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# Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand

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**Summary.** This study is part of a series of investigations on the influence of altitude on structure and function of plant leaves. Unlike most other mountain areas, the Southern Alps of New Zealand provide localities where physiologically effective moisture stress occurs neither at high nor at low elevation, but the changes in temperature and radiation with elevation are similar or even steeper than in most other regions. In comparison with results from other mountains, where moisture may impair plant functioning at low elevation, this study allows an estimation of the relative role of water for the expression of various leaf features typically associated with alpine plants. Maximum leaf diffusive conductance (g), leaf nitrogen content (LN), stomatal density (n) and distribution, as well as area (A), thickness (d) and specific area (SLA) of leaves were studied. Three different plant life forms were investigated over their full altitudinal range (m): trees, represented by *Nothofagus menziesii* (1,200 m), ericaceous dwarf shrubs (1,700 m), and herbaceous plants of the genus *Ranunculus* (2,500 m). In all three life forms g, LN, and n increased, while SLA and A decreased with elevation. Recent investigations have found similar trends in other mountains from the temperate zone, but the changes are larger in New Zealand than elsewhere. Herbs show the greatest differences, followed by shrubs and then trees.

It is concluded that g is dependent upon light climate rather than water supply, whereas SLA and related structural features appear to be controlled by the temperature regime, as they show similar altitudinal changes under different light and moisture gradients. The higher leaf nitrogen content found at high elevations in all three life forms, suggests that metabolic activity of mature leaves is not restricted by low nitrogen supply at high altitude. In general, the leaves of herbaceous plants show more pronounced structural and functional changes with altitude than the leaves of shrubs and trees.

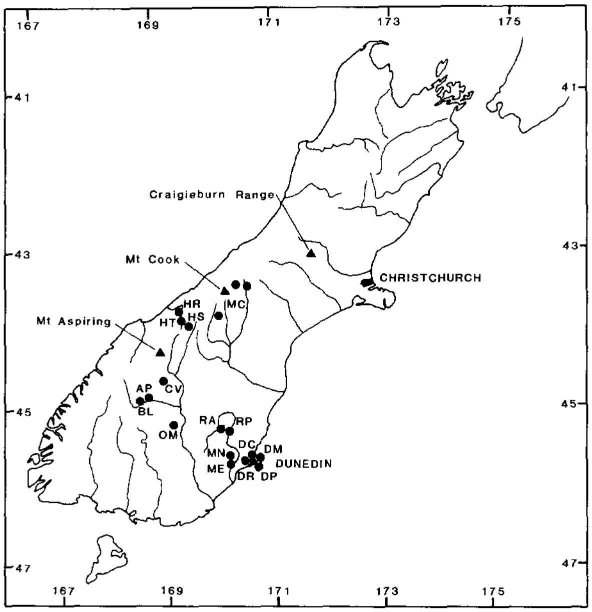

**Fig. 1.** Situation of sites on South Island of New Zealand. For abbreviations see Table 1

Mountain plants differ from lowland plants in many respects, hence changes in physiognomy, anatomy and physiology are observed as elevation increases. It is difficult to separate the influence on these changes of (1) factors that are primarily a function of increased altitude, namely decreases of both pressure and mean ambient temperature, and (2) those which are expressions of the specific local climate and thus are not generally bound to altitude (Larcher 1983). Among the latter, water supply and light regime are particularly important. In fact, several studies of changes of plant characteristics with elevation have been conducted along steep moisture gradients (e.g. Chabot and Billings 1972, Tieszen et al. 1979).

Previous studies (Körner and Mayr 1981, Körner and Cochrane 1985), and in particular an investigation in the humid tropics (Körner et al. 1983), indicate that changes in leaf characteristics with elevation may be divided into at least two groups. The first includes characteristics such as size and specific area of leaves that show similar changes in different mountain regions and are therefore probably related to temperature regime. The second includes leaf conductance, stomatal number (and maybe also photosynthetic capacity) which show variable trends, these were interpreted as responses to local light conditions, although the influence of moisture could not be definitely discounted as short dry periods occur at the lower elevations in all the transects studied so far.

