

The impact of low temperatures in controlling the geographical distribution of plants

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The distribution limits of three species, in the British Isles are discussed. For *Verbena officinalis* and *Tilia cordata* low temperatures are shown to influence distribution, by limiting the capacity either to flower or to fertilize ovules, respectively. In the case of *Umbilicus rupestris*, a long-term transplant population beyond the natural geographical limit of the species has evolved new low-temperature responses of seed germination and winter survival. The effect is a marked change of phenology, compared with populations of the species within its natural range, which enhances the capacity of the population to survive in a colder environment.

1. INTRODUCTION

Low temperatures influence the life cycles of plants through three mechanisms; by limiting the rate of a particular process, by cooling the plant below the non-lethal threshold temperature of a process and by cooling the plant into the lethal temperature region. Each mechanism has been demonstrated to limit the distribution of a plant species, or vegetation type (Patterson *et al.* 1978; Larcher & Bauer 1981; Sakai & Larcher 1987; Woodward 1987).

These extremes of temperature may not occur regularly or frequently at a particular geographical location, and so studies of their importance must, of necessity, cover long periods of observation. In addition it is possible that during the intervening period between extreme events a population of individuals may evolve genetically in response to other features of the local climate (Sakai & Larcher 1987). The end result, particularly for short-lived species, may be a change in tolerance of temperature extremes. This paper describes several long-term observations on the low-temperature tolerances of plant populations. These experimental populations have been established in, and outside of, the natural geographical range of the species, with the aim of detecting the occurrence of long term change in low temperature tolerance.

2. THE HISTORICAL STATUS OF A PRESENT-DAY DISTRIBUTION

It is often tacitly assumed that the present-day distribution limit of a species is controlled by present-day climate. The truth of this assertion will in fact vary with the species under consideration. For a species capable of completing its life cycle in a few months, and with no long-term seed-bank, it appears likely that the climatic conditions in any one year will determine the distribution of the species in the following year. However even that assertion is probably incorrect as, for such a species, presence in any one year must be strongly influenced by presence in several previous years.

A clear and perhaps extreme example of this autocorrelation is seen for the long-lived species, *Tilia cordata* Miller (species authorities from Clapham *et al.* 1981). The distribution of

Tilia in Europe has been reconstructed from the end of the last ice-age to the present day by pollen analysis (Huntley & Birks 1983). This analysis shows that *Tilia* first reached the British Isles about 7000 BP (years before 1950 A.D.). In a careful study of *Tilia cordata* in the British Isles, Pigott & Huntley (1981) have shown that *T. cordata* reached its northern limit (in Cumbria and Northumberland) in the period between 7000 and 5000 BP (figure 1). The present-day distribution of *T. cordata* extends to the same northern limit (fig. 1 in Perring & Walters (1976)). However, the present-day reproductive limit of *T. cordata* is some 200 km south of the absolute northern limit. Such a difference results from the long life of *T. cordata*, which sprouts from the base of fallen trees. As a result it is possible that the northern limit of *T. cordata* in Cumbria and Northumberland is a carry-over of the limit determined by the climatic conditions in the period between 7000 and 5000 BP, with the continued presence of the species due to its great longevity.

