

Evolutionary and Ecophysiological Responses of Mountain Plants to the Growing Season Environment

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I. SUMMARY

The responses of mountain plants to their environment are due to a complex mixture of genetic and environmental influences. There is evidence that some mountain plants have evolved in response to their particular altitudinal environment. Instances include the increased ability to fix CO_2 from lower than sea-level concentrations, use high irradiance levels more efficiently, photosynthesize and grow at lower temperatures, and have intrinsically lower growth rates than their lowland counterparts. However, despite such examples, there is also evidence that many of these features could occur in mountain plants without any genetic component. Whether such developmental plasticity has been selected for is difficult to ascertain. Reduced growth temperatures may cause increased amounts of enzymes, such as Rubisco, per unit leaf area, via the differential effect of temperature on growth and photosynthesis, with changes in leaf thickness and the ratio of mesophyll cell area to leaf area (R^{mes}) being of importance. This would result in increased mesophyll conductance, and hence efficiency of carbon uptake (ECU) and maximum rate of photosynthesis (A_{max}), which may cause an increased maximum stomatal conductance (g_{max}), under high irradiance conditions, via the control of stomatal density. The above scheme is far from proven but is certainly worthy of further investigation. The evidence for changes in the optimum temperature for photosynthesis (T_o) indicates that amounts of Rubisco and Fru- P_2 phosphate activity per unit leaf area are probably very important. Thus increased ECU and A_{max} , and reduced T_o , could all be explained by one scenario, the primal agent being the effect of low temperature on leaf development. The effect of temperature on growth and developmental processes is crucial.

Model simulations of canopy energy balance and CO_2 fixation indicate that canopy structure and leaf area index (LAI) strongly influence both photosynthetic rate (A) and the ratio of ^{13}C to ^{12}C ($\delta^{13}\text{C}$) in leaves. Whereas $\delta^{13}\text{C}$ measurements on expanded leaves provide a time integral of CO_2 discrimination during the photosynthetic life of the leaf, they also include some unknown $\delta^{13}\text{C}$ contribution from photosynthate exported or remobilized from other leaves and organs. It would be interesting, therefore, to investigate the $\delta^{13}\text{C}$ of leaves as they develop during the season. An additional problem is that any mutual shading by other leaves, and any periods of drought, will also influence the ratio of internal leaf to ambient CO_2 partial pressure (p_i/p_a) and therefore $\delta^{13}\text{C}$ (Farquhar *et al.*, 1982).

The model simulations, for just the period of peak irradiance during the day, indicate that the energy balance and gas exchange of a leaf are dependent on its aerodynamic coupling with other leaves in the plant canopy, and with the air at some reference height above the canopy. This degree of coupling must be incorporated when individual leaf measurements of gas

exchange are taken to indicate plant responses to environmental changes with altitude.

The predictions of canopy and leaf photosynthesis by the model have all been obtained with one A/c_i response, based on interpretations of the data of Körner and Diemer (1987). Therefore, tall trees and short herbs do not differ in terms of A , ECU or conductance (g) in the model. Yet this is clearly not so in the real world (e.g. Fitter and Hay, 1987); trees might be expected to exhibit lower A and g . However, Körner *et al.* (1988) showed that $\delta^{13}C$ trends with altitude were broadly similar for trees, shrubs and herbs, indicating that changes in A , ECU or g are closely linked, a feature worthy of further study.

Model simulations have indicated that leaf gas exchange and $\delta^{13}C$ are sensitive to both the expected trends in microclimate with altitude, and plant stature and LAI . There is a decrease in plant stature with altitude. This will cause an increase in stomatal conductance with altitude because the vapour pressure deficit of the air close to the leaves will tend to be lower due to the decreased boundary layer conductance. The poorly documented effects of temperature on stomatal conductance may prove significant and dependent on canopy stature and energy balance.

II. INTRODUCTION

A. Mountain Mesoclimates

Mountains (see Barry, 1981, for a discussion of the problem in defining mountains) cover about 20% of the land surface of the world (Barry, 1981), extending from Antarctica to the Arctic, throughout the east and west hemispheres and, therefore, through a wide range of climatic provinces. During the growing season, an examination of any mountain of reasonable altitudinal extent, will show a clear gradient of plant stature. There will also be a gradient in air temperature, with lower temperatures at higher altitudes. This phenomenon is striking for mountains which extend up to permanent snow.

This decline in temperature is a fundamental feature of all mountains and is due to the drop in atmospheric pressure (Pa) and air density ρ (kg m^{-3}) with altitude (Barry, 1981). The atmospheric pressure falls with altitude because of the monotonic fall in gravitational attraction towards the earth's surface. The atmospheric pressure P_z , at any altitude z (m), can be approximated by the following equation (from Jones, 1983):

$$P_z = \frac{101325}{e^{(z/29.3)(T_k)}} \quad (1)$$

where T_k is air temperature (K). Due to the higher virtual temperatures and

humidities in tropical regions, the equation underestimates P_z by about 1000–1500 Pa (Barry, 1981). The virtual temperature is the temperature at which dry air, at the same atmospheric pressure, is equally dense as the sample air.

The fall in air temperature with altitude occurs because a rising parcel of air expands as the atmospheric pressure decreases. Expansion is an endothermic process and heat for the process is extracted from the air itself, causing it to cool. If this cooling occurs at temperatures above the dew point of the air, the (dry) adiabatic lapse rate may be nearly 10°C km^{-1} . Should the air reach the dew point temperature, water vapour condensation occurs. This process of warming reduces the lapse rate to as little as $4\text{--}5^\circ\text{C km}^{-1}$ (Barry, 1981).

Altitudinal gradients will therefore be associated with a decline in air temperature, a decline which will be dependent on the temperature, the dew point temperature, the radiation load and local wind patterns. Despite all these possible influences, observed lapse rates of temperature decline for meteorological stations (from Müller, 1982) at a range of altitudes (Fig. 1), are rather similar for mountains from a wide geographical range. Water vapour pressure is strongly linked with temperature (Woodward and Sheehy, 1983), and shows similar trends with altitudes (Fig. 2), reflecting the reduced capacity of the air to hold water vapour as temperature declines. The absolute minimum temperature also declines with altitude (Fig. 3), at a similar rate to the mean annual temperature.

The generality of the temperature, or temperature related lapse rates (Figs 1, 2, 3) contrasts strongly with the altitudinal trends in precipitation (Fig. 4), where no two mountain ranges show the same trend. However, Lauscher (1976) has indicated that some global trends may be found. Over altitudinal gradients in which the air, at some altitude, becomes saturated, precipitation generally increases with altitude, as on equatorial, tropical and polar mountains. In contrast, precipitation appears to decrease with altitude on mountains in the middle latitudes. The non-linear relationship between precipitation and altitude for the Himalayas (Fig. 4) indicates the strong influence of the lowland monsoon climate to about 500 m. At higher altitudes, the cooler air holds less water and precipitation decreases. This simple view may vary between individual mountains through local variations in the patterns and strengths of the mountain winds.

Wind speed generally increases with altitude (Geiger, 1965; Grace, 1977), particularly on mountains of the middle and polar latitudes (Barry, 1981), but with marked local variations depending on wind-funnelling and shelter effects by adjacent mountains. On tropical and equatorial mountains, wind speed may change little or even decrease with altitude. The mean wind speed at 4250 m on Mt Jaya, Papua New Guinea is 2 m s^{-1} , while the mean wind speed is 23 m s^{-1} at 1915 m on Mt Washington, USA (Barry, 1981). The mean trend in wind speed is therefore strongly dependent on the strengths of the global wind belts. However, on any particular mountain there will be

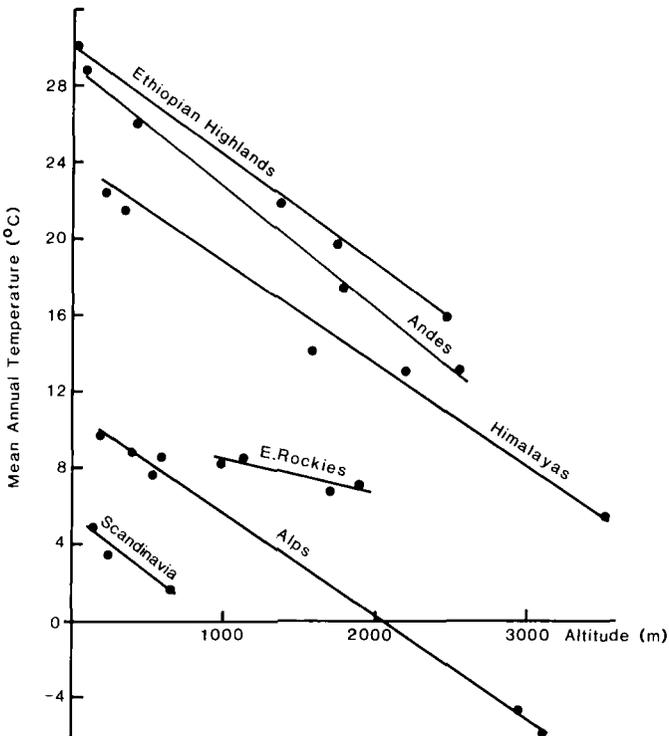


Fig. 1. Trends in mean annual temperature at meteorological stations located on six mountain ranges (from Müller, 1982).

considerable local variations in wind speed dependent on the radiation load, the occurrence of adjacent mountains and topographical variation.

The interaction between the lapse rate in temperature and vapour pressure, plus the characteristics of the lowland regional climate, leads to the complex altitudinal patterns of precipitation (Fig. 4). Associated with these interactions are variations in sunshine duration (Fig. 5). The Himalayas, with a lowland monsoon climate, and mountain ranges with a strong maritime influence such as Scandinavia or Scotland, show a decline in sunshine duration with altitude (Fig. 5; Müller, 1982). The drier continental ranges, such as the European Alps and the American Rockies, show little change in sunshine duration with altitude. Variation in cloudiness strongly influences the receipt of solar and long-wave radiation at ground level. Under both cloudless and cloudy skies, irradiance increases by about $10\% \text{ km}^{-1}$ (Barry, 1981), due to an altitudinal decline in atmospheric scattering and absorption of the solar beam, as atmospheric pressure and air density decrease.

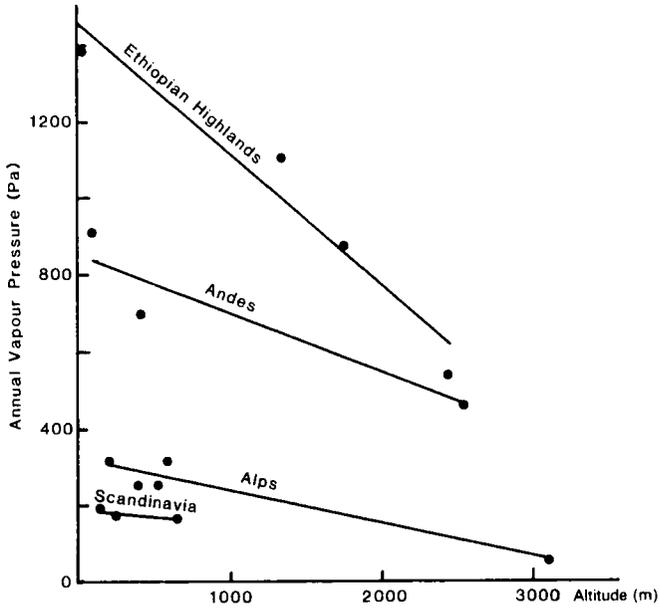


Fig. 2. Trends in the mean annual water vapour pressure (Müller, 1982).

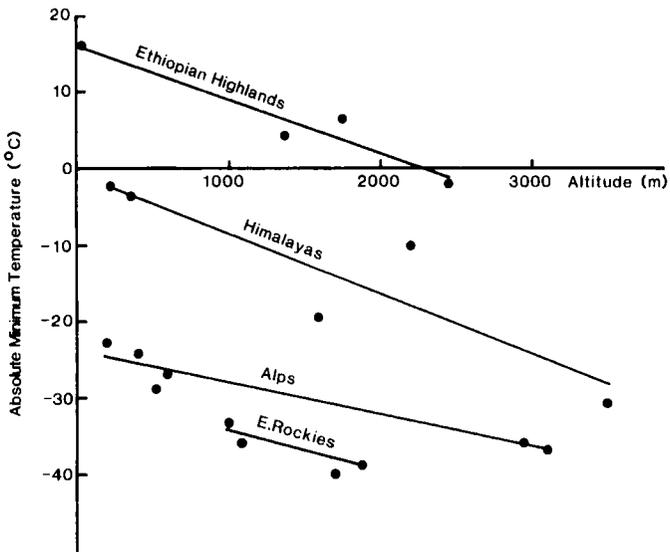


Fig. 3. Trends in the absolute minimum temperature (observed over 30 years) (Müller, 1982).

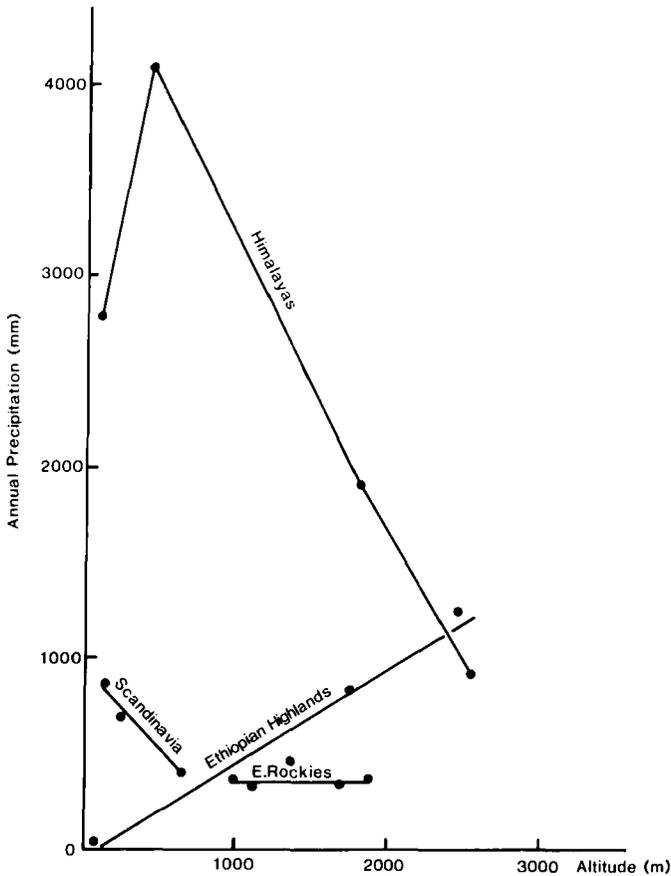


Fig. 4. Annual totals of precipitation along altitudinal gradients (Müller, 1982).

Associated with the increase in solar radiation is an increase in ultraviolet (UV) radiation with altitude. The rate of increase in UV is strongly dependent on cloud cover, but in the Austrian Alps, for example, the increase may be as great as $75\% \text{ km}^{-1}$ (Barry, 1981).

B. Plant Microclimates

Given the striking differences in some aspects of climate between different mountain ranges, it would be expected that vegetation structure and development also vary, negating any recognizable and repeatable altitudinal trends. However, a study of the range of vegetation heights with altitude (Fig. 6) indicates clear and repeatable reductions in height with altitude. The only

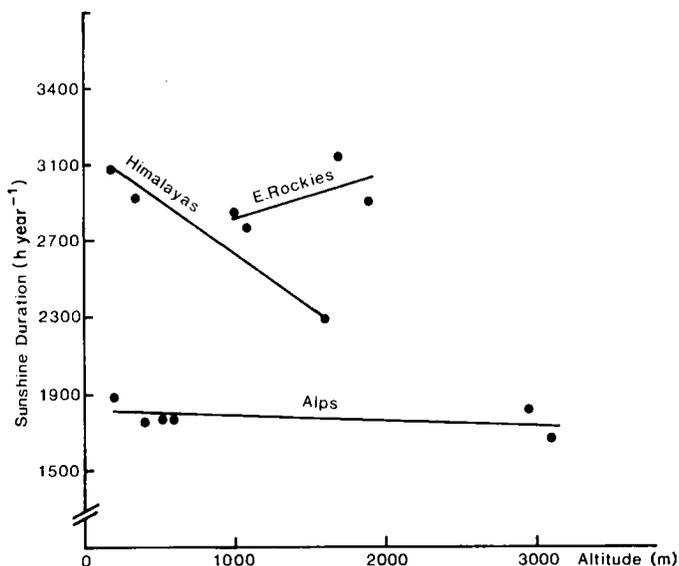


Fig. 5. Sunshine duration for three contrasting mountain ranges (Müller, 1982).

climatic trends which are equally repeatable are those of temperature (Figs 1 and 3) and vapour pressure (Fig. 2), the latter being a function of the former.