The oceanic climate of New Zealand allows a comparative study of structural and functional changes of leaves to be made along an elevational gradient uninfluenced by the availability of plant water. Hence, by comparison with previous investigations, the relative importance of water

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relations for the expression of leaf characteristics in alpine plants can be evaluated.

In order to cover a wide spectrum of plant species and life forms at both high and low elevations, data were collected from two species of sclerophyllous trees and various ericaceous dwarf shrubs and sessile herbaceous rosette plants.

The investigation was designed to complement comparable studies from other mountain environments, both in the temperate zone and in the tropics. Consequently, such characteristics as the size and specific area of leaves, maximum leaf diffusive conductance for water vapour, distribution of stomata, and leaf nitrogen content have been measured from different locations during the peak growing season.

## Site description and climate

The study was conducted along a NW-SE transect crossing the mountains of the South Island of New Zealand from

**Table 1.** Site description

| No./ abbrev. | Name of site | Zone | Elevation m above NN | Annual[a] precipit. mm | Mean[b] temp. of air in January °C | Soil moisture % of total volume (% d.w. of 2 mm fraction) | Depth[c] of soil sample cm | Plant species studied no. from Table 3 |
|---|---|---|---|---|---|---|---|---|
| 1 ME | Maungatua-E (foothills) | coastal | 30 | 1,200 | 14.4 | 31.9 (35.3) | 5–10 | 1 |
| 2 DR | Dunedin (Royal Terrace) | coastal | 50 | 900 | 14.7 | | | 2, 13 |
| 3 HR | Haast Valley (Pleasant Flat) | coastal | 50 | 4,600 | 14.1 | 43.0 (73.6) | 10–15 | 1, 3, 6, 14, 15 |
| 4 DP | Dunedin (Otago Penninsula) | coastal | 0–150 | 700 | 14.5 | | | 11, 15 |
| 5 DM | Dunedin (Mihiwaka) | montane | 260 | 900 | 13.2 | | | 3, 12 |
| 6 MN | Maungatua-N | montane | 320 | 1,000 | 12.4 | 27.1 (27.6) | 3–8 | 1 |
| 7 AP | Arthur's Point (near Queenstown) | montane | 395 | 900 | 15.4 | | | 15 |
| 8 RP | Rock and Pillar Range (pasture) | montane | 550 | 700 | 12.0 | 9.1 (8.1)[d] | 1–6 | 2, 11, 15 |
| 9 DC | Mt. Cargill (Dunedin) | montane | 650 | 1,200 | 10.5 | | | 15 |
| 10 CV | Cardrona Valley (central Otago, semi-arid pasture, Nothofagus menziesii relict stand) | montane | 830 | 600 | 13.2 | 15.4 (7.7) | 1–6 | 1, 14, 15 |
| 11 BL | Ben Lomond (Queenstown) | montane | 910 | 800 | 11.8 | | | 15 |
| 12 RA | Rock and Pillar Range (herbfield) | low-alpine | 1,100 | 1,400 | 8.2 | 24.5 (32.9) | 2–7 | 4, 11, 14 |
| 13 HT | Mt. Armstrong (Haast, Pass, tree line) | low-alpine | 1,200 | 4,200 | 6.0 | 62.1 (107)[e] | 4–9 | 1, 4 |
| 14 OM | Old Man Range (summit plateau) | high-alpine | 1,500–1,650 | 1,800 | 6.0 | | | 5, 9, 10, 11, 14 |
| 15 HS | Mt. Armstrong (Haast Pass, snow bed) | high-alpine | 1,700 | 4,500 | 2.5 | | | 5, 7 |
| 16 MC | Mt. Cook region[f] (Ben Ohau, Mt. Sibbald, Mt. Annan) | subnival/ nival | 1,980<br>2,440<br>2,530 | 4,000 | 5.6<br>2.4<br>1.7 | | | 8<br>8<br>8 |

[a] Estimated from nearest meteorological station and personal observations of A.F. Mark

[b] As above, assuming a dry adiabatic lapse rate of 0.7 K 100 m$^{-1}$

[c] Soil sampled below the organic raw humus and litter layer

[d] Compressed soil in inter-tussock space of sheep pasture

[e] Extremely high organic content

[f] Herbarium material, kindly supplied by DSIR, Botany Division, Christchurch (CHR 96339, 254224, 217997)

