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**CLIMATE, VEGETATION, DISTRIBUTION
OF TAXA AND DIVERSITY:
A SYNTHESIS**

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Abstract

An attempt has been made to investigate from a range of viewpoints the principle of the climatic control of plant distribution. The accumulated plant weight (*w*) is related to the incoming solar radiation (*S*) and is dependent on leaf area index, the incoming solar radiation and the efficiency of solar radiation to dry matter conversion. A review is presented and a model is discussed in order to stimulate interest and knowledge in this crucial and central theme of ecology. The aim is to develop a model based on eco-physiological principles to predict the major vegetational zones of the globe. Predictions were based on various plant responses, such as low temperature survival and evapo-transpiration. Taxonomic diversity declined in a poleward direction; for both the northern and southern hemispheres family diversity is greatest near the equator, declined markedly from latitude 30^0 to 90^0. Strong correlation between family diversity and absolute minimum temperature exists and a regression line suggests a decrease of 3.3 families per ^{0}C reductions in minimum temperature. Analysis of the islands ecology differing in areas at various altitudes of the present and past has been most productive in providing means of investigating dispersal and migration and vertical diversity. Experimental studies have been attempted in herbaceous vegetation at different latitudes (tundra and British Isles) by clearing the native species (*Carex bigelowii*, *Eriphorum vaginatum)* of the area and by introducing exotic species such as *Lolium perenne*. The cover of the exotic species subsequently declined and ultimately became extinct and was covered by the native species. In order to investigate the climatic control of the distribution of taxa it becomes necessary to split the life (life cycles) of a plant into a number of stages, each of which is a link in the chain of survival and each of which can dominate the control of distribution. When a stage of life cycle is broken then extinction is likely. Continued post multiplication of the transition matrix of probabilities by the column vector of population density at each stage leads to a deterministic model of population growth and has been explained with *Eupatorium cannabinum*, *Potentilla reptans* and *Oxyria digyna*. The matrix model and the gap fill model have attempted to satisfy this need in relation to space competition. Two species (*Oxyria digyna* of British upland and *Lolium perenne* of lowlands) were chosen to develop and describe the application of a model for predicting the outcome of competition between species invading a gap and those existing around the gap. It was found that the initial growth rate of invaders is density independent and was expressed by a number of mathematical formulas. It is easy to consider a variety of other effects which are also under climatic control.

1. Introduction

The distribution of the world's vegetation types has been known and documented with some degree of accuracy for at least 180 years, dating back to the foundations of plant geography in von Humboldt and Bonpland (1805). The importance of climate in controlling the observed pattern of vegetation was subsequently accounted by von Humboldt (1807), Schouw (1823), Meyen (1846) and de Candolle (1855). This approach of plant geography adopted by Schimper (1898) and Walter (1931, 1968, 1973, 1976) was one of a physiological explanation for why a particular species was able to survive in a particular area. If the distribution of global vegetation is to be understood in terms of eco-physiology, then the starting points should be the known range of physiological responses of plants to climate. This approach should also establish the value and direction of eco-physiology and establish new problems for investigation. As Box (1981) describes,

> Predictive modeling [sic], i.e., the rigorous application (extrapolation) of quantitative models to environmental data (at sites other than those used to construct the model) in order to predict actually occurring patterns, can be particularly useful in plant geography and plant environment relations, since it provides a ready means of testing the validity of the model and the understanding behind it.

The approach taken by Holdbridge (1947, 1967 and by Box (1981) are representative of an approach to the understanding of the climatic control of plant distribution based on a taxonomy of vegetation and climate. They have established that very strong correlations exist between life form or physiognomy and two broad features of climate, temperature and water budget, measured as the equation of rainfall or precipitation minus evaporation.

2. An eco-physiological basis

Although the correlation approach fails to establish the mechanisms by which climate may control distribution, but it does provide a logical point from which to start. The implications are that the availability of water, or conversely drought, may influence the mass of vegetation, increasing, for example, from an absence of any vegetation in an extreme desert through a sparse mixture of grasses and trees in rather wetter grasslands or savannah, to the dense, galleried structure of a tropical rain forest. The effect of temperature, on the other hand, is multifarious with effects within and beyond the range of plant tolerance. There are many areas which could be logical starting points in a quest for defining a match between physiological response and local climate. What is required is a tautonomous starting point which may subsequently develop and include, step by step, the critical and climatically controlled limitations to the completion and perpetuation of a successful life-cycle.

3. Solar radiation and growth

The growth of a plant is directly related to its ability to intercept solar radiation and to convert the intercepted solar radiation to carbohydrates, or more generally, dry matter. The efficiency of conversion (typically 1.4 g of dry matter, equivalent to about 25 KJ, per mega joule intercepted radiation, or an efficiency of 2.5%) is rather conservative in character, showing little change with season for those herbaceous species which have been investigated (Monteith and Elston, 1983), although Jarvis and Leverenz (1983) show a seasonal drift in efficiency for *Pinus sylvestris*. The absence of further measurements, and for the sake of simplicity, if the efficiency (E) is assumed to change rather little then, over an interval of time t, the accumulated plant weight (w) is related to the incoming solar radiation (S) as,

$$w = E\int_0^t Sidt,\qquad(1)$$

where i is the fraction of the incoming radiation which is intercepted by the canopy. Interception is used rather than absorption (a) because it is easier to measure, where

$$a = 1 - r - t,\qquad(2)$$

and r is reflectivity and t is transmissivity:

$$i = 1 - t,\qquad(3)$$

effectively ignoring canopy reflectivity, which may be as low as 5% or 10% of the incoming radiation. All radiant interception is due to leaves and when a constant fraction of radiation penetrates a layer of leaves, the profile of radiation through a plant canopy will be logarithmic and
$$i = 1 - \exp(-KL),\qquad(4)$$

where K is the extinction co-efficient for solar radiation (Monsi and Saeki, 1953), and L is the leaf area index, the total area of leaves over a unit area of ground. Accumulated plant weight may therefore be described as,

$$w = E\int_0^t S\left(1 - \exp\left(-KL\right)\right)dt,\qquad(5)$$

dependent on leaf area index, the incoming solar radiation and the efficiency of solar radiation to dry matter conversion. The exponential term in the equation for interception indicates a non-linear relationship between L and w, so that for a typical value of 0.5 for K (Jarvis and Leverenz, 1983) and at a leaf area index of 1, 40% of the incoming radiation is intercepted; this increases to 78% at a leaf area index of 3, 92% at a leaf area index of 5, and 97% at a leaf area index of 7. Therefore, changes in L at low mean values will have the greatest effect on w, with small effects once L reaches a value of 5. The maximum leaf area index obtainable by a species in non-limiting climatic conditions will also be result of the ability of the lower leaves to survive in deep shade. Harbinson and Woodward (1984) demonstrated that the photosynthetic rates of the shade leaves of *Fagus sylvatica* and *Ilex aquifolium* were saturated at an irradiance which was only about 1% of maximum incident on the canopy on a sunny day.