Many field observations throughout the world show that as plant height declines with altitude (Fig. 6), so the difference between leaf or canopy temperatures and air temperature increases (Salisbury and Spomer, 1964; Gates and Janke, 1966; Breckle, 1973; Larcher, 1975; Cernusca, 1976; Larcher and Wagner, 1976; Hedberg and Hedberg, 1979; Körner and Cochrane, 1983). This response is due to the direct relationship between the aerodynamic boundary layer conductance to sensible and latent heat transfer and plant height (Grace, 1977), and it can exert a strong influence on leaf temperature. For instance, Körner and Cochrane (1983) found that at an altitude of 2040 m (Australian Snowy Mountains) the leaves of small trees were at air temperature, but adjacent moss cushions were up to 30°C warmer than the air temperature.

Wilson *et al.* (1987) consider that the elevation of leaf and meristem temperatures above air temperatures is a crucial determinant of plant development on mountains. High leaf temperatures will occur only on days of high irradiance, but there will be no differences between leaf and air temperature on days of heavy cloud. Along an altitudinal gradient in the Cairngorm Mountains of Scotland, the lapse rate of air temperature, in sunny conditions, was observed to be 9°C km⁻¹, whereas the lapse rate of leaf temperature, from trees of *Pinus sylvestris* in the lowlands to dwarf-shrubs of *Arctostaphylos uva-ursi* and *Loiseleuria procumbens* in the uplands, was

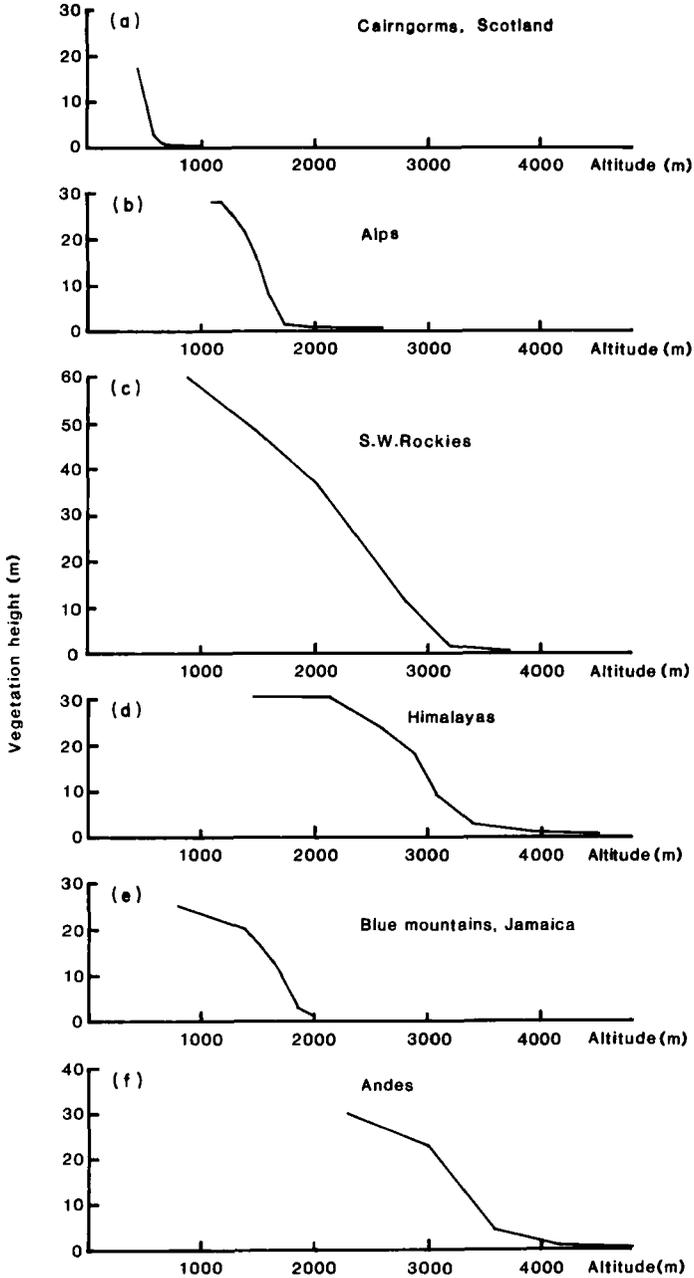


Fig. 6. Trends in vegetation height with altitude. (a) Personal observations; (b) from Cernusca (1976) and Tranquillini (1979); (c) from Barbour (1988); (d) from Osmaston (1922); (e) from J. Healey (pers. comm.); (f) from Beard (1955) and Vareschi (1970).

practically zero (Wilson *et al.*, 1987). This property of vegetation will maximize growth at high altitudes. Because height growth is genetically limited in many species, with dwarf ecotypes often occurring at high altitudes (e.g. Grant and Hunter, 1962; Grant and Mitton, 1977), vegetation cannot grow tall, which would permit higher boundary layer conductances and smaller leaf to air temperature differentials.

The temperature advantage of dwarf vegetation is only realized on days of high irradiance. On very cloudy days, leaf and air temperatures will be similar (Wilson *et al.*, 1987), and so the altitudinal gradient in cloudiness (approximately the inverse of sunshine hours: Fig. 5) will be a crude estimate of the temperature advantage. During nights of clear sky, dwarf vegetation will lose heat by radiation more rapidly than tall vegetation, so that low-temperature tolerance may be an increasing problem with increasing altitude (Larcher and Bauer, 1981; Rada *et al.*, 1985). Woodward *et al.* (1986) demonstrated that leaves of upland species in the Austrian Alps grew both day and night, and in both sunny and cloudy weather, with no measurable low-temperature threshold for growth. In contrast, lowland species, at the same altitude, grew more rapidly at high temperatures but possessed a noticeable low-temperature threshold for leaf growth (3–7°C), with little or no growth on very cloudy days or through the night.

The higher leaf temperatures in dwarf vegetation have a marked effect on photosynthetic rate. At high altitudes (2000–3400 m), for both dwarf trees (Carter and Smith, 1985; Hadley and Smith, 1987; Smith and Carter, 1988) and dwarf shrubs (Grabherr and Cernusca, 1977), the optimum temperature for leaf photosynthesis (T_o) at high irradiance ($> 600 \mu\text{mol m}^{-2} \text{s}^{-1}$) is in the region of 15–25°C, whereas air temperature is often 10°C less than the optimum. Leaf temperatures reach the optimum range for photosynthesis on days of high irradiance, maximizing the photosynthetic rate. However, Körner (1982) has shown that one severe cost of the dwarf life form of the sedge *Carex curvula*, is that the upper-canopy leaves frequently shade lower leaves, reducing the actual photosynthetic rate.

The length of the growing season decreases with altitude (Mooney and Billings, 1961). Any process which enhances the growing season effectiveness, such as by leaf temperature excesses over air temperature (Wilson *et al.*, 1987), will therefore maximize development. One consequence of incomplete leaf development is that immature leaves have incomplete cuticles. These cuticles are readily abraded by the wind and wind-borne particles during winter, leading to leaf desiccation and death (Tranquillini, 1979; Barclay and Crawford, 1982; Hadley and Smith, 1983, 1986; Richards and Bliss, 1986). In the American Rockies, at least, it is considered that the inability of leaves to develop a thick cuticle because of the shortness of the growing season is a crucial factor in determining the treeline (Hadley and Smith, 1986). However, it is also clear that many stages of the life-cycle of a plant are strongly

influenced by the mountain microclimate, with temperature playing a dominant role. Such population effects include vegetative growth and survival (Smith, 1981; Wardle, 1985; Graves and Taylor, 1986), seed germination and seed bank longevity (Miller and Cummins, 1987; Guariguata and Azocar, 1988), seedling emergence and survival (Barclay and Crawford, 1984; Woodward and Jones, 1984), winter survival (Larcher and Bauer, 1981; Larcher, 1983; Woodward and Jones, 1984; Goldstein *et al.*, 1985; Rada *et al.*, 1985; Woodward, 1987a), the frequencies of flower visits by insect pollinators (Arroyo *et al.*, 1985) and seed production (Miller and Cummins, 1982; Young, 1984; Urbanska and Schütz, 1986).

Many processes in the life-cycle of a plant are, therefore, strongly influenced by microclimate, in a manner which exerts its effects on population processes (Woodward and Jones, 1984). Central to many of these processes is the capacity to develop and grow at low temperatures and reduced partial pressures of CO₂. These two features have therefore been selected for the central discussion of this chapter.

III. ECOPHYSIOLOGICAL RESPONSES TO THE MOUNTAIN AERIAL ENVIRONMENT

A. Historical Introduction

The recent use of portable infrared gas analysers (IRGAs) for the *in situ* measurement of photosynthesis, and the application of other sophisticated instruments and techniques, has enabled old ideas about mountain plant ecophysiology to be more thoroughly tested, and has generated new and exciting hypotheses. This chapter concentrates on the above-ground aspects of mountain plant ecology, in particular the interaction of leaf physiology and the environment.

Much of the early work on mountain plants was primarily concerned with the nature of species (e.g. Clausen *et al.*, 1940). In Section IV we briefly discuss evolutionary issues in the light of more recent ecophysiological work. These recent studies have given us a much deeper understanding of the changes in plant ecophysiology with altitude, but comparatively little attention has been given to how they might have arisen.

Mountain plant ecology can be traced back at least as far as the forest provenance work of von Wangenheim (1787, cited in Langlet, 1971). He stressed the importance of the climate at the sites from which seeds are collected, it being correlated with the response of the trees when grown under non-native conditions. He found that trees grown from seeds collected from northern sites in Canada grew better at high altitudes in Germany than plants from more southerly populations. For planting at lowland sites, he

stated that seeds should be collected from sites of lower latitude. According to Langlet (1971), such knowledge of ecotypic differentiation with respect to altitude was known even prior to this by other German foresters working in mountain districts. Hooker (1853) reported how differences in frost resistance of pine and rhododendron populations were correlated with the altitude of their origin in the Himalayas. Hooker was obviously aware of ecotypic differentiation with respect to altitude in plant populations. Following this, Hoffmann (1886, cited in Langlet, 1971) demonstrated the existence of altitudinal ecotypes in herbs differing in time of flowering. Langlet (1971) cited much of the early work on altitudinal differentiation of genotypes.

Wagner (1892) found that non-woody plants growing at high altitudes in the European Alps, often exhibited structural and physiological modifications, compared to those of low altitudes, and suggested that these were due to the influence of climate on development. Bonnier (1895) showed that these responses could be induced in ramets of the same plant by growing them at different altitudes, in the same soil, for 2–4 decades. Among the structural modifications found by Bonnier to be caused by the high-altitude environment were greater relative below-ground growth, shorter above-ground parts, smaller and thicker leaves, more palisade tissue, more chloroplasts and more stomata (especially adaxial). These are all features commonly found when lowland and upland plants of the same species are compared (e.g. Wagner, 1892; Billings and Mooney, 1968). Bonnier saw these alterations of the plants by the environment as enabling the species to survive at both low and high altitudes. By measuring rates of photosynthesis, Bonnier concluded that at high altitudes the "feeble development" of the aerial parts is compensated for by increased photosynthetic rate (A), thus enabling complete development and carbohydrate reserve accumulation during the short growing season. He also noticed the development of certain "protective tissues" against the "climatic rigours of high altitude". Though he never actually measured any physical environmental variables, he concluded that the morphological and physiological changes were due primarily to the greater irradiance, drier air and lower temperatures at high, compared to low, altitudes. Overall, he implied that genetic differentiation is unnecessary for plant survival at high altitudes, at least in the 81 species that he studied. However, this plasticity may be genetically controlled, perhaps representing an adaptation enabling the species to exploit many habitats. Mountain plants may be very plastic and respond to the environment in particular ways.

The inheritance of acquired characteristics and the universality of the plastic viewpoint were questioned by the Swede, Göte Turesson (1922, 1925, 1927, 1930–31, 1931), the first worker to use the term *genecology* (Turesson, 1923). He showed that many plant species, which span a range of altitudes, are genetically differentiated in such a way that the high-altitude ecotypes

display characteristics seemingly making them fitter under high-altitude conditions, and thus constituting adaptations to the alpine environment. Dobzhansky (1970) has advised that it may be best "to restrict the term ecotype to races that occur mosaic fashion in a quasi-continuously inhabited territory, wherever a certain type of environment (e.g. sand, clay, or calcareous soils) appears". Otherwise, he prefers Mayr's (1963) use of the term "race", such as climatic race. Turesson showed that alpine ecotypes are smaller and flower earlier than their lowland counterparts. Many alpine ecotypes, such as *Myosotis silvatica* Hoffm [sic] (Turesson, 1925), also had much thicker leaves. Although Kerner did not publish details of his experiments, he demonstrated genotypic divergence between populations growing at different altitudes, for features such as time of flowering (Langlet, 1971).

Clausen *et al.* (1940) demonstrated the importance of both genetic and environmental factors in the production of plant phenotypes. They discovered genetic races in *Achillea lanulosa* and *Potentilla glandulosa* from sea level, 1402 m and 3048 m in the Colorado (USA) mountains. The main features associated with the high-altitude races were genetically controlled dwarfism, greater frost resistance and phenological differences such as earliness of flowering. Dobzhansky (1970) and Briggs and Walters (1984) gave excellent summaries of this and other works on plant races and ecotypes.

Clements *et al.* (1950) made the most extensive study to that date of the effect of the environment at different altitudes on plant development. They made transplants of many species between three altitudes and assiduously recorded the responses of these plants to the natural environment, as well as to different light, water and nutrient treatments. They regarded the large part played by the environment in determining plant form as being overbearing evidence against the theory for the origin of species by means of natural selection, as proposed by Darwin in the earlier editions of his most famous work (e.g. Darwin, 1859). They went on to include the following statement in their summary: "Natural Selection does not operate upon the forms produced by adaptation [i.e. 'the complete response of plant and species . . . to the habitat complex'], since they are immediately in harmony with the environment that produces them."

Following on from the work of Clements *et al.*, *Oxyria digyna* became a favourite plant for the investigation of plant ecophysiology under arctic and alpine conditions in North America during the 1960s. This very wide-ranging species was shown to display ecotypic differentiation in photosynthetic rate with respect to altitude (Billings *et al.*, 1961). Plants with a high-altitude genotype showed greater photosynthetic rates than those with a low-altitude genotype at all CO₂ concentrations measured. No clear differentiation with respect to temperature was found. However, higher dark respiration rates were found by Mooney and Billings (1961) in alpine ecotypes, and this was

thought to allow these plants to continue normal metabolism at low temperatures but limit their ability to thrive south of their distribution.

Three important reviews on mountain plant ecology were also published during the 1960s: Bliss (1962a), Billings and Mooney (1968) and Tranquillini (1964). The first two were about North American mountain ecology. They characterized the properties of angiosperms at high compared to low altitudes by the following features: relatively more root and rhizome reserves; limitation by drought at their upward limit; higher daily productivity during the growing season (see Scott and Billings, 1964); higher calorific and lipid content; growth often limited by soil nitrogen and phosphorus availability; rates of assimilation of nitrogen into organic compounds reduced by low temperatures; less chlorophyll (both on a fresh weight and a leaf area basis); lower temperature optimum for photosynthesis (T_o); greater rates of dark respiration (R_d); higher light levels required for maximal rates of photosynthesis (A_{max}); more fructans; and fewer seeds. The review by Tranquillini (1964) was European-based, being particularly concerned with the eastern Alps. Tranquillini stressed the lack of drought at high altitude, stating that drought becomes less likely with increased elevation. It was concluded that high-altitude plants were adapted photosynthetically to high irradiance, low temperature and low CO_2 concentrations. Soil and leaf temperatures may become very high; leaves have thick palisade layers, high dark respiration rates, with more storage of reserve carbohydrate for insurance against unproductive seasons, and adaptations to high irradiances of ultraviolet (UV-B) radiation.

The leaves of plants from high altitudes were thought to be capable of positive net photosynthesis at lower CO_2 concentrations, and lower temperatures, than those from lower altitudes (Tranquillini, 1964; Billings and Mooney, 1968). It was also suggested that high-altitude leaves achieved maximal photosynthetic rates at higher irradiances. Because CO_2 concentrations and temperature both generally fall with altitude (Fig. 1), and irradiance often increases (Fig. 5), these features might be considered as adaptations.