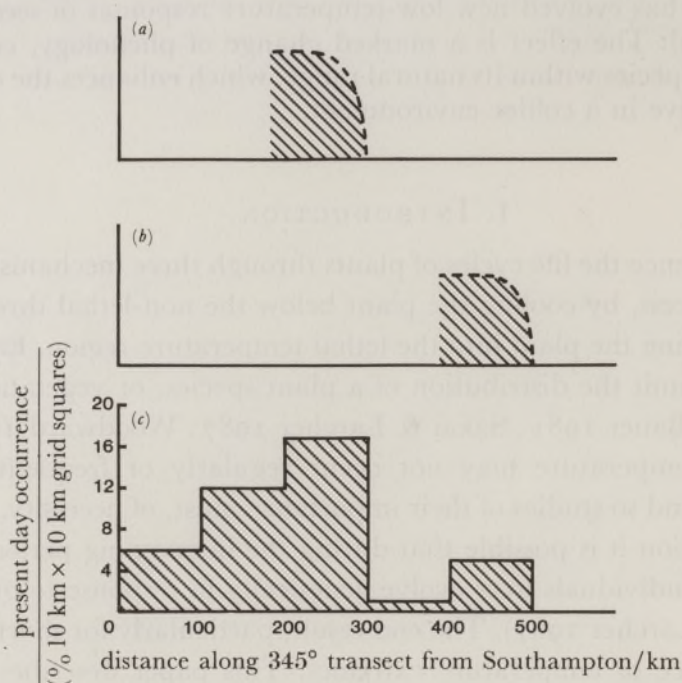


FIGURE 1. The distribution limits of *Tilia cordata*, estimated along a transect 100 km wide running at 345° from Southampton; (a) reproductive limit at the present day; (b) reconstructed northern limit 7000–5000 BP; (c) present-day distribution, estimated as the percentage occurrence in 10 × 10 km squares in a grid square of 100 × 100 km. (Data for (a) and (b) from Pigott & Huntley (1981); data for (c) from Perring & Walters (1976).)

Present day geographical limits must, therefore, be treated with some caution when investigating mechanisms of control, because of the likelihood of wide spatial and temporal separation between distributional and climatic limits. Nevertheless Pigott & Huntley (1981) were able to show unequivocally that the present-day reproductive limit of *T. cordata*, in the British Isles, is caused by a low temperature threshold effect during the flowering phase. Below a temperature of about 18 °C the pollen-tube grows too slowly to reach the unfertilized ovule before the style degenerates. This single mechanism appears crucial in controlling the northerly spread of present day *T. cordata*; such a feature may also have controlled the northern limit in the period between 7000 and 5000 BP. However, work in Scandinavia (Pigott 1981) indicates that other mechanisms, also involved in reproduction, may be equally important.

3. EXPERIMENTAL STUDIES AT DISTRIBUTION LIMITS

Reproduction

One problem with experimental work and observations on extant populations of a species is that the response of the species just beyond its natural range limit cannot be considered. This is a serious limitation because the geographical limit of a species could just as equally result from restricted dispersal, as to a physiological limit on a particular process. The technique of transplantation can overcome the problem of dispersal and allows further investigations of physiological limitations. In addition, the long term establishment of a population, beyond the natural limits of the species as whole, also allows investigations on genetic change within the population.

Verbena officinalis L. is a perennial herb that is not found at altitudes above 220 m in Great Britain (Yaqub 1981). In the autumn of 1979 six transplant populations of *V. officinalis* were established, in the same soil type, at a range of altitudes between 76 m and 305 m. Five populations were established in the Wye Valley and one near to Cardiff in South Wales. In 1980, an additional population was established in Cambridge. Each population consisted of 20 mature plants and about 200–300 seeds, originated from an altitude of 76 m in South Wales. Flowering of the mature plants was first recorded in 1979 (figure 2). The period of flowering was July and August at all sites, and so the mean temperature of these months has been used as a measure of the environment. In 1979, the response of flowering to temperature falls along

