Tree Lines [and Discussion]

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Tree lines

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Trees do not generally grow in places where the mean temperature of the warmest month is less than about 10 °C. At their limit, trees are often short and crooked, the condition known as *krummholz*; and the transition from tall forest to dwarf shrubby vegetation is often abrupt, forming a distinct tree line.

Tree lines fluctuate with climatic change. There is compelling evidence to suggest that they shift to higher elevations and higher latitudes in warmer periods. In northern Europe, they were about 200 m higher in the Boreal period when the temperature is believed to have been 2 °C warmer than now. Controlled-environment studies and tree-ring evidence also point to considerable sensitivity of growth at the tree line to fluctuations in the summer temperature.

Forest vegetation differs aerodynamically from dwarf vegetation in being aerodynamically rough. Consequently, the temperatures of above-ground tissues are closely coupled to temperatures of the air. In contrast, shorter vegetation experiences tissue temperatures and microclimates that depend substantially on other climato-logical variables, notably radiation and wind speed. Short vegetation is, on average, warmer than the air; this is the main reason why dwarf shrubs can succeed in cold climates where trees fail to grow and reproduce.

Water stress commonly occurs in late winter and early spring when soil water is frozen. The foliage of trees at the tree line displays an inability to restrict water loss, either because the epidermis is damaged by abrasion or because the cuticle does not properly develop in the reduced growing season. Consequently, the longevity of leaves is reduced. Winter damage to trees is also likely as a result of gales and the deposition of ice in the canopy, both of which break branches and may contribute to the generally misshapen form of the crown.

1. Climate and the life forms of plants

One of the most notable features of the distribution of plants over the earth's surface is the correlation between life forms and climate. Early botanists seem to have enjoyed collecting data on the life forms to be found in different climatic zones. Raunkiaer (1909) devised a system of botanical classification, based on the height of the perennating organs above the ground. He pointed out that any stand of vegetation contains a spectrum of life forms; that the humid tropics contain a particularly broad spectrum, but that this spectrum becomes progressively narrower towards colder or dryer climates. Trees (known as phanaerophytes in Raunkiaer's scheme) are especially unsuccessful in cold places.

The tendency of vegetation to become shorter in colder places is evident in any mountain region. Local amelioration of the mountain climate, as produced naturally by topographic shelter or experimentally by building stone walls, leads to colonization by taller plant species (Whitehead 1959). Moreover, many individual species that are tall at low altitude occur as short forms at higher altitudes. That the dwarfness observed in such species at high altitude

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is the product of evolution, and not just the consequence of repeated dying back has been illustrated by transplanting individuals from the uplands to gardens at low altitude (Clausen *et al.* 1948; Grant & Hunter 1962). There must be distinct advantages in being short, or the dwarf character would not be fixed by natural selection.

2. Tree lines

The most conspicuous tall–short transition in the vegetation of mountainous regions is the tree line, where trees give way to dwarf shrubs. The general appearance of trees at their altitudinal limit is remarkably similar in different parts of the world, irrespective of whether the species is a gymnosperm or an angiosperm. Most of the tree species that occur at the tree line show characteristic 'deformed' growth, with crooked and decurrent stems (see, for example, Norton & Schonenberger 1984). The German word for these deformed tress is *krummholz*, though some authors may prefer to reserve this word for individuals that are definitely of a dwarf race, such as *Pinus mugo* Turra var. *prostrata* (Holtmeier 1981). Generally, without embarking on a prolonged programme of research, it is impossible to tell if a particular individual is a genetic dwarf rather than a tree that has merely been stunted by periodic damage caused by snow, ice, wind and desiccation.

The altitude of the tree line is quite variable geographically, but everywhere coincides approximately with the 10 °C summer isotherm (Daubenmire 1954; Wardle 1965, 1971; Grace 1977). The same generalization has been made for the latitudinal tree line (Mikola 1962; Kullman 1979). In both cases, however, local variations in the altitude of the tree line can be attributed to shelter from the wind and variations in aspect in relation to the solar beam (Kullman 1979; Piussi & Schneider 1985).