A tradition of ideas about the process by which plants are seemingly adapted to high altitudes has therefore been established. How do these ideas stand up in the light of subsequent work and what new aspects are of importance? Though the ecophysiology of mountain plants will be discussed under a number of different headings, these various features are all closely related to each other, particularly efficiency of CO_2 uptake (ECU), measured by the initial, linear slope of the A/p , response (Fig. 7), and the rate of photosynthesis at ambient CO_2 concentrations under saturating irradiance (A_{max}). Irradiance, CO_2 concentrations and temperature all interact in a complex way with the biochemistry of photosynthesis. Because of this, a

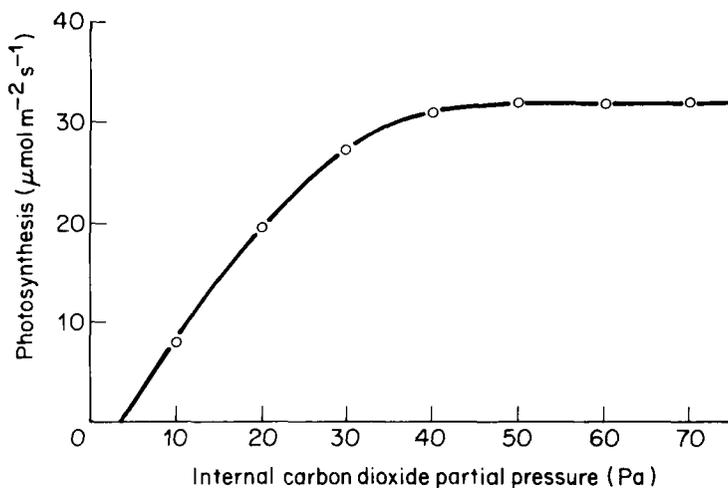


Fig. 7. Example of an A/p_i curve for a C_3 leaf.

reductionist approach is necessary to understand the measured responses of plants at the biochemical level.

B. Photosynthesis at Reduced Carbon Dioxide Levels

1. General

What is the evidence that leaves of plants growing at high altitudes are better at capturing CO_2 from partial pressures lower than the mean at sea-level (34 Pa), than are plants from low altitudes? This question is asked with the possibility of genetic adaptation to low CO_2 levels having occurred. An examination of the available evidence makes such a claim unlikely to be true, except in a very few cases. It seems that any increased ability of high-altitude plants to fix CO_2 from low concentrations could be explained by factors other than adaptation.

At saturating irradiance, the capacity to fix more CO_2 at a given concentration could be due to a greater absolute rate of photon capture, and/or a greater efficiency in converting these captured photons into chemical bond energy. The former could involve more chlorophyll molecules, or those present working more efficiently; the latter could involve greater efficiency of energy conversion to the carboxylase reaction, and/or an increased CO_2 partial pressure at the site of carboxylation, and/or more carboxylation sites per unit leaf area (Sharkey, 1985). This last possibility of more carboxylation

sites seems to be the one that best fits the evidence for differences between high- and low-altitude plants.

Ecotypic differentiation with respect to altitude for CO₂ fixation was found by Billings *et al.* (1961) in *Oxyria digyna*. Alpine populations displayed greater photosynthetic rates (*A*) at all CO₂ concentrations than arctic populations from sea-level, with the alpine population showing positive *A* down to a CO₂ concentration equivalent to an altitude of 12 200 m. However, Decker (1959) found no such differences within the *Mimulus cardinalis-lewisii* complex. Also working with altitudinal races of *Mimulus* spp., Milner and Hiesey (1964a) found no differences between the populations at a slightly elevated CO₂ mole fraction (425 μmol mol⁻¹); however, at a higher mole fraction (1500 μmol mol⁻¹), the lowland races had higher rates than the upland races. In addition, the increase in *A* at the higher mole fraction declined most rapidly in upland races. This could well be due to the upland race being more limited by orthophosphate (Pi) regeneration rates (Leegood and Furbank, 1986; Sage *et al.*, 1988). If internal leaf CO₂ mole fraction (*c_i*), or partial pressure (*p_i*), limits photosynthesis more at high altitudes than at low, then it is expected that for leaves at high altitudes and saturating irradiance, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) will be at maximum activation. This is because ribulose bisphosphate (RuP₂) or P-regeneration limitation will not be apparent under such conditions. The absolute concentration of Rubisco will be limiting *A* at the biochemical level (Sage *et al.*, 1988; Evans, 1989), and photosynthesis will be occurring on the linear part of the *A/p_i* response (see Fig. 7). It should be stated that a change in the ratio of photosynthesis to photorespiration will not be caused by the change in CO₂ partial pressure with altitude. This is because the partial pressure of CO₂ and O₂ will change at the same rate. However, changes in temperature with altitude will have an effect on this ratio (Brooks and Farquhar, 1985).

McNaughton *et al.* (1974) found that ecotypes of *Typha latifolia* from a range of altitudes, did not differ in their capacity to fix CO₂ at low mole fractions (below 300 μmol mol⁻¹). At higher CO₂ mole fractions (300–550 μmol mol⁻¹), however, the high-altitude ecotypes showed the highest values of *A*. They inferred higher concentrations of Rubisco in the upland ecotypes, but with identical kinetic properties to the lowland ecotypes. Mooney *et al.* (1964, 1966), working with a large number of species from various altitudes, found no clear relationship between altitude of origin and ability to fix CO₂ from low concentrations; the ability to fix CO₂ at high concentrations was not investigated. Again working with the *Mimulus* complex, Hiesey *et al.* (1971) made extensive investigations into the eco-physiology of *M. cardinalis* and *M. lewisii*, concentrating on comparisons between plants from different altitudes. They grew *M. cardinalis* clones from different altitudes under controlled growth conditions and found that, under

increased CO_2 mole fractions (i.e. $1250 \mu\text{mol mol}^{-1}$ vs $300 \mu\text{mol mol}^{-1}$), lowland clones responded more favourably, in terms of dry weight accumulation and stem height, than those from high altitudes. The clones from higher altitudes grew faster than the lowland ones at $300 \mu\text{mol mol}^{-1}$. McMahon and Bogorad (1966) have shown that Rubisco in the leaves of the upland clones of this species from the same sites used by Hiesey *et al.* (1971) had a lower Michaelis constant ($K_m(\text{CO}_2)$) than in those from lower altitudes. In this species it appears that genetic differentiation with respect to altitude has occurred for the ability to fix CO_2 at reduced concentrations, though this was not found in earlier work. Increased CO_2 concentrations caused leaves of all races to be thicker, narrower and shorter, especially in the upland clones.

2. Stomatal Responses and Efficiency of Carbon Uptake (ECU)

In order to investigate the increases in stomatal density with altitude found by workers such as Wagner (1892) and Bonnier (1895), it is necessary to examine the literature not directly concerned with altitude. Madsen (1973a, b) investigated the response of young tomato plants to increased CO_2 levels: both dry matter and leaf thickness increased as CO_2 was increased from ambient ($350 \mu\text{mol mol}^{-1}$) up to $2200 \mu\text{mol mol}^{-1}$. In contrast, stomatal number and epidermal cell density decreased. Madsen (1973b) attributed the decrease in stomatal density to increased expansion due to greater carbohydrate concentrations, lower osmotic potentials and higher rates of water flow into enlarging cells. Woodward (1986, 1987b) found that increasing the mole fraction of CO_2 from $200 \mu\text{mol mol}^{-1}$ caused the stomatal density of leaves in *Vaccinium myrtillus*, *Acer pseudoplatanus*, *Quercus robur*, *Rhamnus catharticus* and *Rumex crispus* to fall, up to a threshold value of about $340 \mu\text{mol mol}^{-1}$, beyond which no further change was observed. Subsequently, Woodward and Bazzaz (1988) have shown that CO_2 partial pressure induces a similar response, particularly below ambient partial pressure (from 22.5 to 34 Pa), and that at different atmospheric pressures stomatal density responds to CO_2 partial pressure and not mole fraction. An interpretation of this change in stomatal density may be implicated from the review by Mott *et al.* (1982) on the general significance of amphistomaty. They concluded that a high photosynthetic rate per unit leaf area is often correlated with a high stomatal conductance. Hence stomatal density may be partly controlled by the relationship between CO_2 partial pressure (p_i) and ECU for a given leaf. For a developing leaf with a given ECU, there will be an optimum p_i for the mature leaf under full irradiance. Hence if p_a (ambient CO_2 partial pressure) is altered, it may be that this is sensed by the leaf and the stomatal density adjusted accordingly. There is, however, no conclusive evidence for such a mechanism. Jarvis and Morison (1981) found that "the evidence for a functional dependence of [stomatal conductance] . . . on mesophyll photosynthesis is unconvincing". They pointed out that though stomatal conduc-

tance may be independent of the absolute value of p_i , it is sometimes dependent on the CO_2 concentration around the guard cells.

This capacity to control stomatal density and optimise p_i is an extension of the conclusions of Field *et al.* (1983). They found that during photosynthesis, the steady state CO_2 concentration in the leaf air spaces is maintained at a nearly constant value for a given species. In addition, Wong *et al.* (1979) found that in *Gossypium hirsutum*, stomatal conductance is a compromise between water conservation and the maintenance of internal CO_2 concentration at the optimum level for the intrinsic mesophyll capacity; increasing CO_2 concentration caused stomatal conductance to fall. It is possible that stomatal density is somehow controlled during leaf development by the amount of a substance directly related to the balance between mesophyll carboxylation capacity and internal CO_2 concentration. A similar system may operate to control stomatal aperture once the leaf is mature; Wong *et al.* (1979) suggested ATP. Such a mechanism could explain the results of Woodward (1986, 1987b) and Woodward and Bazzaz (1988). However, stomatal density itself may not uniquely determine conductance because, as stomatal density increases, the size of the guard cells often falls; thus the total pore area per unit leaf area may remain almost constant, and consequently stomatal density is only rarely correlated with conductance (Jones, 1987). More work is clearly necessary to establish the causes and physiological implications of changes in stomatal density.

3. Low Temperature Effects

Körner and Diemer (1987) investigated *in situ* the responses of various plant species to different partial pressures of CO_2 and irradiances at 600 and 2600 m in the Austrian Alps. Species occurring at 2600 m had both greater efficiency of carbon uptake (i.e. a higher ECU , based on the initial A/p_i slope) and greater values of A at CO_2 saturation. They attributed these differences to a greater mesophyll area per unit of leaf area (R^{mes}), and nitrogen content per unit of leaf area. The greater R^{mes} was due to thicker leaves, with a greater volume of palisade mesophyll. Because of the differences in ECU , mean A at ambient CO_2 partial pressure did not change with altitude, even though atmospheric and CO_2 partial pressure changed by 21% between the two altitudes. Because these measurements were made on material *in situ*, it is not possible to state whether the genotype, or the environment, or both, gave rise to these anatomical and physiological differences.

To understand these findings fully, it is necessary to examine the general literature on the physiology and biochemistry of C_3 photosynthesis. Farquhar *et al.* (1980) proposed that ECU is largely controlled by Rubisco activity per unit leaf area, and that A at saturating CO_2 and irradiance reflects limitations in the regeneration of ribulose biphosphate (RuP_2) (see also Evans, 1989). Thus Rubisco activity and RuP_2 regeneration rates determine

the form of A/p_i curves. Chabot *et al.* (1972) found that Rubisco activity per unit fresh weight of leaf, and per unit weight of protein, increased dramatically in an alpine *Oxyria digyna* population, when grown in a low-temperature regime compared to one at higher temperatures. An arctic population did not show any change. Bunce (1986) noted that leaves which developed at low temperatures had higher photosynthetic capacities (rates of photosynthesis under optimal conditions) than those grown at higher temperatures. This is because the rates of leaf expansion are reduced more by low temperatures than is the manufacture of the photosynthetic system components ("photosynthetic machinery"). Leaves formed at low temperatures will therefore contain greater amounts of photosynthetic machinery per unit area. Also, Chabot *et al.* (1972) found a 58% increase in leaf protein per unit weight in low-temperature grown alpine *O. digyna* compared to high; however, an arctic population showed only a 5% increase. Bunce (1986) suggested that the low temperature effect will only be important for A if stomatal conductance (g_s) also increases. This is possible, given the observations by Wong *et al.* (1979) of the importance of maintaining internal CO_2 partial pressure at the intrinsic mesophyll capacity. Indeed, it seems that the amount of CO_2 within a leaf is often maintained at a point close to the inflexion of the leaf's A/p_i response curve (Long and Hallgren, 1985). This is the point at which the photosynthetic system becomes limited by the regeneration of RuP_2 (Farquhar *et al.*, 1980). Evans (1989) proposed that nitrogen within a leaf is distributed between the Calvin cycle and thylakoid proteins so as to cause a co-limitation to photosynthesis by carboxylation and RuP_2 regeneration (except at high irradiances). Such an optimal distribution would tend to maintain photosynthesis and p_i at the inflexion point.

Any change in ECU with altitude might therefore be explained by low temperatures during leaf development, causing an increased mesophyll capacity for CO_2 fixation, with maximum conductance (g_{max}) also increasing. Raven and Glidewell (1981) indicated that the amount of Rubisco per unit leaf area will not affect ECU unless R^{mes} also increases. Also, Sharkey (1985) described how mesophyll conductance (conductance of CO_2 through the cell to the sites of carboxylation, per unit leaf area) is higher than stomatal conductance, so that a marked increase in photosynthesis occurs only if stomatal conductance also increases. Körner and Diemer (1987) found only a small increase in g_{max} with altitude, less than the increase in g_{mes} , leading to an increase in the stomatal limitations of photosynthesis. It is probable that g_{max} is controlled by other factors as well as the mesophyll conductance/ p_i balance. A caveat with regard to the ideas of Bunce (1986) is that growth at low temperatures does not necessarily lead to an increase in A_{max} , as found for arctic plants (Körner and Diemer, 1987). Interestingly, Körner and Diemer (1987) found that plant species which have a wide altitudinal distribution did not have higher $ECUs$ at high altitude. It would be

interesting to know the growth rates of these species at different altitudes, and how they differ from specifically upland species under high-altitude conditions.

Some caution should be used in the interpretation of A/p_i relationships. Under conditions of water limitation, leaves possess a non-uniform distribution of open stomata, leading to an overestimation of p_i (Terashima *et al.*, 1988). In such a situation, ECU will be underestimated due to an apparent non-stomatal inhibition of A (Downton *et al.*, 1988). The generality of leaf patchiness in conductance is unknown but an interesting subject.

4. Leaf to Air CO_2 Ratios

If a plant at high altitude has a higher ECU than one at low altitude, and/or conductance increasingly limits photosynthesis, the ratio of CO_2 partial pressure inside the leaf air spaces (p_i) to that outside (p_a) will decrease with altitude. Farquhar *et al.* (1982) and Downton *et al.* (1985) showed that the time integral of the p_i/p_a ratio can be obtained for a leaf by measuring the relative proportions of the stable isotopes ^{13}C to ^{12}C . The ratio of these two isotopes is affected by diffusion through the stomata and by the enzyme Rubisco. The isotopic ratio, calculated relative to the Pee Dee Belemnite (PDB) standard, is known as $\delta^{13}C$. Because of its higher mass, $^{13}CO_2$ does not diffuse into leaves as quickly as $^{12}CO_2$, and seemingly binds less readily to Rubisco. Thus plant carbohydrates contain lower ratios of ^{13}C to ^{12}C (i.e. lower values of $\delta^{13}C$) than observed for air, because of these discriminations. The scale of $\delta^{13}C$ is set arbitrarily at zero for the standard. Any substance containing a lower ratio of ^{13}C to ^{12}C than this standard will have a negative $\delta^{13}C$ value. Most values for C_3 plants range from -30 to -22‰ (Troughton *et al.*, 1974) and only C_3 species will be considered in this review. $\delta^{13}C$ values are believed to measure the average p_i/p_a ratio for the life of a leaf by the following equation:

$$\delta^{13}C = \delta^{13}C_a - \frac{a(p_a - p_i)}{p_a} - \frac{b(p_i)}{p_a} \quad (2)$$

where $\delta^{13}C$ and $\delta^{13}C_a$ are the ^{13}C to ^{12}C ratios in the leaf and air (-7.8‰) respectively, and a and b are thought to be 4.4 and 27‰ respectively for C_3 plants (Farquhar *et al.*, 1982).

From this equation it can be seen that if average p_i/p_a falls with altitude, the $^{13}C/^{12}C$ ratio of the leaf would be expected to increase. This is what was indeed found by Körner *et al.* (1988), who measured the $\delta^{13}C$ of 100 C_3 species from different altitudes around the world. They found slopes for the regression lines of 0.78 ($P < 0.0001$) for forbs, 0.42 ($P = 0.009$) for shrubs and 0.88‰ km^{-1} ($P = 0.002$) for trees. It was suggested that the lower slope

and significance for shrubs may be due to the effects of intra-canopy carbon recycling. Water stress is also known to cause increased $^{13}\text{C}/^{12}\text{C}$ ratios, but Körner *et al.* (1988) chose plants from sites reputed not to suffer from drought.