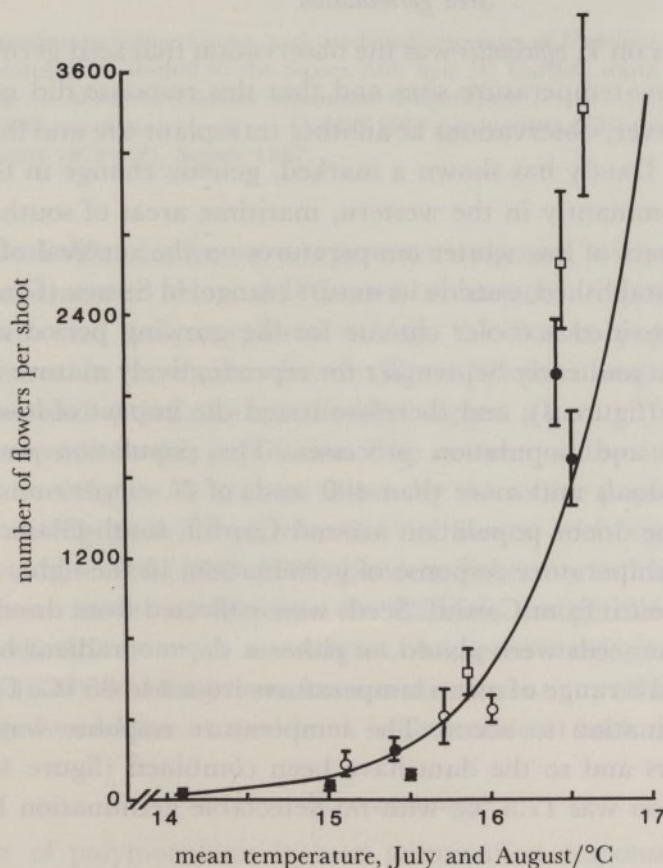


FIGURE 2. Flower production by *Verbena officinalis*. Mean observations with 95% confidence limits. Observations in 1979 (●); 1981 (○) and 1987 (□). Line is exponential regression ($r = 0.949$) between temperature and flower production for 1979 observations on Wye Valley transplants (all ●, except at 16.3 °C).

an exponential regression line, for the population in the Wye Valley. This correlation was repeated in 1981, and indicated that a mean temperature between 16 °C and 16.25 °C was a threshold between poor and profuse flowering. Further studies on the seed produced indicated the same general relationship with temperature, therefore a reduction in flower production is not compensated for by increased seed production.

The sites were revisited at intervals up to 1987. Over this period, at the sites in Cambridge and South Wales, the original mature individuals had died and were replaced by mature individuals establishing from seed. At the remaining sites the transplant populations of *V. officinalis* became extinct. Flower production was measured in 1987. There was no obvious change in the threshold temperature between poor and profuse flowering. Above the threshold, the populations in the warmest climates produced more flowers than the relation indicated for 1979.

That this temperature response is due to a threshold temperature effect was demonstrated by growing mature transplants of *V. officinalis* (collected from the field in Cambridge in May 1984) in the controlled environment. Plants were grown at a mean temperature of 20 °C for one month. One set of plants was then transferred to a mean temperature of 15 °C. These plants remained in the vegetative phase for three months, with no obvious reproductive development. In contrast plants retained at 20 °C flowered profusely, as did the plants from the low temperature when they were transferred to 20 °C.

Seed germination

One finding of the studies on *V. officinalis* was the observation that seed germination was poor at the high-altitude and low-temperature sites and that this response did not change over a period of eight years. However, observations at another transplant site and for another species, *Umbilicus rupestris* (Salisb.) Dandy has shown a marked, genetic change in this response.

U. rupestris occurs predominantly in the western, maritime areas of southern Britain. As a part of a study on the impact of low winter temperatures on the survival of this wintergreen species, a population was established, outside its natural range, in Sussex (Crowborough) at an altitude of 157 m. This provided a cooler climate for the growing period of the species (all months except July, August and early September for reproductively mature individuals) than in the west of the country (figure 3), and therefore tested the impact of low temperatures in controlling plant survival and population processes. The population was established by planting 20 mature individuals and more than 400 seeds of *U. rupestris* on a wall, the same habitat as that found in the donor population around Cardiff, south-Glamorgan.

In 1978 and 1984 the temperature response of germination, in the light, was tested in the donor population of *U. rupestris* from Cardiff. Seeds were collected from dried flower heads, in the field in September. The seeds were placed on either a thermogradient bar or plate (Ellis *et al.* 1982), which provided a range of mean temperatures from 4 to 35 °C. The seeds required no stratification for germination to occur. The temperature response was not statistically different between the years and so the data have been combined (figure 4). The optimum temperature for germination was 17.5 °C, with no detectable germination below 8 °C, after four weeks.

By 1987, reproductively mature individuals of *U. rupestris* had established in Sussex from the original seed source. None of the original mature individuals had survived to this date. Seeds were collected and the temperature response of germination was tested over a four week period.