3. Past fluctuations in the tree line

Information about fluctuations in the tree line comes from various sources. In central Scotland, where the tree line is now at an elevation of about 600 m, Pears (1968) dated tree-stumps found in the peat above the present-day limit of trees. From this, it seems the tree line was at 800 m in the Boreal period (5000–9000 years ago). Similar observations in Norway and central Sweden also suggest that the tree line has declined by 200 m in the period from about 8600 years ago to the present day (Küllman 1988). It is thought that the decline was brought about by the deteriorating climate, with cooler summers, wetter and perhaps windier weather. Some idea of the extent to which the tree line may have been influenced by climatic change over the past few thousand years may be obtained by combining Kullman's data with the probable trends in temperature that have been inferred independently by Lamb (1977). Lamb's temperature curve was obtained mainly from a consideration of the pollen zones. The pollen record of the post-glacial period shows a thermal maximum about 6000 years ago, when, over much of Britain, warmth-loving species like hazel and lime were frequent, according to the pollen record. The summer temperature then is believed to have been about 2 °C warmer than now.

The data indeed show a correlation between the altitudinal limit of trees and the 'pollen' temperature, suggesting that the tree line migrates by about 100 m for every degree change in temperature (figure 1). There are, however, some notable anomalies in figure 1: the tree line

seems to have been lower than expected in the period just before 6000 years BP. This indication may of course be the result of poor sampling or poor preservation in the peat. On the other hand, it may be a real phenomenon, caused by the influence of an unknown variable or a catastrophe.
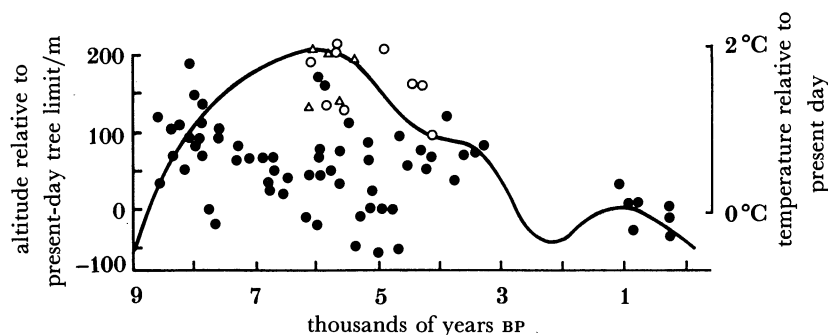

FIGURE 1. Past fluctuations in the elevation of the tree line inferred from radiocarbon dating of tree stumps found in the peat above the present-day tree line (Kullman 1988). Symbols represent different species; ●, *Pinus sylvestris* L.; ○, *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman; △, *Alnus incana* (L.) Moench. The smooth curve and the right-hand axis show the likely temperature trends over the same period, based on Lamb (1977).

Kullman (1979) reviews the considerable Scandinavian literature on the location of the tree line in the 20th century. He also presents new data obtained from the age structure of present-day populations of trees. Before 1930, when the summer temperatures were rather low, the tree line was in a phase of retreat. However, between 1933 and 1939 there was a succession of warmer-than-average summers, and *Betula pubescens* ssp. *tortuosa* regenerated at much higher altitude than before. Kullman (1979) argues that the tree line is determined by the summer temperature acting on germination and seedling establishment, possibly influenced by the duration of snow cover.

4. TEMPERATURE AND TREE GROWTH

We have seen how the fluctuations in the tree line seem to be correlated more strongly with temperature than with any other variable. It is desirable to examine data from other sources, to see how sensitive the growth of trees is to changes in temperature. Two species are considered here.

Scots pine, *Pinus sylvestris* L., is a widely distributed tree, native from northern Norway to southern Spain, and extending across Europe from Scotland in the west to the Pacific Ocean in the east (Carlisle & Brown 1968).

Information about its sensitivity to climatic change comes from several sources. It has attracted more attention than other species perhaps because of its status as a native tree and also because of its wide distribution. Thus measurements of growth increments have been made on cores taken from mature stems (Hustich 1947; Mikola 1962; Schweingruber *et al.* 1979, Hughes *et al.* 1984). Mikola's trees were growing near the latitudinal limit in Finland. Kullman (1981) has examined the temperature dependency of regeneration at the climatic limit in Sweden. Others have measured growth directly in the field or on young plants grown in controlled environments (Jensen & Gatherum 1965; White 1974; Juntilla 1986).

