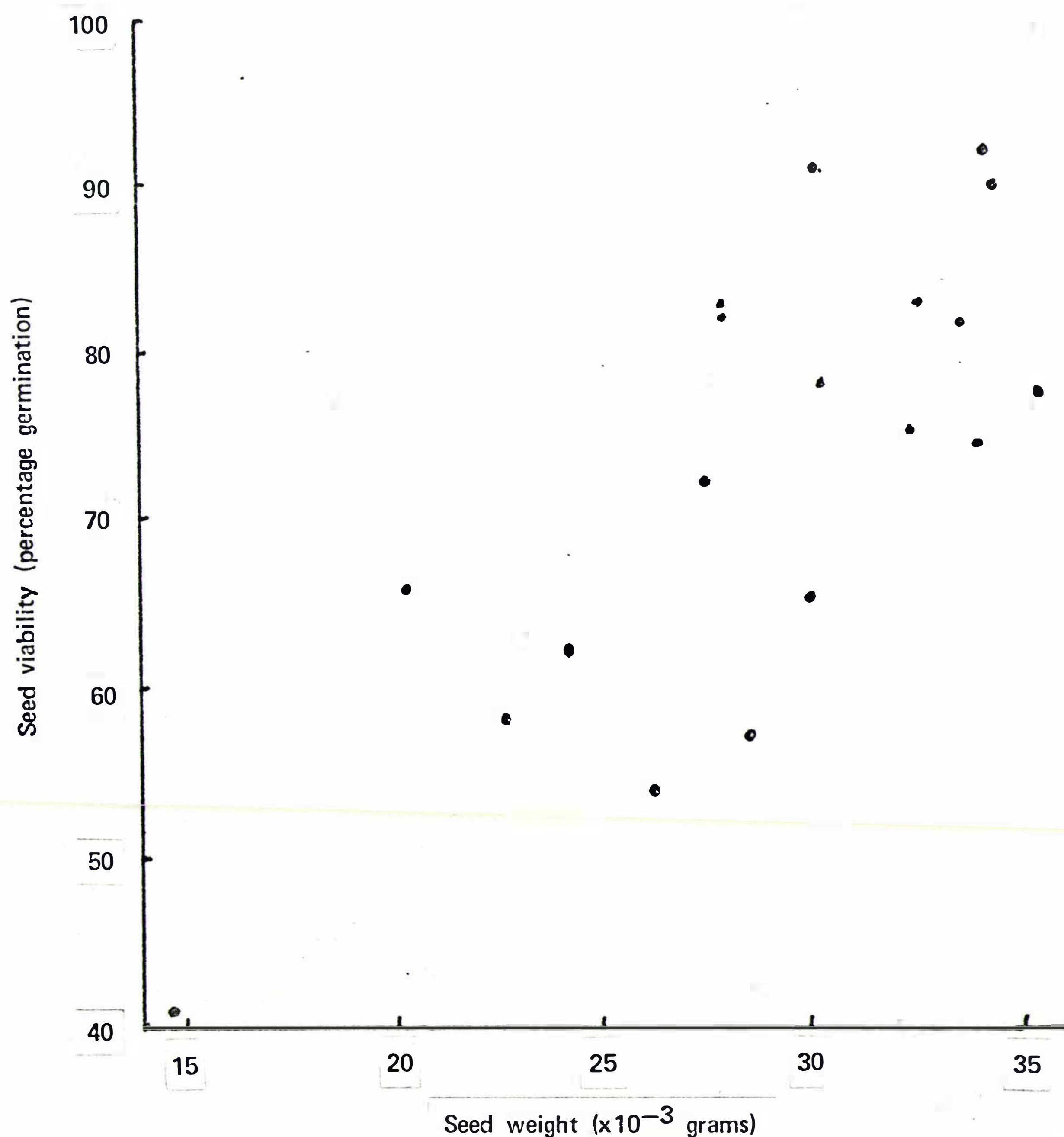


Figure 5: Seed weight-viability relationship (wild material).

Bocher and Larsen (1958) in Europe, and Basnyat (1957) in New Zealand, have described differentiation in perenniality in Yorkshire fog. Short-lived types were considered, by these authors, to be adaptations to summer drought. These types were found to die subsequent to abundant flowering and seed production, probably as a result of the inability of the reduced roots to obtain water or nutrient. It was considered that adaptation of Yorkshire fog to the excessively drained (summer drought) sand dunes (habitats T10, T02 and to a lesser extent, T07) might have been accompanied by a reduction in perenniality. However, no topodeme was seen to behave differently from any of the others, for either panicle production, or survival subsequent to flowering; the only characters relating to perenniality measured. These data indicated the absence of stable selection differences between habitats. The considerable genetic variation displayed by these characters reflected the unstable, widely fluctuating environmental conditions associated with this temperate region, and so indicated how adaptation was achieved; that is, by the possession of a genetic system allowing extensive recombination, followed by a more or less intense selection for adapted types. Such adapted plants may possess broad adaptability, as exhibited by plastic response in various environments. Evidence for this is presented in chapter 4.

Figure 6. Survival-vigour of spaced plants at the termination of the field experiment.

Above: Survival-vigour score 0; plant dead.

Below: Survival-vigour score 1; plant weakly growing, with few tillers.

Figure 6. Survival-vigour of spaced plants at the termination of the field experiment.

Above: Survival-vigour score 2; plant healthy but small. (note erectness of growth habit).

Below: Survival-vigour score 3; plant large, healthy, vigorous.

CHAPTER 4

RESPONSE OF TOPODEMES TO DIFFERENTIAL WATER REGIMES

4.1 Introduction

The aim of the present investigation was to determine whether or not adaptation of the collected Yorkshire fog topodemes to their source habitats involved genecological differentiation. The most notable variable in the natural environment of the source habitats was soil water. It was therefore considered that genecological differentiation might have occurred in response to such habitat variation. The experiment described in this chapter was designed to test this hypothesis.

Genecological differentiation in response to moisture in the environment has been reported numerously in grass species. Several examples of such differentiation have been given previously (see sections 1.2.2 and 3.1). However, in none of these examples was the differentiation shown by direct experiment to be related to water. Experimental studies of intraspecific variation related to water have been carried out on several North American range grasses (e.g. Dactylis glomerata, Keller, 1953; blue panicgrass, Dobrenz et al., 1969a, 1969b; and Boer lovegrass, Wright and Dobrenz, 1970). In these studies, differences in water use efficiency (defined as amount of water transpired to dry weight produced) were demonstrated between samples, and the relationships between this and numerous other characters determined. For example, in Boer lovegrass, the highest water users were the most seedling drought tolerant (Wright and Dobrenz, 1970), and in blue panicgrass the most efficient water users had more vascular bundles than the least efficient clones (Dobrenz et al., 1969a). However, Dobrenz et al. (1969b) found in blue panicgrass that when the water use efficiency and stomate density were correlated, a non-significant association was obtained. In this study, they also found that clones with the least stomate density were the most drought tolerant. However, in all these investigations on North American range grasses, selected genotypes were utilised rather than samples of natural populations. The emphasis of these studies was not therefore on the establishment of genecological differentiation.

4.2 Experimental procedures.

4.2.1 Experimental design and statistical analysis.

In this experiment, nine Yorkshire fog topodemes were tested under three different water treatments, so that not only differences between topodemes, but also the effects of the different water treatments on the topodemes, could be analysed. In order to study these two questions simultaneously, each of the 180 plots, formed from the nine topodemes replicated 20 times, arranged in a randomised complete block design, was sub-divided into three subplots. To each subplot, represented by a single plant established individually in a 5-inch plastic pot, one of the three different water treatments was randomly applied. Such an arrangement is called a split-plot design (see figure 6). An analysis of variance for this design was applied to the data, so that differential topodeme response to the water treatments could be recognised.

From the experimental material, 84 plants were selected on which all the plant characters studied were measured. For each pair of these characters a correlation coefficient, r, was determined (see table XX). The square of r, the coefficient of determination, was also determined and expressed as a percentage (see table XXI). Various methods for testing the significance of the calculated correlation coefficients were considered (see appendix VI). Of these, that which tested the assumption that each correlation coefficient was derived from a sample of a population in which no relationship existed between that pair of characters, was applied to the data.

4.2.2 The glasshouse environment.

No attempt was made to regulate the physical environment of the glasshouse, which showed wide fluctuations (diurnal, seasonal, and random) in such factors as temperature, humidity, light intensity and

day length throughout the duration of the experiment. As well as these variations, uniformity of the environment within the glasshouse could not be assumed. Thus, the experimental design had to account for this largely uncontrollable, suspected variation. This was achieved by incorporating into the design a large number of blocks (20) and by a randomisation procedure whereby the position of each block within the glasshouse, plot within each block and subplot within each plot was altered weekly.

The effectiveness of these procedures in randomizing the effects of the differential environment within the glasshouse can be determined by the significance of the 'block' and 'topodeme x block interaction' terms in the analyses of variance (appendix V).

4.2.3 Pre-experiment treatment of seedlings.

The ability of a plant to respond to various environmental conditions may be affected by the conditions under which the plant is grown (Rook, 1969). In the present study, the plants were grown under conditions as close as possible to those under which measurements were ultimately made. This, therefore, reduced the doubt that plants were not well acclimatised to the experimental conditions.

The test plants were grown from seed, which was germinated on filter paper, then transferred to 5-inch plastic pots, one seedling per pot, in a 1:1 sand:peat mixture with adequate fertiliser (see appendix I). All pots were kept well watered, maintaining soil water around field capacity, to ensure extensive distribution of the roots throughout the soil medium. Plants were grown for six weeks prior to imposition of the differential water treatments, and one week before this plants were clipped to within 3 cm of the soil surface. Thus, direct effects of the source environment mediated by the seed, and manifest in seedling characters, were nullified, or at least diminished.

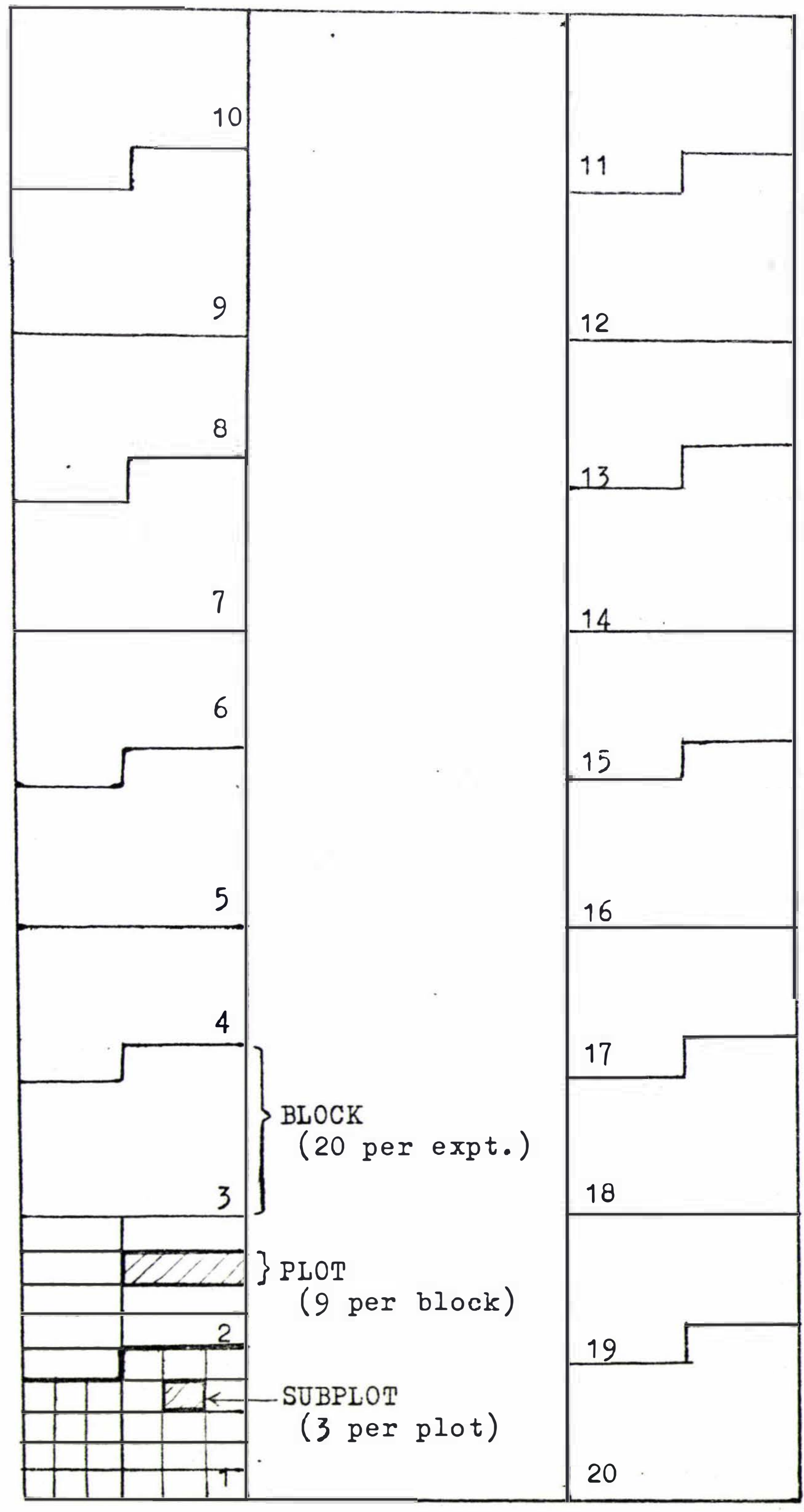


Figure 7: Layout of glasshouse experiment.

4.2.4 The water treatments

The three water treatments to test the topodemes were chosen to simulate various environmental water conditions found within the limited geographical region sampled. They involved a waterlogged, a frequently watered, and an infrequently watered treatment. Thus, three levels of soil water were made available to the plants, being maintained in the following ways:-

(1) Wet. The 5-inch pots containing the experimental plants were placed into water-filled watertight 6-inch plastic pots. The water-level was maintained at the soil-air interface by daily replenishment. A layer of gravel covered the bottom of the 6 inch pot so ensuring distribution of water completely throughout the soil.

(2) Medium. Water (250 ml) was added to the soil every three days to replace that lost through evaporation from the soil surface and transpiration by the plant, thereby maintaining soil water around field capacity.

(3) Dry. Each day at around 0800 hours, when the evaporative demand of the atmosphere was expected to be low due to high humidity, individual plants were observed for wilting. When the wilted condition was observed on two consecutive mornings, soil water was assumed to be at around permanent wilting percentage, and so water (350 ml) was added to rewet the soil to field capacity (see appendix I for estimation of amounts of water required in the water treatments to bring soil water back to field capacity).

The water treatments were initiated on July 12, 1972, and terminated on September 11, 1972.