4. Low temperatures

Predictions of the local water budget can be used to predict canopy development, measured as leaf area index, but cannot be used to predict the physiognomy; i.e. whether the local vegetation is needle leaved coniferous forest or broad leaved deciduous or evergreen forest, or grassland, shrub land or tundra. The considerations of leaf area index have been confined to the summer growing season; however it is clear for species of conifers which must endure freezing temperatures during the winter that leaf water potentials are likely to be more extreme at that time than during the summer (Kozlowski, 1976). As leaf temperature declines below 0^0C, the water potential also falls, with a co-efficient of about 1.2 MPa ^{0}C^{-1} (Jones, 1983). All these features may be crucial to the survival of the characteristic species of a particular physiognomy.

The impact of these low temperature responses on plant distribution may be readily observed for species which are grown outside their natural geographical range. In Cambridge, UK, for example, minimum air temperatures during the winter of 1981-82 fell to -16.1^{0}C. Species from

warmer winter climates such as *Cistus* and *Hebe* were killed outright, whilst the evergreen oak, *Quercus suber*, suffered complete defoliation. Presumably, if the defoliation of *Quercus suber* was a regular event the species would be less competitive, also requiring more energy to make the leaves which are thicker than the native, but winter deciduous, *Quercus robur* (Woodward, 1987). Competitive exclusion might limit the pole ward spread of a species sensitive to low winter temperatures before low temperature mortality, which itself would define a precise geographical limit. The implications are here that winter deciduous species should be more competitive than evergreen species in areas of low winter temperature. On the south Island, the Southern Alps (New Zealand) have a permanent snow cover and the dense cold air at these high altitudes (3000 m and greater) drains into lowland valleys. The resulting low temperatures have been shown to be fatal for the locally dominant and evergreen *Nothofagas solandri* (Wardle, 1971), leading to a low altitude or 'inverted' timberline. It is only in these areas, where low winter temperatures limit the survival of the evergreen *Nothofagus*, that the deciduous tree *Hoheria glabrata* is dominant (Wardle, 1977). It fails to spread into the *Nothofagus forest*, although it is well able to survive in the climate (Bussell, 1968*b*), suggesting poor competitive ability. The *Nothofagus*, on the other hand, also fails to dominate *Hoheria* in these areas because of the restricting influence of low winter temperatures. The low winter temperatures control the facultatively deciduous behaviour of the New Zealand deciduous trees has been demonstrated experimentally (Bussell, 1968a) and is suggested by field observations which show the species to be evergreen in warmer areas of New Zealand (Cockayne, 1928). Zimmerman (1964) has shown that temperatures of only $-1\ ^0$C or $-2\ ^0$C are sufficient to cause ice formation in the xylem of the trunk of *Quercus rubra*. This has two powerful effects. First, no water is available to replace that lost by evaporation, even if only through the cuticle, and so frost drought may be a severe problem because the leaf store of water will be small. The second effect of ice formation in the xylem is the mechanism of recovery following xylem thaw. Once the xylem thaws, air bubbles will form and block the vessels. In the hardwood species this will inhibit water movement along the pipes of the xylem.

It is not obvious why species which are able to survive the low winter temperatures (e.g. the boreal zone) are prevented from occurring naturally in winter climates. Many conifers such as *Larix gmelinii*, *L. laricina*, *Picea glauca* and *Pinus sylvestris* grow well in gardens of the temperate zone, far south of their natural ranges. The suggestion again is that competition will play a key role in limiting their distribution, as has been demonstrated for herbaceous species (Woodward, 1975; Woodward and Piggot, 1975). Certainly many of the trees grow poorly in the warmer climates and some, such as *Picea mariana* and *Populus balsamifera*, become much shorter lived. Competitive ability can be described as maximal dry weight accumulation, which is dependent on canopy leaf area index and the extinction coefficient for solar radiation (5). The most competitive individuals would therefore have the highest product of leaf area index and extinction co-efficient, or interception.

5. Frost drought

When low temperatures cause freezing in the leaf, extracellular ice forms. The cause of the spatial organisation of freezing is unclear but is presumably related in part to gradients of osmotic potential. The appearance of intracellular ice is thought always to be fatal (Levitt, 1980). The formation of ice removes liquid water from the leaf and so the solute concentration increases. In addition, the vapour pressure over ice is lower than over liquid water at the same temperature. These two properties ensure further movement of water from the cell to the site of extracellular ice formation and a subsequent tendency for the cell to contract.

Frost drought is clearly an appreciable problem for plant survival. Some species avoid freezing by the super cooling of water below the freezing point that is predicted from water potential.

Super cooling is the rule for most species, which differ rather in their degree of super cooling (Burke *et al*., 1976). Although the mechanisms for surviving low temperatures are still not known with any certainty, it is clear that the ability to survive temperatures of 10 ^{0}C and less is dependent on a range of energy requiring processes, many of which are concerned with protecting the integrity of cell membranes. When the range of plant responses to low temperatures is investigated then particular cardinal temperatures, or ranges of temperature, may be recognized.

The temperatures over which chilling sensitivity is commonly observed lie between -1 ^{0}C (without freezing and +12 ^{0}C (Larcher and Bauer, 1981). It is likely that species may be able to control the threshold for chilling resistance by changes in membrane structure.