Other workers have also examined the relationship between $\delta^{13}\text{C}$ ratios and altitude. Vitousek *et al.* (1988) found that $\delta^{13}\text{C}$ increased with altitude in the dominant tree species *Metrosideros polymorpha* on a tropical volcano, and that $\delta^{13}\text{C}$ was negatively correlated with *SLA*, but offered no explanation. Friend *et al.* (1989) investigated the relationship between $^{13}\text{C}/^{12}\text{C}$ ratios and altitude in *Vaccinium myrtillus* and *Nardus stricta* for two growing seasons in Scotland. They found that the slope of the relationship between carbon isotope ratios and altitude varied from positive to near zero, dependent on season, and concluded that, even in the Scottish climate, changes in water relations could account for the differences between the years.

There has been some argument as to whether plants at high altitude really do experience reduced availability of CO_2 . Verduin (1953) proposed that an alpine plant at 3500 m would experience CO_2 rarefied by a factor of 1.7 compared with one at sea-level, but that because this will also be true for all the other molecular species, the volume % of CO_2 (mole fraction) will be very similar. The product of concentration and diffusivity proved to be very similar at all altitudes; it was thus concluded that the measured high rates of photosynthesis at high altitude are not as surprising as they might first appear. Similarly, in a theoretical paper, Gale (1973) concluded that plants growing at different altitudes will not experience the extremes of CO_2 supply expected directly from the observations of partial pressures. This was explained in similar terms to Verduin with regard to the diffusion coefficient of CO_2 in air, which increases as atmospheric pressure decreases (i.e. altitude increases). This effect to a large degree compensates for the fall in partial pressure. This is also the case for water vapour, with a potential for increasing transpiration rates at reduced atmospheric pressure. Gale (1973) concluded that the reduction in ambient CO_2 partial pressure with altitude will only have a minor effect on plants. However, the diffusion coefficients decrease with temperature, and so when temperature falls with altitude (as is most frequently the case), the changes in CO_2 partial pressure will become important. Therefore, changes in CO_2 availability to plants with altitude will be dependent on the temperature of the air and the leaf. These issues were debated in a series of letters (Cooper, 1986; Gale, 1986; La Marche *et al.*, 1986) following the publication of a paper purporting to show that subalpine conifers growing at high altitudes have responded more to the increased atmospheric CO_2 levels since 1850 than those from lower altitudes (La Marche *et al.*, 1984). If Gale's (1973) conclusions are valid, then the results of

Billings *et al.* (1961) and Hiesey *et al.* (1971) are incongruous given that no selection for increased ability to fix CO_2 at low partial pressure would have been possible.

Overall, however, plants growing at high altitudes do frequently have higher rates of photosynthesis at lower CO_2 concentrations than plants at low altitudes. Körner and Diemer (1987) found differences in *ECU* between plants at different altitudes, but these differences may have been plastic, rather than genetic. Only Billings *et al.* (1961) and Hiesey *et al.* (1971) found ecotypic differentiation between altitudinal clones for this feature. It seems possible that observations of changes in *ECU* with altitude, as well as in stomatal density and g_{max} , may be explained by developmental responses to the environmental conditions, in particular low temperatures, as shown by Bonnier (1895), Clements *et al.* (1950) and Chabot *et al.* (1972). Controlled environment and reciprocal transplant studies are necessary to separate genetic from environmental influences on the ability of plants to fix CO_2 at low concentrations.

C. A_{max} : The Maximum Rate of Photosynthesis at Saturating Irradiance and Ambient CO_2 Concentration

1. General

A_{max} is the rate of photosynthesis, measured at saturating irradiance, occurring on an A/p_i curve where p_i is that partial pressure occurring within the leaf under ambient CO_2 conditions. Thus any differences in *ECU*, and/or CO_2 -saturated rates of photosynthesis, will result in differences in A_{max} . Any mechanism responsible for differences in A/p_i curves between plants at different altitudes, as discussed in the previous section, might also explain differences in A_{max} .

What evidence is there that leaves of plants growing at high altitudes have higher irradiance-saturated rates of photosynthesis (A_{max})? Because irradiance often increases with altitude, at least on sunny days (Barry, 1981, pp. 29–32), one might expect the leaves of plants at high altitudes to have evolved towards a morphology closer to the classic “sun leaf” than those of lower altitudes, enabling full utilization of the high levels of irradiance present during clear summer days. A sun leaf, relative to a shade leaf, is thicker, of lower area, and it has a lower volume of intercellular air space, a higher proportion of palisade cells, longer palisade cells, greater R^{mes} (the ratio of mesophyll to leaf surface area), more and smaller chloroplasts per cell, greater stomatal density and a thicker cuticle (Nobel and Walker, 1985). There are many reports in the literature of leaf thickness increasing with altitude (e.g. Tranquillini, 1964; Hiesey *et al.*, 1971; Woodward, 1979a;

Körner and Cochrane, 1985; Körner *et al.*, 1986; Körner and Diemer, 1987; Körner and Renhardt, 1987). Thicker leaves generally have a lower specific leaf area (SLA), more nitrogen per unit area and a higher A_{\max} (e.g. Mooney *et al.*, 1978). Increased leaf thickness can be caused by high irradiance levels during development (see, e.g. Mott *et al.*, 1982) or low temperatures (Wardlaw *et al.*, 1983), and so it may prove possible to find a causal explanation for increased leaf thickness in these factors. Because thicker leaves are likely to have an increased R^{mes} , then they will probably also have a higher A_{\max} (Charles-Edwards and Ludwig, 1975; Raven and Glidewell, 1981; Nobel, 1983). However, there are instances in which A_{\max} has not been correlated with leaf thickness, such as found by Patton and Jones (1989).

Rabinowitch (1951, p. 997) reported that the highest rates of photosynthesis (with very high quantum yields) found under natural conditions were for alpine plants, in particular those measured by Henrici (1918), Blagowesthenskij (1935) and Kjær (1937). Verduin (1953) and Zalensky (1954) have made similar claims. Clebsch (1960) found that alpine *Trisetum spicatum* populations had higher A_{\max} values than arctic populations. Mooney and Billings (1961) found the same for *Oxyria digyna*, the leaves from the alpine plants possessing a greater internal leaf surface area (Au, 1969). It was suggested by Tranquillini (1964) that plants growing at high altitudes were extreme sun plants able to make good use of high irradiances, and Glagoleva (1962, 1963, cited in Tranquillini, 1964) demonstrated that this may be due to the thickness of the palisade tissue. Milner and Hiesey (1964b) found that light-saturated levels of photosynthesis for six races of *Mimulus cardinalis* increased with their native elevation. These results are particularly interesting as they demonstrated ecotypic differentiation for A_{\max} between altitudes. However, Mooney and Johnson (1965) found that alpine clones of *Thalictrum alpinum* had lower A_{\max} values and genetically thinner leaves than arctic clones. Also, Godfrey (1969) showed that high-altitude populations of *Geum turbinatum* and *O. digyna* had lower photosynthetic rates than lower-altitude populations at several irradiances.

Hiesey *et al.* (1971) described how upland clones of *M. cardinalis* produced thicker leaves which had higher A_{\max} values and irradiance absorptivity than their lowland counterparts. Grabherr (1977) suggested that A_{\max} was related to chlorophyll content in *Loiseleuria procumbens*, with two peaks, one in the spring and a higher one in summer. Further evidence for ecotypic differentiation of A_{\max} was provided by Mächler and Nösberger (1977), who noted how high-altitude clones of *Trifolium repens* had higher photosynthetic rates than lowland clones when grown under controlled conditions. It should be borne in mind that A_{\max} occurs at a higher irradiance level for the canopy than it does for an individual leaf, owing to self-shading of the leaves in the canopy, as found by Grabherr and Cernusca (1977) for *L. procumbens*.

2. *Effects of Leaf Morphology*

Tieszen (1978) found a negative correlation between A_{\max} and SLA for Alaskan tundra species, while Mooney *et al.* (1978) described a negative correlation between SLA and water use efficiency (WUE : carbon gained per unit water lost), and a positive correlation between SLA and nitrogen use efficiency (NUE : carbon gained per unit leaf nitrogen) in *Eucalyptus* spp. Correlations occurred between A , SLA and leaf nitrogen contents per unit leaf area. Species from drier habitats tended to produce smaller, thicker leaves, with a higher content of leaf nitrogen per unit area, lower $SLAs$, and correspondingly higher levels of A_{\max} . This form of leaf, they concluded, must have a higher WUE , but lower NUE , than the larger and thinner leaves produced by species from wetter habitats. Because leaves are frequently thicker at higher altitudes, one might thus expect them to have higher $WUEs$ under identical water vapour pressure deficits. It may also be that any increase in WUE is counteracted by an increase in conductance due to the reduced ambient CO_2 concentration. Because the WUE of leaves possibly increases with altitude, an increase in potential conductance may be of high selective advantage.

Also of relevance to the relationship between SLA and A_{\max} is the work of Ledig and Korbobo (1983), in which *Acer saccharum* seedlings were grown from seeds collected along an altitudinal gradient. They found that the population from the highest altitude displayed the highest values of A , but, curiously from what has been said above, also had the highest $SLAs$. The mid-altitude population displayed lowest A rates but lowest $SLAs$. This pattern was found to repeat itself along another transect. No other data were given which might suggest a possible explanation for these unusual results. The authors did suggest that the differences in A could be caused by differences in stomatal density, pore size, mesophyll resistance or carboxylation capacity, but did not provide any data in support of these claims.

It is thought that g_{\max} may be an important limitation to A_{\max} (Sharkey, 1985). Körner *et al.* (1979) investigated g_{\max} for many C_3 vascular plants, and found that plants with a high g_{\max} tend to have a high A_{\max} , but that a given leaf would not benefit greatly from increasing g_{\max} because of the much more important role played by mesophyll conductance. This correlation between g_{\max} and A_{\max} concurs with the observations by Mott *et al.* (1982) of greater stomatal densities (especially amphistomaty) occurring in leaves with greater values of A_{\max} , when developed under high irradiance, as a high mesophyll conductance usually indicates a high carboxylation capacity (e.g. Nobel and Walker, 1985). Körner (1982) highlighted the ability of alpine plants to make full use of high irradiance levels. In a *Carex curvula* canopy, he found that irradiance is by far the major factor limiting photosynthesis over a whole growing season, this limitation being due to clouds, fog and mutual leaf

shading. Mott *et al.* (1982) showed that thicker leaves will not necessarily have increased g_{\max} unless high irradiance levels also occur during development. It appears that a high A_{\max} is only realized by a leaf with a high mesophyll conductance *and* high irradiance levels during development. Thus we might expect to find different relationships between altitude, stomatal density and A_{\max} depending on the changes in irradiance with altitude. This idea is supported by the data in Körner *et al.* (1983), which show stomatal density decreasing with altitude in New Guinea, where the climate is maritime and irradiance falls with altitude.

Körner *et al.* (1983) discussed the significance of changes in stomatal density with altitude. As already noted, the most general trend is for an increase in the adaxial density (e.g. Wagner, 1892; Berger-Landefeldt, 1936; Au, 1969; Scheel, 1979, cited in Körner and Mayr, 1981; Körner and Mayr, 1981; Woodward, 1986). This may enhance diffusion, an important feature if the leaves are also thicker (Mott *et al.*, 1982). Körner *et al.* (1983) concluded that as features such as stomatal density, stomatal index and g_{\max} do not always change in the same manner with altitude, they must in part be related to specific local environmental factors (such as water availability and/or irradiance levels), and not entirely due to (i.e. selected, or caused by) environmental features which change in the same direction on all mountains, such as temperature and the partial pressure of gases. Increased irradiance frequently has a substantial effect on adaxial stomatal density in dicotyledons (Mott *et al.*, 1982). Bonnier (1895) found increased stomatal density in lowland genotypes when grown at high altitudes, indicating both the plasticity of plants for this feature, and that there were probably increased levels of irradiance and/or reduced growth rates. Clements *et al.* (1950) also found that both increased irradiance and altitude were correlated with increased stomatal density in a wide range of species transplanted between altitudes, and subjected to different shade treatments. The increase in density with altitude was not thought to be due to the increased irradiance levels (irradiance was not found to change with altitude), but rather to reduced leaf expansion at the lower temperatures. However, "[in] some cases, the inverse relation did not hold between growth and number, indicating a more deep-seated modification of the meristem". When transported to the same altitude, plants grown at higher altitudes had equal or greater rates of transpiration than those grown at lower altitudes, reflecting the increased stomatal densities. It may be that both irradiance levels and leaf temperature during development are of importance in determining stomatal density (Körner *et al.*, 1986), as may be CO_2 concentration (see Section III.C.1).

3. Soil Nutrient Effects

Field (1983) showed that A_{\max} can be limited by levels of enzymes such as Rubisco, and Field *et al.* (1983) demonstrated a positive relationship between

total leaf organic nitrogen content and A_{\max} between species. Because levels of leaf nitrogen and enzymes such as Rubisco are closely correlated (e.g. Huffaker, 1982, p. 387; Field, 1983; Evans, 1989; see also Chapin *et al.*, 1980), it is to be expected that leaf nitrogen content and A_{\max} will be highly correlated. There is good evidence that leaf nitrogen content generally increases with altitude and latitude (Ehrhardt, 1961; Babb and Whitfield, 1977; Chapin *et al.*, 1980; Nordmeyer, 1980; Haselwandter *et al.*, 1983; Körner and Cochrane, 1985; Körner *et al.*, 1986; Körner and Diemer, 1987; Körner and Renhardt, 1987). This seems surprising, because soil nitrogen availability might be expected to decrease with the altitudinal (and latitudinal) decline in soil temperature, and with the increase in soil moisture, reducing mineralization and nutrient cycling rates (Grubb, 1971; Marrs *et al.*, 1988; Vitousek *et al.*, 1988). Grubb (1989) cited evidence that the growth of montane tropical forest is limited by nitrogen supply, due to decreased rates of organic matter decomposition. However, the overall decline in productivity with altitude is also directly attributable to decreased irradiance and lower temperatures (Grubb, 1989). Vitousek *et al.* (1988) found that concentration of foliar N, P, Mg and K, on a leaf weight basis, declined with altitude in *Metrosideros polymorpha*. However, concentrations per unit leaf area fell less, because SLA declined with altitude. Körner and Cochrane (1985), studying *Eucalyptus pauciflora* along an elevational gradient in the Snowy Mountains of south-eastern Australia, found that leaf thickness, number of palisade layers and leaf nitrogen per unit leaf area all increased with altitude. Körner *et al.* (1986) found the same pattern in New Zealand, with a positive correlation between leaf nitrogen and g_{\max} , suggesting that high photosynthetic rates are possible in these high-altitude plants. In addition, Körner and Diemer (1987) found that mean total nitrogen per unit leaf area in plants growing at high altitudes was 34% greater compared to those growing at low altitudes. ECU in these plants correlated strongly with leaf nitrogen concentration.

Holzmann and Haselwandter (1988) discovered high concentrations of nitrogen in both roots and shoots of plants in an alpine sedge community. Rehder and Schäfer (1978) found that in three alpine dwarf shrub communities of the central Alps, there was greater productivity than expected from the concentrations of mineralizable N in the soil. They concluded that mycorrhizal fungi must contribute to nitrogen uptake, or that some form of root exudation occurs to stimulate N-mineralizing organisms in the rhizosphere. As might be expected, Holzmann and Haselwandter (1988) found that low soil temperatures largely inhibited biological nitrogen fixation in an alpine sedge community. The nitrogen supply per unit ground area by fixation, mineralization and precipitation did not appear to be sufficient to support the measured growth. However, the plants studied were mostly infected with vesicular-arbuscular (VA) mycorrhizas, as are most plants. This, together

with evidence for movement of N to the roots for storage towards the end of the growing season for release in the spring, greater relative root length at higher altitudes for absorbing and storage (see also Körner and Renhardt, 1987), and the possibility of large inputs of nitrogen following snow melt (Haselwandter *et al.*, 1983), may help to explain the enigma. Also, it has been found that some commonly occurring ectomycorrhizal fungi can utilize organic nitrogen in peptides and proteins (Abuzinadah and Read, 1986; Abuzinadah *et al.*, 1986), but it is not known how important this may be for alpine plants, most of which are VA mycorrhizal.