4.2.5 Characters measured.

The characters measured on all experimental plants during the course of the experiment were:-

(1) Number of tillers. The number of tillers per plant were counted

on days 01, 12 and 22. Subsequently numbers became uncountably large. One value, tiller production, given by number of tillers on day 22 less number of tillers on day 01, was defined and used in subsequent analyses.
(2) Gross leaf dimensions. The length and breadth of the lamina of the youngest, fully-expanded leaf on a standard tiller was measured, to the nearest mm and 0.5 mm respectively, on days 08, 22, 36, 50. Leaves measured could have been present as primordia before the experiment started. However, environmental reversal experiments (Mitchell and Soper, 1958) indicated that dimensions of mature leaves were typical of the conditions during their growth. Leaves measured on day 08 would probably have expanded to some extent before the experiment began and so these values were ignored, since they probably did not reflect plant response to the experimental conditions. From the data one value, the mean for days 22, 36 and 50 for lamina length, and for breadth, was obtained.
(3) Leaf emergence. Leaf emergence was defined as the time at which a leaf tip just emerged above the level of the ligule of the youngest fully-expanded leaf. Whenever this was observed between 0800 and 0930 hours on a standard tiller, subsequent to day 28, the date was recorded, and the youngest mature leaf was marked with paint to facilitate rapid appraisal. When two such dates were recorded for a plant, the period between emergence of successive leaves was determined. Where more than two dates were recorded, mean values were calculated.
(4) Dry weight. On day 61, the aerial parts of each plant were removed, placed into a paper bag, sealed with a staple, oven-dried at 80°C for 24 hours, and weighed.
(5) Basal diameter. The diameter of the plant base at ground level was measured after the removal of the aerial plant parts. (Maximum diameter).

Four parameters associated with growth form of individual plants (Hickey, 1961) were measured on a random selection of nine plants from each topodeme x water treatment combination. Two measurements were taken

on undisturbed plants in the natural position:-

(6) Plant diameter. This measure of the aerial spread of the crown of the plant was taken as the maximum horizontal distance from leaf collar to leaf collar.

(7) Plant height. This was perpendicular distance from the soil to the tallest leaf collar.

From these, an index of growth form given by

$$\frac{\text{Natural height}}{1/2\ (\text{natural diameter-basal diameter})}$$

was also determined. This growth form index is an estimate of the tangent of the angle at which tillers protruded from the base of the plant.

Two further measurements were made after the foliage was raised to its maximum vertical position ("compressed" position):-

(8) Compressed diameter. The diameter of the compressed aerial parts at average height of the collars.

(9) Compressed leaf length. Length from the soil to the tallest leaf collar in the compressed position.

On day 61 the second youngest fully expanded leaf was removed below the level of the ligule and fixed in a formalin: acetic acid: ethanol (5:5:90 FAA) solution. Several techniques were considered for the preparation of this material for microscopic examination (see appendix III). Finally, a 1 cm segment was sampled from each leaf 2 cm above the ligule and placed in a clearing solution (phenolic acid: saturated choral hydrate: lactic acid 1:1:1) at 70°C, for 24 hours. Cleared leaf material was then mounted in the clearing solution on a microscope slide and examined under a dissecting microscope (40X). Two measurements were made:-

(10) Leaf width.

(11) Number of primary and secondary vascular bundles across the leaf.

Next, the abaxial leaf surface was examined under a Zeiss Ergaval research microscope (100X) with microphotographic accessories. One standard-sized microphotograph per leaf segment was taken of an area immediately adjacent to the second primary vascular bundle from the leaf margin. From these photographs five observations were made, the latter three from a standard intercostal region between adjacent stomatal files.

(12) The number of hair cells.

(13) The number of stomata.

(14) The number of cross-walls (hair cells counted as one cross-wall).

(15) The number of epidermal cell files.

(16) The width of this region, between adjacent stomatal files.

From these data the following indices were calculated:-

(i) $\text{Cell Length} = \dfrac{\text{No. of files X length of photograph}^{1}}{\text{Cell No.}}$

(ii) $\text{Cell Width} = \dfrac{\text{Width of intercostal region}}{\text{No. of Files}}$

(iii) $\text{Cell Number} = \dfrac{\text{No. of cross-walls}}{\text{Width of intercostal region X length of photo.}^{1}}$

(17) Plant water status. Plant water status was measured on a random selection of 10 plants per topodeme x water treatment combination, by the relative water content (RWC) method of Barrs and Weatherley (1962). Wet and medium treatment plants, whose respective drying cycles were all

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1 Multiplication by this constant may be disregarded since it will make no difference to either comparative values of cell length and cell number, or the analysis of variance.

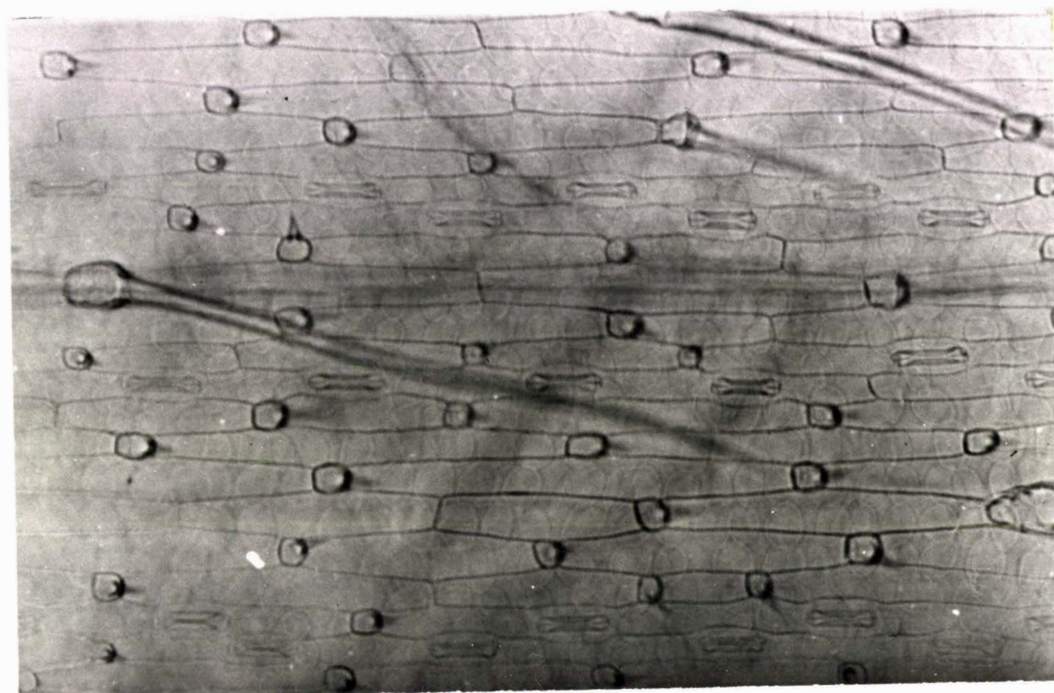

Figure 8. Abaxial leaf lamina surface.

S = stomatal file (guard cells dumbbell shaped)
VB = vascular bundle (out of focus below the surface)
I = intercostal region between adjacent stomatal files
Epidermal hairs are those cells not elongated in longitudinal direction. Two types are obvious from the photograph; one with short barb-like hairs, the other with long flaxen hairs. (Objective lens = 10X; projective lens = 6.3X; film 35mm).

in phase due to watering of plants in each of these treatments at the same time, were sampled on day 61. So comparative values of RWC that were meaningful could be determined for dry treatment plants whose drying cycles were not necessarily in phase, sampling was spread over a period, days 50 - 61, so that each sample was obtained at the same relative position of the drying cycle. The plants were sampled at the driest part of cycle, immediately before rewatering (see criterion for rewatering, section 4.2.4). Thus, the RWC values determined for these plants represent the most extreme (low) values that existed during the dry treatment.

At each sampling three leaf lamina segments, each 1 cm long, were cut from the base, middle and tip of the lamina of the youngest fully-expanded leaf on a standard tiller using sharp razor blades. These segments were placed in a stoppered weighing-bottle and weighed. The segments were then floated on distilled water in a covered petri dish for 40 minutes, removed, blotted dry with filter paper, and reweighed in the same bottle. Dry weight was determined after drying the segments for 1 hour at 90° C.

Relative water content, RWC, was given by

$$\frac{FW - DW}{TW - DW} \times 100$$

where FW = weight of segments at sampling

TW = weight of segments after floating

DW = dry weight of segments.

Relative water content is synonymous with relative turgidity but was preferred to the latter term because the technique measured water content, not turgidity. Details of the preliminary evaluation of the technique are given in appendix IV.

4.3 Results.

The experimental data were analysed to reveal significant

differences[1] between topodemes in their response to water treatments. A summary of the results of this experiment (analysis of variance tables, tables of means, standard errors and significant differences) can be found in appendix V. Where the analysis of variance procedure has indicated significant differences between various means, these means have been included in this section.

Tiller production. In the three midwinter weeks immediately after the imposition of the water treatments on July 12, 1972 plants produced tillers at a rate of almost one per day. The mean rate of tiller production for dry treatment plants (19 ± 0.432) was significantly less than that for either medium (20.8 ± 0.432) or wet treatment (20.7 ± 0.432) plants. However, the difference between no one pair of overall topodeme means was found to be significant, nor could differences between any pair of individual topodeme x water treatment means be considered significant.

Of note was the highly significant topodeme x block interaction (analysis of variance, appendix V) indicating that there was at least one topodeme for which tiller production was not constant in all blocks. Such an effect was indicated for only two other plant characters (dry weight of foliage and lamina breadth).

Table VII: Leaf lamina; water treatment means.

	Length (mm)	Breadth (mm)		Shape
Medium	152.44	8.62	Dry	18.66
Dry	138.94	7.51	Medium	17.93
Wet	132.07	7.67	Wet	17.35
	d.05	d.01		d.05

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1 Significant differences have been based on the 1% and 5% levels. Where they have been based on the 1% level the term "highly significant" has been used.

<u>Leaf lamina</u>. Mean length and breadth of leaf laminae produced by medium treatment plants (table VII) was greater than that produced by either wet or dry treatment plants ($p = 0.01$). Thus, the size (length x breadth) of leaf laminae produced by medium treatment plants was significantly larger than that produced by either wet or dry treatment plants. The difference between mean lamina length of wet and dry treatment plants was also significant.

<u>Table VIII: Leaf lamina; topodeme means.</u>

	Length (mm)		Breadth (mm)		Shape
T02	149.133	T09	8.345	P04	19.466
L02	147.550	T01	8.123	L02	18.735
P04	147.300	T02	8.118	T02	18.541
T10	146.116	T10	8.003	T10	18.353
P01	140.150	P01	8.001	L00	18.298
L00	136.566	L02	7.985	P02	18.013
P02	136.116	P02	7.638	P01	17.678
T01	133.866	P04	7.633	T01	16.601
T09	133.583	L00	7.578	T09	16.111
	d.05		d.05		d.05

Table VIII shows for lamina length and breadth those pairs of topodemes whose means can be considered significantly different at the 5% level. Where two topodeme means are not bracketed by a line, they can be considered different at the given level of significance. From the data for gross leaf lamina dimensions, an index of lamina shape (lamina length/lamina breadth), was obtained. The pairs of topodeme means for lamina shape that differ significantly can also be seen in table VIII. The shape of laminae for wet and medium treatment plants (table VII) were no different from each other. However, laminae for wet treatment plants were wider in comparison with length than those of

dry treatment plants (p = 0.01). And at the 5% level, laminae of medium treatment plants were also relatively broader than those of dry treatment plants.

No difference between any pair of individual (topodeme x water treatment) means could be considered significant for any of these lamina characters, since at the 5% level, the topodeme x water treatment interaction term did not reach significance. At least one topodeme was indicated (significance of topodeme x block interaction term, analysis of variance, appendix V) for which lamina breadth was not constant in all blocks.

Rate of leaf emergence. The rate at which leaves appeared on a standard tiller varied little between topodemes (range, 9.65 to 10.11 days between emergence of successive leaves), with an overall mean of one leaf per 9.85 days. The mean rate of leaf emergence for wet (one per 9.22 days) and medium (one per 9.12 days) water treatment plants

Table IX: Leaf emergence, water treatment means.

	Days between successive leaf emergence
Dry	11.208
Wet	9.216
Medium	9.116
	d.01

was almost identical. However, the rate for dry treatment plants (one per 11.21 days) was significantly less than the two former water treatment mean rates, at the 1% level (table IX). Differences between all pairs of individual (topodeme x water treatment) means were attributed to chance (non-significance of TDMS X WATER interaction term in the analysis of variance, appendix V).

Dry weight of foliage. The overall mean dry weight of foliage for plants harvested at the conclusion of the experiment was 5.131 ± 0.07 gm.

Table X: Dry weight of foliage, water treatment means.

	Dry weight (grams)
Medium	6.769
Wet	5.003
Dry	3.621
	d.01

The differences observed between overall topodeme means can be attributed to chance. Similarly, no difference between any two individual (topodeme x water treatment) means can be considered significant. However, the difference between each pair of overall water treatment means for dry weight of foliage was highly significant (table X).

As mentioned previously in this section under Tiller production, the error within whole-plots term for dry weight (that is, topodemes x blocks interaction) was highly significant (analysis of variance table, appendix V). This indicated that there was at least one topodeme for which dry weight was not constant in all blocks. This analysis of variance table also had a significant 'Blocks' term. This indicated that there were at least two blocks that could be considered significantly different with regard to this plant character.

Basal diameter. The mean basal diameter over all topodemes, under each of the three water treatments was different from that under the other two water treatments. Also, when mean topodeme response over all the water treatments was considered, topodeme L02 had a greater mean basal diameter than topodemes T01, P01, P02, L00 and T10; topodeme T09 had a greater basal diameter than did L00 and T10; and P04 also had a greater basal diameter than T10. Differential response (in terms of basal diameter) of individual topodemes to the three water treatments was indicated by the significance of the topodemes x water treatment interaction term in the analysis of variance for this plant character (appendix V). Under

the dry treatment, the mean basal diameter for all topodemes, except PO1, PO2 and LOO, was smaller than that under either the wet or medium treatments. The medium and dry treatments did not induce different basal diameters in either PO1 or PO2, but for these two topodemes the basal diameter under these treatments were both smaller than under the wet treatment. Topodemes LO2, PO4 and LOO were also able to respond

Table XI: Basal diameter means.

	Wet	Medium	Dry	
LO2	36.736	33.052	23.368	31.052
TO9	32.842	34.105	22.842	29.929
PO4	36.105	29.684	23.473	29.754
TO2	31.736	29.368	25.631	28.912
TO1	32.052	31.052	21.684	28.263
PO1	32.000	25.105	27.315	28.140
PO2	33.368	25.578	24.631	27.859
LOO	32.263	21.842	27.368	27.157
T10	29.631	28.947	22.526	27.035
	32.970	28.748	24.315	

to the wet treatment by producing larger basal diameters than under the medium treatment. Topodemes T10, TO2, TO1 and TO9 were not able to do this (table XI).

Plant height and diameter. The analysis of variance tables for these two characters indicated that no two overall topodeme means, or water treatment means for individual topodemes, can be considered to differ significantly. However, each of the three overall water treatment means, for both plant height and diameter, were found to be different from the other two overall water treatment means, at the 5% level (table XII).