6. Low temperatures and plant distribution

The ability of a species to survive low winter temperatures to a certain threshold has been an attractive starting point for describing the climatic control of plant distribution. Raison *et al*. (1979) describe a clear correlation between the temperature at which the cell membrane changes from the liquid crystalline to the gel state and the geographical range of a number of species. Temperature is strongly correlated with latitude, with minimum temperatures decreasing in a poleward direction (Larcher and Bauer, 1981), therefore establishing a strong correlation between the proposed cause and effect. The critical temperatures for leaf survival may be the lowest in winter for species with winter green leaves, even though the leaves will be at their most resistant due to hardening. Less extreme low temperatures during the period of maximum growth and in the dehydrated condition may also prove to be effective in limiting plant distribution (Lyons *et al*., 1979a). Moving in a poleward direction, from low altitudes in the tropics, will be associated with periods of the year in which the minimum temperature falls below the chilling range into the subzero, or freezing, range. Gusta *et al*. (1975) have shown that the freezing resistance of a range of cereals is closely correlated with the tolerance of diminishing quantities of liquid water at freezing temperatures. It emerges, therefore, that both frost drought and membrane sensitivity to low temperatures are likely to be the mechanisms which control plant survival and therefore distribution at freezing temperatures. Sakai (1978) has shown clearly that distribution of dominant species of trees in Japan is strongly correlated with their winter freezing resistance. Broad-leaved, evergreen trees dominate the warm, southern regions of Japan, where the minimum temperature rarely falls below about – 15 ^{0}C. The frost resistance of these species correlates strongly with the trend of the isotherms for extreme minimum temperatures. The region dominated by evergreen trees rapidly changes to a region dominated by broad leaved deciduous trees, once the minimum temperature drops below about – 15 ^{0}C. The work of Sakai, and conclusions drawn by de Candole (1855), Parker (1963), Sakai and Weiser (1973) and Larcher and Bauer (1981), all suggest that the pole ward spread of a species or a physiognomic type of vegetation is controlled by the minimum temperature.

7. Global perspective

The major global zonations of vegetation based on eco-physiological responses to temperature have been mentioned. Even these large scale considerations show substantial eco-physiological differences between species common to a particular vegetation type. The mechanisms by which climate may control such variations in distribution of plant taxa and in particular, considers the dynamic aspects of plant responses in terms of dispersal and in the ability to occupy space will be described.

Taxonomic diversity should decline in a pole ward direction. This hypothesis has been tested by investigating latitudinal variation in a number of families of angiosperms (Heywood, 1979) and arboreal gymnosperms (Hora, 1981). A total of 313 families were included in the analysis. The distribution of the families in latitudinal bands of 15^0 is given on Fig.1. For both the northern and southern hemispheres family diversity is greatest near the equator, declining markedly from latitudes 30^0 to 90^0. The same pattern may also be seen for species diversity (Rejmanek, 1976).

The absolute minimum temperature for each of the latitudinal bands has been extracted from the climatic data presented in Muller (1982) and is plotted against family number in Fig. 2. There is a strong correlation between family diversity and absolute minimum temperature. The regression line shown in the figure suggests a reduction of 3.3 families per ^{0}C reduction in minimum temperature.

An intriguing feature to emerge from the correlation is the way in which the regression line differentiates between the northern and southern hemispheres when the minimum temperature is below 0 ^{0}C. It is interesting to consider whether this is an 'artefact' derived in the averaging process which produces the mean values, or it has some significance to the control of plant diversity. The mean minimum temperature will be a function of the frequency and topographical and altitudinal diversity of the meteorological stations selected for the analysis, but a single mean value will clearly mask the range of diversity within a longitudinal range. In the same way, the number of families may also be a function of habitat diversity. If this is the case then larger areas of land should have a greater probability than smaller areas of presenting the complete spectrum of variation which might be required for the differing habitat requirements of different families (Preston, 1960; MacArthur, 1965; MacArthur and Wilson, 1967; Connor and McCoy, 1979).
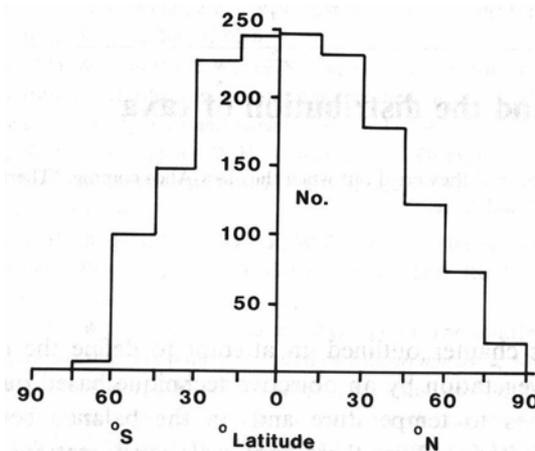

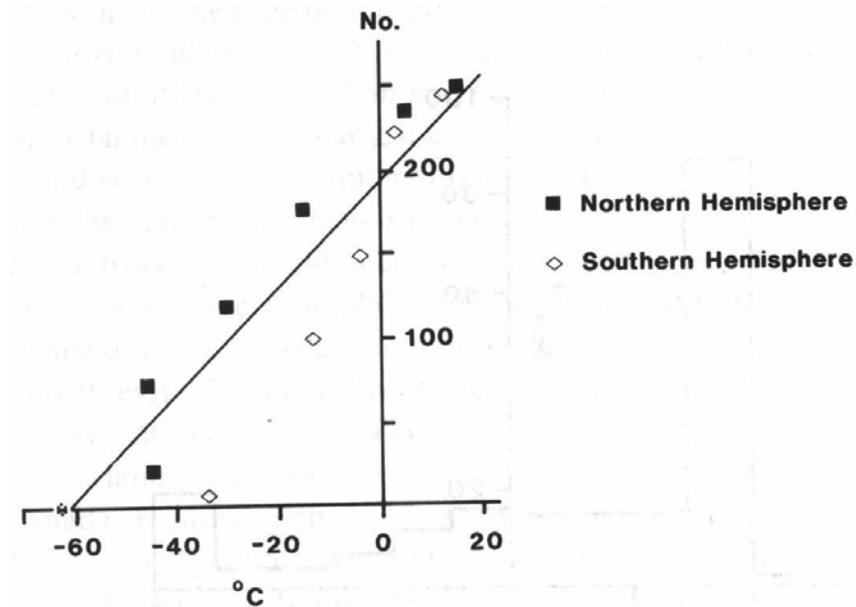Fig.1. Latitudinal distribution of major plant species