As already pointed out, Holzmann and Haselwandter (1988) found no evidence of nitrogen deficiency in the 12 species they examined. Recalling Bunce's (1986) suggestion that low-temperature leaf development can cause increased values of A_{\max} , it may be that low temperatures at high altitudes reduce the growth rates of the plant more than the supply of N. Therefore, the concentration of plant nitrogen will increase with altitude, a possible explanation for some of the observed increases in A_{\max} . Similarly, the concentration of phosphorus may also increase. Chapin (1980) concluded that plants from infertile habitats may be characterized by the maintenance of high nutrient concentrations as a result of reduced growth rates.

4. *The Importance of Growth Temperature*

To conclude this discussion of increased A_{\max} with altitude, it is significant that Bunce (1983) described the dependence of A_{\max} not only on irradiance levels during development (as suggested by Chabot *et al.*, 1979), but also on the leaf expansion rate, with increasing expansion causing a dilution of the photosynthetic components. The expansion rate is closely linked to temperature (see below). Bunce (1983) demonstrated that when A_{\max} increased with irradiance during development, the increase in the R^{mes} ratio could not on its own explain the increase in A_{\max} . It appears that absolute concentrations of critical enzymes such as Rubisco might be involved, or even be of primary importance. Raven and Glidewell (1981), in a review of the literature, concluded that Rubisco activity (i.e. the amount of Rubisco in an activated form per unit leaf area) plays an important role in determining net CO_2 fixation, and that the activity is intimately related to leaf anatomy, especially the R^{mes} ratio. The leaf temperature during development is important for determining A at a given temperature, and hence g_{\max} .

D. T_o : The Optimum Temperature for Photosynthesis

1. *General*

As temperature is reduced, A_{\max} occurs at lower irradiance levels (e.g. Pisek *et al.*, 1973) and quantum efficiency may fall (Billings, 1974a; Berry and

Björkman, 1980). Wilson (1966) has suggested that this reduced efficiency may be due to a reduction in demand for sugars resulting in product inhibition. There is also evidence that the phosphate status of the chloroplast may be critical for rates of photosynthesis at low temperatures. Such an increase in phosphate limitation may cause a decrease in Rubisco activity, thus altering ECU and A_{max} , though Rubisco activity may change in direct response to temperature (Chabot *et al.*, 1972; Labate and Leegood, 1988). If a given plant has a higher photosynthetic rate at a low temperature than another plant, then this may be an adaptation to low temperatures, caused by the same physiological changes which influence A_{max} . If an upland plant has a greater A_{max} at low temperatures than a lowland plant, we may speak of differentiation with respect to altitude for the optimum temperature for photosynthesis (i.e. T_o). Evidence for this and its possible physiological explanation will now be discussed.

2. Evidence for Genotypic Differentiation

Björkman *et al.* (1960) found that alpine ecotypes of *Solidago virgaurea* from Sweden had lower T_o values than lowland ecotypes. The alpine ecotypes also had higher rates of dark respiration (Björkman and Holmgren, 1961). Similarly, Mooney *et al.* (1964) found that species from high altitudes in the White Mountains of California, when grown under controlled conditions, displayed lower values of T_o than species from lower altitudes. *Eriogonum ovalifolium* from 3947 m had maximal photosynthetic rates at around 20°C, whereas for *Hymenoclea salsola* from 1372 m they were around 30°C. The photosynthetic rate of lowland ecotypes of *Mimulus cardinalis* increased more rapidly with temperature than upland ecotypes (Milner and Hiesey, 1964b). Tieszen and Helgager (1968) found that an alpine ecotype of *Deschampsia cespitosa* had a higher T_o value for the Hill reaction than an arctic ecotype. Also, alpine populations of *Thalictrum alpinum* have been shown to exhibit higher T_o values than arctic ones (Mooney and Johnson, 1965), but alpine populations of *Oxyria digyna* had lower T_o values than arctic populations, by exhibiting greater acclimation potential (Billings *et al.*, 1971). There are many reports of such acclimation of T_o to growth temperature, for example: *Chamaebatiaria millefolium*, *Artemisia tridentata* and *Haplopappus apargioides* (Mooney and West, 1964); *Erigeron clokeyi*, *H. apargioides*, *C. millefolium* and *Encelia californica* (Mooney *et al.*, 1966); *D. cespitosa* (Pearcy, 1969); *Arenaria nuttallii* (Chabot and Billings, 1972); *Eucalyptus pauciflora* (Slatyer, 1977); and *Geum urbanum* and *G. rivale* (Graves and Taylor, 1988). However, the mechanisms leading to this dependency have not been elucidated.

Even though Hiesey *et al.* (1971) measured minimal reductions in leaf temperature with altitude, they found that growth of *M. cardinalis* clones showed genetic differentiation with respect to temperature for dry weight

accumulation. The clones from sea-level had a significantly greater increase in dry weight between 10 and 20°C than clones from higher altitudes. Woodward (1975) reached similar conclusions in comparisons of growth at different temperatures between the lowland *Sedum telephium* and the upland *S. rosea*. This differential growth response to temperature was thought to be responsible for changes in the outcome of competition experiments at different altitudes (Woodward and Pigott, 1975). In addition, Woodward (1979b) found that the growth of the lowland species *Dactylis glomerata* and *Phleum bertolonii* responded much more to an increase in temperature, from 10 to 20°C, than did the growth of the upland species *Sesleria albicans* and *P. alpinum*. However, it is not clear whether these differences were due to differences in T_o or to differences in the temperature response of leaf extension rate, or both (the latter subject is discussed in Section III.D.3).

T_o decreased with the altitude of origin of populations of *Abies balsamea*, when grown from seed under uniform environmental conditions. The change with altitude in T_o was similar to the adiabatic lapse rate, suggesting adaptation (Fryer and Ledig, 1972). Similarly, Slatyer (1977) found that under controlled environmental conditions, T_o for populations of *E. pauciflora* fell as the altitude of the seed source increased. Probable adaptation was also reported by Tranquillini (1979), who found that T_o values for spruce (*Picea abies*) from the timberline were 3°C lower than for spruce from the valley floor, irrespective of irradiance levels. Similar results were reported for larch (*Larix decidua*) and birch (*Betula verrucosa*; *B. pendula*). Thus there is substantial evidence for the evolution of T_o in response to altitude. It should be noted that the optimum temperature for photosynthesis of the whole canopy may be lower than for individual leaves, as has been found for a *Loiseleuria procumbens* canopy (Grabherr and Cernusca, 1977). This may in part be explained by greater self-shading of leaves together with the drop in T_o with a decline in irradiance (e.g. Pisek *et al.*, 1973, p. 113).

Pisek *et al.* (1973) and Billings (1974a) have both written reviews on the T_o values of alpine plants. In the former, it was reported that T_o values of 24°C occurred for *Citrus limon* from 80 m, 19°C for *Taxus baccata* from 550 m, 14°C for *Betula pendula* from 1900 m, and 12.5°C for *O. digyna* from 2500 m. Vegetative propagation of clones of *Trifolium repens* from different altitudes in Switzerland has shown the presence of high-altitude ecotypes which display higher rates of photosynthesis at all temperatures, particularly so at low temperatures (Mächler *et al.*, 1977). It is possible that photosynthetic adaptation to low temperatures may also involve high rates of photorespiration when warm, leading to a drop in net CO₂ fixation. This was confirmed by Neama (1982), who found that growing *Salix herbacea* at low temperatures caused increased rates of both dark respiration and photorespiration, when transferred to higher temperatures.

3. Mechanisms

In order to understand better the differences in T_o between plants we must examine the literature not specifically aimed at mountain plant ecology. Björkman and Badger (1979) found *Nerium oleander* to be very plastic for T_o when grown at different temperatures. Until this work, no insight had been made into the possible mechanism by which T_o changes in response to growth temperature (Björkman, 1973), despite its obvious widespread occurrence. Any theories in this connection will have important implications for ecotypic differentiation of T_o with altitude. Björkman and Badger investigated the differences between plants differing in T_o values. Differences in stomata, anatomy, amount of photosynthetic machinery per unit leaf area, electron transport capabilities and general enzyme levels could not explain the differences in photosynthetic rates. However, the maximum activities of the chloroplast enzymes Rubisco and fructose-1,6-bisphosphate phosphatase (Fru-P₂ phosphatase) differed substantially, but only Fru-P₂ phosphatase changed by an amount comparable to the changes in photosynthetic rates at suboptimal temperatures. Photosynthetic capacity of plants grown at 45°C, and then transferred to 20°C, was closely correlated to increases in the levels of Fru-P₂ phosphatase activity. Thus it may be that the levels of this enzyme are critical in photosynthetic acclimation, and adaptation, to low temperatures. Rubisco levels changed in a similar fashion, but not to such an extent. Rubisco does not appear to be particularly temperature-dependent at CO₂ partial pressures typical for C₃ plants. Photosynthetic adaptation to low temperatures may, therefore, lie in the metabolic pathway control mechanisms which regulate the metabolic pools in the Calvin cycle. Fru-P₂ phosphatase catalyses one of the key steps for regulation of the Calvin cycle: the hydrolysis of the phosphate from the C-1 atom of fructose-1,6-bisphosphate, to form fructose-6-phosphate (Portis *et al.*, 1977). It is possible that changes in the storage of phosphate in the vacuole and its release into the cytoplasm may play a significant role in the adaptation of photosynthesis to low temperatures (Labate and Leegood, 1988).

Of particular significance to T_o at different altitudes, Raven and Glidewell (1981) described how a number of workers have found a correlation between low-temperature growth and both net CO₂ fixation and Rubisco activity per unit leaf area. This is known as capacity adaptation and seems to be more dependent on absolute Rubisco amounts than any kinetic changes. Leaf thickness can also be increased by growth at low temperatures (e.g. Wardlaw *et al.*, 1983). Peet *et al.* (1977) found that both Rubisco activity and leaf thickness increased in *Phaseolus vulgaris* when grown at low temperatures, hence R^{mes} probably also increased. Raven and Glidewell (1981) suggested that increases in Rubisco/ R^{mes} ratios are not required for increased A at low temperatures, an increase in R^{mes} being sufficient. Klikoff (1969) sampled a

number of species from different altitudes and found that the low-temperature activities of isolated chloroplasts were positively correlated with altitude. Similar conclusions were reached by May and Villareal (1974). In Puma rye (*Secale cereale* L. cv. Puma), Rubisco itself changed in response to a low growth temperature by increasing its low-temperature stability (Huner and MacDowell, 1979a). These changes were shown to enhance the activity of Rubisco at low temperatures (Huner and MacDowell, 1979b).

4. Significance of T_o

In a previously mentioned study of CO_2 exchange in an alpine *Carex curvula* canopy, it was found that the optimal temperature for photosynthesis, at an altitude of 2310 m in the Austrian Alps, was 22.5°C, close to the mean leaf temperature on clear summer days (Körner, 1982). Thus leaf temperature, on days of high irradiance, does not severely limit photosynthesis in this alpine plant. Körner and Diemer (1987) reached similar conclusions for 8 lowland (600 m) and 11 upland (2600 m) species. At 4°C, the plants at 2600 m maintained 50% of A_{max} , whereas this was achieved at 8°C by the plants at 600 m.

Thus it might appear that low temperatures may not be of great direct significance to carbon gain per unit leaf area because of a combination of changes in T_o and the elevation of leaf temperature above air temperature (Körner and Larcher, 1988). However, it should be noted that the latter will only occur on days of high irradiances, when A is at maximum. On cloudy days, low irradiance and temperatures occur, making rates of A at low temperature crucial. The importance of elevation of leaf temperature above ambient will depend on how much CO_2 is fixed in these two types of climate. Local cloudiness will be very important; the Alps may be very different from Scotland or Scandinavia, for example (Fig. 5).

The effect of low temperatures on A during development can be considerable. In barley, for instance, cold hardening causes a doubling of A_{max} per unit chlorophyll, resulting in a 30% increase per unit leaf area (Sicher *et al.*, 1988). The mechanism whereby a plant developing in the cold has a higher rate of photosynthesis at low temperatures than a plant developing in the warm, is most probably a combination of growth being more reduced than photosynthesis during development (Bunce, 1986), resulting in an increased A_{max} , and some type of change in metabolic pool control as suggested above (Berry and Björkman, 1980). However, the general significance of these processes in the reduction of T_o values is not known.

E. Growth

Whereas low temperatures on mountains may, at least in some cases, be of little significance to carbon gain per unit leaf area, they are crucial to the

expansion of leaf area, and hence for the productivity of the whole plant. Plant stature usually declines with altitude (Körner and Renhardt, 1987; Woodward, 1986; Fig. 6), though on some tropical mountains it may increase (e.g. Smith and Young, 1987). That high-altitude ecotypes can be genetically of lower stature has been known for some time (Zederbauer, 1908, cited in Langlet, 1971; Turesson, 1925; Clausen *et al.*, 1940). Plants taken from the lowlands and grown at high altitudes are of lower stature than when they are grown in the same soil at lower altitudes (Bonnier, 1895). Woodward (1986) grew populations of *Vaccinium myrtillus* in a controlled environment and found that the low stature of high-altitude populations is unchanging, and probably has some genetic control. He suggested that this resulted from selection by high wind speeds, and reduced competition for light. The reduction of vegetation stature with altitude may well be due to a combination of environmental and genetic factors. High wind speeds may lead to severe abrasion by ice particles and sand, and to drought during winter. Shorter plants may be protected by snow, except in very exposed sites where the lower boundary layer conductance, associated with the small stature, will reduce the impact of the wind. All these factors will give shorter plants a selective advantage as well as causing dwarfism in otherwise taller plants. In addition, summer growth and metabolism will occur at the higher temperatures experienced closer to the ground (e.g. Körner and Cochrane, 1983). Fitter and Hay (1987) give a full description of the possible selective advantages of dwarfism in arctic and alpine environments.

Ollerenshaw and Baker (1981), Chapin and Oechel (1983), Woodward *et al.* (1986) and Sakai and Larcher (1987), have all demonstrated that plant growth dynamics in response to temperature are genetically controlled and vary between latitudes and altitudes. The earlier work in this regard was discussed in the excellent review of genecology from an historical perspective by Langlet (1971). Cline and Agatep (1970) demonstrated that upland ecotypes of the *Achillea borealis-lanulosa* complex had greater growth at low temperatures than lowland ecotypes under the same conditions. There is also evidence that upland ecotypes and species do not respond to increased temperature as well as their lowland counterparts (e.g. Hiesey *et al.*, 1971; Woodward and Pigott, 1975; Woodward, 1975, 1979a, b).

In situ measurements of leaf growth have demonstrated that upland populations and species are able to grow at lower temperatures than lowland populations and species (Woodward *et al.*, 1986; Körner and Woodward, 1987). Woodward and Friend (1988) found the same for seed-grown material under controlled conditions. It was suggested that the ability to grow at low temperatures was related to adaptation in either, or both, the rate of cell production and the rate of cell expansion in the growing zone of the leaves. An examination of the factors involved in cell expansion suggested that the high-altitude species were able to grow at low temperatures by maintaining

significant cell wall extensibility; this capacity was lost by lowland species. Cell wall extensibility is the degree to which the cell walls can irreversibly extend due to turgor pressure. The cell walls of plants have both plastic and elastic properties; it is their plastic properties that are most important to growth. The ability to maintain growth at low temperature was negatively correlated with the rate of growth at higher temperatures, which was more dependent on cell turgor potentials.

Of possible relevance to the decline in stature with altitude, Hiesey *et al.* (1971) found that the stem height of low-altitude clones of *Mimulus cardinalis* increased more with CO₂ mole fraction (from 175 to 1250 $\mu\text{mol mol}^{-1}$) than the upland clone. However, as photosynthetic rates do not appear to decline with altitude (e.g. Körner and Diemer, 1987; Friend *et al.*, 1989), at least on a leaf area basis, it is unlikely that changes in the partial pressure of CO₂ on mountains are responsible for any plant height differences.

The effect of altitude-related changes in the environment on plant height has attracted much attention in terms of the control of the Alpine treeline. Daubenmire (1954) wrote the first review on treeline research, and later Wardle (1971) concluded that treelines are caused by winter desiccation producing death in trees unable to mature fully because of low rates of production of lignin, cuticle and epicuticular wax. This was supported by Tranquillini (1979), who has suggested that the principal cause of the Alpine treeline is winter desiccation, due to high evaporative demand, low root permeability and frozen soil water. Evergreen conifers are especially prone, with the cuticle of the youngest needles unable to develop fully in one short growing season. Baig and Tranquillini (1976) found that the cuticle and cutinized cell wall thicknesses decreased with elevation for stone (Arolla) pine (*Pinus cembra*) and Norway spruce (*Picea abies*) in Austria, causing needle damage and death at high altitudes. This was also found by DeLucia and Berlyn (1984) for *Abies balsamea*, though the cutinized cell wall thickness increased dramatically at the level of the Krummholz trees, whereas elsewhere it decreased with altitude. Stomatal density also increased with altitude, though not significantly, and measured rates of stomatal and cuticular water losses were very high at high elevations. It was concluded that the treeline of *A. balsamea* is caused by desiccation, a conclusion similar to that reached by Hadley and Smith (1986). Grace (1989) pointed out the correlation between summer temperatures and the treeline. The faster reduction in the temperature of photosynthesizing leaves in a tree canopy compared to short vegetation ultimately causes trees to fail to grow and reproduce. This was thought to occur when the mean temperature of the warmest month is below about 10°C. However, it is still not clear whether one main factor, or a number of interacting factors, limits tree distribution at high altitudes.