Table XII: Plant height and diameter, water treatment means.

	Diameter (mm)	Height (mm)
Medium	230.0750	47.4583
Dry	155.1625	42.0972
Wet	172.1625	31.8333
	d.05	d.05

Compressed leaf length. Each of the water treatment means, over all the topodemes, differed from the other two water treatment means ($p = .05$). The mean topodeme response over all the water treatments, could not be considered to differ for any pair of topodemes. However, differences were indicated between topodemes in the way they responded to individual water treatments. Such differences are indicated in table XIII.

Table XIII: Compressed leaf length means.

	Wet	Dry	Medium
P04	41.8888	44.0000	58.6666
L02	48.3333	51.3333	53.2222
T09	37.3333	48.7777	56.8888
T01	46.1111	49.4444	62.5555
P02	37.7777	56.0000	51.3333
L00	45.1111	47.4444	47.6666
T02	49.0000	54.2222	58.6666
T10	52.6666	43.5555	65.1111
	44.7777	49.3472	56.7638

Compressed diameter. Those compressed diameter means that can be considered to differ are indicated in table XIV. Each of the water treatment means (over all topodemes) differed from each of the other

Table XIV: Compressed diameter; means.

	Wet	Medium	Dry
P04	48.6666	45.5555	36.8888
L02	59.8888	47.3333	36.0000
T09	52.4444	47.0000	39.2222
T01	52.7777	48.3333	39.1111
P02	51.1111	45.3333	34.4444
L00	53.5555	53.2222	37.6666
T02	49.6666	44.5555	39.2222
T10	43.2222	45.8888	38.3333
	51.4166	47.1527	37.6111

two (p = .01). No differences in mean topodeme response over all the water treatments were indicated, although differences did exist between topodemes in the pattern of response to the individual water treatments (table XIV). For T10, wet and dry treatment means were no different.

Plant form. No significant differences between any two topodeme means were found (in mean response over all water treatments or to individual water treatments). The mean for dry treatment plants (over all topodemes) was larger than the means for either medium or wet treatment plants, at the 1% level (table XV). These two latter means were no different from each other (at the 5% level).

Table XV: Plant form - water treatment means.

	Index (tan θ)	Angle, θ (degrees)
Dry	0.6480	33
Medium	0.4863	26
Wet	0.4665	25

d.01

Number of vascular bundles per unit leaf width. Both the number of primary and secondary vascular bundles across the width of the leaf were counted. Since the number of primary bundles was constant for all leaves counted, only one value - total number of bundles - was analysed. The overall mean number of vascular bundles per unit leaf width was 3.798 ± 0.027. None of the differences observed between any means for either water treatments or topodemes were significant.

Epidermal hair density. Plants under the dry treatment produced a significantly greater density of epidermal hairs than those under the wet treatment (table XVI). This was the only difference between water treatment means for this character that was significant. In addition, significant differences were found between overall topodeme mean epidermal hair densities. Topodemes T02 and T10 differed from P04, T09 and P01, and L02 and T01 also differed from P01 (table XVI).

Table XVI : Epidermal hair density - (number per unit lamina area).

Topodeme means	
T02	51.523
T10	50.523
L02	48.904
T01	48.190
P02	46.380
L00	45.666
P04	41.666
T09	41.428
P01	39.809

d.05

Water treatment means	
Wet	43.857
Medium	45.015
Dry	49.158

d.05

Stomate density. In general plants under the wet treatment produced more stomata per unit leaf area than they did under the medium treatment (means over all topodemes), whereas plants under the dry treatment produced an intermediate number of stomata per unit leaf area (which could not be said to be statistically different from that under either of the other treatments). The topodemes for which the pattern of response to the three water treatments differed (in terms of stomate density) are indicated in table XVII. Stomate density for topodemes T09, P04, P02, P01 and T02 was stable (non-plastic) over the water treatments; whereas for topodemes

Table XVII: Stomata; means.

Density (number per unit lamina area)

	Wet	Dry	Medium
P04	15.428	18.142	15.428
L02	20.714	20.428	14.142
T09	19.000	16.285	15.571
T01	18.000	20.285	12.285
P02	15.285	15.714	17.428
L00	19.571	15.000	14.428
P01	14.714	13.857	16.857
T02	16.714	13.857	16.714
T10	17.857	15.428	11.571
	17.476	16.555	14.936

L02, T01, L00 and T10 the density of stomata under the medium treatment was lower than that under the wet treatment. For L02 and T01 the density of stomata under the medium treatment was also lower than that under the dry treatment.

Epidermal cell dimensions. The mean epidermal cell breadth for all leaves measured was 12.174 ± 0.0857 units. No significant differences between

Figure 9. Typical response of a Yorkshire fog topodeme to the experimental water treatments.

W = wet treatment; M = medium treatment; D = dry treatment;

L02 = topodeme name (see text).

any of the topodemes or water treatments were indicated. The size (inversely related to number per unit.leaf area) and length of epidermal cells produced by medium treatment plants (mean over all topodemes) was generally larger than those produced by either wet or dry treatment plants (table XVIII). The difference between no two topodeme means (over all the water treatments or for individual water treatments) was seen to be

Table XVIII: Epidermal cell dimensions - water treatment means.

	Width	Length	Number/unit lamina area (1/size)
Medium	12.290	111.655	26.276
Wet	12.053	101.879	28.689
Dry	12.179	100.949	29.380
	d.05	d.01	d.05

significant, for either size or length of these epidermal cells. However, epidermal cell length was not constant for all blocks in the experiment (significant 'Blocks' term, at 5% level, see analysis of variance table for this character, appendix V).

Relative water content. The data obtained for relative water content of leaf lamina tissue have been summarised in table XIX. From this table it can be seen that plants in each of the three water treatments (means over all topodemes) had a different RWC than plants in each of the other two treatments ($p = .01$). The mean RWC for topodemes (means over all water treatments) was lower for topodemes L02, T10 and P02 than they were for all other topodemes ($p = .05$). Similarly, mean RWC for T09 was greater than that for T02 and L00. When a comparison of individual topodeme x water treatment means was carried out, it was found that the pattern of topodeme response to the water treatments was not the same for all topodemes. In all topodemes the mean for dry treatment plants was considerably lower than for either medium or wet treatment plants.

However, for topodemes T02, L02, T10 and P02, the mean RWC in the wet treatment was no different from that in the medium treatment; whereas, for topodemes T09, P04 and L00, mean RWC in the wet treatment was significantly lower than that in the medium treatment.

Table XIX: Relative water content; means.

	Wet	Medium	Dry	
T09	88.46	95.43	69.14	84.34
P04	86.32	95.99	66.66	82.99
T02	90.17	91.98	64.13	82.09
L00	85.60	92.16	65.98	81.25
L02	86.95	85.77	63.97	78.90
T10	86.36	88.69	59.36	78.13
P02	84.26	83.63	64.10	77.33
	86.88	90.52	64.76	d.05

Correlation coefficients. The correlation coefficients determined for pairs of characters in this experiment can be seen in table XX. The most practicable test for the significance of these coefficients was that in which the population coefficient, ρ, for each pair of characters was assumed to be zero:-

Given that sample size $n = 83$,

then $r > 0.199$ (or $r < -0.199$) would be obtained

less than or equal to 5% of the time.

Similarly $|r| > 0.282$ would be obtained less than

or equal to 1% of the time (appendix VI).

These r-values were, then, taken as the correlation coefficient threshold values for significance at the 5% and 1% levels, respectively. For those pairs of characters for which a significant correlation was found, the coefficient of determination, r^2, was determined, and expressed as a percentage (table XXI). However, since the correlation coefficients

were based upon a relatively large number of plants (and so the number of degrees of freedom was high), a value as small as 0.20 indicates a significant correlation.

Key for Correlation coefficient matrix (table XX)
and Coefficient of determination matrix (table XXI)

BD = basal diameter
CD = compressed plant diameter
CH = compressed plant height
PD = natural plant diameter
PH = natural plant height
TP = tiller production
LL = lamina length
LB = lamina breadth
LE = leaf emergence

DW = dry weight of foliage
SD = stomate density
ED = epidermal cell density
EW = epidermal cell width
EL = epidermal cell length
HD = epidermal hair density

* significant at 5% level
** significant at 1% level

Table XX: Correlation coefficient matrix II

	BD	LL	LB	TP	LE	DW	PD	PH	CH	CD	SD	ED	HD	EW
BD	1.000													
LL	.012	1.000												
LB	.169	.487	1.000											
TP	.154	-.222	-.189	1.000										
LE	-.257	.287	-.041	-.080	1.000									
DW	.502	.354	.530	.237	-.259	1.000								
PD	.249	.368	.391	.155	-.269	.758	1.000							
PH	.170	.401	.274	.154	.075	.536	.591	1.000						
CH	.096	.516	.407	.073	-.005	.626	.759	.596	1.000					
CD	.552	-.129	.348	.239	-.605	.524	.288	0.000	.065	1.000				
SD	.136	-.345	-.236	.039	.016	-.251	-.236	-.318	-.317	-.002	1.000			
ED	-.078	-.220	-.247	.024	.188	-.214	-.302	-.286	-.220	-.168	.525	1.000		
HD	-.170	-.135	-.168	0.000	.222	-.192	-.198	-.191	-.121	-.217	.318	.810	1.000	
EW	.021	.131	.095	-.030	-.083	.087	.042	.125	-.036	-.005	-.289	-.544	-.395	1.000
EL	.029	.208	.231	-.030	-.210	.244	.378	.323	.339	.143	-.501	-.908	-.757	.251

Table XXI: Coefficient of determination matrix

	BD	LL	LB	TP	LE	DW	PD	PH	CH	CD	SD	ED	HD	EW
BD	100													
LL	NS	100												
LB	NS	23.7**	100											
TP	NS	4.9*	NS	100										
LE	6.6*	8.2**	NS	NS	100									
DW	25.2**	12.5**	28.1**	5.6*	6.7*	100								
PD	6.2*	13.5**	15.3**	NS	7.1*	57.5**	100							
PH	NS	16.1**	7.5*	NS	NS	28.7**	34.9**	100						
CH	NS	26.6**	16.6**	NS	NS	39.2**	57.6**	35.5**	100					
CD	30.5**	NS	12.1**	5.7*	36.6**	27.5**	8.3**	NS	NS	100				
SD	NS	11.9**	5.6*	NS	NS	6.3*	5.6*	10.1**	10.0**	NS	100			
ED	NS	4.8*	6.1*	NS	NS	4.6*	9.1**	8.2**	4.8*	NS	27.6**	100		
HD	NS	NS	NS	NS	4.9*	NS	NS	NS	NS	4.7*	10.1**	65.6**	100	
EW	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	8.4**	29.6**	15.6**	100
EL	NS	4.3*	5.3*	NS	4.4*	6.0*	14.3**	10.4**	11.5**	NS	25.1**	82.4**	57.3**	6.3*

4.4. Discussion

The types of response to water treatments displayed by the plant characters studied in this experiment ranged from stable to differentially plastic (table XXII). This information may help to explain the wide ecological distribution of this species in the limited geographical area sampled. For example, the ability of a topodeme to respond preferentially to the wet treatment may be of adaptive significance in a waterlogged environment. The problem then is to relate the types of responses displayed by the topodemes to the source environmental conditions.

Plastic response to the water treatments was displayed by all characters measured, except for density of vascular bundles and epidermal cell width (table XXII). Therefore it can be surmised that each of the three water treatments was empirically different from the other two. The differences between the water treatments probably involved numerous soil factors. Examples of the response to three of these factors are given. (1) The plasticity in plant water status (as measured by relative water content of leaves, see table XIX) probably reflects differences between treatments in soil water status. However, plant water status depends upon numerous soil, plant and atmospheric factors (e.g. soil conductivity, root distribution, root permeability, resistance to flow in roots, Evans, 1973; stage of plant development, Langer and Ampong, 1970; physiological condition of the plant, Rook, 1973; evaporative demand of the atmosphere, Miller et al., 1968). Thus, a given plant water stress does not necessarily relect an equivalent soil water stress. (2) Under waterlogging the Yorkshire fog plants were found to produce a mass of fine aerial roots (see figure 10) indicative of reduced amounts of oxygen in the soil under this treatment. (3) Waterlogging also possibly increased the amount of various soluble ions in the soil and thus some of the effects of this treatment, for example, reduced length of leaves and plant height, could be a result of high levels of particular ions in the soil. (For example, Jones, 1973, showed that under waterlogging, the mineral content of plants was significantly higher than under drier water regimes).

Table XXII : Hierarchy of plant response

Response	Characters
Non-plastic (stable) response to water treatments	
No differentiation between topodemes................	vascular bundle density
	epidermal cell width
Plastic[1] response to water treatments	
No differentiation between topodemes................	tiller production
	rate leaf emergence
	plant height
	plant diameter
	plant shape (form)
	dry weight foliage
	epidermal cell length
	e pidermal cell size
Differentiation	
In mean topodeme response...	epidermal hair density
	leaf lamina breadth
	leaf lamina length
	leaf lamina shape
	basal diameter
	relative water content
In pattern of response to water treatments........	compressed diameter
	compressed leaf length
	basal diameter
	relative water content
	stomate density

1. The term plasticity is used in these pages to denote the degree and direction of change in topodeme response to a change in water treatments.

The stability in density of vascular bundles in response to the water treatments was surprising in view of the variability previously observed in this character in response to water (e.g. in wheat, Ridley and Todd, 1966; in Pelargonium, Metwally et al., 1970; and in blue panicgrass, Dobrenz et al., 1969a). The stability in this character and in epidermal cell width may be explained by a physiological homeostasis whereby constant character values were maintained despite differences between treatments in, for example, plant water stress (table XIX, relative water content means). Such homeostatic mechanisms, which may confer survival value in changing and/or stress environments (see, for example, Parker, 1968) have been numerously described in plant species (e.g. Boyer, 1973). This stability in response to water could also be related to the genetic invariability found for these two characters (error variance for vascular bundles and cell width = 0.13 and 1.43, respectively, see tables A XIX and A XXIII). The lack of genetic diversity could have come about as a result of a strong stabilizing selection for either of these two characters or a developmentally-related character. Expansion of the epidermis and vascular and mesophyll tissues are closely related during the latter stages of leaf development (Mitchell and Soper, 1956; Tomlinson, 1970). Thus, stabilizing selection for, for example, mesophyll cell size, which is related to rates of light-saturated photosynthesis (Wilson and Cooper, 1967, 1969, for Lolium), could explain the constancy in cell width and vascular density.

It is notable that both non-plastic characters discovered were measured on leaf material collected at the termination of the experiment (day 61). At that stage not all drying cycles for all dry treatment plants were in phase. For example, the final watering that some of these plants received was 14 days before day 61, others 3 days. Thus, within the dry treatment, leaves on which epidermal measurements were made did not represent a similar stage of water stress. The effect of this on a character sensitive to water would be to increase the within-treatment variance and so reduce the chance of finding significant differences between treatments. In retrospect, it would have been more prudent to have harvested leaves for microscopic examination when plants within the dry treatment

were at a similar stage in their drying cycle.