Fig.2. Relationship between absolute minimum temperature and family number at different latitudes

The areas of land in the different latitudinal ranges are shown in Table 1. The terrestrial surface area of the northern hemisphere is considerably more extensive than the southern hemisphere at latitudes exceeding 15 ^{0}. It is possible therefore that the variation shown in Fig. 2 is simply a measure of hemispherical differences in surface area. Some measure of habitat diversity may be realised by calculating the number of families per unit of land surface, the family area. Considerations of the pole ward decline of diversity shown on Fig.1 suggest that, irrespective

Table 1. Approximate terrestrial surface areas of the globe

Latitudinal range	Area Mm^2 (10^6 Km^2)
0 – 15 ^{0} N	14.4
15 – 30 ^{0} N	19.4
30 – 45 ^{0} N	19.8
45 – 60 ^{0} N	24.6
60 – 75 ^{0} N	14.8
75 – 90 ^{0} N	1.2
0 – 15 ^{0} S	14.9
15 – 30 ^{0} S	14.3
30 – 45 ^{0} S	9.3
45 – 60 ^{0} S	1.1
60 – 75 ^{0} S	4.8

of habitat diversity, family area might decrease with latitude, reflecting the reduced diversity resulting from the selective forces of low temperatures. The latitudinal range of family area has been presented in Fig. 3.
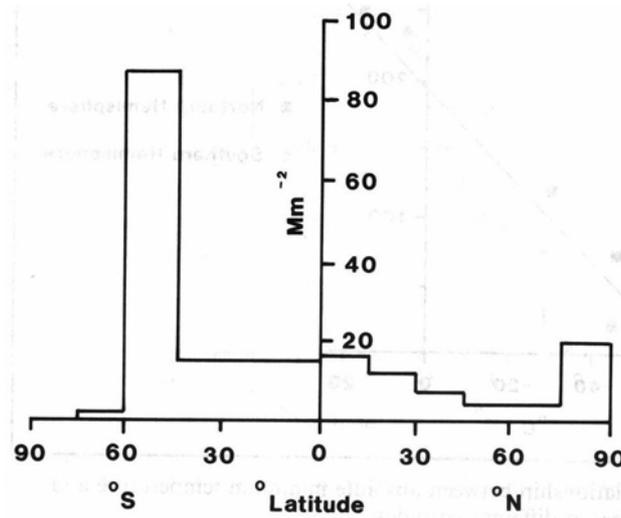
Fig.3. Latitudinal variations in the number of families per unit area

The latitudinal change in family area is not monotonic, although in the northern hemisphere a clear reduction in family area progresses to 75^0 N. In both hemispheres the family area increases markedly at the margins of the major land masses between $75 - 90^0$ N and $45 - 60^0$ S. The area of land between 60^0 and 70^0 S with a low family area is well isolated from any major continent, perhaps reflecting the limitations of plant dispersal across ocean surfaces.

The explanation for the two peaks in family area is not clear. Both latitudinal ranges have virtually identical surface areas (1.1 to 1.2 Mm[2)] and, particularly in the southern hemisphere, are the dwindling expanses of the large continents at lower latitudes (Woodward, 1987).

Within the latitudinal range of 45^0 to 60^0 S, which lies in the main at the foot of South America, 93% of the families are also common to the lower latitudes of South America. Of the remaining 7%, 6% are found in Australia and 1% in South Africa. In fact, 21% of the families in South America between 45^0 and 60^0 S have their geographically closest neighbours in either of South Africa or Australasia, or both, providing some quantitative measure of the relevance of at least 60 million years of history to the present day distribution of families. This historical connection may be an important feature of diversity in the latitudinal range of $45 - 60^0$ S.

Diversity in the northern latitudes is lower than in the south and 91% of the families are truly cosmopolitan compared with 68% in the southern range. Land in the latitudes from 75^0 to 90^0 N is confined to three areas: part of Greenland, Ellesmere Island and the Queen Elizabeth Island to the north and north east of Canada, Svalbard in the Arctic Ocean and the north of Novaya Zemlya and the Taymyr Peninsula of the USSR. The majority of the land area consists of Greenland and the islands to the north of Canada. However only 57% of the families occur in this area. Svalbard has the smallest area, containing only 43% of the species. The Taymyr Peninsula, which is comparable in area to Svalbard is, in contrast, floristically richer, containing 96% of the families present throughout this range of latitudes. The limited diversity of the Islands compared with the Taymyr Peninsula at the tip of the vast Eurasian continent suggests the crucial importance of the probability of plant dispersal to diversity. It is possible to suggest that the diversity in the latitudes between 45^0 and 60^0 S and 75^0 and 90^0 N is due largely to dispersal efficient contact with the large diversity of large continents. Once this efficiency of dispersal is reduced then diversity is also reduced, as in Svalbard or in the latitudes between 60^0 and 75^0 S (Woodward, 1987).The high diversity in these selected areas, measured as family area, implies that much of the ground area in the adjacent continents is redundant in terms of diversity.

8. Dispersal and migration

The distribution of taxa should be concerned with the rate and extent to which dispersal of different species responds to changes in climate. The response of species to changes in climate can only be understood as the combined phenomenon of the dispersal or spatial spread of plant propagules and the migration of plant populations. It is unlikely that the two processes can be studied independently because of the random nature of the actual dispersal process.

One of the most productive areas for the investigation of migration is at the limits to a particular area of distribution. Such a limit may be very sensitive to changes in climate if a threshold phenomenon is the cause of the limit and can provide evidence for the mechanisms by which species adjust their range. Kullman (1979, 1983) has provided careful analysis of the variations in the tree and forest limits of birch, *Betula pubescens*, in central Sweden since the turn of the century. This work re-enumerated the same area that Smith (1920) had surveyed in the period between 1915 and 1916. The evidence provides an accurate assessment of any changes in the tree limit of birch over a period of about 60 years.