Of the work on tree rings, that of Mikola (1962) enables a simple relation to be made between annual increment and temperature. This has been done after obtaining a linear regression between July temperature and growth: the relation is apparently linear over the

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range of temperatures (9–16 °C) occurring in Mikola's study and the correlation coefficient is quite high ($r = 0.8$). By using this relation (figure 2) it seems that growth can be expected to be nil at 8 °C and thereafter to increase rapidly with temperature.
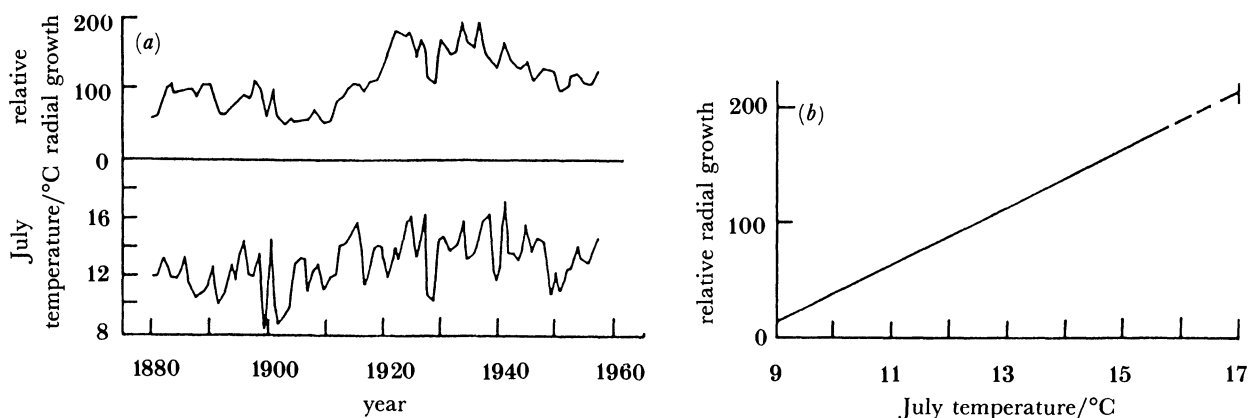

Figure 2. (a) Fluctuations in the radial growth of *Pinus sylvestris* near the latitudinal tree line in Finland and corresponding July temperatures (Mikola 1962). (b) Linear regression derived from the data.

There are many similarities between the *Pinus sylvestris* tree line and tree lines in other places. For example, in New Zealand, radial growth of *Nothofagus solandri* (Hook. f.) Oerst. was progressively more correlated with summer temperature as the tree line was approached (Norton 1984).

Tree rings represent a useful archive of information about past productivity, although the dry matter production of the tree obviously depends on the extension growth as well as the height growth. Moreover, it is not only the width but also the density of the wood formed in the radial increment that is influenced by the climate (Schweingruber *et al.* 1979; Hughes *et al.* 1984). Despite the difficulty in interpreting radial increments in the absence of associated data on wood density and height, it is noteworthy that Mikola's data from the tree rings of *Pinus sylvestris* (figure 2) are consistent with the recent data obtained from controlled environment work on growth of the same species (Juntilla 1986). Juntilla's data lead us to expect no growth at all at 7 °C and thereafter a nearly linear relation between temperature and growth in the range normally encountered at the tree line.

In Britain, the tree most often planted to high altitude is Sitka spruce, *Picea sitchensis* (Bong.) Carr., a native of North America, where it occurs along a coastal fringe in a markedly oceanic climate.

Its planting at a range of altitudes in northern Britain provides an opportunity to assess the influence of a cold climate on growth, although it must be remembered that variables other than temperature change with altitude. Several investigators have assessed its performance in relation to altitude and site (Malcolm & Studholme 1972; Mayhead 1973; Worrell 1987). The forester is able to estimate the future yield many years before the harvest is taken from a knowledge of the dimensions of the trees and the age of the plantation. By using Forestry Commission tables, the general yield class (GYC) may be found, this being the volume of timber that the plantation is expected to produce in cubic metres per hectare† per year, averaged over the rotation of the crop.