**Table 2.** Incoming radiation at different altitudes in New Zealand (means for December–February period)

| Meteorological stations | Altitude (m) | Daily mean $(MJ\ m^{-2}\ d^{-1})$ | | | |
|---|---|---|---|---|---|
| | | 1977 | 1979 | 1980 | 1977–1980 |
| Christchurch[a]<br>(Eppley pyranometer) | 30 | 22.0 | 23.2 | 20.7 | 22.0 |
| Dunedin[b]<br>(Robitzsch bimetallic radiation recorder) | 1 | 20.0 | 20.2 | – | 20.1 |
| Invercargill[c]<br>(as Christchurch) | 0 | 19.8 | 19.8 | 20.7 | 20.1 |
| Mount John[d]<br>(as Christchurch) | 1,027 | 22.2 | 24.0 | (20.5) | 23.1 |
| Craigieburn Range[e]<br>(Fuess actinograph) | | | | | 1969–1974 |
| a) Forest Stn | 914 | | | | 20.0 |
| b) Ski Basin | 1,550 | | | | 20.7 |
| Old Man Range[f]<br>(Rimco Pyranometer | | | | | 1976–1977 |
| 400–1,100 nm) | 1,220 | | | | 21.5 |
| Dunedin[g]<br>(see footnote) | 20 | | | | 17.5 |
| Central Alps[h]<br>(star pyranometer) | | | | | longterm<br>mean |
| 47° N, | 2,000 | | | | 20.0 |

[a-d] NZ Meteorological Service, Misc. Pub 109 (1977, 1979, 1980)

[e] McCracken (1980)

[f,g] Greer (1978). Data for Dunedin estimated from regression equations of bright sunshine (Campbell-Stokes recorder) against monthly radiation at Invercargill (Eppley pyranometer) and Dunedin(Robitzsch-type bimetallic recorder)

[h] Fliri (1975)

latitudes of about 44 to 46 degrees south. The sites and some relevant environmental data are listed in Tables 1 and 2. The climate of the particular region of New Zealand that was studied is described below.

As a result of the regular and abundant precipitation, the moisture supply in the top soil is unlikely to restrict plant functioning at our study sites (see also Mark and Sanderson 1962; Mark 1965), except the specially selected dry location in Central Otago and the pasture soil on the Rock and Pillar Range (CV and RP in Table 1). Although there may occur sporadic summer drought situations also on the eastern side of the South Island, but this was not the case in the 1980/81 season, when this investigation was conducted.

Unfortunately radiation data are not available for the study sites near the main divide of the Southern Alps. The data shown in Table 2 from Craigieburn Range (about one degree north) indicate little altitudinal change. The absolute values are similar to those reported for the Central European Alps. Annual mean incoming radiation at Ski Basin, Craigieburn Range amounts $48.10^8\ J\ m^{-2}\ a^{-1}$ compared to 51 in Innsbruck (sources as in Table 2). Horizontal plane interception of incoming radiation seems to increase between 0.6 and 1.2% per 100 m of elevation. The measurements, by Greer (1978), of short wave radiation in Dunedin (near sea level) and the Old Man Range (1,220 m) are more relevant to this study. His data show an increase by 23% over this altitudinal range (midsummer values for two years). As all the study sites were on hill slopes or in valleys with some screening of the horizon, the effective elevational gradient of total light interception is possibly even steeper. The annual mean of bright sunshine hours (1935–1960) near sea level reaches 1734 in Dunedin (east coast) and 1816 in Haast (west-coast) and represents 39% and 43% of the possible maximum. For comparison, Innsbruck in the Central Alps has 1,766 hours or 40% of the possible (1931–1966, Fliri 1975).