Kullman (1979) demonstrated that the altitude of the 1915- 1916 tree limit had increased in about 75% of the localities that was investigated by him with the remaining 25% being unchanged. He concluded that the rise in the tree limit was caused by the increased frequency of warm summers during the period of 1930 to 1949. Birch establishment occurred well above the original tree limit, although decreasing significantly with altitude. A climatic explanation of this expansion in the range of birch is encouraged by the strong correlation between the high mean temperatures and establishment, and the sharp cut - off in establishment in the period of 1950 – 1955 when temperature fell and remained cool to 1975. Kullman (1983) points out that the reverse situation for *Betula pubescens*, with adult individuals surviving, with normal mortality, in the cooler years when there is no establishment from seed. As Kullman (1979, 1983) has pointed out, it is clear that an understanding of the eco-physiological responses of different stages of the life cycle are crucial in understanding the control of plant distribution..

The deviation of the observations of species number from the overall prediction based on distance has been investigated by fitting the following curve to the data:

$$N = A^z D^m \tag{6}$$

where N is the number of species on a particular island of area A (km^2) and D km from the source of propagules. The powers of z and m are a measure of the degree of influence of island area and source distance on the total species diversity of an island. The relationship A^z is the familiar relationship resulting from the theory of island biogeography (MacArthur and Wilson, 1967). The values of z and m are 1.33 and -1.1 for the Soviet species and 0.55 and - 0.19 for the American species. Without attaching too great a biological significance to the absolute values of these equations, it appears that the probability of species migration is less from the USSR. The influence of distance in migration, as measured by the co-efficient m, is nearly an order of magnitude more negative for the Soviet species, compared with the American species, again emphasizing a lower probability of migration. It is not clear why the migration of species from the USSR has a lower probability but investigation of wind and sea current transport may prove valuable (Heusser, 1983).

The divergences between the observations of species number and the numbers of predicted species using the above equation have been done. For the species which are most probably Soviet in origin, the greatest divergences are found on the largest and most distant islands from the Soviet coast: Umnak, Unalaska and Unimak. It is clear that the probability of dispersal is so low for these islands that it completely dominates the overall species / area relationship of the

above equation. Species diversity on the remaining islands appears to be adequately described by the product of the species / area relationship and the probability of dispersal.

9. Vertical diversity

An analysis of the ecology of the islands at the present and in the past has been most productive in providing a means of investigating dispersal and migration, the effect of dispersal on plant distribution and the importance of climate on the processes of dispersal and migration. How important is climate in controlling vertical and horizontal diversity? This question has been investigated by applying a Bray and Curtis ordination (Bray and Curtis, 1957). Three islands at different latitudes were selected for the comprehensive vegetational analyses of the vascular plants. The area of the islands was 380 km^2 (71^0 N; altitude 2277 m; most northerly island Jan Mayen); 75 km^2 (40^0 S; altitude 910 m; Gough Island at Edingburgh Peak) and 986 km^2 (0^0 S; altitude 846 m; Santa Cruz, in the Galapagos Islands). Hamann (1981) has made extensive vegetational studies of the Galapagos Islands and is the source of quantitative information of the major vegetational types.

Two dimensional ordinations were prepared for the major communities of the islands, with the axes providing a measure of the similarities in species composition between stands: the smaller the difference on the axes, the greater the similarity between the stands (Woodward, 1987). Only two growth forms (shrub and herbaceous) are found in Jay Mayen. The two major dwarf shrubs are *Salix herbacea* and *Empetrum hermaphroditum*. All four growth forms are found in Gough Island, albeit sparsely for the tree, *Sophora macnabiana*. The stands dominated by *Sophora* and the bush *Phylica arborea* were three layered, or storeyed, consisting of a uniform upper story of the tree or shrub, a central storey mainly of ferns and a lower storey, or ground cover, of both ferns and bryophytes. The stands of Santa Cruz are clearly separated by the ordination into stands of deciduous trees, evergreen trees and herbaceous species. The deciduous forests consisted of a diverse upper canopy of 15 or more species such as *Bursera graveolens*, *Zanthoxylum fagara*, *Opuntia scouleri* and *Jasminocereus thouarsii*. The climates of these three islands are quite distinct and are given in Table 2, with data from Wace (1961), Hamann (1979) and Muller (1982). Both the mean and minimum temperatures decline with latitude, although the islands do not fall into a monotonic series with respect to precipitation. Santa Cruz is considerably drier than the other islands. Small scale variations in local topography and hydrology are typical features of mountainous islands. These variations clearly lead to local variations in the distribution of species, but within the constraints of the general climate.

Table 2. Island Climates

Name of the Island	Temperature ^{0} C			Total annual Precipitation (mm)
	Latitude	Annual Mean	Absolute Mean	
Santa Cruz	0^0 S	23.8	17.8	364
Gough Island	40^0 S	11.7	2.0	3225
Jan Mayen	71^0 N	- 0.2	-27.9	628

In the very wet climate (40^0 S), 40% of the vascular plant species are under storey pteidophytes, which are generally considered to be drought intolerant (Richards and Evans, 1972; Page 1979*a*, *b*). On the much drier island (0^0 S), pteridophytes account for about 16% of the vascular plants (van der Werff, 1983); On Jan Mayen Island which is wet but cold (71^0 N), the pteridophytes only account for 5% of the vascular plants, although one species, *Equisetum arvense*, is particularly widespread and often locally dominant. These examples of the occurrences of the pteridophytes highlight one of the many problems in phyto-geography, which is the large swing between geographical areas in those features of climate which may be critical in controlling the

distribution of plants. On the island of southern latitude water availability is critical and in the island of northern latitude low temperatures may be more important.

One other critical feature is the correlation, at least, between the increase in vertical diversity and temperature. The increase diversity created by the locally dominant, drought and high irradiance-insensitive trees, ensures the occurrence of a cool and moist shade, which may be an obligate habitat for the survival of many pteridophytes.

Under a coniferous canopy, Young and Smith (1979) have shown that the short periods of high irradiance and leaf temperature during sun flecks can exert a strong influence on the local distribution of the ground layer species, *Arnica cordifolia* and *Arnica latifolia*. For these species it was found that *A. latifolia* was more common where the shade environment was most constant with infrequent sun flecks, whilst the reverse was true for *A. cordifolia*.

It appears therefore that the climate amelioration associated with an equatorial shift in latitude leads to an increase in vertical and horizontal diversity, with greater dissimilarity between stands. This climatic control of vertical diversity is also critical in increasing the local range of habitat diversity.