Worrell (1987) examined the variation in GYC and elevation at 18 sites in Scotland, selecting
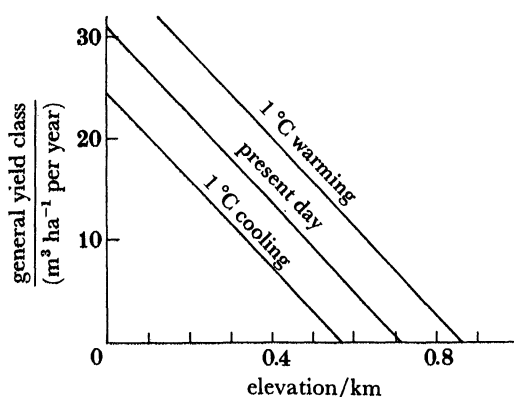
† 1 hectare = 10^4 m².

FIGURE 3. The average decline in productivity of *Picea sitchensis* in Scotland, based on field data of Worrell (1987). The sensitivity of this relation to changes in temperature has been estimated on the assumption that the decline with altitude is entirely caused by a decline in temperature ($7\ °C\ km^{-1}$ was taken as the temperature lapse rate).

plantations that were 20–30 years old. The average regression line suggested that plantations will produce $31\ m^3\ ha^{-1}$ per year at sea level, declining by 4.3 of these units for every 100 m of elevation (figure 3).

Temperature, radiation, rainfall and wind speed are all correlated with altitude. Moreover, soils deteriorate with increasing altitude. Thus several variables are likely to have a direct or indirect effect on growth, but temperature probably has the overriding influence (Grace 1987; Grace & Unsworth 1988). If this is assumed to be the case, and knowing that temperature declines by about $7\ °C$ per km of altitude, it becomes possible to show how the GYC might change as a result of a small climatic warming or cooling, or how the tree line might fluctuate in response to a change in temperature (figure 3). According to this, a fairly average site now expected to yield $14\ m^3\ ha^{-1}$ per year at an elevation of 400 m will produce $20\ m^3\ ha^{-1}$ per year of timber if the temperature rises by only $1\ °C$, and the tree line will rise by rather more than the 100 m estimated from figure 1.

5. INFLUENCE OF WIND AND RADIATION ON MERISTEM TEMPERATURES

Temperature operates at several points in the life cycle of a woody perennial. Leaf primordia are formed at the shoot apices throughout much of the growing season, and the number of primordia that enter the winter enclosed in the resting bud seems to depend quite closely on the accumulated temperature (Sucoff 1971). In the spring, the onset of growth occurs when a certain temperature sum has been reached. Thereafter, the extension of the shoot and leaves occurs at a rate that depends on temperature. As a first approximation, the photosynthetic production is the product of the quantity of leaf material thus formed and its leaf-specific photosynthetic activity. The latter is also a strong function of temperature, declining from an optimum, which, in north-temperate conifers is around $15\ °C$, to a low value at freezing temperatures (Neilson *et al.* 1972).

The temperatures of leaves and meristems are not the same as that of the air. Recently, meristem temperatures of tall and short vegetation were recorded at an altitudinal transect in the Cairngorm mountains (Wilson *et al.* 1987). The hypothesis under examination here was that dwarf vegetation is aerodynamically smoother than tall vegetation, and thus dissipates

heat less rapidly and, whenever the radiation balance is positive, becomes substantially warmer than tall vegetation.