Chapin (1983) concluded that the characteristic morphologies, metabol-

isms and life-histories of alpine and arctic plants are so well adapted to low temperatures that their distribution was limited by the secondary effects of low temperatures on water and nutrient supply. These areas are both very poorly understood for high altitudes and latitudes. Körner and Larcher (1988) suggested that the most important influence of low temperatures on plants is on growth and development, but the results of ecophysiological experiments and observations of plant life in cold climates will not be fully understood until more basic developmental physiology is known. They suggested that selection for short plants at high altitudes may be due to increased warming closer to the ground surface, and that intrinsic low growth rates may be due to an adaptation to long-term low resource availability (see Grime, 1979, p. 30 *et seq.*). Reduced competition at high altitudes may make selection for reduced stature possible (e.g. Körner and Diemer, 1987). Woodward (1979a) found that growing *Phleum alpinum* at low temperatures caused the leaves to be thicker with larger cells. Similarly, Körner and Larcher (1988) found that the smaller leaves produced at low temperatures did not have smaller cells, suggesting that a low rate of cell division was responsible for their size; alternatively, they suggested that low rates of cell expansion might reduce the rate of mitosis by some process of negative feedback.

Important relationships between growth rate, low temperature hardening and tolerance to low temperatures can be inferred from the findings of Pollock *et al.* (1988). They found that the growth rates of *Lolium perenne* were negatively correlated with freezing tolerance and accumulation of soluble carbohydrate. Eagles (1967a, b) came to similar conclusions with regard to *Dactylis glomerata*.

F. Pigments

Bonnier (1895) found that lowland plants, when grown at high altitudes, produced many more chloroplasts in each cell than in their natural habitat, each chloroplast being darker than at lower altitudes. However, there is much evidence that leaves of *in situ* alpine plants contain less chlorophyll on both a leaf area and fresh weight basis than either lowland or arctic leaves (Henrici, 1918; Seybold and Eagle, 1940; Mooney and Billings, 1961; Mooney and Johnson, 1965; Billings and Mooney, 1968; Godfrey, 1969; Tieszen, 1970). There is also evidence that the ratio of chlorophyll a to b is higher for alpine plants than arctic plants (Tieszen, 1970), a characteristic of sun leaves, which also tend to have a greater ratio of chlorophyll a to b than shade leaves (Björkman, 1981, p. 67). Billings and Mooney (1968) and Billings *et al.* (1971) found that the reduced level of chlorophyll in alpine *Oxyria digyna* plants was under partial genetic control, and suggested that this may have been selected for as a mechanism for reducing damage by UV

irradiance. Tieszen and Helgager (1968) found that reduction of ferricyanide per unit chlorophyll was much greater for alpine than for near sea-level arctic clones of *Deschampsia cespitosa*. Similarly, Billings *et al.* (1971) found higher rates of photosynthesis per unit chlorophyll in alpine than in arctic ecotypes of *O. digyna*. Chlorophyll may also play a role in cold hardening. As mentioned with respect to T_o , Sicher *et al.* (1988) found that cold hardening in barley caused A_{\max} per unit chlorophyll to double, and despite a simultaneous reduction in chlorophyll concentration the photosynthetic rate increased by 30%. Clearly, the photosynthetic impact of a reduction in chlorophyll with altitude may be small because of the ability of plants to increase R^{mes} and A per unit chlorophyll.

Leaves of alpine species frequently contain a high concentration of anthocyanins, causing them to appear very dark (Billings and Mooney, 1968; Klein, 1978). Fitter and Hay (1987) suggested that this may be due to selection for increased absorption of solar radiation, and therefore enhanced leaf temperature. Klein (1978) described how high concentrations of anthocyanins may have been selected for, along with flavenoids and epidermal waxes, because of their ability to reduce damage from UV radiation.

G. Dark Respiration

At the same temperature, alpine species and populations frequently exhibit higher mitochondrial respiration rates (R_d) than those from the lowlands (e.g. Björkman and Holmgren, 1961; Mooney, 1963; Tranquillini, 1964, 1979; Mooney *et al.*, 1964; Klikoff, 1966, 1968; Billings and Mooney, 1968; Billings *et al.*, 1971; Chabot and Billings, 1972; Ledig and Korbobo, 1983). These include examples of genetic differentiation for increased dark respiration at high altitudes. Klikoff (1969) found that the low-temperature activities of isolated mitochondria from a number of widely distributed species were positively correlated with the altitude from which the populations were isolated. High mitochondrial respiration rates are probably an advantage for plants in cold climates because of the short, cool growing season for metabolic activity (Stewart and Bannister, 1974; Klikoff, 1968). There is much evidence that rates of dark respiration in some plants are enhanced if the plants are grown at low temperatures (Billings and Godfrey, 1968; Chatterton *et al.*, 1970; Chabot and Billings, 1972; Neama, 1982), the species with the widest altitudinal range exhibiting the greatest change in dark respiration rates (Chabot and Billings, 1972). However, a high dark respiration rate in the cold will mean a very high rate when warm and a rapid exhaustion of carbohydrate reserves (Crawford and Palin, 1981), hence possibly limiting altitudinal (e.g. Dahl, 1951; Stewart and Bannister, 1974) or latitudinal (e.g. Mooney and Billings, 1961) distribution. Elevated rates of dark respiration enable cold-climate plants to operate with enhanced specific

metabolic activities; they are probably a compensatory mechanism in response to low temperatures and will not cause excessive losses of carbon as long as the plants remain cold (Körner and Larcher, 1988).

The importance of dark respiration rates (R_d) for altitudinal distribution was highlighted by Graves and Taylor (1986, 1988). They found that the differential altitudinal distribution of the species *Geum rivale* (upland) and *G. urbanum* (lowland) could not be explained by a climatic limitation of relative growth rate (Graves and Taylor, 1986). They went on to show that the growth rate of *G. urbanum* roots was lower than that of *G. rivale* at low temperatures, and suggested that this may be due to lower rates of root respiration. *G. urbanum* was thought to be unable to use the excess assimilate it was capable of producing at low temperatures because of inherently low R_d , and hence was limited to lower, warmer altitudes (Graves and Taylor, 1988).

Because dark respiration occurs mainly at night, when leaf temperatures are closely tied to the air temperature, the ambient temperature for dark respiration will decrease with altitude. Thus the respiration rates of plants may be similar at all altitudes.

H. Photorespiration

Like dark respiration, photorespiration at high temperatures is enhanced by cold acclimation (e.g. Mächler and Nösberger, 1978; Neama, 1982). The ratio of CO_2 to O_2 remains approximately constant with altitude (Barry, 1981), and hence photorespiration changes will be influenced primarily by temperature (Brooks and Farquhar, 1985). Genotypic adaptation to low temperatures may restrict the distribution of plants in higher-temperature regions because of excessive photorespiration (Zetlich and Day, 1973). High-altitude ecotypes of some species (e.g. *Trifolium repens*: Mächler *et al.*, 1977; Mächler and Nösberger, 1978) exhibit higher photorespiration at high temperatures than low-altitude ecotypes. The ratio of Rubisco to phosphoenolpyruvate carboxylase has also been observed to increase with altitude in the alpine plant *Selinum vaginatum* (Pandey *et al.*, 1984), reflecting the reduced advantage of C_4 metabolism as temperature is reduced.

J. Non-enzymic Biochemical Changes

Golley (1961) described a significant increase in the calorific content of plants from tropical to temperate to alpine environments. Bliss (1962b) suggested that this increase may result in part from the greater lipid content in alpine tundra plants. He further suggested that the high rates of R_d found in arctic and alpine plants may be provided by lipid-rich reserves as well as carbohydrates, and that the high R_d rates may account for rapid growth and

development at low temperatures. The implications of these findings for estimates of primary productivity and yield were discussed by Billings and Mooney (1968). They described how alpine shrubs and herbs have higher calorific values than many tropical and temperate plants, especially in evergreen prostrate shrubs, because of their high lipid content. Zachhuber and Larcher (1978) found that the content of energetically expensive compounds increases with altitude in plant tissue. Baruch (1982) found an increase in calorific energy content of giant rosettes with altitude in Venezuela, and argued that this increase in energy content is consistent with the views of Grime (1979) on stress tolerators. Grime describes stress tolerators as plants with low growth rates and a capacity to store and conserve captured resources. These plants must be able to store energy (and nutrients) for environmentally unfavourable periods, in terms of growth, and hence allow rapid development when a brief favourable period arrives. However, McCown (1978) suggested that increased lipid content is not the result of increased storage but simply of rapid synthesis. Levitt (cited in Grill *et al.*, 1988) suggested that resistance to frost requires increased thiol contents, this being important for the stability of cell structure and frost resistance. Increased levels of thiols were found by Grill *et al.* (1988) in high-altitude grown Norway spruce (*Picea abies*). With regard to the storage and transport of metabolites, Berry and Raison (1981) highlighted how movement of assimilate in plants is highly sensitive to temperature. The importance of this at high altitudes is unexplored.

IV. MODELLING THE EFFECTS OF ALTITUDE ON PLANT GAS EXCHANGE

A. General

The discussion on the effects of altitude-related changes in CO_2 partial pressure and temperature on photosynthetic rate and stomatal conductance indicates considerable degrees of freedom in plant responses. The limited observations that have been obtained in the field (Körner and Diemer, 1987; Friend *et al.*, 1989) indicate that mesophyll and stomatal conductance increase with altitude, while A_{max} either increases or is unchanging. In this work, the vegetation was herbaceous at both low and high altitudes, with measurements of gas exchange usually made at constant leaf-to-air water vapour pressure deficit (VPD). However, stomatal conductance is sensitive to VPD (Lösch and Tenhunen, 1981), a feature which will influence *in situ* stomatal conductance and photosynthetic capacity. Despite this limitation in the range of environments for analysis, Körner and Diemer (1987) were able to state unequivocally that the increase in mesophyll conductance with

altitude exceeded that observed for stomatal conductance. As a consequence, the ratio p_i/p_a decreased with altitude, indicating an increasing stomatal limitation of CO_2 uptake. This conclusion was strengthened by a global survey of $\delta^{13}\text{C}$ along altitudinal gradients (Körner *et al.*, 1988), which indicated that the time integrated measure of p_i/p_a , as extracted from the measurements of $\delta^{13}\text{C}$ ratios (Farquhar *et al.*, 1982), also decreased with altitude. However, the variation of the measurements of $\delta^{13}\text{C}$ were very large. This in part must reflect varying degrees of leaf shading, or perhaps stomatal closure due to high leaf temperatures or short-term drought. Both of these effects will influence $\delta^{13}\text{C}$ (Farquhar *et al.*, 1982).

Additional sources of variation which need to be considered are those due to variations in plant height and, therefore, the aerodynamic coupling between the vegetation and the air above. Tall vegetation will be well coupled, with a temperature close to air temperature, whereas dwarf vegetation may be less well coupled, with a temperature often very different from that of the air (McNaughton and Jarvis, 1983). These temperature variations will directly influence the photosynthetic rate (Grabherr and Cernusca, 1977; Carter and Smith, 1985). Stomatal conductance may also be influenced directly by temperature (Jarvis, 1976). In addition, the *VPD* of the leaves, and therefore stomatal conductance, will be strongly influenced by temperature and aerodynamic coupling.

The parallel findings of Körner and Diemer (1987), with *in situ* observations at constant *VPD*, and Körner *et al.* (1988), with *in situ* observations over a range of *VPDs*, encourage the view that these effects of temperature, aerodynamic coupling and plant stature are either unimportant or, perhaps, balance out and have little impact on the relation between CO_2 supply to, and fixation at, the chloroplast. The problem is that neither $\delta^{13}\text{C}$ nor the value of p_i/p_a indicate the absolute values of stomatal and mesophyll conductances, or rates of photosynthesis and transpiration. In view of the many aspects of microclimate which can influence these conductances and rates, it seems clear that a model which could identify the sensitivity of $\delta^{13}\text{C}$ to microclimate is an important development, for clarification and for considering the large variance shown by Körner *et al.* (1987).

A model of vegetation gas exchange and energy balance has therefore been developed with the specific aim of investigating the relationship between canopy height (Fig. 6), canopy energy balance, leaf area index (*LAI*), photosynthetic rate, stomatal and boundary layer conductances and $\delta^{13}\text{C}$.

B. Model Development

1. CO_2 Exchange

Central to the model are the data obtained by Körner and Diemer (1987) for A/p_i curves (Fig. 7, page 73), at saturating irradiance, of a very large selection

of herbaceous species at altitudes of 600 and 2600 m. The averaged results from these observations are used in this model, no account being taken of expected differences in photosynthetic capacities between plants of different stature (e.g. trees vs. herbs). They indicate that the initial slope of the A/p_i curve (g_m) increases with altitude, as does the transition point from the Rubisco to the RuP₂ limitation of photosynthesis. However the A/c_i curve (from Körner and Diemer, 1987) is virtually unchanging with altitude, as is A_{\max} , such that:

$$A = \frac{A_{\max}}{(275 - c_{i,r})} \quad (3)$$

where $A_{\max} = 18.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $c_{i,r}$ is the CO₂ compensation point where $A = 0$. Bauer *et al.* (1983) have shown that the CO₂ compensation point is a conservative property of a wide range of species with C₃ metabolism.

However, it is temperature-sensitive according to the following relationship:

$$c_{i,r} = 23.71 + (0.695 \times T_c) + (0.062 \times T_c^2) \quad (4)$$

where $c_{i,r}$ is measured in $\mu\text{mol mol}^{-1}$ and T_c is temperature ($^{\circ}\text{C}$).

Körner and Diemer (1987) showed that the optimum temperature for photosynthesis decreases slightly, by 2.7°C over 2000 m of altitude. In addition, the photosynthetic response to temperature is quadratic, as has been shown elsewhere (Ehleringer and Björkman, 1978). The estimate of A from (3) must therefore be modified in terms of leaf temperature. The following quadratic equation includes, and assumes, a linear decrease in the optimum temperature for photosynthesis with altitude, plus the quadratic response to temperature from the data of Körner and Diemer (1987):

$$A_t = A \times 0.01 \times [(-13.52 \times (0.0136 \times z)) + (9.128 - (0.000645 \times z)) \times T_c] - ((0.182 + (0.0000015 \times z)) \times T_c^2) \quad (5)$$

where z is altitude (m) and A_t is the temperature-adjusted photosynthetic rate. Given an estimate of the stomatal and boundary layer conductances to CO₂ uptake (from eqns 17, 19, 21 and 34) it then becomes possible to estimate c_i :

$$c_i = \frac{((c_{i,r} \times g_m) + (c_a \times g))}{(g_m + g)} \quad (6)$$

where g_m is the mesophyll conductance ($\mu\text{mol m}^{-2} \text{s}^{-1}$), g is the combined stomatal and boundary layer conductance to CO₂, and c_a is the ambient CO₂ mole fraction ($345 \mu\text{mol mol}^{-1}$). The mesophyll conductance is determined from the relationship:

$$g_m = \frac{A_t}{(0.000275 - c_{i,r})} \quad (7)$$

The predicted photosynthetic rate, A_a , may then be calculated from:

$$A_a = g_m \times (c_i - c_{i,r}) \quad (8)$$

The intercellular mole fraction of CO_2 , c_i , may be adjusted for the confounding effect of the opposing mass flow of water vapour through the stomata (estimated by the rate of transpiration ET , $\text{mol m}^{-2} \text{s}^{-1}$, which is in turn calculated from eqn 28) according to the equation (von Caemmerer and Farquhar, 1981):

$$c_i = \frac{((g - ET/2) \times c_a) - P}{g + ET/2} \quad (9)$$

The $\delta^{13}\text{C}$ of the leaf may then be predicted from the following equation (from Farquhar *et al.*, 1982):

$$\delta^{13}\text{C} = -7.8 - (4.4 \times \frac{(c_a - c_i)}{c_a}) - 27 \times \frac{c_i}{c_a} \quad (10)$$

2. Energy Balance

The radiant energy balance of the leaf, or canopy, determines leaf temperature. One aim of this model is to predict the effect of changing environmental conditions, at different altitudes, on some typical and initial stomatal conductance, g_o , to water vapour. For the simulations described here, g_o is equal to $275 \text{ mmol m}^{-2} \text{ s}^{-1}$, a value typical of those observed by Körner and Diemer (1987) and Friend *et al.* (1989).