10. The impact of variations in life cycle characteristics on plant distribution

The considerations of vertical diversity, and in particular the distribution of pteridophytes, suggest the need for more detailed investigation on the life cycles of species, to determine the importance of specific variations in the life cycle in limiting the distributions of plants in deep shade, full sunlight or xerophytic or mesophytic habitats. The large scale mesoclimate of an area is critical in controlling the dominant physiognomy (Woodward and Shelly, 1983). Within such an area there may be abundant smaller scale variation in the distribution of species. Some of this variation may be because of vertical diversity. Harper and White (1974), Grubb (1977) and Harper (1977) have emphasized the importance of variations at all stages in the life cycle in controlling plant distribution. An example is provided by *Sophora macnabiana* which is the only tree found in Gough Island. Wace and Dickson (1965) found that seeds of *Sophora macnabiana* (and a number of other species on Gough) are able to germinate after at least three years of immersion in sea water. Of the available sources of seeds that may reach the island (40^0 S) by sea, only those which are tolerant of long periods of immersion, and which are appreciable in number, can colonise the island. As far as this colonisation is concerned, the dispersal phase of the life cycle is most crucial. The end result of the successful dispersal and establishment of *S. mecnabiana* is the development of a vertical diversity of species which is associated with *S. mecnabiana*. The mechanism, by which this diversity develops, presumably with the exclusion of some species, was studied experimentally. Such experimental studies have been attempted in herbaceous vegetation at different latitudes which demonstrate the effect of broad changes in climate on the local abundance of species. Chapin and Chapin (1980) in an experimental study showed the response of a cleared area of tundra in Alaska (65^0 N) to seeding by an exotic species *Lolium perenne*, itself not found naturally beyond about 55^0 N in North America. Before clearance (years 0 to 1) the area was completely vegetated with tundra species of *Carex bigelowii* and *Eriophorum vaginatum*. The area was cleared of vegetation and sown with the temperate species, *L. perenne*. At the end of the first growing season the cover of *L. perenne* had reached 20%. The cover of *L. perenne* subsequently declined to 2% at the end of the third year and became extinct by the fifth year. During this time *C. bigelowii* and *E. vaginatum* invaded the cleared area and increased in abundance, forming a nearly complete cover by the fifth year. In this case, the extinction of *L. perenne* is unlikely to result from competitive relationships with the native species because the cover of these species is quite low, suggesting that the extinction of *L. perenne* is more likely to be caused by its inability to survive the local climate. It is also

interesting to note that the native species took at least five years to recolonise this cleared area in the cold tundra, emphasising the limited potential growth in this climate.

Woodward (1987) did a similar type of experiment in the British Isles at latitude of 50^0 N and an altitude of 90 m. Local vegetation was *Lolium perenne*, which was locally dominant. Small areas of this vegetation (0.06 m^2) were cleared in the early spring (year 1) and plants of *C. begelowii*, which does not occur below about 600 m in England, were introduced, providing a cover of about 90%. The cover of *C. begelowii* declined to 50% by the end of the second year, following invasion and shading by the local species, including *L. perenne*. *C. begelowii* disappeared by the end of the third year. It appears that competitive relationships with local species are crucial in controlling distribution, because *C. begelowii* grows well and completes its life cycle at low altitudes on the same soil but in the absence of interspecific competition. Grubb (1982) in Cambridge initiated an experiment by clearing areas of vegetation followed by sowing with equal quantities of seeds of *Arrhenatherum elatius*, *Dactylis glomerata*, *Plantago lanceolata* and *Festuca rubra*. The fates of the four species were traced for 9 years. By the sixth year *A. elatius* had established its dominance over the community, while *D. glomerata* and *P. lanceolata* had been eliminated, presumably through competition with *A. elatius*. However the small grass *F. rubra* persisted in the community, even increasing its cover by the eighth year. *F. rubra* remained established as an understorey component in deep shade but failed to reproduce sexually. Survival of *F. rubra* but the extinction of *C. begelowii* in temperate grassland clearly relates to specific differences in shade tolerance of the adult phase of the life cycle. Turitzin (1978) has developed a model based on the photosynthetic and architectural features of plants to show that these characteristics are sufficient to explain the occurrence or absence of the grass *Bromus mollis* in various competitive situations. Yaqub (1981) investigated the altitudinal distribution of two perennial herbaceous species, *Eupatorium cannabinum*, which has an upper limit of about 270 m in Wales, and *Verbena officinalis*, with an upper limit of 220 m. *V. officinalis* overwinters as an evergreen rosette, whilst *E. cannabinum* is winter deciduous. Mature individuals of both species were transplanted in 1977 to a range of altitudes up to 400 m, above the natural limits of both species. The evergreen rosettes of *V. officinalis* died when the minimum temperature reached – 7.8 0C. *E. cannabinum* survived at all sites, showing an insensitivity to the local winter climate. Woodward and Jones (1984) predicted that such a response should occur for the lowland species *Potentilla reptans*, at a site about 240 m above its observed altitudinal limit (610 m) in the British Isles. They also observed the number of individuals of a range of species which survived from one stage of the life cycle to next in 90 mm diameter patches cleared of the native vegetation. In addition they established the density dependence of each probability in the life cycle, by sowing the patches at a range of densities. The resulting observations on each stage of the life cycle over 2 years, and for a range of densities, species and altitudes, are too extensive to be simply used for predicting survival. However the actual probabilities of the stages in the life cycle can be inserted into a (mathematical) transition matrix, which when multiplied by the number of individuals at different stages, or phases, serves to predict the growth in number of the whole population. Leslie (1945), Lefkovitch (1965) and Usher (1969, 1972) described the mathematical details of the technique. The technique has recently proved to be valuable and applicable to a range of vegetation types, such as annuals (Law, Bradshaw and Putwain, 1977), herbaceous perennials (Sarukhan and Gadgil, 1974; Woodward and Jones, 1984), temperate trees (Enright and Ogden, 1979) and tropical trees (Hartshorn, 1975; Pinero *et al.,* 1984).
Continued post multiplication of the transition matrix of probabilities by the column vector of population density at each stage leads to a deterministic model of population growth, described by:

$N = N_0 e^{rt}$ (7)

where N is the population number at time t, with N_0 the initial population size and r the intrinsic rate of increase in number. When r has a value of zero, population increase is also zero and N is constant with time, reflecting a perfect balance of birth and death. When r is greater than zero, the population will be increasing in number, and the population will decrease when r is less than zero. Repeated multiplication of the model with $r > 0$ predicts continuous but unrealistic exponential growth, although a stable population in terms of the relative numbers in each stage or phase is soon established.