At the lowest altitude, where the vegetation is tall *Pinus sylvestris* forest, the temperatures measured in the meristems with fine thermocouples were on average just a few degrees warmer than those of the air by day (figure 4). By night, there was scarcely any difference between meristem and air temperatures. In contrast, for the short vegetation types the temperatures recorded at the meristems in the day were considerably higher than those of the air (figure 4).
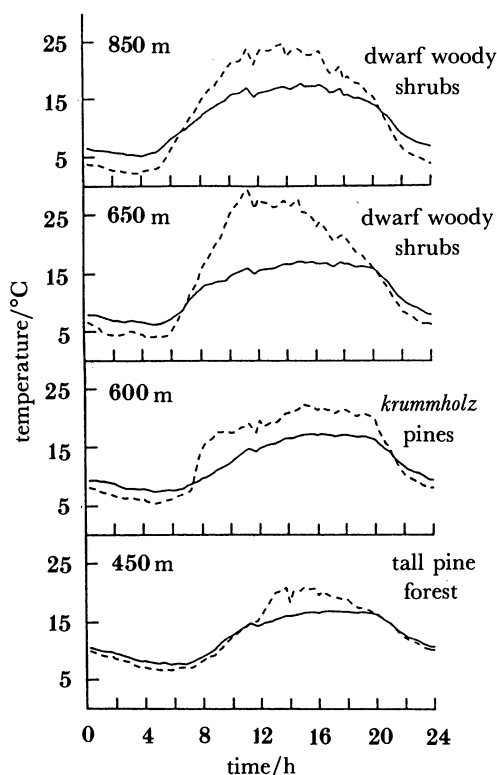

FIGURE 4. Mean diurnal trends of temperature in the period 27 May to 30 June 1985 at four sites near the tree line in the Cairngorm mountains of Scotland. Solid lines are air temperatures, broken lines are the temperatures of terminal meristems (Wilson *et al.* 1987).

To model the influence of wind and radiation on meristem temperatures it was assumed that heat transfer from terminal meristems to the atmosphere occurs via two diffusive resistances in parallel, representing forced and free convection (Grace *et al.* 1989). The term for forced convection depends on the wind speed and the vegetational height, and these were calculated using relations that have been widely used in classical micrometeorology. The free convection term uses the Grashof number, calculated iteratively from the surface temperature and the diameters of the shoots (Grace *et al.* 1989).

The model shows how the temperature difference between meristems and the air depends on radiation, wind speed and the height of the vegetation (figure 5). According to the model, the meristems of short vegetation respond very strongly to any increases in radiation and any reductions in wind speed. For tall trees, the influence of radiation and wind speed are much less. However, tree lines increase in altitude by regeneration above the existing tree line, and
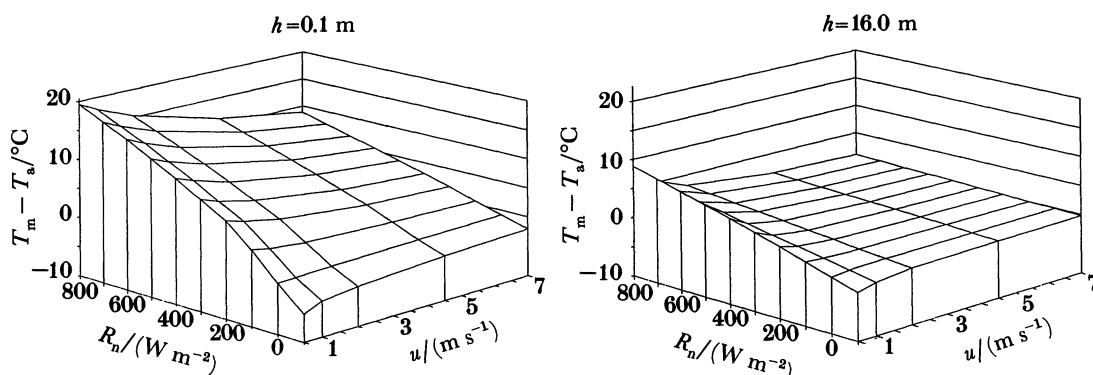
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$h=0.1$ m $h=16.0$ m

FIGURE 5. Influence of wind u and net radiation R_n on the meristem–air temperature difference ($T_m - T_a$), calculated from a model incorporating calculations of heat and mass transfer (Grace *et al.* 1989). The vegetation height h is set for dwarf shrubs and tall trees.

the exercise shows very clearly how a southerly aspect or shelter from the wind might confer a large thermal advantage on a population of seedlings.