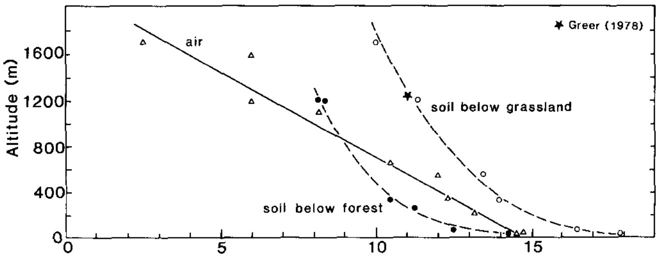

Fig. 2. The altitudinal variation of air and soil temperature in the study area. Mean monthly air temperatures for midsummer are obtained from Table 1. Soil temperatures were measured at midday in 20 cm depth during the course of this investigation in adjacent Nothofagus forests and grassland (values from semiarid Central Otago not included)

According to McCracken (1980), again in the Craigieburn Range, the dry adiabatic lapse rate of the mean annual air temperature is 0.66 K/100 m, and reaches 0.70 to 0.75 in midsummer. Monthly mean maxima in summer reach 1.07 K/100 m. Similar lapse rates are reported by Greer (1978). Corresponding values for the Central Alps are 0.5, 0.65, and 0.7 K/100 m (Fliri 1975). Thus, altitudinal temperature gradients are particularly steep in New Zealand, as is typical for islands, and are expressed in a comparatively compressed altitudinal zonation of the vegetation (Mark 1965; Wardle 1974; Heine 1978; Franz 1979; Benecke and Havranek 1980).

No microenvironmental information is available for the studied plants. The strong winds and frequent midday cloud cover on the higher mountains of New Zealand will reduce the likelihood of massive heat accumulation in the canopies of alpine vegetation that has been described for continental sites (Gates et al. 1964; Cernusca 1976, Smith and Geller 1979; Körner and Cochrane 1983). Thus, plant temperatures in the mountains of New Zealand may be assumed to be, on average, somewhat closer to ambient temperature than in other less maritime mountain areas. There is, however, some evidence that snow tussocks from subalpine grassland can show substantial heat accumulation for short periods (McCracken 1980). Probably the same is true for cushion plants. According to Greer (1978) the mean maximum air temperature, in February, within tussock canopies from the Old Man Range is about 4 K higher than that above the canopy (mean for two years).

Unreplicated readings of soil temperature were made at 20 cm depth below various grassland types under dry midday conditions during the current study. These are 1–6 K above mean monthly air temperature in midsummer (January), and are significantly warmer (3–4 K) than soil temperatures from below a dense forest canopy. Figure 2 shows the good agreement between the measured soil temperatures and the monthly mean maximum recorded at −20 cm by Greer (1978).

In conclusion, it may be assumed that the study areas have somewhat steeper altitudinal gradients of light interception and plant temperature than more continental mountain areas, and no physiologically significant differences in moisture between coastal and montane sites, at least in the western part of the transect.

## Material and methods

### *Plant species*

A list of the studied plant species is shown in Table 3. Some of these species have been used only for studies of leaf anatomy. Fully sunlit, mature leaves from adult plants have been used for all investigations, unless stated otherwise. In the evergreen species only the current season's leaves have been studied. The altitudinal amplitude of occurrence of the three life forms represented by these species, is approximately 1,200 m for the trees, 1,800 m for the shrubs and 2,500 m for the forbs.

For the two species introduced from the Northern Hemisphere, it should be noted that *R. acetosella* is found up to the lower alpine belt in the European Alps, whereas *H. radicata* only rarely climbs above timberline.

Voucher specimens of the species are deposited in the herbaria of the Botany departments in Dunedin and Innsbruck unless stated otherwise. All field measurements and collections were made during peak growing season in February 1981, when Ranunculus species had flowered, and ericaceous shrubs were bearing full-sized fruits.

### *Methods*

Maximum leaf diffusive conductance for water vapour was determined by a ventilated, dynamic response porometer, which was calibrated absolutely in terms of water vapour influx by the micropipette technique (Körner and Cernusca 1976). The design of the porometer head was modified to allow the attachment of both flat leaves (clamp-mode) and narrow leaved branchlets (insert mode; Debrunner-Walz AG, Geroldswil, Switzerland). In leaves larger than 0.8 x 2.5 cm separate readings where made for both sides of the blade (clamp-mode). All conductances are based on total leaf surface (not projected area), even when leaves showed no stomata in certain parts of their green surface, so that data from plants with different leaf anatomies are readily compared (Körner et al. 1979). The same instrument and sensors were also used in the previously cited comparative studies from the Australian Alps and New Guinea, as well as in New Zealand, and calibration characteristics did not change during all three consecutive investigations. The pressure dependency of the equipment was tested in an aeronautic flight simulator up to the equivalent of 5,600 m above sea level. There was an approximately 6% decrease of response time, at equal rates of transpiration, for a pressure drop equivalent to a 1,000 m increase of altitude. This was accounted for in all calculations (cf. Körner et al. 1983).