A number of physical properties in the energy balance equation are influenced by either altitude or temperature, or both. These are described below, using data provided in Monteith (1973), Jones (1983), Woodward and Sheehy (1983) and Landsberg (1986).

The change of pressure with altitude is described in (1). The change in the saturation vapour pressure (Pa) with temperature, e_{svp} is:

$$e_{svp} = 6.108 \times \exp((17.269 \times T_c)/(237.3 + T_c)) \times 100 \quad (11)$$

The latent heat of vaporization (λ , J g^{-1}) changes with temperature as:

$$\lambda = 2500 - (2.367 \times T_c) \quad (12)$$

The psychrometric constant (γ , Pa K^{-1}) changes with pressure as:

$$\gamma = \frac{P \times c_p}{0.622 \times \lambda} \quad (13)$$

where c_p is the specific heat capacity of air ($1.012 \text{ J g}^{-1} \text{ K}^{-1}$). The density of air (ρ , g m^{-3}) is dependent on temperature and atmospheric pressure (P , Pa):

$$\rho = \frac{P}{101325} \times (1288.4 - (4.103 \times T_c)) \quad (14)$$

The diffusion coefficients of water vapour (D_h , $0.0000242 \text{ m}^2 \text{ s}^{-1}$ at N.T.P.) and CO_2 (D_c , $0.0000147 \text{ m}^2 \text{ s}^{-1}$ at N.T.P.) are sensitive to both temperature and pressure. These effects may be incorporated as:

$$D_a = D \times \frac{(T_k)^{1.75}}{293} \times \frac{(101325)}{P} \quad (15)$$

3. Sensible Heat Transfer

Meteorological station data, or some given value of wind speed, are used to determine the boundary layer conductance to momentum ($g_{n,a}$, in non-molar units of m s^{-1}) by vegetation differing in height (h , m), and leaf area index (LAI). It is assumed that wind speed (u , m s^{-1}) is measured at 10 m (u_{10}) above the ground. This speed is adjusted to a reference height of 50 m (u_{50}), which exceeds the maximum canopy height used in the model simulations, by:

$$(u_{50}) = (1.219 + (0.038 \times h)) \times (u_{10}) \quad (16)$$

The boundary layer conductance of the vegetation is then calculated as follows – ignoring the effects of buoyancy and the radiative conductance (Jones, 1983); and assuming that the conductance to momentum is equal to the conductance for sensible heat:

$$g_{n,a} = \frac{0.168 \times u_{50}}{(\log_e(50 - d))^2 / z_0} \quad (17)$$

where d is the displacement height ($0.7 h$) and z_0 is the roughness length. The roughness length may be estimated as $0.1 h$, or the effects of plant spacing on z_0 may be approximated from LAI (this assumes that as LAI decreases plant spacing increases), in a simplified linear-log relationship of Garratt (1977) and Landsberg (1986). Roughness length may then be estimated as:

$$z_0 = \exp(-3.51 + (0.62 \times \log_e(LAI))) \times h \quad (18)$$

The boundary layer conductance and the stomatal conductance may be converted between molar units (as in eqns 6, 7, 8 and 9) and non-molar units (g_n , as in eqn 17) as follows:

$$g_n = g \times \frac{(R \times T_k)}{P} \quad (19)$$

where g has units of $\text{mol m}^{-2} \text{s}^{-1}$, R is the gas constant and T_k is temperature (K). Molar units are used here when predicting rates of photosynthesis, while non-molar units are used in the energy balance predictions.

4. Canopy Transfer Characteristics

The initial stomatal conductance, g_0 , is likely to have a direct response to temperature, with a peak conductance at some optimum temperature. Observations of this nature are limited, but on the basis of Jarvis (1976) a quadratic relation between conductance and temperature has been assumed, with the same coefficients as for the photosynthetic response to temperature (eqn 5). This stomatal conductance is for a leaf, but given a knowledge of canopy LAI , the distribution of LAI into strata (LAD) within a canopy (Woodward, 1987a), and the penetration of solar radiation through the canopy, the canopy conductance g_c may be calculated as follows:

$$S_i = S_0 \times \exp(-0.5 \times \sum LAD) \quad (20)$$

where S_0 is the incident irradiance (W m^{-2}), S_i the irradiance at stratum i within the canopy, $\sum LAD$ is the sum of the LAD from the top of the canopy to layer i and -0.5 is a typical extinction coefficient for radiation within the canopy (Woodward, 1987).

The decline in irradiance through the canopy causes a decrease in stomatal conductance as (from Woodward, 1987a):

$$\frac{1}{g_i} = \frac{1}{g_0} + \frac{710}{S_i} \quad (21)$$

Canopy stomatal conductance is then estimated from:

$$g_c = \sum_{i=1}^{i=5} (g_i \times LAD_i) \quad (22)$$

where LAD_i is the LAD of layer i . The canopy has been divided into 5 strata (from Woodward, 1987a) and the following fractions of canopy LAI are found in the five layers: LAD_1 (top) 0.11; LAD_2 0.38; LAD_3 0.26; LAD_4 0.21; LAD_5 0.04.

The canopy boundary layer conductance is determined from the wind speed profile (eqn 17). This conductance needs to be apportioned to each stratum of the canopy, so that leaf photosynthesis (eqn 8) can be predicted for leaves in the top (or any) layer of the canopy. The heights of the canopy strata are arranged as follows: $LAD_1 = 0.9 h$; $LAD_2 = 0.7 h$; $LAD_3 = 0.5 h$; $LAD_4 = 0.3 h$; $LAD_5 = 0.1 h$. The fractional height f_i therefore has values from 0.9 to 0.1, moving from the top to the bottom of the canopy.

The wind speed at 50 m above ground surface has been estimated (eqn 16), as has the canopy boundary layer conductance (eqn 17). These measurements may then be used to calculate the eddy velocity, u_* :

$$u_* = \sqrt{u_{50} \times g_{n,a}} \quad (23)$$

The wind speed at the top of the canopy, u_h , may then be estimated from:

$$u_h = \frac{u_*}{0.41} \times \log_e \frac{(h-d)}{z_0} \quad (24)$$

It is difficult to predict the wind speed within the canopy, but taking the lead of Landsberg (1986), wind speed at depth i in the canopy is estimated from:

$$u_i = u_h \times \exp(-3 \times (1 - f_i)) \quad (25)$$

The expected boundary layer conductance at a wind speed u_i is then calculated for each level of the canopy (from eqn 17). The inverse of these conductances (resistances) act in parallel for the loss of sensible and latent heat. The parallel sum of these resistances is then added and multiplied by a coefficient so that $1/g_{n,a}$ estimated from eqn 17 equals the parallel sum of these resistances. The boundary layer conductance of any layer i may then be extracted.

The conductances to water vapour (in molar units) are converted to the total canopy conductance to CO_2 by:

$$\frac{1}{g_{CO_2}} = \frac{(D_h/D_c)}{g_c} + \frac{1.37}{g_a} \quad (26)$$

5. Calculating the Energy Balance

The canopy stomatal and boundary layer conductances are used in the equation of the energy balance of the canopy. In addition, the response of stomatal conductance to VPD and the aerodynamic coupling between the canopy and the climate above, as measured at a meteorological station, must

also be incorporated. This is achieved using the model described by Choudhury and Monteith (1986). It has not been feasible to model the VPD profile through the canopy (McNaughton and Jarvis, 1983) and so the response of the total canopy conductance (g_c) to VPD has been modelled. Choudhury and Monteith (1986) use non-molar units in their models and this approach is carried on here, so that:

$$g_{n,c} = g_{n,c,0} \left(1 - \frac{VPD}{VPD_m}\right) \quad (27)$$

where VPD is the VPD of the air, as measured at a meteorological station and VPD_m is the VPD at which $g_{n,c}$ is zero, because of the stomatal response to VPD (Lösch and Tenhunen, 1981). There are few measurements of VPD_m , and so the value of 7000 Pa, as selected by Choudhury and Monteith (1986) for annual crops and deciduous trees, has been used.

The VPD -dependent value of $g_{n,c}$, and the canopy boundary layer conductance $g_{n,a}$, are incorporated in the Penman-Monteith equation (Monteith, 1981) to predict canopy transpiration (ET , $W m^{-2}$):

$$ET = \frac{s \times R_n + \rho \times C_p \times g_{n,a} \times VPD}{s + \gamma(1 + g_{n,a}/g_{n,c})} \quad (28)$$

where s is the change of saturation vapour pressure with temperature ($Pa K^{-1}$).

The temperature dependence of s is determined as:

$$s = 48.7 \times \exp(0.0532 \times T_c) \quad (29)$$

R_n is the net radiant balance of the canopy and is determined by iteration of the following two equations and eqn 28, by varying canopy temperature ($T_{k,c}$, in K):

$$R_n = L_d + (-0.95 \times s \times T_{k,c}^4) + ((S_0 \times (1 - \exp(-0.5 \times LAI))) - (S_0 \times (r \times (1 - \exp(-0.5 \times LAI))))) \quad (30)$$

$$0.96 \times R_n = C + ET \quad (31)$$

where L_d is the downward flux of long wave radiation ($W m^{-2}$) from the atmosphere (Monteith, 1973) calculated from the air temperature ($T_{c,a}$):

$$L_d = 208 + (6 \times T_{c,a}) \quad (32)$$

In eqn 30, LAI may either be the canopy leaf area index or a modification of

the plant leaf area index (LAI_p). The modification may be incorporated when leaf area index is low and individual plants are somewhat isolated (a feature incorporated in eqn 18). The end result of this situation is that plant leaf area index will exceed the mean canopy leaf area index (Woodward, 1987a). In this situation, the equation $LAI_p = \exp(-0.05 \times LAI)$ has been employed.

The constant 0.96 in eqn 31 allows for the flux of radiation into the soil beneath the plant canopy. The net radiant balance of the canopy calculates the input of longwave radiation (L_d), and the input of solar radiation (S_0), minus the fraction of solar radiation penetrating through the canopy ($S_0 \times (1 - \exp(-0.5 \times LAI))$), which is dependent on leaf area index (LAI) and the extinction coefficient (-0.5). In addition, the proportion of reflected solar radiation is calculated from ($S_0 \times (r \times (1 - \exp(-0.5 \times LAI)))$), where r is the canopy albedo (typically 0.15). The upward flux of long wave radiation from the canopy is calculated using the Stephen-Boltzmann equation, where s is the Stephen-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$).

In eqn 31, the radiant balance of the canopy is balanced by transpiration (eqn 28) and by sensible, or convective, heat loss (C , W m^{-2}):

$$C = (\rho \times C_p(T_{k,a} - T_{k,s})) \times g_{n,c} \quad (33)$$

The Penman-Montieth equation (eqn 28) treats the plant canopy as a single layer of leaves, a treatment which excludes the necessity of calculating VPD profiles within the canopy. However, an important variable in eqn 28 is the VPD itself. The data input for VPD is the VPD of the air, but stomata respond to the VPD between the canopy surface temperature and the air, at some reference height. Choudhury and Monteith (1986) assume that the VPD of the air at the reference height is independent of the vegetation beneath. However, this may not be so, with differences occurring between aerodynamically rough and smooth surfaces (McNaughton and Jarvis, 1983). Due to uncertainty in this respect (Paw and Gao, 1988), and following Choudhury and Monteith (1986), this aspect of the model is not included. The approach of Choudhury and Monteith (1986) to estimate the "canopy VPD ", i.e. the VPD that all of the stomata in the canopy respond to, VPD_c , has also been employed. The reference height VPD is retained in eqn 28 but the effect of VPD on stomatal conductance (eqn 27) is modified as:

$$g_{n,c} = g_{n,0} \frac{(1 - VPD_c)}{VPD_m} \quad (34)$$

where VPD_c is estimated from:

$$VPD_c = \{b - (b^2 - 4 \times a \times h)^{0.5}\} / 2 \times a \quad (35)$$

where,

$$\mathbf{a} = (1 + s/\gamma)(g_{n,0}/(g_{n,a} \times VPD_m)) \quad (36)$$

and,

$$\mathbf{b} = 1 + (1 + s/\gamma)(g_{n,0}/g_{n,a}) \quad (37)$$

and,

$$\mathbf{h} = VPD + s \times R_n/(\rho \times C_p \times g_{n,a}) \quad (38)$$

C. Model Simulations

The model described above has been applied using climatic data for the Austrian Alps (from Müller, 1982; Körner and Diemer, 1987). The responses of vegetation, ranging in height from 0.031 to 32 m, to the climatic gradient over an altitudinal range of 3000 m, have been investigated. The mean sea-level climate and the lapse rates of the selected and various climatic variables are shown in Table 1.

The responses of stomatal conductance, photosynthetic rate and $\delta^{13}\text{C}$ of leaves in the top layer of the canopy and the mean canopy temperature have been investigated. Fig. 8 shows the results of a simulation which assumes that *LAI* decreases with altitude, according to the relation (from data presented by Körner and Mayr, 1981):

$$LAI = 7 \times \exp(-0.001056 \times z) \quad (39)$$

where z is altitude (m). Over this altitudinal range, plant height decreases (Fig. 6) from 25 m at an altitude of 800 m, to 0.05 m at 2500 m.

From Fig. 8, it may be seen that canopy temperatures will increasingly

Table 1
Climatic conditions for model simulation

Mean temperature at 0 m	21.9°C
Temperature lapse rate	-6.5°C km ⁻¹
Relative humidity at 0 m	64%
Lapse rate in relative humidity	2.7% km ⁻¹
Irradiance at 0 m	800 W m ⁻²
Lapse rate in irradiance	80 W m ⁻² km ⁻¹
Wind speed at 0 m	4 m s ⁻¹
Lapse rate of wind speed	1 m s ⁻¹ km ⁻¹

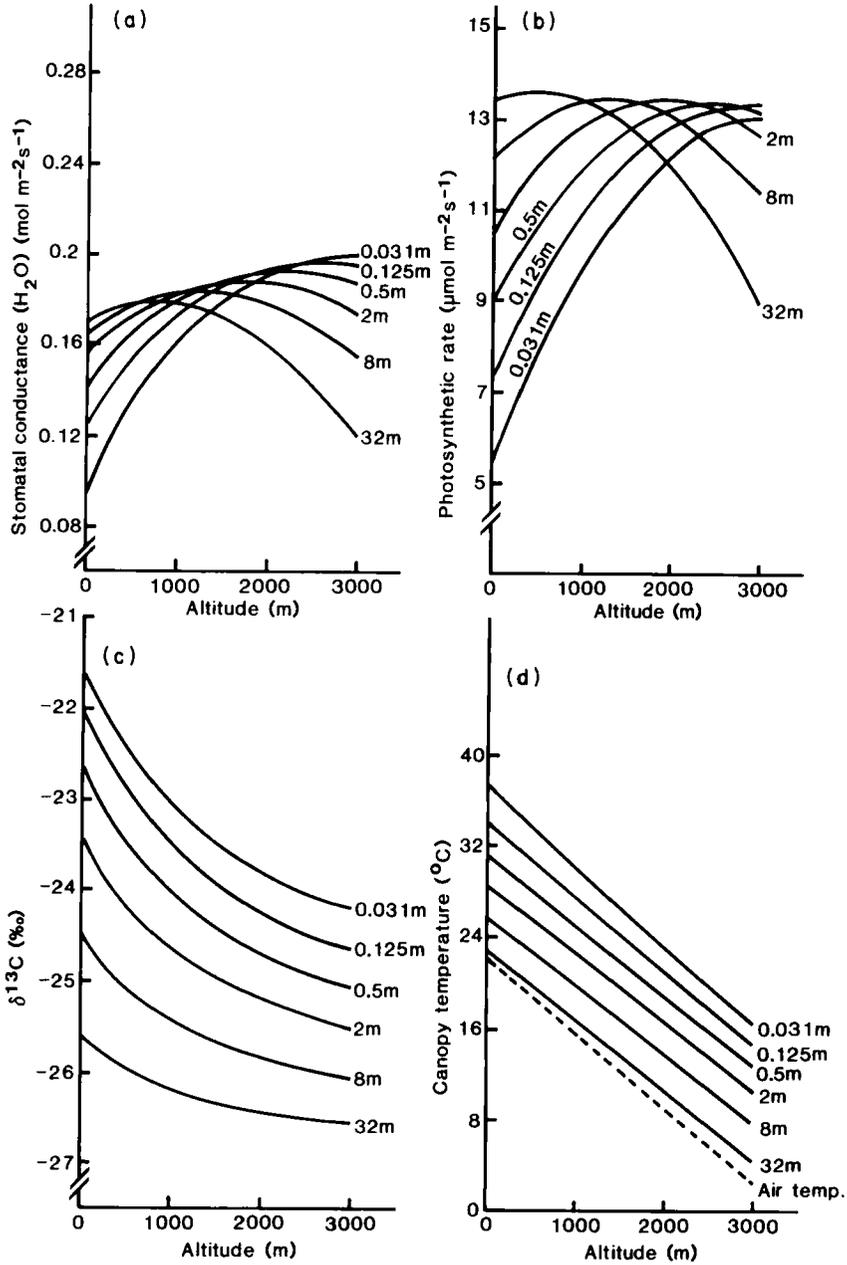


Fig. 8. Model simulations of the responses of (a) stomatal conductance, (b) photosynthetic rate, (c) $\delta^{13}\text{C}$ and (d) canopy temperature, to the changes in climate with altitude and to vegetation height.

exceed air temperature, with altitude, and as vegetation stature decreases. For vegetation 32 m tall, the temperature excess (for the maximum daily irradiance) does not exceed 2°C, while for vegetation 0.03 m high the excess may be 16°C. These values are similar to those observed by Körner and Cochrane (1983) in the southern hemisphere.