The data and the model also provide a possible explanation of why dwarf shrubs thrive above the tree line, where trees will not grow. It is not necessary to postulate that these two life forms have different physiological responses to (tissue) temperature. It appears that dwarfness *per se* implies a reduction in turbulent transfer because of the scaling of turbulence by the roughness elements of the canopy. Thus surface temperatures are considerably dependent on radiation and wind speed. In a cold climate the elevated tissue temperature enables survival and reproduction.

6. WEATHER VARIABLES AND GAS EXCHANGE

Spruce trees growing at high altitude in the Austrian Alps displayed much lower rates of net photosynthesis than those at lower altitude (Pisek & Winkler 1958). Even in the summer the rates at high altitude were 30–50 % less than those at high altitude. In the winter, the period during which the net photosynthesis was zero or negative was only five weeks in the case of trees at 600 m, whereas near the tree line, at 1840 m, the corresponding period was nearly five months (Pisek & Winkler 1958). The loss of photosynthetic capacity appeared to be related to the minimum daily temperatures. Since the work of Pisek & Winkler, the effect of low temperature on photosynthesis has become more thoroughly understood. When plants are exposed to low temperatures their quantum yield declines mainly as a result of damage at photosystem 2 involving the loss of a protein electron acceptor, Q_b (Öquist 1983; Evans 1987). This protein turns over very rapidly in normal, warmer, conditions. The phenomenon whereby quantum efficiency is lost until such time as the leaves are warmed and the photosystem becomes fully operational, is known as photoinhibition. In northern coniferous forests photoinhibition occurs for much of the winter and the rates of photosynthesis are rather low as a result. During prolonged mild spells recovery may occur, and substantial rates of photosynthesis may be possible (though never as much as in the summer because the irradiance is much lower). It would appear very likely that the incidence of photoinhibition is much greater at the tree line, and if so, one might expect a measurable effect of winter temperatures on growth.

Recent work generally confirms the findings of Pisek & Winkler, whose pioneering studies preceded development of the infrared gas analyser (see, for example, Benecke & Havrand 1980). Small differences in microclimate, such as occur between north- and south-facing slopes have been found to exert a surprisingly large influence on rates of photosynthesis in *Pinus mugo* and *Larix decidua* Miller (Hasler 1982, 1984).

7. Water relations at the tree line

The phenomenon of frost drought is widespread in the alpine tree line (Tranquillini 1963, 1979; Hansen & Klikoff 1972; Marchand & Chabot 1978). Frost drought is evident as browning of needles in the spring, particularly on the windward side of the canopy, leading to a large reduction in the leaf area. Studies of the transpiration of detached shoots or needles in their winter condition show that those taken from the tree-line population display an impaired ability to restrict water loss (Tranquillini 1979, 1982; Baig & Tranquillini 1976, 1980) Thus, when the water in the soil and stem is frozen and the sun shining on the foliage, the water potential of the needles declines over days and weeks to a lethal point. It is likely that freezing temperatures are not an absolute requirement, as cold (liquid) water is considerably more viscous than water at summer temperatures. Frost drought is not restricted to trees: it also occurs in dwarf woody shrubs (Watson *et al.* 1966).

There are some tree lines in the world where the winters are mild and the soil is seldom at freezing temperatures. At the Snowy Mountains of southeastern Australia the main cause of leaf mortality in *Eucalyptus pauciflora* Sieb. ex Spreng is not frost drought but frost killing of unhardened foliage (Slatyer 1976).

Wardel (1971) and Tranquillini (1979) advance an ingenious explanation as to why the tree line is apparently determined by summer temperatures yet mortality is so obviously caused by frost drought occurring in the late winter and spring. The cuticle is supposed to grow in thickness as the season progresses and finally to 'ripen' to produce a suitable barrier to transpiration. This process of growth and ripening requires a suitably long and warm summer, so that at high elevation the needles enter the winter with an imperfectly developed cuticle. Subsequently, when the ground is frozen and aerial conditions favour transpiration, water stress occurs in the foliage.