Plastic response to the water treatments was displayed for all other plant characters studied (table XXII). The significance of the plasticity can in many cases be inferred from the direction and amount of the response to the treatment differences ; examples are given below.(1) Epidermal hair density was found to be greatest under the dry, and least under the wet treatment (table XVI). In terms of reducing wind speed immediately adjacent to the surface of the leaf, and so increasing the depth and resistance of the boundary layer resistance to gaseous exchange between the leaf and the surrounding atmosphere (Slatyer, 1967), densely hairy leaves would be advantageous under conditions of limited water supply. (2) Plant size was found to be reduced under the dry treatment, in comparison with the medium treatment. This observation made on various estimates of plant size (i.e. lamina, length and breadth, table VII; rate of leaf emergence, table IX; rate of tiller production, page 55; plant height and diameter, table XII; compressed diameter, table XIV; compressed leaf length, table XIII; basal diameter, table XI; and dry weight of foliage, table X) can also be explained in terms of water use. By reducing water requirement and so water loss, a smaller plant would be more able to withstand limited water conditions than a larger plant. The reduction in plant size under the dry treatment was almost certainly a result of reduced cell expansion growth (epidermal cell size was smaller under the dry than either of the other treatments, see table XVIII). This was probably related to the reduced turgidity of tissues under the dry treatment as indicated by the comparatively lower relative water content of the leaves (table XIX). (3) Plants grown under the wet treatment possessed smaller leaves (table VII) and tillers, and so smaller plant diameters, heights (table XII) and compressed leaf lengths (tableXIII), smaller intercostal epidermal cells (table XVIII), and more frequent stomata per unit lamina area (table XVII) than those under the medium treatment. These observations can be explained by a comparative decrease in cell expansion growth under the wet treatment, as a result of a water deficit in the tissues of these plants (table XIX). Water deficits in plants growing in excess water

conditions have previously been described (Rook, 1973). However, some other factors must also be important here, since the length of leaves, plant height and compressed leaf length were shorter under the wet, than under the dry treatment. The reverse would have been predicted using the relative water content values as an indication of turgor and so cell expansion growth. Soil factors in the supra-optimal water treatment that could be involved in the limitation of leaf expansion growth include limited oxygen (figure 10) and excess minerals. A more complete picture of the comparative contributions of cell expansion and division to leaf and plant growth would have been gained from a count of the number of cells within an epidermal file, along the length of the lamina. This would have provided information on cell division.

However, the biological significance of the plastic response to water treatments could not always be inferred from the direction of the response. For example, growth form was found to be more erect under the dry treatment, than under either the medium or wet treatments. These results are contrary to those of Hickey (1961) who, in his study of the effects of site and grazing on growth form of crested wheat-grass, found that plants from wet sites tended to be more erect than plants from drier sites. Hickey explained his observations in terms of reduced water loss by the more prostrate (dry site) types. Another example where biological significance could not be inferred from the direction of the response involved basal and compressed diameters. Under the wet treatment these measurements were found to be greater than under the medium treatment. Despite their relationship with number of leaves per tiller and tillers per plant (table XXI), the increase in these diameters under the wet treatment cannot be fully explained by the measured rates of leaf emergence and tiller production, neither of which showed a difference between medium and wet treatments. It is possible that if counts of the number of tillers per plant had been continued throughout the duration of the experiment, a difference between the wet and medium treatments may have developed.

The evidence presented above for adaptation to the environmental conditions that induced the differences observed

gure 10: Aerial roots produced by plants under waterlogging.

between plants under the different water treatments is merely circumstantial. Direct evidence for such adaptation was not obtained in this experiment. In retrospect, it could have been achieved through reciprocal reversals of the water treatments, followed by some measurement of " adaptability " to the new conditions (e.g; Survival or water use efficiency). However, it must not invariably be considered that plasticity is adaptive. In some circumstances plasticity may have mortal consequences for the species. Such an example was presented in Chapter 3 in relation to the plasticity observed in seed weight (see figure 5).

The plasticity discussed above was indicated by the significance of the water treatments term in the analysis of variance for each plant character (appendix V). This plasticity is a characteristic of the species as a whole in the temperate region from which the samples were collected, and is related to environmental variability characteristic of this region as a whole. Such environmental variability, to which plants respond by phenotypic plasticity, is random with respect to time. The climate, for example, of this temperate region varies between years and within seasons in such an unpredictable fashion. For the plasticity discussed above, then, no topodeme differences were considered. Such differential topodeme plasticity, indicated for only five plant characters by the significance of the topodemes x water treatment interaction term (see analysis of variance tables appendix V), will be discussed later.

Genetic differentiation, involving quantitative differences between overall topodeme means was discovered for epidermal hair density, lamina dimensions, basal diameters, and relative water content (table XXII). Such differentiation suggests specific, stable environmental differences between the source habitats of those topodemes that were found to be different. That is the genetic divergence exposed probably came about as a result of disruptive selection. Several examples of such differentiation are given. Topodemes T02 and T10, from exposed habitats in which water drained rapidly from the soil after rain, possessed more densely hairy leaves than plants of topodemes P04, T09 and P01, from more moist habitats.

The effect of increased hair density is to reduce water loss from the leaf (see discussion above). The observation of greater hair density on leaves of T01 plants (from a marshy yet very exposed coastal sand dune habitat where rate of water loss was high) than on leaves of P01 plants can also be explained in terms of reduced water loss. Habitat P01 was moist throughout the year, sheltered and of higher altitude and so cooler than the coastal T01 habitat. Under such conditions the rate of water loss would be low, and epidermal hair density selectively neutral. This was one occasion where a statistical analysis for exposing differences between sample variances, rather than sample means (as in the analysis of variance used), would have been profitable.

Mean topodeme lamina breadth was found to be greater for topodemes T09, T01 and T02, than for topodemes P02, P04 and L00. The effect of increased lamina width is to decrease water loss from the leaf surface. One effect of increased leaf width is to increase the degree of leaf roll. Differentiation in this character, a typical xerophytic adaptation, was found between regional samples of Yorkshire fog in New Zealand (Basnyat, 1957). However, no direct estimate of this character was attempted in this experiment. Another effect of increased leaf width is to reduce the " edge effect " (see for example Lewis, 1969) on leaf water loss. The broadness of laminae of topodemes T09, T01 and T02 is probably related to the exposed situations of their source habitats, and so can be considered an adaptation against water loss, Such an adaptation would have especial significance for T02 plants from a rapidly-draining sand dune habitat. Topodemes P02, P04, and L00 were from more sheltered habitats in which the water table level was continuously high, and in such situations selection for adaptations preventing excess water loss would be unlikely.

The mean topodeme lamina length for topodemes T02, L02, P04 and T10, topodemes from the two extremes in the range of habitat water regimes, was greater than that for topodemes T01 and T09. The topodeme X water treatment interaction term (see analysis of variance, table AVII) was not significant and so it was assumed that the above topodeme differentiation was the result of an

increased response of the four former topodemes to each of the water treatments. Inspection of the table of individual lamina length means (table AVII) showed that this was not so. The explanation of the apparent differentiation lies in the response of the topodemes from the extreme source habitats to the extreme water treatments. Under the dry treatment, topodemes T10 and T02, from rapidly draining sand dune habitats, produced disproportionately longer laminae ; and under the wet treatment, topodemes P04 and L02, from continuously waterlogged habitats, responded in the same manner. However, the ability of these topodemes to respond differentially to the extreme water treatments was not so great as to be indicated by the analysis of variance, at the 5 % level of significance. Thus, it cannot be concluded with the conventional confidence (95 % level) that the above observation of differential topodeme response to water treatments was real.

The topodeme differentiation discussed above involved quantitative differences between some topodemes in their mean response over all the water treatments. For this differentiation no differences between topodemes in their response to individual water treatments were involved. Such differentiation was seen to be related to specific, stable environmental differences between source habitats. A further type of topodeme differentiation, that in pattern of response to the water treatments, was also displayed by some topodemes, for some plant characters. Such differentiation involved both degree and direction of response of the topodemes to the water treatments ; that is, differntial plasticity. Plasticity is considered to be a characteristic response of plants to randomly fluctuating environmental variability (Bradshaw, 1965). The differential plasticity observed between particular topodemes must then reflect differences between their source habitats in randomly fluctuating environmental factors. However, these environmental differences between habitats must have been relatively stable with time, otherwise it would have been impossible for topodemes to have diverged genetically, as demonstrated. The plant characters for which differential plasticity was observed were compressed diameter and leaf length, stomate density, basal diameter and relative water content

(table XXII). For the two latter characters, topodeme differentiation in mean topodeme response was also demonstrated. However, for these characters such differentiation will not be discussed due to the uncertainty of its interpretation.

For relative water content, the direction of the response to the water treatments to all topodemes was similar (table XIX). Water deficits in leaf laminae, as measured by RWC, were in general induced by the wet treatment and to an even greater extent by the dry treatment. However, the degree of plastic response to some water treatment differences was seen to differ quantitatively between some topodemes. For example, the increase in plant water deficit induced by the dry treatment was relatively greater for T10 than for the other topodemes. The explanation of this observation probably lies in the ability of T10 plants, from an excessively drained habitat, prone to drought, to withstand a relatively greater degree of internal moisture stress before showing signs of this stress. This view was supported by the observations of plant size measurements for which comparison of individual means was valid (i.e. compressed and basal diameters, and compressed leaf length). Plant size for topodeme T10 under the dry treatment was not as small in comparison with other topodemes as would have been predicted using the RWC values. This relatively greater water deficit induced in T10 plants by the dry treatment was probably a consequence of the criteron for watering plants under this treatment. Plants were watered when they indicated soil water to be at permanent wilting percentage (see section 4.2.4). Thus, if T10 plants under the dry treatment were able to withstand greater levels of internal moisture stress before showing signs of wilting, then they would have been rewatered when soil moisture status was relatively lower than that for other topodemes. Critical evidence for this would have been achieved by a direct measurement of soil water status immediately before rewatering. Such a measurement would have provided a quantitative means for comparison of the ability of topodemes to extract water from the soil, and so have provided supporting evidence for the differential ability of topodeme T10 to withstand internal water stress. A further example for the character relative water content, in which the degree of plastic response to a water treatment difference was seen to differ quantitatively between some topodemes, involved response to

the wet and medium treatments. No significant difference was found between these treatments for topodemes T02, T10, L02 and P02, unlike topodemes T09, P04 and L00. The source habitats of the four former topodemes represent the range in source environmental water regimes. Therefore, the topodeme differences cannot be considered to be related to differences in absolute amounts of environmental water , but rather to differences in the degree of random fluctuation in some aspect of this environmental factor.

Low stomate frequency was associated with high levels of drought resistance in blue panicgrass (Dobrenz et al., 1969b). This was probably related to the high stomatal resistances and low transpiration rates associated with low stomate frequencies (see Miskin et al., 1972). In the present investigation, no Yorkshire fog topodeme was found to possess a consistently lower stomate density over all the water treatments than any of the other topodemes. However, in response to the dry treatment, the treatment simulating periodically droughty conditions, topodeme differences were found. Topodemes T02, P01 and L00 produced a lower stomate density than topodemes T01 and L02. The latter topodemes were from habitats in which water was in excess of plant requirements throughout the year ; whereas the source habitats of the former, lower stomate density, topodemes were characterised by periods of water deficit. In the source habitat of topodeme T02, in particular, it is probable that water was continually in short supply due to the sand dune soil of this habitat being unable to maintain water for long periods after rain. Thus, the reduced stomate density for topodeme T02, and perhaps for topodemes P01 and L00, under the dry treatment, can be considered an adaptive response to these conditions.

Further topodeme differentiation, involving quantitative differences in degree of plastic response to the diverse water treatments, was found for stomate density; For topodemes P04, T09, P02, P01 and T02, this character was stable in response to the water treatments, whereas for topodemesL00, T10, L02 and T01 fewer stomates per unit leaf area were observed under the medium than under the wet treatment. For the latter two topodemes the mean density under the medium treatment was also significantly less than that under the

dry treatment (table XVII). The relatively lower stomate density under the medium treatment was expected since epidermal cell expansion growth (to which this character was inversely related, table XXI) was greatest under this treatment (table XVIII). However, the differences in plasticity displayed between the above groups of topodemes cannot be explained by topodeme differences in expansion growth of the epidermis ; no topodeme differentiation was displayed for any of the epidermal cell dimensions that were related to expansion growth. Nor can this differential plasticity be explained by the observed differential plasticity in leaf water stress, as measured by RWC of leaf laminae, although it is certain that leaf water stress cannot be fully eplained by relative water content (Barrs, 1968). The inability of topodemes P04, T09, P02, P01 and T02 to respond by plasticity to diverse water treatments is probably related to the relative stability within their source habitats of the environmental factors determining stomate density. Metwally et al. (1970) showed that soil water level was one such determining factor. These workers showed that in young leaves of *Pelargonium* decreased water levels decreased density of stomata by inhibiting cell divisions for stomate formation. However, the absolute level of water in the environment cannot be the sole determining factor since the source habitats of the topodemes for which stability in stomate density was displayed represented the whole range in environmental water regimes.

As suggested above, stomate density was directly related to cell division in young leaves. When it and the one estimate obtained in this experiment of the amount of cell division in the epidermal surface (I.e. number of cells per unit leaf area) were correlated, a highly significant positive association was obtained (table XXI). In older leaves, in which cell divisions for stomate formation would have been completed, and cell expansion growth continuing, stomate density can be expected to be inversely related to characters directly related to expansion growth. Such negative associations were found when this character was correlated with leaf length and breadth, dry weight of foliage, plant height and diameter, and compressed leaf length (table XXI).

The two compressed plant dimensions were measured when foliage of the plant was raised to its maximum vertical position by grasping it together at average leaf length. Compression facilitates comparison of measurements of heights and diameters by minimizing differences in growth form (Hickey, 1961). The obtaining of these measurements, as estimates of plant size was particularly felicitous since plants were grown under water treatments that induced differences in plant form (table XV). When these two compressed dimensions were correlated a non-significant association was found. Compressed leaf length was found to be associated with those characters most closely related to cell expansion growth (i.e. epidermal cell length, leaf length, plant height and diameter) ; whereas, compressed diameter was associated withthose characters for which cell division was more important (i.e. tiller production, rate of leaf emergence, leaf breadth and basal diameter, see table XXI). Topodeme differentiation in plasticity for both of these compressed dimensions was discovered.

The differential plasticity for compressed leaf length merely involved quantitative differences in the degree of plastic response. In general topodemes possessed greater compressed leaf lengths under the medium treatment and least under the wet treatment (c.f. pattern of plant response to the water treatments for leaf length (table VII) which when correlated with compressed leaf length (table XXI) showed a high positive association). However, for some topodemes, the difference in compressed leaf length between some water treatments was not so great as to be considered significant. For example, the difference between the wet and the dry treatment for topodemes P04, L02, T01,L00,T02, and T10 was not significant ; nor was the difference between the dry and the medium treatments for topodemes L02, T09, P02, L00 and T02. The differences between topodemes in the degree of plasticity (stability) for compressed leaf length probably reflect stable environmental differences between their source habitats in randomly fluctuating factors that were related to this plant character. Likely factors include those that determine cell expansion growth.