The absolute temperature of the vegetation influences stomatal conductance and photosynthesis by the quadratic responses of these processes to temperature (eqn 5). In addition, the reference height and "canopy" *VPDs* decrease with altitude. As a consequence, the responses of photosynthesis and stomatal conductance are broadly quadratic with altitude. For dwarf vegetation in the lowlands, the temperature is supraoptimal for photosynthesis and stomatal conductance. However, as altitude increases, the optimal temperature is approached. For tall vegetation, temperature is suboptimal at altitude.

The maximum rate of photosynthesis predicted for vegetation of any stature remains about constant with altitude. In contrast, maximum stomatal conductance increases. These findings agree with the observations of Friend *et al.* (1989) on Scottish mountains.

The predictions also agree with the observations of Körner and Diemer (1987), the originators of the raw data in the model. However, it should be pointed out that their observations were obtained at a constant *VPD* and therefore independently of the canopy boundary layer conductance.

The $\delta^{13}\text{C}$ of leaves in the top of the plant canopy decreases with altitude, a trend which is opposite in sign from the global observations of Körner *et al.* (1988). However, there is a marked effect of vegetation height on $\delta^{13}\text{C}$. Assuming that the majority of carbon fixation occurs in the highest irradiance, which is the environment selected in the model simulation, there could be $\delta^{13}\text{C}$ differences between the tallest and shortest canopies in the order of 4‰. This difference is equivalent to the trend in $\delta^{13}\text{C}$ associated with a 6000 m change in altitude (Körner *et al.*, 1988).

Körner *et al.* (1988) found significant differences between trees, shrubs and herbs in $\delta^{13}\text{C}$. This difference is most likely to be due to the generally lower stomatal conductances and rates of photosynthesis in trees and shrubs, in comparison with herbs (Larcher, 1980; Jarvis, 1976).

If the typical plant height is assumed to be about 32 m at sea-level, decreasing to 0.03 m at 3000 m, then $\delta^{13}\text{C}$ should increase from -25.7‰ at 0 m to -24.2‰ at 3000 m, a trend which is about 70% of the trend measured by Körner *et al.* (1987). It does seem possible to interpret global trends of $\delta^{13}\text{C}$ in vegetation, at least partially, in terms of plant height, and therefore boundary layer conductance.

The influence of *LAI* alone on the model predictions is shown in Fig. 9. In this case, *LAI* has a constant value of 1, simply simulating the observation on some Scottish mountains where sheep grazing may be intense at all altitudes.

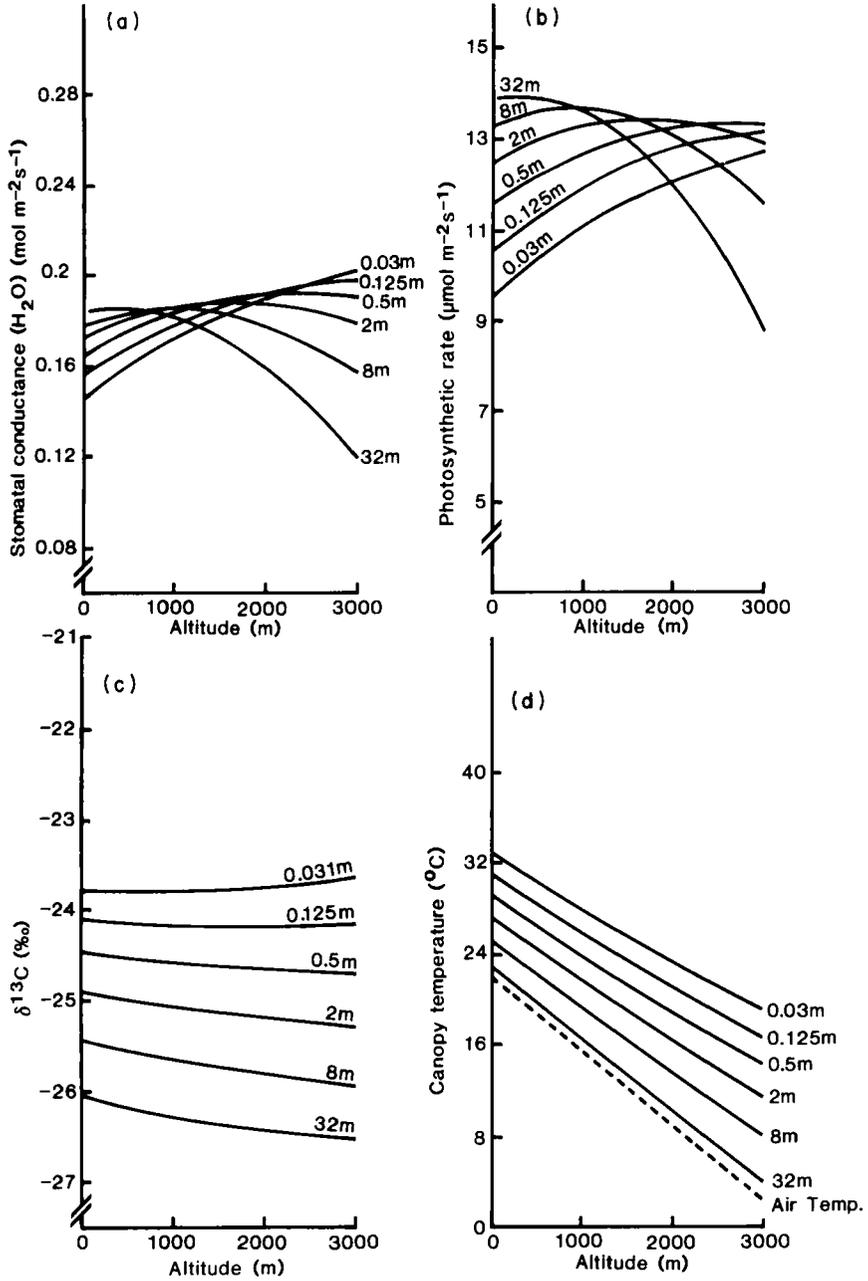


Fig. 9. As Fig. 8, but $LAI = 1$ at all altitudes.

The effect of the change in LAI is to flatten the response of $\delta^{13}C$ to altitude. For vegetation of 0.125 m and less, $\delta^{13}C$ is constant with altitude, a response observed by Friend *et al.* (1989). However, the altitudinal trend in photosynthetic rate and stomatal conductance, for vegetation of a fixed stature, such as 0.125 m, is rather less than that for vegetation which shows a decrease in LAI with altitude (Fig. 8). This effect is due to the change in canopy excess temperature at constant LAI . In this case (Fig. 9), the excess increases with altitude, so that vegetation of height 0.031 m has a temperature range from 33°C at sea-level to 19°C at 3000 m. For the case of decreasing LAI with altitude (Fig. 8), vegetation of the same stature would have a temperature range from 37 to 16°C.

It appears therefore that vegetation stature and LAI can strongly influence plant $\delta^{13}C$, and presumably lead to significant variation in global surveys of $\delta^{13}C$. The variations of $\delta^{13}C$ in the model simulations result from the effects of vegetation stature and LAI on boundary layer conductance, canopy temperature and VPD . These responses, in turn, influence photosynthesis and stomatal conductance. Given this strong effect, it appears surprising that gas exchange measurements on leaves isolated from the vegetation canopy, and at a constant VPD , show such efficiency in predicting altitudinal trends in plant $\delta^{13}C$.

V. PLANT EVOLUTION IN THE MOUNTAIN AERIAL ENVIRONMENT

A. Historical and Geographical

Billings (1974b) gave a good account of the possible origins and evolution of alpine floras. These mountain plants spread in the late Tertiary and Pleistocene, moving upwards and possibly evolving. The present-day floras of temperate mountain chains are the products of migration and natural selection subsequent to the last Pleistocene ice age. Bliss (1962a) related the importance of establishing the areas of periglacial survival from which populations subsequently migrated, and comparing this to the present-day distributions. He remarked how good use could be made of autecological and cytogenetic studies for this purpose. Many of the plants which now make up the European mountain floras are thought to have survived the last ice age to 14 000 years ago in the Mediterranean region; others survived in the more northern unglaciated steppe and tundra regions (Grabherr, 1987), recolonizing as the climate ameliorated. This was put eloquently by Darwin (1859, p. 367):

As the warmth returned, the arctic forms would retreat northward, closely followed up in their retreat by the productions of the more temperate regions.

And as the snow melted from the bases of the mountains, the arctic forms would seize on the cleared and thawed ground, always ascending higher and higher, as the warmth increased, whilst their brethren were pursuing their northern journey. Hence, when the warmth had fully returned, the same arctic species, which had lately lived in a body together on the lowlands of the Old and New Worlds, would be left isolated on distant mountain summits (having been exterminated on all lesser heights) and in the arctic regions of both hemispheres.

During the ice ages, the lowland periglacial plains of Europe were rich in arctic-alpine and boreal species, and some alpine plants survived on nunataks, and re-established in a downward direction (Godwin, 1956, pp. 297, 319–320). It should not be forgotten that vegetation change since the end of the last ice age has not been a simple successional process, as alternating periods of warmer and colder climates have caused fluctuations in species distribution. Because of the ecological and geographical isolation of mountains, vicariance, speciation and genetic drift are thought to have occurred frequently. Alpine regions are floristically diverse, the European Maritime Alps containing more species than the whole of Germany (Grabherr, 1987). The migration of species after the last ice age is thought to have brought formerly isolated but closely related species into contact, with subsequent hybridization and possibly the production of allopolyploids.

B. General

Changes in environment with altitude are important in causing genetic differences within plant populations (e.g. Slatyer, 1977; Ledig and Korbobo, 1983). Indeed, the classic demonstration of ecotypes was made for populations from different altitudes (Turesson, 1931). As described in Section III, many of the genetic differences found between populations at different altitudes appear to be of selective advantage, such as those that cause differences in the optimum temperature for photosynthesis (T_o) (e.g. Fryer and Ledig, 1972). However, Larcher (1983) warned that typical morphological and physiological responses may not be directly adaptive, but incidental and not essential for fitness and survival at high altitudes. Awareness of a panglossian approach in mountain plant ecology is as important as in other areas of biology (Gould and Lewontin, 1979).

It is important to point out that even if there were no genetic differentiation with altitude, the word adaptation may still be applicable when discussing plasticity, such as that found by Bonnier (1895) and Clements *et al.* (1950). Acclimation (in the sense that Bonnier, 1895, used “adaptation” to mean changes in development which occur in response to the environment of a plant during growth) may be of primary interest, but if it is important to establish whether modifications in plants with altitude are selective adaptations, or whether they are simply the passive consequence of the environ-

ment, a problem presents itself with regard to plasticity. Does a modification of physiology that can be induced in a leaf by growing it in an appropriate environment, and which increases the plant's ability to pass its genes on to future generations in that environment, constitute an adaptation? This question is not easily resolvable. Indeed, it was the great plasticity of plants, particularly in response to growth at different altitudes, that led Bonnier (1920) and Clements *et al.* (1950) to conclude that there is no reason to invoke natural selection in the formation of new species. It is perhaps best to avoid the use of the word adaptation and concentrate on those works where genetic differentiation with respect to altitude is proven. This includes differences between species which have restricted altitudinal distributions, implying that these differences may be, in some way, responsible for their different distributions.

Perhaps with some surprise we find that it is not at all obvious which environmental or plant processes are important for plant success at high altitudes (Körner and Diemer, 1987). Grabherr (1987) wrote that it is because of the relatively low importance of any one environmental factor that a specific alpine plant type has not evolved. There are, however, examples of convergent evolution, such as unbranched, or little branched, giant rosette plants in the tropics (Smith and Young, 1987), and cushion-type plants in more temperate regions (Bliss, 1962a).

With increased altitude there is probably less inter-plant competition for light, water and nutrients (Körner and Renhardt, 1987). Thus the potential for natural selection driven by competition for these resources is perhaps reduced. This view is reinforced when considering the preponderance of apomixis and vegetative reproduction in alpine areas, with a resultant decrease in genetic variation, although Silander (1985) suggested that clonal plants may not necessarily be less genetically diverse than sexual ones. It seems possible that the upper distributional limits of plants on mountains are not set primarily by competition, with the capacity for leaf and root growth, long-term carbon balance and low-temperature survival being of greater importance (Bunce *et al.*, 1979). K-type selection may therefore be more likely at high than low altitudes (Bliss, 1985), and one might thus expect to find life-histories that correspond to the "stress-tolerators" of Grime (1979). Present-day alpine floras may consist mostly of those genera and species which possessed sufficient plasticity of physiology and morphology to survive the incumbent environment. Adaptation need not be invoked to explain features typically associated with alpine plants.

VI. CONCLUSIONS AND SUGGESTIONS FOR FURTHER WORK

Plants growing on mountains experience reduced temperatures and vapour pressures with altitude, as well as a reduction in the partial pressure of air.

The most obvious general trend in plant morphology is a decrease in stature with increasing altitude. When examined in more detail there are many other morphological, physiological and biochemical features of plants which change with altitude. However, whether these changes are direct consequences of the changing environment, or are the result of genetic differentiation, has only rarely been ascertained. It is possible to explain many of the changes with altitude as being developmental responses to the environment alone, with no genetic component. However, such plasticity may have been selected for if it thus results in greater fitness in many environments.

The observed increased efficiency of carbon uptake with increased altitude might be entirely due to the influence of low temperature on leaf development, as could be the increases in A_{\max} . Controlled environment and reciprocal transplant studies could easily test this. Of worthy investigation is the control of stomatal density, and whether the observed increases with altitude have any effect on maximal conductance in the field.

T_o is frequently found to fall with altitude, but again this could be due to developmental responses to low temperature alone. We need to know its biochemical explanation, particularly the role played by phosphate and Fru- P_2 phosphatase levels, and changes in the K_m of critical enzymes by low temperatures. The possibility of alterations in metabolic pool control at different temperatures should also be addressed. We need to have a much more general picture of the relationship between genetically controlled stature and altitude. At low temperatures, is it cell expansion or cell division rate which limits growth, or is there some form of self-regulating system between the two? What is the importance of cell-wall extensibility? Is it really this aspect of plant physiology which changes to allow plants to grow in low-temperature environments?

With regard to plant pigments, we still do not know why there is generally less chlorophyll and more anthocyanin in leaves with increased altitude, at least on temperate mountains. Also, growth at low temperatures tends to produce leaves with greater rates of dark respiration and photorespiration when measured under high-temperature conditions than does growth at higher temperatures. The mechanism for this change is not understood, nor is the effect it may have on the differential mean rate of dark respiration and photorespiration between different altitudes. It may be that intrinsically high rates of dark respiration and photorespiration do not allow high-altitude genotypes to colonize warmer habitats.

We do not know the functional significance of the high calorific contents of alpine plants. We also do not know how important reduced temperatures might be for the movement of assimilates in plants at high altitudes. This may be crucial. From the model proposed, it is clear that vegetation stature and leaf area index are probably very important determinants of leaf $\delta^{13}\text{C}$ values. The use of $\delta^{13}\text{C}$ gives us a powerful tool with which to characterize plant responses to altitude. The model should be subjected to examination

using long-term field measurements, and controlled environment measurements, on the influence of boundary layer conductance, canopy temperature and VPD on $\delta^{13}C$ values.

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