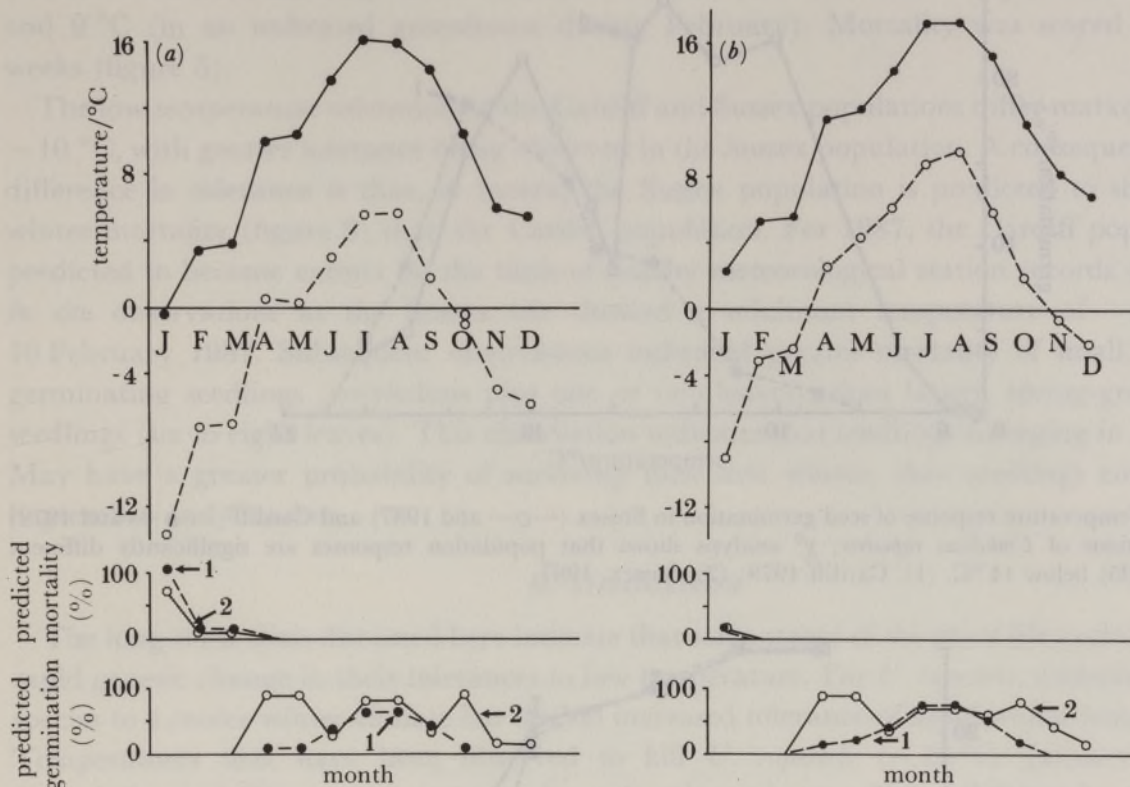


FIGURE 3. Mean and minimum temperatures, and predicted responses of *Umbilicus rupestris*, at (a) Goudhurst, Kent (the nearest meteorological station to the Sussex site) and (b) Cardiff, south Glamorgan. (i) Mean monthly temperature (—●—), absolute monthly minimum temperature (---○---); (ii) predicted seedling mortality (—○—, Sussex 1987 population; ---●---, Cardiff 1978 population); (iii) predicted germination (symbols as for (ii)); (1), Cardiff 1978; (2), Sussex 1987.

There was a remarkable change in temperature response, with an enhanced capacity to germinate at temperatures below 14 °C and a bimodal response to temperature. This presumably reflects seed polymorphism, within the Sussex population, in terms of the temperature responses. In the Sussex climate (figure 3) such a response enhances germination in both the autumn and spring, and predictions suggest a greater frequency of seeds with the low temperature response in this population. The autumn and spring peaks of germination by the Sussex population (figure 3) are not shown by the native population.

The predicted spring peak of germination in Sussex with significant germination and seedling growth was observed (1987–1989) between February and May. Germination was also observed, to a lesser extent in October. In Cardiff, the germination peak of the native population is predicted to occur in August, however most germination is observed in September (1977–1979), with little germination observed at any other time (J. R. Etherington, unpublished data). In addition, a seed bank is detectable at both sites, although its longevity is unknown.

Over-wintering

The occurrence of polymorphism in seed germination responses to temperature, in the Sussex population, indicates genetic change, probably in response to selective forces. The presence of both high- and low-temperature forms also suggests that either the selection for only one temperature form is rather weak, or that genetic change is still occurring and that stability