**Table 3.** List of plant species (nomenclature following Allan 1961 and Mark and Adams 1973)

| | Sites | Number |
|---|---|---|
| 1. *Sclerophyllous tree species* | | |
| Nothofagus menziesii (Fagaceae) | HR, HT, MN, ME, CV | 1 |
| Griselinia littoralis (Cornaceae) | DR, RP | 2 |
| 2. *Sclerophyllous shrubs and dwarf shrubs (Ericaceae)* | | |
| Gaultheria antipoda | HR, DM | 3 |
| Gaultheria depressa | HT, RA | 4 |
| Pernettya alpina | HS, OM | 5 |
| 3. *Herbaceous rosette plants (Ranunculaceae)* | | |
| Ranunculus hirtus | HR | 6 |
| Ranunculus sericophyllus | HT | 7 |
| Ranunculus grahamii | MC | 8 |
| Ranunculus pachyrrhizus | OM | 9 |
| Ranunculus enysii | OM | 10 |
| Ranunculus lappaceus | OM, RA | 11 |
| Ranunculus repens L. | DM | 12 |
| Ranunculus foliosus | DR | 13 |
| Cosmopolitan weeds: | | |
| Rumex acetosella L. (Polygonaceae) | HR, OM, RA, ME, CV | 14 |
| Hypochoeris radicata L. (Asteraceae) | HR, AP, DC, DP, CV, RP, BL | 15 |

For abbreviations of sites see Table 1

**Table 4.** Maximum leaf diffusive conductance for water vapour (mmol $m^{-2}$ $s^{-1}$) based on total i.e. upper plus lower leaf surface area)

| Plant species | Site | Elev. (m) | Mean | ±s.e. |
|---|---|---|---|---|
| Nothofagus menziesii | HR | (50) | 96 | 6 |
| | HT | (1,200) | 168 | 11 |
| | ME | (30) | 78 | 6 |
| | MN[a] | (320) | 75 | 2 |
| | CV[a] | (830) | 94 | 4 |
| Griselinia littoralis | DR | (50) | 66 | 7 |
| | RP | (550) | 88 | 4 |
| Gaultheria antipoda | HR | (50) | 72 | 7 |
| | DM | (260) | 82 | 4 |
| Gaultheria depressa | RA | (1,100) | 226 | 14 |
| | HT | (1,200) | 225 | 21 |
| Ranunculus hirtus | HR | (50) | 207 | 11 |
| Ranunculus lappaceus | RA | (1,100) | 368 | 17 |
| Ranunculus repens | DM | (260) | 197 | 3 |
| Ranunculus lappaceus | RP[a] | (550) | 412 | 19 |
| Ranunculus foliosus | DR[a] | (50) | 544 | 42 |

Means calculated from the 5 highest values obtained in different leaves during the day

[a] Indicates data for individuals from sites with "special" environmental conditions (i.e. animal manuring (MN), drought (CV), heavy grazing pressure (RP), and lawn mowing (DR). These data are excluded from the transect analysis, but indicate potential variability due to factors unrelated to altitude

Maximum leaf conductance was determined by taking a series of porometer readings during the morning until leaf conductance started to decline or showed no further increase. The five highest values obtained during such a series of measurements were averaged, and this value was considered as maximum conductance. Individual readings were obtained from different leaves or branchlets, and from different, unshaded, plants within the same area. Similar samples were used for subsequent anatomical studies and the determination of specific leaf area and nitrogen content.

The weather on the days of investigation was sunny with intermittent clouds and the maximum vapour pressure deficit exceeded 1.0 kPa only at the dry site in Central Otago (CV). In the principal study sites, maximum conductance occurred at vapour pressure deficits of between 0.3 and 0.7 kPa (cf. Körner and Bannister 1985).