The differential plasticity observed forcompressed diameter involved not only differences in the degree of plastic response to

water, but also a difference in the direction of the plasticity. For all topodemes, but L02 and T10, the pattern of the response to the water treatments was the same ; wet treatment means were slightly larger than medium treatment means, although never significantly so, and the dry treatment means were significantly less than either of the former means. However, under the wet treatment, topodeme T10 possessed a smaller compressed diameter than under the medium treatment ; and, therefore, the means for this dimension under the wet and dry treatments were no different. For no other topodeme was this observed. The reduction in compressed diameter for this topodeme under waterlogging probably reflects its lack of adaptation to these environmental conditions. Such conditions could not have existed in the source habitat of T10, due to the inability of the sand dune soil of this habitat to hold water after rain. The differential plasticity observed for topodeme L02 also involved differential response to the wet treatment; However, in this instance the differential response was merely one of degree, not direction, to the treatment difference. Under the wet treatment, this topodeme possessed a significantly larger compressed diameter than under the medium treatment. The ability of these plants to respond differentially to the wet treatment (in comparison with the other treatments) probably reflects their adaptation to such waterlogged conditions ; the source habitat of topodeme L02 was waterlogged throughout most of the year.

Basal and compressed diameters were probably closely related genetically and physiologically. This was suggested by the high positive association found between these characters when they were correlated at the individual plant level (table XX). Thus, it was not unexpected that patterns of response to the water treatments for these two characters were similar (tables XI and XIV). For example, the response of topodemes T01, T02 and T09 for basal diameter reflected those patterns found for compressed diameter. In addition, the ability of topodeme L02 to be more responsive to the wet than the medium treatment in terms of compressed diameter was also observed for basal diameter. However, these two characters were not so closely related that differences between them in patterns of topodeme response

were not found. For example, topodemes P04, P01, P02 and L00 were able to respond to the wet treatment by producing larger basal diameters than they did under the medium treatment (c.f. pattern of response for L02). Such abilities were not observed for these topodemes in terms of compressed diameter, although the differences were merely of degree of plastic response. A further example in which topodeme response in terms of basal diameter was different from that for compressed diameter involved topodemes P01 and P02. Mean basal diameters under medium and dry treatments were not significantly different for these two topodemes. For no other topodeme was this found. The stability in response to the difference in these water treatments for P01 and P02 appeared to be due to their inability to respond to the medium treatment. Such an inability could be related to the low soil fertility, high altitude conditions of their source habitats. The final example of a difference in topodeme response between these two diameters involved topodeme L00. For this topodeme, mean basal diameter under the medium treatment was significantly lower than that under the dry treatment. Such a pattern of response, involving a change in direction of response to the medium treatment, was different from that for all other topodemes for either basal or compressed diameters. Nor was this pattern of response for L00 observed for dry weight of foliage for which no differentiation was discovered. Thus, the significance of this differential adjustment to this particular water treatment was difficult to explain. It is possible, however, that L00 under the medium treatment allocated proportionally more of its energy than other topodemes to sinks other than those that contribute to basal diameter, and dry weight of foliage. The roots were one such possible sink.

The types of responses displayed in this experiment by the Yorkshire fog topodemes have provided information on the means by which this species became adapted to the ecologically diverse situations from which it was sampled. Differentiation between some topodemes was observed in their ability to respond to the experimental water treatments, in terms of some plant characters. Where such plant variation was related to known environmental variation, genecological differentiation can be

suggested. For some characters measured, however, no topodeme differentiation was observed. These characters (tiller production, rate of leaf emergence, plant height and diameter, vascular bundle density, dry weight of foliage, and epidermal cell length, width and number per unit lamina area) were, therefore, considered to be of least importance in the adaptation of these topodemes specifically to their source habitats. However, they could have been of importance in the adaptation of these topodemes under the environmental conditions characteristic of this region as a whole.

For those characters in which differentiation was revealed, the differences did not always involve the same groupings of topodemes, even where the character was seen to be related developmentally (table XXI). Nor did the differences invariably involve those groupings of topodemes for which differences in environmental water regimes were described. Therefore the differentiation could not always be explained in terms of habitat water regimes. However, topodemes T02 and T10 consistently appeared where differentiation was displayed: stomate density under the dry treatment (T02); epidermal hair density over all treatments (T02, T10); leaf lamina length under dry treatment (T02, T10); lamina breadth over all water treatments (T02); relative water content under the dry treatment (T10); and compressed and basal diameters in pattern of response to the three water treatments (T02, T10). The direction of the responses displayed by these topodemes, from rapidly drained sand dune habitats in which soil water deficits were probably continually high, was usually interpretable in terms of adaptation to periodically dry conditions or lack of adaptation to waterlogging. The differentiation involving these topodemes can then be considered to have arisen as a result of selection, by factors involving environmental water.

In the present investigation topodemes of Yorkshire fog were sampled from ecologically diverse habitats and grown under uniform environmental conditions in order to discover whether or not genetic divergence existed between them. For

some pairs of topodemes, no such divergence was observed. In these cases, broad adaptability of individual genotypes was suggested to account for this lack of differentiation. Genetic divergence observed between pairs of topodemes for various characters studied in the glasshouse and field experiments could not in many cases be related to environmental variation. Therefore, although it could not be concluded that such divergence was the result of genecological differentiation, this possibility could not be disregarded. The evidence was insufficient. This genetic divergence could also have come about as a result of several chance sampling effects.

APPENDIX I : Experimental control of water

Numerous publications have described attempts to control moisture supply to the soil and to regulate its distribution throughout the soil. However, it is impraticable to attempt to maintain the water content of the soil continuously at any value other than saturation, field capacity, or permanent wilting percentage (Kramer, 1969).

In attempts to circumvent this problem, numerous workers (e.g. Slatyer, 1961) have used osmotic solutions of known concentrations in place of soil, on the assumption that (1) plant response to osmotic stress is the same as to an equivalent soil moisture tension and (2) plant roots do not take up the solute of the osmotic solution. There are, however, objections to both these assumptions. Firstly, Gingrich and Russell (1957), comparing the effects of soil moisture tension and osmotic stress on growth of corn roots, claimed that the effects were not the same. Secondly, some substances used as osmotic agents have been shown to be absorbed by plant roots (e.g. mannitol, Slatyer, 1961), and may produce toxic effects within the plant (e.g. polyethylene glycol 1500, Macklon and Weatherley, 1965). Finally, water stress in plants may originate through soil water conductivity being too low to allow rapid rewetting of the soil around the roots during periods of rapid transpiration (Macklon and Weatherley, 1965). Such rewetting will occur when transpiration falls, subject to water availability in the soil outside this root zone. Thus, osmotic solutions cannot be regarded as a reliable substitute for drying soils.

The water treatments of the glasshouse experiment involved the supply of different amounts of water to the experimental material. In one treatment the soil was maintained in a waterlogged condition. In the other two treatments the plants were allowed to deplete the soil of water to different moisture contents below field capacity before rewatering (i.e. two drying cycles of different periods were imposed). Hundreds of papers have been published on plant response to such water treatments (recently, for example, by Vough and Marten, 1971; and Jones, 1973) and

these have provided the subject material for numerous reviews (e.g. Richards and Wadleigh, 1952; Stanhill, 1957; Kramer, 1963), and several books (e.g. Kramer, 1949, 1969; Slatyer, 1967; Kozlowski, 1968) and symposia proceedings (e.g. Soil and plant water, N.Z.D.S.I.R. Symposium, 1973).

The experimental water treatments chosen required (1) that the soil held effectively different amounts of water at field capacity and at saturation and (2) that the plants depleted the available moisture rapidly, so that several drying cycles could be completed before termination of the experiment.
A 1:1 plasterer's sand:peat potting medium, the water retention characteristics of which were known (Wilson, 1973), was therefore employed. To this soil a fertilizer mixture of osmocote : superphosphate : dolomite lime : uramite (20:14:8:3) was added. The rate of fertilizer application (225 grams per bushel of soil) was considered great enough to supply the plant with adequate nutrient for the duration of the experiment.

The amount of water held by this soil between permanent wilting percentage and field capacity was estimated. This information was required for determination of the watering schedule for each of the drying cycles. Samples of dry soil were suturated with water and left to drain for 24 hours, weighed, oven-dried at 80°C for 24 hours and reweighed. The weight difference was anestimate of the water available for plant growth (i.e. that held between permanent wilting percentage and field capacity). It was probably an overestimate, since oven-drying dried the soil to moisture contents well below these moisture contents at which plant roots could absorb water.

TABLE a I : Soil water content

Medium		Weight (grams)
Soil, plus water at field capacity, Sample........	1	1379
....	2	1334
Oven-dried soil	1	1015
....	2	984
Difference	1	364
....	2	350

APPENDIX II: Percentage seed germination. The determination of significant topodeme differences.

The significance of differences in percentage germination between topodemes (Section 2-3) was determined by the Chi-square test. An analysis of variance procedure could not be applied owing to the form of the data (one value, percentage germination, taken from counts on 200 seeds for each topodeme). The problem in a Chi-square test is to test the (null) hypothesis that no relationship exists between two classifications; in this case, various topodemes and percentage germination. This is done by comparing the observed values with those expected on the basis of the null hypothesis. In this case the data was tested on the basis of equal percentage germination between topodemes; that is, deviation from the overall mean for percentage germination (Table aII).

Chi-square, $\chi^2 = \sum(O-E)^2/E$, (Alder and Roessler, Ch.5)
where O is the observed percentage germination for each topodeme,
E is the expected percentage germination for each topodeme on the basis of the null hypothesis, i.e. $\sum O/n$, and
n is the number of topodemes.

In each of the four cases below, E takes on a new value since in each case a different set of topodemes, n was considered.
In (1), twenty-one topodemes were considered for which $\sum O = 1535$ and thus E = 73.10; in (2), n = 20, $\sum O$ = 1535-41 and thus E = 75.15; in (3) n = 19, $\sum O$ = 1494-54 and thus E = 75.79; and in (4), n = 18, $\sum O$ = 1440-57 and thus E = 76.83.

(1) All topodemes. (20 degrees of freedom; expected percentage germination, 73.10). Chi-square calculated, $\chi^2 = 52.98$. This value was much higher than that expected by chance from a set of topodemes in which percentage germination was equal. The most deviant topodeme was P03, 41% seed germination.

(2) PO3 removed. (19 d.f.; expected percentage germination, 75.15). Chi-square calculated, $\chi^2 = 37.19$. This value was also in excess of that expected by chance from a set of topodemes in which percentage germination was equal. The most deviant topodeme was PO5, with 54% seed germination.

(3) PO3 and PO5 removed. (18 d.f.; expected percentage germination, E = 75.79). χ^2 calculated was found to be 30.86, a value expected by chance about 3% of the time from a set of topodemes in which percentage germination was equal. Thus, at the 5% level the percentage seed germination for all remaining topodemed cannot be considered equal. The most deviant topodeme was, in this case, LO5 with 57% germination.

(4) PO3, PO5 and LO5 removed. (17 d.f.; expected percentage germination = 76.83). χ^2 -calculated = 25.6. Such a χ^2 -value might well be expected by chance from a set of topodemes in which the percentage germination was equal. In fact, $\chi^2 = 25.6$ with 17 d.f. can be expected almost 10% of the time from such a set of topodemes. Thus, the differences between the remaining topodemes can be attributed to chance; they were not significantly different.

TABLE aII: Percentage germination (wild Material)

		Percentage germination	Chi-square $(O-E)^2/E$
Topodeme	T01	66	0.69
	T02	82	1.08
	T09	65	0.90
	T10	82	1.08
	P01	90	3.91
	P02	83	1.34
	P04	91	4.38
	L00	74	0.01
	L02	92	4.89
	T00	83	1.34
	T03	58	3.12
	T04	78	0.32
	T05	75	0.05
	T06	72	0.02
	T07	77	0.21
	L03	62	1.69
	L04	90	3.91
	L05	57	3.55
	P00	63	1.40
	P03	41	14.10
	P05	54	4.99
		$\Sigma O = 1535$	$\chi^2 = 52.98$

See text for meaning of symbols.

APPENDIX III : <u>Preparation and examination of fixed leaf material.</u>

On day 61 of the glasshouse experiment, the second youngest fully-expanded leaf on each plant was removed below the level of the ligule and fixed in a formalin: acetic acid: ethanol (5:5:90 FAA) solution.

Of the numerous techniques devised for preparation of leaf material for anatomical and morphological study (see Johansen, 1940), several were considered. Firstly, cellulose-acetate replicas from silicone-rubber impressions of biological surfaces (Sampson, 1961) have recently been extensively used, although the use of this technique for estimation of stomatal dimensions has been questioned (Lesham and Thaine, 1969, see appendix IV). The technique was judged unsuitable for the often densely pubescent epidermal surfaces of Yorkshire fog. Secondly, various techniques for exposing the surface by scraping away the remainder of the leaf of dissolving the leaf in a macerating fluid that would leave only the cuticular layer of the epidermis, a "surface impression" (Skipworth, 1973), were found to be either too time-consuming or impraticable due to the fragility of the cuticular layer. Finally, a technique based on that of Arney (1954), who killed his leaf material in boiling water, decolourised it in warm alcohol, then cleared it in hot lactic acid, was found to be suitable. This technique (outlined in section 4.2.5.) cleared the leaf tissue sufficiently to allow the epidermal surface of an intact leaf segment to be examined microscopically.

A number of epidermal characters (e.g. stomate and hair density, and cell size) were to be studied, and therefore microphotographs of the leaf surface were taken since this would be an accurate means of recording this information. The leaf material was mounted in the clearing fluid on a glass side and placed onto the platform of a Zeiss Ergaval microscope (16 X objective lens, 10 X eyepiece lens). The microscope was set up for microphotography with a 35mm Zeiss camera with automatic exposure control (projective lens = 6.3X).

Preliminary examination of the two leaf surfaces revealed that the abaxial surface was relatively flat in contrast with the deeply furrowed adaxial surface. The abaxial surface also displayed intercostal cells of much greater uniformity than the adaxial surface, where large bulliform cells were associated with the furrows. These observations were confirmed by examination of transverse sections through this same leaf material. Also, it has been claimed that the cells of the abaxial surface in some grass species show greater variation in response to various treatments than those of the adaxial surface (Mitchell and Soper, 1958). Therefore, the abaxial surface alone was examined and photographed The camera was positioned so that the second primary vein from the leaf margin lay just outside the camera's field of view and parallel to the length of the photograph. This standard position for each photograph therefore included at least two adjacent stomatal bands. Preliminary trials for correct exposure settings were required. Labelled slides were photographed in a predetermined order so that recognition of a particular leaf segment was possible by position in the sequence of frames on the film. The films were each labelled by taking a photograph of a number (10,20,30...100) on a micrometer eyepiece.

APPENDIX IV : The glasshouse experiment - plant characters measured.