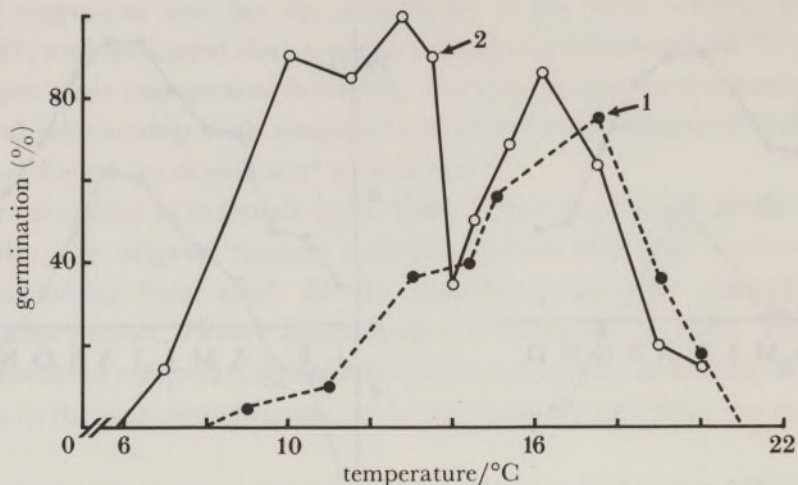


FIGURE 4. Temperature response of seed germination in Sussex (—○— and 1987) and Cardiff (---●--- and 1978) populations of *Umbilicus rupestris*; χ^2 analysis shows that population responses are significantly different ($p = 0.05$) below 14 °C. (1), Cardiff 1978; (2), Sussex, 1987.

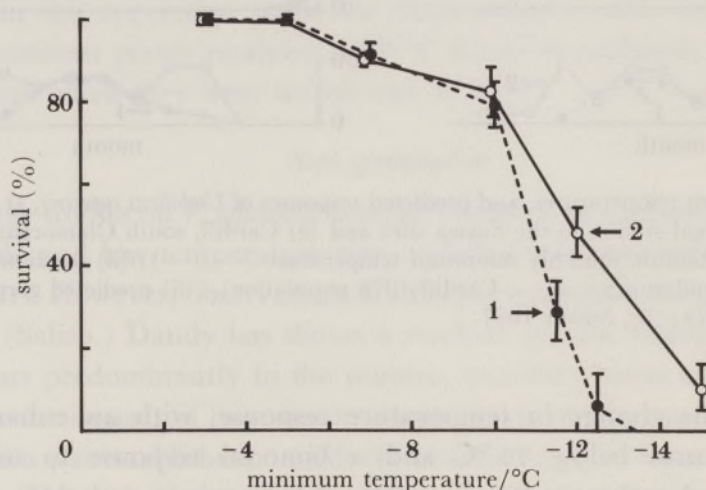


FIGURE 5. Low-temperature survival of populations of *Umbilicus rupestris* in Sussex (—○— and 1987) and Cardiff (---●--- and 1978). Means shown with 95% confidence limits. Confidence limits calculated from inverse sine transformations of percentage data. (1), Cardiff 1978; (2), Sussex 1987.

has not been reached. In either event the significance of the change may be realized at a later stage of the life cycle. Woodward & Jones (1984), for example, found that the winter survival of young plants of *Digitalis purpurea* and *Eupatorium cannabinum* was positively correlated with plant size at the onset of winter. Plants that were small, either through late germination, or growth in high plant densities and marked competition, were killed more readily by winter frosts. As a result of these observations it was decided to investigate the low-temperature tolerance of *U. rupestris*, with the specific aim of detecting any changes in low-temperature tolerance at the Sussex site.

Young plants of *U. rupestris* (four to eight leaf stage) were collected intact with soil medium in January, from Cardiff in 1978 and Sussex in 1987. Their tolerance of sub-freezing temperatures was tested by placing the young plants, in soil, in a deep-freeze and cooling them to different temperatures. The plants were then maintained at the selected temperature for

1 h, removed from the deep-freeze and allowed to recover at a mean temperature between 3 and 9 °C (in an unheated greenhouse during February). Mortality was scored after two weeks (figure 5).

The low temperature tolerances of the Cardiff and Sussex populations differ markedly below -10 °C, with greater tolerance being observed in the Sussex population. A consequence of this difference in tolerance is that, in Sussex, the Sussex population is predicted to show lower winter mortality (figure 3) than the Cardiff population. For 1987, the Cardiff population is predicted to become extinct on the basis of nearby meteorological station records (figure 3). *In situ* observations at the Sussex site showed a minimum temperature of -13 °C on 10 February 1987. Subsequent observations indicated greater mortality of small, autumn-germinating seedlings (cotyledons plus one or two leaves), than larger, spring-germinating seedlings (six to eight leaves). This observation indicates that seedlings emerging in April and May have a greater probability of surviving their first winter, than seedlings emerging in September and October.