The anatomical studies included determination of stomatal number and size from hand sections, and (for *Nothofagus* only) studies of stomatal and epidermal structure from microtome sections of resin embedded material. Five randomly sampled leaves from each species and site were used. Leaf area was measured by a belt-photoplanimeter (Li-3100, Licor Inc., Lincoln, Nebraska, USA). Nitrogen was analysed by Kjeldahl-digestion and subsequently by an auto-analyser (Technicon Instr., Tarrytown, N.Y., USA).

## Results

### Maximum leaf conductance

Table 4 presents the maximum conductances for the three plant life forms. A logarithmic transformation (log e) has been used for all statistical analyses in order to obtain a more normal distribution of data.

*Nothofagus*. Differences between sites are highly significant, except for the two Maungatua sites (MN, ME) which are not significantly different from all the rest. The altitudinal component accounts for a highly significant (64%) proportion of the variation between sites.

*Griselinia*. The two sites are significantly different from each other ($P<0.05$) with the higher value obtained from the mountain site.

*Gaultheria*. There is a highly significant difference between conductances obtained at low and high altitude. No significant difference exists between the data from the two different sites examined at each elevation. The altitudinal component accounts for 99% of the total variation between sites.

*Ranunculus*. Analysis of the total data shows a highly significant difference between sites. *R. repens* and *R. hirtus* from low elevation (HR and DM) show similar values and are significantly different from the conductance of *R. lappaceus* at high elevation (RA). It is interesting to note that additional data obtained in dwarfed and non flowering individ-

**Table 5.** Frequency, distribution and area of stomata

| Plant species | Site | Elev. (m) | d/v | Frequency no mm$^{-2}$ | ±s.e. | Area % | *n* |
|---|---|---|---|---|---|---|---|
| Trees | | | | | | | |
| N. menziesii | ME | (30) | – | 149 | 8 | 4.1 | 10 |
| | HR | (50) | – | 168 | 12 | 4.4 | 10 |
| | HT | (1,200) | – | 180 | 6 | 4.6 | 10 |
| | MN[a] | (320) | – | 207 | 5 | 4.6 | 5 |
| | CV[a] | (830) | – | 182 | 9 | 5.0 | 10 |
| G. littoralis | DR | (50) | – | 110 | 6 | 3.2 | 5 |
| | HR | (50) | – | 99 | 5 | 4.3 | 5 |
| | RP | (550) | – | 94 | 5 | 3.3 | 5 |
| Shrubs | | | | | | | |
| G. antipoda | HR | (50) | – | 146 | 17 | 5.9 | 5 |
| | DM | (260) | – | 129 | 13 | 5.9 | 5 |
| G. depressa | RA | (1,100) | – | 241 | 24 | 11.0 | 5 |
| | HT | (1,200) | – | 179 | 21 | 7.7 | 5 |
| P. alpina | HS | (1,700) | 1.17 | 222 | 25 | 14.5 | 5 |
| Forbs | | | | | | | |
| R. hirtus | HR | (50) | 0.07 | 30 | 3 | 7.3 | 5 |
| R. repens | DM | (260) | 0.06 | 38 | 4 | 7.5 | 5 |
| R. lappaceus | RA | (1,100) | 1.05 | 67 | 8 | 11.2 | 5 |
| | OM | (1,500) | 1.19 | 68 | 7 | 12.9 | 5 |
| R. enysii | OM | (1,650) | 1.09 | 81 | 9 | 11.6 | 5 |
| R. pachyrrhizus | OM | (1,650) | 1.35 | 110 | 10 | 14.6 | 5 |
| R. sericophyllus | HS | (1,700) | 1.82 | 72 | 8 | 9.2 | 5 |
| R. grahamii | MC | (1,980) | 2.71 | 58 | (3) | 6.6 | 2 |
| | MC | (2,440) | 1.78 | 50 | (9) | 4.5 | 1 |
| | MC | (2,530) | 1.86 | 53 | 3 | 5.7 | 3 |

d/v, dorsal/ventral ratio of stomatal frequency; area, relative proportion of leaf area covered by stomata; *n* number of investigated leaves (10–20 counts per leaf)