Differential plant response to the water treatments of the glasshouse experiment was measured in terms of structural features of the leaves. Such features play an important part in the resistance to gaseous and heat exchange between the leaf and the surrounding air, and consequently impinge upon all plant processes. For example, stomate density was measured. The dimensions and distribution of stomatal pores determines the efficiency of control of gaseous exchange (Metwally et al., 1971). Certain aspects of stomatal dimensions, pore width and depth, are both very difficult to measure, and in the case of pore width subject to rapid changes. Therefore, this dimension measured on excised leaves probably bears little relation to the width prior to excision. Also, the validity of surface impression methods (Sampson, 1961) has recently been questioned by Lesham and Thaine (1969), who show that in some grass species with sunken stomata (and Yorkshire fog is one such species), the pores observed in surface impressions probably do not represent stomatal apertures which penetrate to sub-stomatal cavities. Because of these difficulties of making meaningful measurements of stomatal dimensions, this component of gaseous exchange control was not measured.

Leaf size and epidermal cell size were also measured. The size and shape of leaves, as well as their orientation and wind speed, determines the resistance to gaseous and heat exchange of the layer of non-turbulent air immediately adjacent to the leaf surface, i.e. the boundary layer resistance (Slatyer, 1967). Final leaf size and shape is said to be determined by expansion of the epidermis through the latter's control of the expansion of the mesophyll and vascular tissues (Soper and Mitchell, 1956). Therefore, variation in lamina length in grass species might be expected to be primarily related to changes in epidermal cell length (Cooper, 1964). However, Forde (1966) pointed out that this generalization tends to obscure the importance of epidermal cell number. The depth and consequently the resistance of the boundary layer might be expected to be increased by leaf hairs (Slatyer, 1967), which significantly decrease wind

speed near the surface of the leaf. But if the hairs are filled with water, they may contribute to the non-stomatal component of water movement (Wooley, 1964). Thus, the presence of hairs may not contribute to the reduction in water movement from the leaves.

Differential plant response to water treatments was also measured in terms of relative water content of leaf tissue by the relative turgidity method of Barrs and Weatherley (1962). Relative water content, RWC, has become a standard expression of plant water status. Recently, Barrs (1968) reviewed the methods used in determination of water status in plant tissues showing it to be described variously by water content, total water potential, and structural characteristics of the plant. However, the full description of the water status of plants is complicated since plant water status is a highly dynamic parameter. Is is strongly influenced by atmospheric and soil conditions and also regulated to different degrees, in different situations, and with different species, by physiological factors (Slatyer, 1970). Thus, any one description using only one of the methods in common use cannot be said to describe the water status of the plant completely.

The determination of Relative water content

Segments of leaf tissue floated on distilled water take up water. The pattern of uptake with time is clearly divided into two phases. The initial rapid uptake (Phase I) satisfies the water deficit of the tissue; the second phase (Phase II), which is slower, and prolonged, was shown by Barrs and Weatherley to be associated with growth of the tissue segments. Phase II does not begin until Phase I is complete. For accurate determination of RWC, the tissue should be removed from the water at the conclusion of Phase I. If this is not done, and Phase II is allowed to commence, the additional uptake of water results in an under-estimation of RWC.

The duration of Phase I differs among species (e.g. in wheat, 4 hours, Yang and de Jong, 1968) and may also vary with the magnitude of the water deficit of the tissue (El-Sharkawy and Hesketh, 1964). It is therefore necessary to determine the duration of Phase I to uptake for any species for which the method is used, and also to ascertain the constancy of this duration at various levels of water stress.

RWC may also be under-estimated if there is a bulk entry of water through the cut edges of the tissue segments; an effect known as injection. The importance of injection was minimised by using the whole width of the lamina and by cutting the segment from the lamina using very sharp razor blades.

Thus, before the technique was judged suitable for use with Yorkshire fog leaf lamina tissue, it was necessary to determine the duration of Phase I uptake, at various levels of water stress.

Duration of Phase I uptake

Razor blades were used to cut segments (1cm long) from the lamina of Yorkshire fog plants. The complete lamina width was included. In each case the segments were bulked. Three samples were obtained, one for non-wilted leaf material, the other two for wilted leaf material; that is, low water stress and high water stress, respectively. Each sample was placed in a stoppered glass bottle

TABLE aIII: RWC - Duration of Phase I uptake

Non-wilted material 1.

Time (minutes)	Weight (grams)	Weight (% FW)
0	0.0906	100.0
10	0.1047	115.6
17	0.1047	115.6
24	0.1057	116.7
31	0.1057	116.7
38	0.1060	117.0
101	0.7068	117.9
166	0.1104	121.9

Wilted Material 2.

Time (minutes)	Weight (grams)	Weight (% FW)
0	0.0494	100.0
12	0.0628	127.1
22	0.0684	138.5
33	0.0733	148.4
40	0.0765	154.9
50	0.0806	163.2
98	0.0916	185.5
151	0.0954	193.2
197	0.0973	197.0

Wilted Material 3.

Time (minutes)	Weight (grams)	Weight (% FW)
0	0.0700	100.0
20	0.1120	160.0
40	0.1239	177.5
65	0.1314	188.0
95	0.1364	195.0
125	0.1342	192.0
155	0.1350	193.0

and weighed. The segments were then floated on distilled water in a covered petri dish (one sample per petri dish) and at intervals were removed, blotted dry on filter paper, weighed in the original bottles, and replaced in the dish. The weight of the samples at each weighing was expressed as a percentage of the original fresh weight, and these percentage weights plotted against time (figure A1).

It is apparent from figure A1 that Phase I (initial rapid uptake of water) was completed in all samples within about 40 minutes. For sample 1 (medium-low water stress) this initial uptake of water was probably completed in a considerably shorter time than 40 minutes. However, the Phase II water uptake within the first 40 minutes for this sample was negligible.
Thus, in all subsequent routine determinations of RWC, 40 minutes was adopted as the time for which the segments were floated. Therefore, with 40 minutes floating period, the RWC technique appeared suitable for use with Yorkshire fog, in this investigation.

Comparisons of RWC values for dry treatment plants would have been meaningless if the tissue had not been sampled at comparative stages of the drying cycle. Samples were obtained immediately prior to rewatering (i.e. at the greatest soil moisture tensions developed). RWC values at this stage would reflect the most extreme water deficits experienced by these plants.

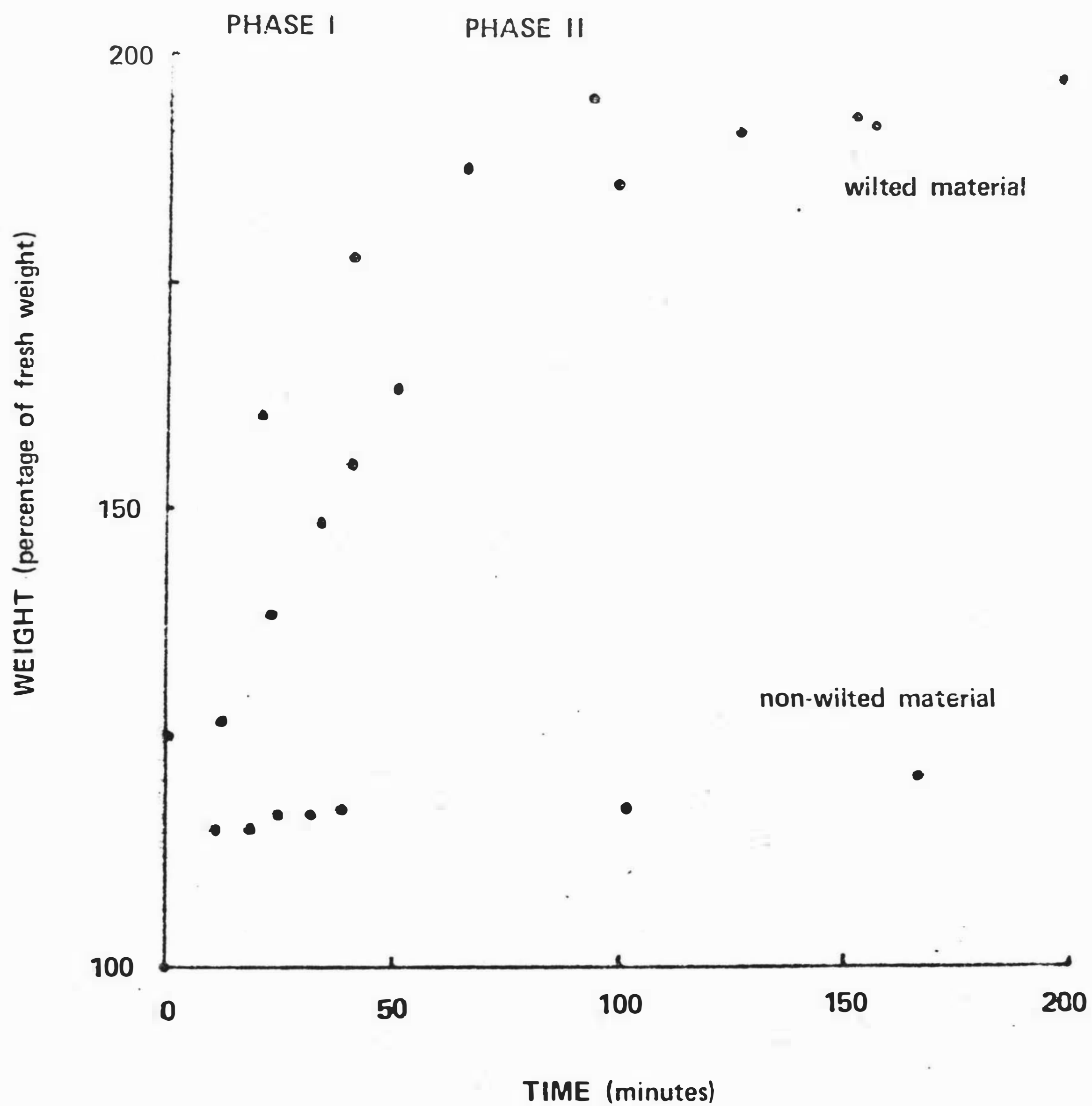

figure A1 Determination of floating period

APPENDIX V: Statistical analysis and results

Two types of analysis were available for the recognition of differential response of topodemes to the various water treatments. They were analysis of variance (for splitplot design) and form or regression analysis. Regression analysis, which has been revived recently, (e.g. Findlay and Wilkinson 1963; Breese, 1969), involves quantification of the test environments (water treatments) by their biological potential. Thus, each environment can be measured and graded by the mean of any plant response for all plants grown in that environment. The performance of individual topodemes may then be expressed as the regression of their individual values on this mean. However, three test environments (water treatments) were considered too few to obtain a reliable regression line. Also, much debate has centred around the use and interpretations of this technique (see, for example, Easton, 1971). Therefore, regression analysis was avoided in favour of the less contentious analysis of variance.

TABLE AI: 100 Seed Weight I (Wild material)

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOTAL	79					
TOPODEMES	19	119.647	16.595	**	1.78	2.26
REPLICATES	3	18.533	2.570	NS	2.79	4.20
ERROR (TDMS X REPS)	57	7.21				

TOPODEME MEANS

L04	35.50
T07	34.50
P01	34.50
L02	34.25
L00	34.00
T10	33.75
T00	32.75
T05	32.50
T04	30.50
P04	30.25
T09	30.00
L05	28.50
P02	28.00
T06	27.25
T02	26.50
P05	26.25
L03	24.25
T03	22.75
T01	20.25
P03	14.75
	29.05

STANDARD ERROR SE = 1.343

SIGNIFICANT DIFFERENCES d.05 = 3.3973

d.01 = 5.0500

TABLE AII: Survival-vigour.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	20	3.417E-00	1.312	NS	1.75	2.20
BLOCKS	3	2.676E-00	1.027	NS	2.77	4.14
TDMS X BLOCKS	60	2.605E-00	2.0803	**	1.35	1.52
ERROR	588	1.252E-00				
TOTAL	671					

MEANS

	BLOCK I	BLOCK II	BLOCK III	BLOCK IV	
T00	3.0000	2.2500	1.3750	2.5000	2.2812
T01	1.0000	2.8750	2.2500	2.5000	2.1562
T02	2.6250	1.0000	2.3750	2.0000	2.000
T03	3.0000	1.0000	1.3750	2.2500	1.9062
T04	2.8750	2.2500	2.7500	2.6250	2.6250
T05	1.7500	3.0000	3.0000	3.0000	2.6875
T06	2.0000	2.0000	3.0000	1.5000	2.1250
T07	1.3750	2.5000	2.5000	2.6250	2.2500
T09	2.1250	2.7500	1.5000	3.0000	2.3437
T10	2.5000	2.7500	2.8750	2.7500	2.7187
P00	1.5000	2.6250	1.7500	1.8750	1.9375
P01	1.6250	2.0000	2.2500	2.2500	2.0312
P02	2.3750	1.5000	1.7500	1.6250	1.8125
P03	1.2500	1.0000	1.7500	1.7500	1.4375
P04	1.3750	1.5000	3.0000	2.3750	2.0625
P05	2.5000	2.5000	1.3750	3.0000	2.3437
L00	3.0000	2.0000	1.5000	2.3750	2.2187
L02	2.2500	2.0000	3.0000	2.2500	2.3750
L03	2.1250	2.1250	1.7500	3.0000	2.2500
L04	3.0000	2.2500	3.0000	3.0000	2.8125
L05	2.1250	2.6250	2.3750	2.2500	2.3437
	2.1607	2.1190	2.2142	2.4047	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	0.198	0.5483	0.7206
BLOCKS	0.086	0.2393	0.3145
TDMS X BLOCKS	0.396	1.0966	1.4413

TABLE AIII: Panicle emergence.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	20	1.348E+02	3.271	**	1.75	2.20
BLOCKS	3	2.332E+01	0.566	NS		
TDMS X BLOCKS	60	4.121E+01	2.1828	**	1.30	1.45
ERROR	672	1.887E+01				
TOTAL	755					

MEANS

	BLOCK I	BLOCK II	BLOCK III	BLOCK IV	
T00	24.4444	20.0000	17.7777	19.3333	20.3888
T01	17.4444	17.7777	19.2222	20.0000	18.6111
T02	20.0000	18.0000	19.3333	18.2222	18.8888
T03	14.8888	17.6666	16.8888	17.6666	16.7777
T04	14.4444	19.3333	21.2222	19.3333	18.5833
T05	15.6666	21.1111	22.4444	23.3333	20.6388
T06	14.3333	17.4444	17.1111	18.8888	16.9444
T07	15.3333	13.7777	14.8888	17.0000	15.2500
T09	18.7777	23.8888	18.2222	24.5555	21.3611
T10	18.8888	14.7777	14.1111	15.6666	15.8611
P00	19.1111	19.7777	17.2222	18.5555	18.6666
P01	20.1111	20.1111	23.7777	19.5555	20.8888
P02	13.6666	17.8888	19.5555	18.2222	17.3333
P03	18.6666	16.1111	15.7777	17.5555	17.0277
P04	19.2222	19.1111	17.0000	18.0000	18.3333
P05	20.7777	16.8888	20.1111	21.5555	19.8333
L00	22.7777	21.8888	19.5555	17.3333	20.3888
L02	19.0000	14.6666	12.3333	14.6666	15.1666
L03	18.8888	15.1111	15.3333	15.0000	16.0833
L04	17.3333	19.1111	16.7777	18.1111	17.8333
L05	13.8888	16.0000	15.4444	18.6666	16.0000
	17.9841	18.1164	17.8148	18.6296	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	0.724	2.0073	2.6382
BLOCKS	0.316	0.8760	1.1514
TDMS X BLOCKS	1.374	4.0146	5.2764