6. DISCUSSION

The long-term trials discussed here indicate that some stages of the plant life cycle may show rapid genetic change in their tolerances to low temperature. For *U. rupestris*, transplanting the species to a cooler winter climate has led to increased tolerance of sub-freezing temperatures. Temperatures that have been observed to kill *U. rupestris* (-12 °C, January 1979 in Caerphilly, mid-Glamorgan) can now be endured, to about a 50% tolerance by the Sussex population (figure 5). Both populations had the same origin (areas of Cardiff, south-Glamorgan) but the Sussex population had a period of nine years in which to evolve. The mechanism by which tolerance has evolved is not certain, although it appears to be one consequence of a change in the low-temperature response of seed germination (figure 4). The Sussex population is polymorphic in the temperature response of seed germination. This feature leads to significant increases in spring germination in comparison with the Cardiff donor population. Seedlings that develop during the spring are larger than those that develop in autumn, and have been observed, in the field, to be more frost tolerant.

The explanation does not end at this point because a significant problem for seedlings of *U. rupestris* that remain summergreen (unlike the summer deciduous reproductive individuals) is the need to endure summer drought in the small volumes of soil of their native, or cultivated habitat on walls and cliffs. Investigations on the photosynthetic physiology of *U. rupestris* (Daniel *et al.* 1984; 1985) show that the species is able to switch to crassulacean acid metabolism (CAM) during drought. In *U. rupestris*, induced CAM has the classic property of low stomatal conductance during the photoperiod, with a higher conductance at night (Neales 1975). Unlike obligate CAM species (Neales 1975) and many other species with facultative CAM (Winter *et al.* 1978), *U. rupestris* shows no net CO₂ fixation during the night (Daniel *et al.* 1984; 1985). This property is known as CAM-idling and has been observed in other genera, such as *Peperomia* and *Pereskia* (Hanscom & Ting 1978; Rayder & Ting 1981; Ting & Rayder 1982).

The lack of significant CO₂ fixation in *U. rupestris* following the induction of CAM-idling led Daniel *et al.* (1985) to propose that the primary function of this physiological change was to endure periods of drought. The evolutionary trends seen for *U. rupestris* lends credence to this view. In the drier climate of Sussex (15% less precipitation in the May to August period than Cardiff, from Meteorological Office, Monthly weather reports 1978-1987), summer drought

may be a severe problem, particularly in drier years, for the survival of small seedlings in small volumes of soil. *U. rupestris* appears to be particularly drought tolerant, easily enduring leaf water potentials of -3 MPa (F. I. Woodward, unpublished observations (in controlled environment)). Few other wall species in Sussex (e.g. *Geranium robertianum*, *Cymbalaria muralis*) appear capable of enduring such drought, so that competition is not severe.

In the damper climate of South Wales, cliffs and walls may be wet all through the summer, perhaps with occasional short periods of drought, and so a competitive suite of species may exist through the summer. In such a climate, with a milder winter (figure 3) late-summer and autumn germination may prove an effective method of avoiding competition during the typical growing season between March and August.

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Discussion

G. E. FOGG (*Marine Science Laboratories, Gwynedd, U.K.*). It is worth recalling that some of the earliest work in this field was done by Joseph Hooker when he accompanied James Clark Ross on the Erebus and Terror voyage of 1839–43 to the Antarctic. He studied plant distribution in relation to latitude by using the ratio of number of species to numbers of familiar represented as an index. During a landing on an island off the tip of the Antarctic Peninsula he noted that the delicate green alga *Prasiola* flourished equally with coriaceous lichens and concluded that cold hardiness did not depend on mechanical toughness.

U. HEBER (*Institute of Botany and Pharmaceutical Biology, University of Würzburg, F.R.G.*). Would it be possible for Dr Woodward to comment on how far to the north the range for profitable planting of a crop could be extended if cold tolerance of the plants could be increased by 1 °C?

F. I. WOODWARD. For crop plants such as maize, which must endure periods of limiting low temperatures during the period of growth, a 1 °C increase in cold tolerance could enhance the spread of cultivation by as much as 150–200 km, in a poleward direction. This assumes that soil nutrients and water supply are not limiting to growth.