[a] "special" sites, see Table 4

**Table 6.** Anatomical data for *Hypochoeris radicata*

| Site code | DP | HR | AP | DC | CV | RA | BL |
|---|---|---|---|---|---|---|---|
| Altitude (m) | 0 | 50 | 395 | 650 | 830 | 900 | 910 |
| Leaf thickness (mm) | 0.31 | 0.29 | 0.30 | 0.33 | 0.26 | 0.31 | 0.31 |
| Stomatal density ($n/mm^2$ total surface) | 43 | 38 | 58 | 57 | 69 | 38 | 47 |
| Dorsal/ventral ratio | 0.89 | 0.92 | 1.00 | 0.98 | 0.92 | 0.93 | 0.97 |
| % leaf surface area covered by stomata | 1.63 | 1.63 | 2.40 | 2.50 | 2.13 | 1.63 | 1.50 |
| Projected leaf area ($mm^2$) | 1,267 | 1,588 | 557 | 433 | 163 | 746 | 415 |

Partitioning of variance:

| | Leaf thickness | Stomatal density | d/v ratio | % stomatal area | Log leaf area |
|---|---|---|---|---|---|
| Altitude | n.s. | n.s. | n.s. | n.s. | 57%*** |
| Log rainfall | n.s. | 32% ** | n.s. | n.s. | 38% *** |

Where there are significant differences between sites, the variance has been partitioned by linear regression to expose any relationships with altitude or rainfall. The percentages give the amount of between-site variation accounted for by the the regression. Asterisks indicate significance: n.s. not significant, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

uals of *R. lappaceus* and *R. foliosus* from sites at low elevation with heavy grazing (pasture, DP) or mowing (city lawn near DR) showed significantly higher conductances than the rest (360 and 450 mmol $m^{-2}$ $s^{-1}$).

### *Stomatal number, distribution and area*

Table 5 shows the variation in stomatal density and the percentage of leaf area covered by stomata (guard cells plus pore). *Nothofagus* and *Griselinia*, both hypostomatous, show no significant altitudinal change (a slight tendency towards higher densities in *Nothofagus* from timberline). The ericaceous shrubs show a highly significant elevational increase in both stomatal number and total stomata area. *Gaultheria* species (lower elevations) are hypostomatous, whereas the related prostrate alpine shrub *Pernettya alpina* is amphistomateous, with more stomata on the upper leaf side (240 per square millimeter) than on the lower side (204).

Similar results for stomatal density and area are obtained for the herbaceous plants, except for the samples from the subnival zone of Mount Cook, at the upper limit of higher plant growth in New Zealand. Here a reversal of the trend becomes apparent.

In the herbaceous plants, the partitioning of stomata between the two sides of the leaf shows marked and consistent changes with altitude. *Ranunculus* species from low elevations show only few stomata on their upper leaf surfaces whereas the species from high elevations have twice as many stomata on their upper as on their lower.

**Table 7.** Anatomical data for *Rumex acetosella*

| Site code | DP | HR | CV | RA | OM |
|---|---|---|---|---|---|
| Altitude (m) | 0 | 50 | 830 | 1,100 | 1,500 |
| Stomatal density ($no/mm^2$ of total surface area) | 62 | 50 | 78 | 62 | 61 |
| Dorsal/ventral ratio | 0.85 | 0.79 | 0.95 | 0.94 | 0.84 |
| % leaf area covered by stomata | 5.4 | 5.9 | 6.6 | 5.2 | 5.6 |
| Projected leaf area ($mm^2$) | 185 | 213 | 61 | 102 | 167 |
| Specific leaf area (SLA, $cm^2$ g d.w.$^{-1}$) | 313 | 349 | 161 | 294 | 233 |

Partitioning of variance:

| | Stomata density | d/v ratio | % area | Log leaf area | SLA |
|---|---|---|---|---|---|
| Altitude | n.s. | 32%* | 36%* | 16%* | 35%** |
| Log rainfall | 76%** | 53%* | 76%** | 40%*** | 43%*** |

Further explanations as in Table 6

There is little variation in stomatal size (length × width) within each group. No significant differences were found in the tree species (21 × 16 μm) and within *Gaultheria* (27 × 20). *Pernettya alpina*, the ericaceous shrub from the highest altitude, has significantly larger stomata than any other woody species examined (32 × 26). *Ranunculus* species have the largest stomata, but their size decreases from 63 × 44 at low altitude to 45 × 35 at high altitude.