Active growth of natural populations ultimately leads to a density dependent effect (usually reduction) on one or more of the probabilities in the matrix. Law (1975) and Woodward and Jones (1984) have shown that the effect of this density dependence is on asymptotic trend in population growth, reaching a more or less steady population size.
If (7) is differentiated, then the growth rate in a continuously exponential phase is:

$$\frac{dN}{dt} = rN \tag{8}$$

However, the growth rate falls to zero when the population size reaches an asymptote, so that if the population size at the asymptote is K, then:

$$\frac{dN}{dt} = r\frac{N(K-N)}{K} \tag{9}$$

This equation is known as the logistic equation and K is a measure of the carrying capacity of the local environment. The bracketed part of the equation varies from 1 (when $N = 0$) to 0 when $N = K$, and simply modifies (7), to account for the carrying capacity.

The application of density dependent transition matrices to predicting population growth has been done (Woodward, 1987). Three predictions based on field observations are given.

- *Eupatorium cannabinum* growing at an altitude of 360 m (the populations died at 610 m).
- *Potentilla reptans* and
- *Oxyria digyna*, growing at 360 m and 610 m respectively.

Symonides (1979) observed very similar patterns of population increase for *Corynephorus canescens* when it invades sand dunes. In both cases the initial increase in population density was rapid, then moving to a more or less constant equilibrium density. The matrix approach to predicting population growth, resulting from variations both subtle and obvious of different stages of life cycle, is particularly valuable. The best is shown by *P. reptans* when grown at 610 m. At this stage the prediction is that the species should decline slowly and ultimately become extinct because of overall reductions in the success of a number of stages of the life cycle, such as seed germination, winter survival and fecundity. Mortality resulting from extremes of temperature, may explain the extensive and uniform boundaries to vegetation as seen particularly clearly at the tree lines on mountains. Where investigated, the clear cut boundary appears to result from frosts rather than through the results of competition with plants from higher altitude (Wardle, 1985).

Population growth of *Oxyria digyna* shows little sensitivity to altitude, either within or outside (below) its natural range. Indeed Salisbury (1926) and Dahl (1951) have pointed out many examples of upland species which can complete their life cycles in low land environments far from their natural range. This success may be observed for isolated plants, but in competition

with more rapidly growing lowland species extinction appears to be inevitable (Woodward and Jones, 1984; Woodward and Piggot, 1975), as was clearly demonstrated in the field for upland species S*edum rosea*, when growing in competition with the lowland *S. telephium*. This example provides a clear case for the basis of the mechanism by which climate can control plant distribution on mountains.

The very nature of the experiments which are central to the matrix predictions mentioned above is that both intra- and interspecific competition are measured. If, as might be expected, the upland species *O. digyna* will become extinct in the lowlands, then an improved model should attempt such a prediction. It is known that differences in growth rates are critical in the competition for irradiance (Woodward, 1975; Woodward and Piggot, 1975) and also for soil nutrients and water, yet absolute differences in the growth rates of species cannot be extracted from the predictions. However Jones (1983) clearly demonstrated that the lowland species *E. cannabinum* had a higher growth rate in the lowlands than *O. digyna*.

11. Competition for space

A more precise model for predicting geographical distributions should aim to embody both life cycles and growth characteristics of the species under investigation. A starting point for this aim may be met by predicting the ultimate fate of a monospecific stand of seedlings which have germinated in a bare patch of ground, encircled by established plants of the same or different species. The model assumes that, at least in this case, range extension may occur by growth and establishment of individuals in gaps denuded of vegetation. The invading seedlings in the patch may survive in two ways. One way is by survival in the understorey beneath the encroaching plants. The other way is for the species to grow sufficiently rapidly to equal or overtop the encroaching species, therefore effecting, rather than being affected by, shade.

Species capable of incorporation into the understorey must be shade tolerant, such as *Festuca rubra* in the shade of *Arrhenatherum elatius*. There is abundant evidence to support this proposal in forests. Examples include the long-term survival in the forest understorey by *Prunus serotina* in North American forests of *Quercus alba* and *Q. macrocarpa* (Auclair and Cottam, 1971); *Tsuga canadensis* under *Pinus strobus* (Henry and Swan, 1974).

Contrary evidence for the elimination of shade intolerant species in shade can also be found in forests. Young individuals of the pioneer and shade intolerant *Betula alleghaniensis* fail to survive longer than three years under a canopy of *Acer saccharum*, *Fagus grandiflora* and *Betula alleghaniensis* in North America (Forcier, 1975); and also in North America the occurrence of the short lived and shade intolerant *Populus grandidentata* declines rapidly under the *Acer saccharum* and *A. rubrum* (Spurr and Barnes, 1980). In addition, the spectral quality of the shade cast by the canopy may inhibit seed germination (King, 1975), so that the life cycle fails to be initiated. Shade tolerance can therefore define the ability of a species to survive the encroachment of a gap. Within any canopy the frequency of occurrence and longevity of gaps will be critical in maintaining a diverse mixture of shade intolerant and shade tolerant species. This is a universal phenomenon of closed vegetation. In forests the average annual creation of gaps is about 1% of the total area in northern boreal forests (Heinselman, 1973), subalpine forests (Kanzaki, 1984), temperate evergreen forests (Naka, 1982), temperate deciduous forests (Runkle, 1982) and tropical forests (Hartshorn, 1975).