Unfortunately, the development of conifer cuticle has so far been studied only with the light microscope. Such studies, in which the cuticular lipids have been stained with one of the Sudan stains, suggest that the cuticle does indeed increase in thickness over the entire growing season (Lange & Schulze 1966), and that cuticles at high altitude are thinner than those from valley populations (Baig & Tranquillini 1976, 1980). In parallel studies, the transpiration rates of the high-altitude foliage were shown to exceed those from the valley, and it appears that the apparent cuticular resistance, like the cuticle thickness, does increase progressively over the growing season (Sowell *et al.* 1982). Whether this increase in resistance is caused by development of cuticle, as claimed, is open to question as cuticle is difficult to measure with the light microscope and sometimes its thickness scarcely exceeds the optical resolution of the instrument. Moreover, modern views of cuticle structure suggest that the diffusive resistance is not particularly dependent on the thickness of the cuticle, but more on the ultrastructure and lipid chemistry (Schönherr 1982).

In samples of *Pinus sylvestris* from different altitudes near the tree line in Scotland, no difference in cuticle thickness could be detected, even though the needles from the high altitude

did display increased surface conductance (J. Grace, unpublished data). It may well be that the increased conductance was caused by the failure of the stomata to shut completely. It is known that stomatal function in grasses is impaired by physical damage to the epidermis caused by wind and abrasion (Grace 1974; Pitcairn *et al.* 1986). At the tree line physical damage is likely to be caused by blown particles of ice and soil. A similar suggestion has been made recently by Hadley & Smith (1986). The distribution of needle mortality within the canopy is certainly consistent with the view that wind abrasion, or abrasion by wind-dispersed particles, has an important part to play in the process.

Isolated or scattered trees and open stands may be particularly susceptible to frost drought because the soil is more prone to radiative heat exchange with the sky and so water in the soil profile may be frozen more often than where the canopy is closed. Perhaps this is one of the reasons why the tree line is often so abrupt.

8. Other adverse effects of the weather at high altitudes

Mountain and upland environments are often described as exposed. A satisfactory definition of exposure has never been made, but perhaps the closest one can come to it is through the concept of coupling. This term was proposed by Monteith (1981), who defined it in terms of an electrical analogy (resistances and capacitors) to link the plant environment with the atmospheric environment. Later, McNaughton & Jarvis (1983) introduced the omega factor, ranging between nought and unity, to express the extent to which the regional climate is coupled with the climate that impinges at the surface of plants.

Mountain forests, more than any other type of vegetation, are closely coupled to the atmosphere. They are aerodynamically rough, and they occur in an aerodynamically rough landscape. As a consequence, they experience a climate that is relatively little-affected by processes occurring in the planetary boundary layer at a local scale, and more akin to that of the regional circulation.

In the context of an oceanic climate, this means that wind speeds are much higher than in a lowland environment, the amplitude of the diurnal temperature cycle is rather low, and inputs of water and chemicals from rain and cloud are high.

In the British Isles, the mean wind speeds at 600 m are in the range 6–8 m s^{-1}, and the frequency of gales is very high. Mechanical excitation of plants by wind directly influences the partitioning of assimilates between radial and height growth, leading to an alteration in the form of the stem (Telewski & Jaffe 1981). High wind speeds cause the breakage of young shoots shortly after budbreak; this is one of the main causes of the windshaping of trees (Allen 1985). In the winter, the formation of rime ice on the foliage is a major cause of structural failure, leading to misshapen crowns. Given the conditions for rime formation, the deposition rate of cloud water to form further rime is a linear function of wind speed (Foster 1988). Catastrophic gales cause uprooting of trees, although plantations seem to be much more vulnerable to this than native forests.

A recent concern regarding mountain forests is the enhanced deposition of pollutant materials (Fowler *et al.*, this symposium). In the British Isles, a major concern is the chemical content of cloud water and snow in upland regions. Compared with normal rain, the water in upland rain and in the deposited cloud water contains a several-fold enhancement in chemical species (Unsworth & Fowler 1988).