TABLE AIV: Panicle number.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	20	7.881E+03	1.075	NS	1.75	2.20
BLOCKS	3	2.592E+04	3.537	*	2.77	4.14
TDMS X BLOCKS	60	7.328E+03	2.2036	**	1.35	1.52
ERROR	336	3.325E+03				
TOTAL	419					

MEANS

	BLOCK I	BLOCK II	BLOCK III	BLOCK IV	
T00	51.8000	163.0000	137.2000	139.4000	122.85
T01	105.6000	175.0000	150.2000	157.4000	147.05
T02	46.0000	127.0000	218.0000	170.8000	140.45
T03	112.8000	97.4000	179.4000	169.8000	139.85
T04	141.0000	111.8000	146.0000	138.6000	134.35
T05	135.8000	88.2000	76.4000	95.8000	99.05
T06	119.2000	160.8000	185.6000	114.2000	144.95
T07	152.0000	115.0000	108.4000	166.0000	135.35
T09	121.0000	74.4000	102.0000	133.0000	107.60
T10	139.4000	109.4000	206.6000	144.0000	149.85
P00	102.0000	130.8000	106.0000	177.4000	129.05
P01	170.8000	69.0000	85.2000	50.4000	93.85
P02	98.8000	198.4000	126.6000	185.0000	152.20
P03	201.6000	118.6000	176.0000	160.2000	164.10
P04	101.4000	98.4000	102.8000	115.6000	104.55
P05	171.0000	98.4000	172.0000	142.4000	145.95
L00	115.6000	82.8000	187.6000	195.2000	145.30
L02	134.4000	84.2000	129.2000	119.2000	116.75
L03	204.8000	103.0000	112.8000	145.8000	141.60
L04	117.2000	124.0000	204.2000	183.0000	157.10
L05	87.8000	129.6000	202.0000	188.6000	152.00
	125.2380	117.1047	148.2952	147.2285	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	12.89	35.7424	46.9757
BLOCKS	5.63	15.5992	20.5019
TDMS X BLOCKS	25.79	71.4848	93.9515

TABLE AV: Seed weight II. (Field experiment)

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOTAL	335	34.88				
TOPODEMES	20	88.95		NS		
BLOCKS	3	22.00		NS		
TDMS X BLOCKS	60	141.18	26.00	***	1.35	1.52
ERROR	151	5.43				

MEANS

	BLOCK I	BLOCK II	BLOCK III	BLOCK IV	
T01	33.25	37.25	28.75	40.50	34.94
T02	43.50	32.00	26.50	34.25	34.06
T09	29.25	30.50	30.00	32.00	30.44
T10	37.00	30.75	39.00	33.50	35.06
P01	31.75	34.75	37.00	36.75	35.06
P02	33.25	32.00	29.75	33.75	32.19
P04	27.75	37.50	29.00	30.50	31.19
L00	36.50	32.50	28.75	29.00	31.69
L02	35.00	34.25	32.00	39.00	35.06
T00	31.75	30.50	37.00	27.00	31.56
T03	31.00	35.75	27.00	33.50	31.81
T04	40.00	28.75	36.75	30.00	33.88
T05	27.00	45.00	40.50	27.75	35.06
T06	38.50	30.50	38.25	50.75	39.50
T07	32.00	35.75	47.25	32.25	36.81
L03	29.50	26.50	42.00	35.50	33.38
L04	44.25	25.25	32.25	26.25	32.00
L05	33.25	39.75	30.00	38.25	35.31
P03	28.50	44.75	38.25	33.50	36.25
P05	41.25	25.25	29.50	31.75	31.94
P00	31.00	34.75	49.75	34.50	37.50
	34.06	33.52	34.73	33.82	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	0.58	-	-
BLOCKS	0.25	-	-
TDMS X BLOCKS	1.04	7.53	10.00

TABLE AVI: Tiller production.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	19	53.77	.94	NS	1.68	(2.06)
TOPODEMES	8	95.03	1.66	NS	2.01	(2.65)
ERROR I	152	57.10	1.70	**	1.22	(1.32)
WATER	2	116.32	3.45	*	3.03	(4.68)
TDMS X WATER	16	14.37	.42	NS	1.68	(2.06)
ERROR II	342	33.63				
TOTAL	539					

MEANS

	WET	MED	DRY	
P04	21.550	22.850	21.050	21.816
L02	21.800	22.600	19.500	21.300
T09	22.300	23.050	19.450	21.600
T01	20.150	19.500	19.150	19.600
P02	20.100	19.300	19.100	19.500
L00	21.750	20.850	20.000	20.866
P01	21.300	20.100	19.950	20.450
T02	19.500	20.800	17.600	19.300
T10	17.950	17.800	18.300	18.016
	20.711	20.761	19.344	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.975	2.704	3.553
WATER	.432	1.198	1.574
TDMS X WATER	1.296	3.594	4.724

TABLE AVII: Lamina length.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	19	1232.05	1.49	NS	1.68	(2.06)
TOPODEMES	8	2436.12	2.95	**	2.01	(2.65)
ERROR I	152	824.71		NS		
WATER	2	19335.00	27.86	***	3.03	(4.68)
TDMS X WATER	16	404.25	.58	NS	1.68	(2.06)
ERROR II	342	693.89				
TOTAL	539					

MEANS

	WET	MED	DRY	
P04	142.800	153.300	145.800	147.300
L02	142.400	159.800	140.450	147.550
T09	126.150	147.650	126.950	133.583
T01	124.050	147.500	130.050	133.866
P02	127.850	146.950	133.550	136.116
L00	126.850	151.250	131.600	136.566
P01	131.200	151.300	137.950	140.150
T02	137.950	155.750	153.700	149.133
T10	129.400	158.500	150.450	146.116
	132.072	152.444	138.944	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	3.707	10.276	13.506
WATER	1.963	5.442	7.152
TDMS X WATER	5.890	16.326	21.458

TABLE AVIII: Lamina breadth.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	19	1.06	.72	NS	1.68	(2.06)
TOPODEMES	8	4.16	2.84	**	2.01	(2.65)
ERROR I	152	1.46	1.315	*	1.22	(1.32)
WATER	2	64.66	58.01	***	3.03	(4.68)
TDMS X WATER	16	.36	.33	NS	1.68	(2.06)
ERROR II	342	1.11				
TOTAL	539					

MEANS

	WET	MED	DRY	
PO4	7.430	8.210	7.260	7.633
LO2	7.795	8.510	7.650	7.985
TO9	8.165	9.015	7.855	8.345
TO1	7.830	8.965	7.575	8.123
PO2	7.275	8.415	7.225	7.638
LOO	7.175	8.470	7.090	7.578
PO1	7.720	8.790	7.495	8.001
TO2	7.920	8.580	7.855	8.118
T10	7.750	8.645	7.615	8.003
	7.673	8.622	7.513	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.156	.433	.569
WATER	.078	.218	.286
TDMS X WATER	.236	.654	.860

TABLE AIX: Leaf shape index.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	19	24.87	1.53	NS	1.68	(2.06)
TOPODEMES	8	66.14	4.06	**	2.01	(2.65)
ERROR I	152	16.25	1.524	**	1.22	(1.32)
WATER	2	77.66	7.27	**	3.03	(4.68)
TDMS X WATER	16	5.33	.50	NS	1.68	(2.06)
ERROR II	342	10.66				
TOTAL	539					

MEANS

	WET	MED	DRY	
P04	19.355	18.870	20.175	19.466
L02	18.560	19.065	18.580	18.735
T09	15.580	16.475	16.280	16.111
T01	15.935	16.595	17.275	16.601
P02	17.625	17.870	18.545	18.013
L00	17.780	18.280	18.835	18.298
P01	16.975	17.350	18.710	17.678
T02	17.480	18.320	19.825	18.541
T10	16.825	18.545	19.690	18.353
	17.346	17.930	18.657	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.520	1.442	1.896
WATER	.243	.674	.886
TDMS X WATER	.730	2.024	2.660

TABLE AX: Leaf emergence

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	19	3.99	1.62	NS	1.68	(2.06)
TOPODEMES	8	1.35	.55	NS	2.01	(2.65)
ERROR I	152	2.45		NS		
WATER	2	250.55	104.06	***	3.03	(4.68)
TDMS X WATER	16	1.22	.50	NS	1.68	(2.06)
ERROR II	342	2.40				
TOTAL	539					

MEANS

	WET	MED	DRY	
P04	9.073	9.040	10.849	9.654
L02	9.165	9.215	11.149	9.843
T09	8.890	8.902	11.499	9.763
T01	8.790	9.127	11.533	9.816
P02	9.240	9.027	10.800	9.689
L00	9.498	9.515	11.100	10.038
P01	9.365	8.948	11.083	9.798
T02	9.257	9.011	11.458	9.908
T10	9.665	9.262	11.400	10.109
	9.216	9.116	11.208	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.202	.560	.737
WATER	.115	.320	.421
TDMS X WATER	.346	.961	1.264

TABLE AXI: Dry weight of foliage.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	18	7.38	1.99	*	1.68	(2.06)
TOPODEMES	8	5.53	1.49	NS	2.01	(2.65)
ERROR I	144	3.70	1.40	**	1.22	(1.32)
WATER	2	425.81	160.67	***	3.03	(4.68)
TDMS X WATER	16	2.06	.77	NS	1.68	(2.06)
ERROR II	324	2.65				
TOTAL	512					

MEANS

	WET	MED	DRY	
P04	4.770	5.975	3.657	4.801
L02	5.266	7.322	3.828	5.472
T09	5.243	7.568	3.588	5.467
T01	4.737	6.417	3.519	4.891
P02	4.389	6.003	3.437	4.610
L00	4.782	7.138	3.518	5.146
P01	5.361	7.330	3.511	5.401
T02	5.422	6.823	3.697	5.314
T10	5.054	6.346	3.831	5.077
	5.003	6.769	3.621	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.254	.706	.928
WATER	.124	.345	.453
TDMS X WATER	.373	1.035	1.360

TABLE AXII: Basal diameter.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	18	32.77	1.08	NS	1.68	(2.06)
TOPODEMES	8	103.74	3.42	**	2.01	(2.65)
ERROR I	144	30.25		NS		
WATER	2	3202.97	111.88	**	3.03	(4.68)
TDMS X WATER	16	183.30	6.40	**	1.68	(2.06)
ERROR II	324	28.62				
TOTAL	512					

MEANS

	WET	MED	DRY	
P04	36.105	29.684	23.473	29.754
L02	36.736	33.052	23.368	31.052
T09	32.842	34.105	22.842	29.929
T01	32.052	31.052	21.684	28.263
P02	33.368	25.578	24.631	27.859
L00	32.263	21.842	27.368	27.157
P01	32.000	25.105	27.315	28.140
T02	31.736	29.368	25.631	28.912
T10	29.631	28.947	22.526	27.035
	32.970	28.748	24.315	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.728	2.019	2.653
WATER	.409	1.134	1.490
TDMS X WATER	1.227	3.402	4.471

TABLE AXIII: Plant height.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	7	4.018E+02	1.6378	NS	2.01	2.64
WATER	2	4.538E+03	18.4971	***	2.99	4.60
TDMS X WATER	14	2.400E+02	.9783	NS	1.69	2.07
ERROR	192	2.453E+02				
TOTAL	215					

MEANS

	WET	MED	DRY	
P04	35.0000	48.8888	46.8888	43.5925
L02	36.7777	55.0000	42.1111	44.6296
T09	31.4444	45.0000	43.1111	39.8518
T01	37.0000	44.3333	45.3333	42.2222
P02	26.2222	30.8888	40.0000	32.3703
L00	30.4444	51.8888	36.7777	39.7037
T02	35.7777	50.5555	41.4444	42.5925
T10	22.0000	53.1111	41.1111	38.7407
	31.8333	47.4583	42.0972	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	3.015	8.3561	10.9439
WATER	1.85	5.1170	6.7017
TDMS X WATER	5.221	14.4732	18.9555

TABLE AXIV: Plant diameter.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	7	2.535E+03	1.3747	NS	2.01	2.64
WATER	2	1.231E+05	66.7767	***	2.99	4.60
TDMS X WATER	14	1.220E+03	.6617	NS	1.69	2.07
ERROR	216	1.844E+03				
TOTAL	239					

MEANS

	WET	MED	DRY	
P04	180.4000	238.8000	158.2000	192.4666
L02	173.4000	238.2000	143.6000	185.0666
T09	158.1000	209.5000	163.5000	177.0333
T01	171.4000	230.5000	150.5000	184.1333
P02	157.9000	217.7000	152.0000	175.8666
L00	173.4000	214.9000	160.7000	183.0000
T02	175.2000	222.5000	155.3000	184.3333
T10	187.5000	268.5000	158.2000	204.7333
	172.1625	230.0750	155.2500	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	7.840	21.7356	28.5667
WATER	4.800	13.3102	17.4935
TDMS X WATER	13.579	37.6471	49.4791

TABLE AXV: Plant form index.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	7	7.004E-02	1.5947	NS	2.01	2.64
WATER	2	7.137E-01	16.2517	***	2.99	4.60
TDMS X WATER	14	4.275E-02	.9735	NS	1.69	2.07
ERROR	192	4.392E-02				
TOTAL	215					

MEANS

	WET	MED	DRY	
P04	.4855	.5211	.7077	0.5714
L02	.5255	.5488	.7100	0.5948
T09	.4955	.5211	.6055	0.5407
T01	.5644	.4844	.7055	0.5848
P02	.4588	.2777	.6300	0.4555
L00	.4466	.5111	.5388	0.4988
T02	.4544	.5433	.6322	0.5433
T10	.3011	.4833	.6544	0.4796
	0.4665	0.4863	0.6480	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	0.0403	0.1117	0.1469
WATER	0.0247	0.0684	0.0899
TDMS X WATER	0.0698	0.1936	0.2544

TABLE AXVI: Compressed leaf length.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	7	2.296E+02	1.7162	NS	2.71	4.14
WATER	2	2.634E+03	19.6925	**	3.29	5.42
TDMS X WATER	14	2.584E+02	1.9320	*	1.69	2.07
ERROR	192	1.337E+02				
TOTAL	215					