The formation of gaps in forests is due in part to catastrophic disturbances such as fire and storms and also to the death of individuals in the mature canopy. The mortality rate can therefore be critical in maintaining community diversity, which in vertical terms is also climatically controlled. Mortality is also a feature of herbaceous of canopies, and in controlled monoculture. Kira *et al*. (1953) demonstrated that mortality lead to fewer and larger individuals. This process of self thinning is most obvious for a dense group of small individuals, such as the seedlings attempting to establish in a clear patch in herbaceous vegetation. Yoda *et al*. (1963) described the

relationship between the size or weight (w) of an individual and plant density (N) when self thinning is occurring by a power relationship:

$$w = cN^{-3/2} \tag{10}$$

White (1980) has shown that this relationship is true for monocultures of a number of species, both herbs and trees, with a mean value of 6761g m^{-2} for c and – 1.51 for the exponent. During the phase of self thinning no species exceeds the relationship with a much greater weight than would be predicted from the above equation using the mean values provided by White (1980). At large weights and low densities, the exponent may tend to -1, at which point the plants have reached the carrying capacity of the local environment and any increase in size will be at the expense of directly proportionate diminution in plant density. The point of change from slopes of -1.5 to -1 appears to be species related and may be climatically controlled (White and Harper, 1970; Kays and Harper, 1974). At the other extreme, before self thinning occurs, plant growth is apparently density independent, and is not described by the equation (10). The relation between weight and density described by the equation (10), in the absence of any evidence to the contrary, can be accepted as a universal phenomenon for plants in monoculture, with the exponent of – 1.5 (or -3/2) describing the marriage of a volume of plant, with a dimension of 3 to an area of soil, with a dimension of 2 (Whittington, 1984). This relationship therefore defines the upper boundary line or constraint relating plant weight and density.

It has been established that growth rate is critical in determining the survival of patch invaders, and that in the first year of the growth of most perennials sexual reproduction of the patch invaders can be discounted. The patch will be encroached at a rate which, initially at least, is dependent on the growth rates of the species in the existing vegetation. It is assumed in this instance that the individuals of the patch invaders which are encroached and shaded by the advancing front of the existing vegetation are eliminated, i.e. they are shade intolerant juveniles. In addition, once self thinning occurs in the patch, the numbers of individuals will also decline in the manner predicted by the equation (10).

The plant responses to be considered are therefore the density dependent and independent rates of growth of the patch of invaders and the rate of patch infill. Two species have been chosen to develop and describe the application of a model for predicting the outcome of competition between species invading a gap and those existing around the gap. The selected species are the arctic alpine species *Oxyria digyna* found in the British uplands and the continental species *Lolium perenne* found in the lowlands. Data on the growth of the species have been obtained in Cambridge, in addition to data from Jones (1983) and Woodward and Jones (1984) for
O. digyna and Kays and Harper (1974) for *Lolium perenne*. *L. perenne* was grown in greenhouse between February and July in North Wales. *O. digyna* was grown over a similar period at 360 m in mid-Wales and in Cambridge.

It has been assumed that propagules of either *O. digyna* or *L. perenne* have invaded a patch of vegetation surrounded by a number of individuals of native species. The initial growth rate of the invaders is density independent and may be described by the relationship (reviewed by Evans, 1972):

$$w = w_0 e^{Rt} \tag{11}$$

where w is plant weight at time t, with an initial, or starting weight of w_0. The intrinsic rate of increase, or relative growth rate, is R, and is the rate of increase in weight per unit of plant weight. Once the plant weight and density relationship reaches the self thinning line,

$$w = cN^{-3/2} \tag{10}$$

and (11) can be modified as:

$$w = w_\text{T} e^{R_\text{T} t}, \tag{12}$$

where w_T is related to the point of inflexion from the density of independent to the density dependent or self thinning line, and R_T is the relative growth rate during thinning. Rearranging (10) in terms of density,

$$N = \left(\frac{c}{w}\right)^{2/3} \tag{13}$$

allows density to be related to growth during self thinning as:

$$N = \left(\frac{c}{w_T e^{R_T t}}\right)^{2/3} \tag{14}$$

Mean values of the various parameters in (10, 11 &12) for the two species are shown in Table 3 (Woodward, 1987). The constant c has a value of 40 000 g m^{-2} for both species. It emerges that the upland species *O. digyna* has lower growth rates than *L. perenne* in a lowland environment.

Table 3. Growth attributes of *L. perenne* and *O. digyna* (Woodward 1987)

	w_0 (g)	R (d^{-1})	w_T (g)	R_T (d^{-1})
L. perenne	0.0007	0.076	0.0211	0.018
O. digyna	0.0005	0.044	0.0154	0.009

The relative growth rates of the two species have been chosen to be invariant during the two phases of growth. However there should be no problem in introducing both climatically an ontogenetically determined variations in the relative growth rate. The growth curve for *O. digyna* is similar in detail to *L. perenne* but in this case growth is slower, in both density independent and dependent phases of growth (Woodward 1987). The growth of *O. digyna* is much less than *L. perenne* and is likely to be less competitive. The importance of gaps for maintaining species diversity in forests has been a particularly important thrust in plant ecology. Shugart (1984) has provided a synthesis of this work which provides an extensive and fascinating model for predicting the effect of gaps on species diversity. It follows from this work that modelling has great value in amalgamating diverse stands of information. The significance of gaps or diversity in herbaceous vegetation has also been area of keen interest. The survival to flowering of two biennial species, *Daucus carota* (Holt, 1972) and *Verbascum thapsus* (Gross, 1980), has been shown to be dependent on the rate of gap infill. The survival of either *Lythrum salicaria* or *Epilobium hirsutum* in gaps is related to specific differences in growth rate. If both species invade a gap in the spring then *L. salicaria* has a greater growth rate and excludes *E. hirsutum*. If invasion occurs in the autumn, the reverse occurs because of the greater rate of growth of *E. hirsutum* at low temperatures (Whitehead, 1971). It was also found that *E. hirsutum* is unable to survive in some calcareous soil when as a result of water-logging exchangeable manganese increases in the root environment. (Nazrul-Islam, 1986).

The example of two species differing in rates of growth demonstrates that the slow growing *O. digyna* should become extinct in gaps surrounded by aggressive and fast growing individuals. *L. perenne*, on the other hand, has a greater probability of survival in the same situation. The application of this model, which relates plant growth to population density, is a logical addition

to the matrix model and would be strongly dependent on inter-specific differences in rates of growth. Indeed it would predict the outline demise of *O. digyna* at low altitudes, because of its poor ability to fill geometric space.

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