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Discussion

P. G. JARVIS (*Department of Forestry and Natural Resources, University of Edinburgh, U.K.*). Models of needle–air temperature differences in tall trees seem fairly adequate in predicting that the difference is generally close to zero and does not deviate very much (say 0.5 °C), even at low wind speeds. My question relates to the failure of Dr Grace's model adequately to predict small

temperature differences between the meristems and air. It would seem that the model is inadequate in some respect because it predicts a very much larger temperature difference. Does Dr Grace have any explanation for this?

J. GRACE. The very small temperature differences Professor Jarvis mentions are for individual needles. In shoots, needles are grouped tightly around the meristems and the shoot tip itself has a diameter of about 5 mm, much more than for needles. The failure of the model occurs at low wind speeds only, and I think this is a consequence of the flow régime at that wind speed. Vertical motion of the air is not detected by the cup anemometers, and often they stall. Thus the air movements around the meristems were probably higher than the wind speed data suggest.

N. HUTCHINGS (*Macaulay Land Use Research Institute, U.K.*). Where low temperature limits growth, a prostrate growth form is an advantage. In hot climates, a similar elevation of meristem temperature over that of the air could push that meristem beyond its upper tolerance level. Does this mean that taller vegetation is at an advantage in these areas?

J. GRACE. I have not looked into this matter, but it would be interesting to do so. The problem is non-trivial because in hot climates it is necessary to take into account the water balance of the plant and consequent changes in stomatal resistance, which may feed back into leaf and meristem temperature.

J. L. MONTEITH, F.R.S. (*International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India*). Dr Grace has told us about changes of air and meristem temperature with increasing altitude, but what are the associated changes below ground? Does the soil get shallower so that the roots have less access to water and nutrients? Could this be a major cause of stunted growth?

J. GRACE. Soils do generally become shallower with increasing altitude and this site is no exception. The soils are peaty, over a terrain of boulders. I have sampled needles for foliar analysis with the intention of looking at the question, but the analysis has not yet been made.

W. J. SHUTTLEWORTH (*NERC Institute of Hydrology, Wallingford, U.K.*). Dr Grace mentioned tree lines are often dictated by sylvicultural practice in the U.K.; is this a matter of accessibility or economics? How is this likely to alter in response to climate warming?

J. GRACE. The practical limit of planting is dictated by availability of land and by the likelihood of wind damage. The forest industry has not responded noticeably to the prospect of climatic warming.

D. FOWLER (*NERC Institute of Terrestrial Ecology, Penicuik, U.K.*). During this presentation Dr Grace showed that low winter temperatures were associated with reduced growth during the following summer. As unusually high winter temperatures may lead to enhanced respiratory carbohydrate loss does he believe that low winter temperature invariably leads to reduced summer growth?

J. GRACE. All north temperate trees require a chilling treatment in winter. One fear about climatic warming is that they will not get this. Bud break in the spring will then be greatly delayed. Dr Fowler's point, however, is about carbohydrates and carbon balance. For conifers growing in a northern environment. I would expect that higher temperatures would lead to higher rates of winter photosynthesis (less photoinhibition), which would more than offset the effect he mentions. This sort of thing is shown in the classic paper by Pisek & Winkler (1958).

J. CORLETT (*Department of Physiology & Environmental Science, University of Nottingham, U.K.*). How did Dr Grace arrive at a value of one for meristem area index (MAI)? How sensitive is the model to changes in MAI?

J. GRACE. The meristem area index (MAI) is introduced so that measurements made on groups of meristems can be referred to a unit of ground area, in much the same way as leaf area index (LAI) is used to 'scale up' stomatal conductance measurements made with a porometer. In shoots of Scots pine, the terminal meristems and the needles grouped around them constitute about a quarter of the silhouette area of the entire shoot. Old stands of Scots pine often have an LAI of about four, so I estimate an MAI of unity.

Varying MAI in the model affects the meristem temperature very little in the case of forest but very much for the dwarf shrubs.

J. THOMAS (*West Hall, Kew, U.K.*). A relation between the forest limit and the temperature of the warmest month would suggest that the warm month was needed to aid the process of reproduction on seedling germination. Does this not imply that the forest line could be greatly extended both northwards and upwards by forestry planting?

J. GRACE. I do not think it implies that at all.