MEANS

	WET	MED	DRY	
P04	41.8888	58.6666	44.0000	48.1851
L02	48.3333	53.2222	51.3333	50.9629
T09	37.3333	56.8888	48.7777	47.6666
T01	46.1111	62.5555	49.4444	52.7037
P02	37.7777	51.3333	56.0000	48.3703
L00	45.1111	47.6666	47.4444	46.7407
T02	49.0000	58.6666	54.2222	53.9629
T10	52.6666	65.1111	43.5555	53.7777
	44.7777	56.7638	49.3472	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	2.226	6.1702	8.1094
WATER	1.360	3.7784	4.9659
TDMS X WATER	3.854	10.6871	14.0459

TABLE AXVII: Compressed diameter.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	7	1.191E+02	1.342	NS	2.71	4.14
WATER	2	3.597E+03	73.6961	**	3.29	5.42
TDMS X WATER	14	8.877E+01	1.8185	*	1.69	2.07
ERROR	192	4.881E+01				
TOTAL	215					

MEANS

	WET	MED	DRY	
P04	48.6666	45.5555	36.8888	43.7037
L02	59.8888	47.3333	36.0000	47.7407
T09	52.4444	47.0000	39.2222	46.2222
T01	52.7777	48.3333	39.1111	46.7407
P02	51.1111	45.3333	34.4444	43.6296
L00	53.5555	53.2222	37.6666	48.1481
T02	49.6666	44.5555	39.2222	44.4814
T10	43.2222	45.8888	38.3333	
	51.4166	47.1527	37.6111	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	1.345	3.7272	4.8986
WATER	0.824	2.2824	2.9997
TDMS X WATER	2.329	6.4557	8.4846

TABLE AXIX: Veins per unit lamina width.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	6	.18	1.75	NS	2.30	(3.20)
TOPODEMES	8	.12	1.16	NS	2.15	(2.90)
ERROR I	48	.10		NS		
WATER	2	.15	1.08	NS	3.10	(4.81)
TDMS X WATER	16	.12	.93	NS	1.74	(2.20)
ERROR II	108	.13				
TOTAL	188					

MEANS

	WET	MED	DRY	
P04	4.034	3.718	3.892	3.881
L02	3.715	3.965	3.675	3.785
T09	3.618	3.652	3.938	3.736
T01	3.791	3.820	3.968	3.860
P02	3.805	3.755	3.842	3.801
L00	3.731	3.702	3.675	3.703
P01	3.841	3.624	3.635	3.700
T02	3.920	3.837	3.928	3.895
T10	3.561	3.627	4.015	3.734
	3.780	3.744	3.841	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.070	.196	.259
WATER	.046	.131	.173
TDMS X WATER	.140	.394	.521

TABLE AXX: Hair density.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	6	251.53	1.45	NS	2.29	(3.18)
TOPODEMES	8	373.97	2.15	*	2.13	(2.88)
ERROR I	48	173.17		NS		
WATER	2	489.43	2.67	NS	3.07	(4.79)
TDMS X WATER	16	241.54	1.31	NS	1.73	(2.16)
ERROR II	108	183.26				
TOTAL	188					

MEANS

	WET	MED	DRY	
P04	43.285	37.571	44.142	41.666
L02	50.285	36.571	59.857	48.904
T09	38.285	38.000	48.000	41.428
T01	45.142	43.000	56.428	48.190
P02	40.714	46.857	51.571	46.380
L00	39.428	48.285	49.285	45.666
P01	39.857	44.428	35.142	39.809
T02	49.571	57.142	47.857	51.523
T10	48.142	53.285	50.142	50.523
	43.857	45.015	49.158	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	2.871	8.041	10.627
WATER	1.705	4.775	6.312
TDMS X WATER	5.116	14.327	18.937

TABLE AXXI: Stomate density.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	6	61.87	2.09	NS	2.29	(3.18)
TOPODEMES	8	22.92	.77	NS	2.13	(2.88)
ERROR I	48	29.51		NS		
WATER	2	104.14	4.55	*	3.07	(4.79)
TDMS X WATER	16	40.26	1.76	*	1.73	(2.16)
ERROR II	108	22.86				
TOTAL	188					

MEANS

	WET	MED	DRY	
P04	15.428	15.428	18.142	16.333
L02	20.714	14.142	20.428	18.428
T09	19.000	15.571	16.285	16.952
T01	18.000	12.285	20.285	16.857
P02	15.285	17.428	15.714	16.142
L00	19.571	14.428	15.000	16.333
P01	14.714	16.857	13.857	15.142
To2	16.714	16.714	13.857	15.761
T10	17.857	11.571	15.428	14.952
	17.476	14.936	16.555	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	1.185	3.319	4.387
WATER	.602	1.686	2.229
TDMS X WATER	1.807	5.060	6.689

TABLE AXXII: Epidermal cell length.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	6	1038.20	2.56	*	2.29	(3.18)
TOPODEMES	8	733.17	1.81	NS	2.13	(2.88)
ERROR I	48	404.59		NS		
WATER	2	2216.20	5.89	**	3.07	(4.79)
TDMS X WATER	16	524.46	1.39	NS	1.73	(2.16)
ERROR II	108	376.07				
TOTAL	188					

MEANS

	WET	MED	DRY	
P04	108.342	131.542	99.585	113.157
L02	91.100	122.928	89.814	101.280
T09	105.657	115.414	103.957	108.342
T01	101.700	110.857	96.614	103.057
P02	99.100	106.014	92.500	99.204
L00	100.514	108.000	96.300	101.604
P01	114.000	109.800	121.314	115.038
T02	93.714	105.385	99.057	99.385
T10	102.785	94.957	109.400	102.380
	101.879	111.655	100.949	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	4.389	12.290	16.244
WATER	2.443	6.841	9.042
TDMS X WATER	7.329	20.524	27.127

TABLE AXXIII: Epidermal cell width.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	6	2.15	1.27	NS	2.29	(3.18)
TOPODEMES	8	.86	.50	NS	2.13	(2.88)
ERROR I	48	1.69		NS		
WATER	2	.88	.61	NS	3.07	(4.79)
TDMS X WATER	16	2.32	1.62	NS	1.73	(2.16)
ERROR II	108	1.43				
TOTAL	188					

MEANS

	WET	MED	DRY	
P04	12.314	12.271	12.442	12.342
L02	12.014	12.600	11.371	11.995
T09	11.600	13.071	11.685	12.119
T01	12.328	12.928	11.857	12.371
P02	12.414	11.714	12.185	12.104
L00	11.700	12.514	12.314	12.176
P01	12.200	11.914	13.485	12.533
T02	12.114	11.371	12.542	12.009
T10	11.800	12.228	11.728	11.919
	12.053	12.290	12.179	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	.283	.794	1.050
WATER	.151	.422	.558
TDMS X WATER	.453	1.268	1.676

TABLE AXXIV: Epidermal cell number.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
BLOCKS	6	63.72	1.67	NS	2.29	(3.18)
TOPODEMES	8	67.49	1.77	NS	2.13	(2.88)
ERROR I	48	38.13		NS		
WATER	2	167.29	3.93	*	3.07	(4.79)
TDMS X WATER	16	54.09	1.27	NS	1.73	(2.16)
ERROR II	108	42.51				
TOTAL	188					

MEANS

	WET	MED	DRY	
PO4	26.611	23.895	28.572	26.360
LO2	32.327	23.085	35.214	30.209
TO9	28.512	23.130	30.321	27.321
TO1	28.448	25.154	31.421	28.341
PO2	28.405	29.230	30.770	29.468
LOO	29.847	26.137	30.150	28.711
PO1	25.001	27.047	21.372	24.473
TO2	30.405	29.168	28.758	29.444
T10	28.648	29.641	27.841	28.710
	28.689	26.276	29.380	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	1.347	3.773	4.987
WATER	.821	2.300	3.040
TDMS X WATER	2.464	6.900	9.120

TABLE AXXV: Relative water content.

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	D.F.	M.S.	F(CALC)		F(REQ'D).05	.01
TOPODEMES	6	1.887E+02	3.01	*	3.00	4.82
WATER	2	1.223E+04	194.99	**	3.49	5.95
TDMS X WATER	12	6.272E+01	6.0764	**	1.75	2.24
ERROR	168	1.032E+01				
TOTAL	188					

MEANS

	WET	MED	DRY	
P04	86.3233	95.9866	66.6600	82.9900
L02	86.9522	85.7655	63.9666	78.8948
T09	88.4644	95.4266	69.1377	84.3429
P02	84.2622	83.6344	64.1022	77.3329
L00	85.6011	92.1566	65.9811	81.2462
T02	90.1688	91.9788	64.1344	82.0940
T10	86.3566	88.6877	59.3566	78.1337
	86.88	90.52	64.76	

STANDARD ERRORS AND SIGNIFICANT DIFFERENCES

	S.E.	d.05	d.01
TOPODEMES	0.618	1.7138	2.2525
WATER	0.405	1.1220	1.4746
TDMS X WATER	1.071	2.9685	3.9015

APPENDIX VI: The significance of the correlation coefficients calculated.

The correlation coefficient, r, is an estimate of the total variation in a character Y which is due to the linear relationship existing between it and a second character X. For values of r close to zero, no linear relationship is present; for values of r close to ± 1, a very strong linear relationship exists. There is then, a problem of drawing precise conclusions for intermediate values of r.

The distribution of r assumes widely different forms for various sized samples and population correlation coefficients. Two situations will be considered here; that in which the population correlation coefficient, ρ, is assumed to equal zero, and that in which ρ is assumed to have some other value between -0.60 and +0.60, for example ± 0.50.

(1) Where it is assumed that $\rho = 0$. The hypothesis that no linear relationship existed between any pairs of variables in the multivariate population was tested. That is the probability that from such a population a sample was taken for which the correlation coefficient equalled or exceeded the value of r calculated for the sample was determined. Given a correlation coefficient r, and sample size n, from a population in which $\rho = 0$, then

$$t = \frac{r}{\sqrt{\frac{1 - r^2}{n - 2}}} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (1)$$

satisfies the Student's t-distribution with n - 2 degrees of freedom (Alder and Roessler, Chapter 18).

Example: Determine whether a correlation coefficient of -0.107 (see Table VI) estimated from a sample of 420 plants, indicates a significant correlation, on the basis of both the 1% and 5% levels of significance.

Solution: Given $r = -0.107$, $n = 420$ and $\rho = 0$
then, from equation (1),

$$t = \frac{-0.107}{\sqrt{\frac{1 - (-0.107)^2}{420 - 2}}}$$

$$= 2.20$$

From Student's t - distribution table, for 418 degrees of freedom, $t_{.05} = 1.96$ and $t_{.01} = 2.576$; thus, $t_{.01} > t > t_{.05}$.

The correlation coefficient, $r = 0.107$, is, then, obtained less than 5% of the time, but greater than 1% of the time, from a population in which $\rho = 0$. Such a correlation coefficient is significant at the 5% level, but not at the 1% level.

Example: Determine whether or not r equal to 0.086 (see Table VI) estimated from a sample n = 420, indicates a significant correlation on the basis of the 1% and 5% levels of significance.

Solution: Given $r = 0.086$, $n = 420$ and $\rho = 0$
then, from equation (1), $t = 1.764$.

From Student's t-distribution table with 418 d.f., $t < t_{.05} < t_{.01}$. Thus, the value 0.086 for r is obtained rather frequently (about 8% of the time) from a population in which $\rho = 0$. Such a correlation coefficient is, then, not significant at either the 1% or 5% levels.

Example: Determine whether $r = 0.199$ (correlation coefficient estimated for epidermal cell size—the inverse of cell number—and lamina width, LW, see Table XXI), indicates a significant correlation on the basis of the 5% level of significance.

Solution: Given $r = 0.199$, $n = 83$ and $\rho = 0$
then, from equation (1), $t = 1.99$.

From the Student's t-distribution tables with 81 d.f., $t_{.05}$ is equal to 1.99, so that $t = t_{.05}$. Thus, the probability that from a population in which $\rho = 0$ a sample $n = 83$ was taken for which

$r = 0.199$ is 5%. This correlation coefficient is, then, the threshold value for r in such a population at the 5% level of significance.

Similarly $r = 0.282$ is the threshold correlation coefficient at the 1% level of significance.

This procedure may be used only where it is assumed that $\rho = 0$, and so it is merely used to decide whether, in a particular sample, r is significantly different from $\rho = 0$.

(2) In those cases in which ρ cannot be assumed to be zero, or where the confidence limits of ρ are required, a quantity Z has been defined in terms of r. The distribution of Z is approximately normal. The equation

$$z = \frac{Z - m_Z}{\sigma_Z} \quad .. \quad .. \quad .. \quad .. \quad .. \quad (2)$$

satisfies approximately a normal distribution, with

$$m_Z = 1/2 \ln \frac{1 + \rho}{1 - \rho} \qquad \text{and} \qquad \sigma_Z = \frac{1}{\sqrt{n - 3}} \quad .. \quad .. \quad (3)$$

The values for Z for given values of r may be found in statistical tables (e.g. Alder and Roessler, Table V). The value Z may be used to test the hypothesis that ρ is equal to a given value, for example +0.50, at a given level of significance when the correlation coefficient for a given sample size is known.

Example: In a sample $n = 83$, the correlation coefficient $r = 0.287$ (see Table XXI, for leaf length and leaf emergence). Test the hypothesis that $\rho = 0.50$ at both the 1% and 5% levels of significance.

Solution: From the tables (transformation of r to Z) for $r = 0.287$, $Z = 0.299$. Similarly for $= 0.50$, $m_Z = 0.549$.

From (3),

$$Z = \frac{1}{\sqrt{80}}$$

and so from (2),

$$z = (0.299 - 0.549) \times 80$$
$$= -2.44$$

From the area under the normal curve tables (e.g. Table I, Alder and Roessler, 1958) the area to the left of $z = -2.24$ is equal to 0.5 - 0.4875, and this the desired probability $P = 2(0.5 - 0.4875) = 0.025$, which is less than 5% and greater than 1%. Thus we can reject the hypothesis at the 5% level of significance, but must accept at the 1% level, that the sample with correlation coefficient $r = 0.287$ was taken from a population with $\rho = 0.50$.

As suggested above, equation (2) may be used to establish confidence limits for ρ when a sample's correlation coefficient is known.

Example: In the above example the correlation coefficient $r = 0.287$. Determine the 99% confidence limits for the population correlation coefficient, ρ. As above $r = 0.287$, thus $Z = 0.299$ and $\sigma_Z = \frac{1}{\sqrt{80}}$.

From the area under the normal probability curve table, for 99% confidence limits, $z = \pm 2.57$. Thus we have

$$\frac{Z - m_Z}{\sigma_Z} = \pm 2.57$$

$$\longrightarrow \quad 0.299 - m_Z = \frac{\pm 2.57}{\sqrt{80}}$$

$$\longleftrightarrow \quad m_Z = 0.299 \pm 0.288$$

$$= 0.011 \text{ and } 0.587$$

Thus, m_Z lies between 0.011 and 0.587 and correspondingly ρ is between 0.011 and 0.53. (The two latter values were obtained from the r to Z transformation tables).

The most practicable test for the significance of the correlation coefficients determined (Tables VI and XXI) was that in which the population correlation coefficient, ρ, was assumed to equal zero. This test was applied to the data.

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