For comparison, the same anatomical investigations have been made on the two introduced weeds, *R. acetosella* and *H. radicata*. In neither species is the variation in stomatal frequency, ratio of dorsal to ventral stomatal number, or stomatal area strongly related to altitude (Tables 6 and 7). Any differences are more associated with rainfall; this may be due to the inclusion of extreme sites, such as the very dry site in Central Otago (CV), as otherwise differences between sites are small.

### *Leaf size, specific leaf area and leaf thickness*

Leaf size decreased with altitude in all three plant life forms (Table 8). The smallest change ocurred in *Nothofagus* (−40%) followed by the shrubs (ca. −70%) and the forbs (−31 to −85%). In forbs from low elevations, the area of leaflets from compound leaves is used for comparison; otherwise the decrease with altitude would be 97%.

Specific leaf area (SLA) also generally decreases with altitude. The drop is about 25% in the trees and shrubs and about 53% in the forbs. Apparently both dry inland conditions (CV) and the humid, but rather cool, environment at the alpine timberline (HT) affect SLA in the same way.

Leaf thickness was studied in *Nothofagus* (Table 9). Leaves from timberline (HT) show a highly significant increase in leaf thickness over those from low elevation, where no significant difference was found between leaves from the two sites. These results reflect changes in SLA. Table 10 shows that, while all leaf components contribute to the

**Table 8.** Leaf area, specific leaf area and nitrogen content

| Plant species | Site | Elev. (m) | Area cm$^2$ | SLA cm$^2$ g$^{-1}$ | N-content mmol m$^{-2}$ (% dw) | *n* |
|---|---|---|---|---|---|---|
| Trees | | | | | | |
| N. menziesii | ME | (30) | 1.11 | 73.5 | 148 (1.52) | 74 |
| | HR | (50) | 1.09 | 66.4 | 144 (1.35) | 48 |
| | HT | (1,200) | 0.65 | 51.7 | 197 (1.43) | 46 |
| | MN[a] | (320) | 1.77 | 63.2 | 195 (1.73) | 16 |
| | CV[a] | (830) | 1.35 | 55.5 | 167 (1.29) | 63 |
| G. littoralis | DR | (50) | 30.5 | 96.3 | 84 (1.13) | 30 |
| | HR | (50) | 53.3 | 93.5 | 80 (1.05) | 31 |
| | RP | (550) | 9.0 | 57.1 | 130 (1.04) | 29 |
| Shrubs | | | | | | |
| G. antipoda | HR | (50) | 0.88 | 88.2 | 74 (0.92) | 46 |
| | DM | (260) | 0.90 | 90.6 | 75 (0.95) | 61 |
| G. depressa | RA | (1,100) | 0.28 | 73.6 | 102 (1.05) | 44 |
| | HT | (1,200) | 0.24 | 73.1 | 122 (1.25) | 72 |
| P. alpina | HS | (1,700) | 0.21 | 68.1 | 120 (1.14) | 58 |
| Forbs | | | | | | |
| R. hirtus | HR | (50) | 4.1 | 166.6 | 60 (1.40) | 6 |
| R. repens | DM | (260) | 28.9 | 246.6 | 62 (2.14) | 7 |
| R. lappaceus | RA | (1,100) | 1.16 | 149.6 | 72 (1.51) | 9 |
| | OM | (1,500) | 0.59 | 133.5 | 78 (1.46) | 9 |
| R. enysii | OM | (1,650) | 0.80 | 106.0 | 94 (1.39) | 11 |
| R. pachyrrhizus | OM | (1,650) | 0.61 | 95.5 | 132 (1.76) | 14 |
| R. sericophyllus | HS | (1,700) | 0.96 | 96.4 | 189 (2.55) | 7 |

*n* number of leaves per mixed sampel. All values calculated for the unit projected leaf area

[a] "special" sites, see Table 4

**Table 9.** Leaf thickness in *Nothofagus menziesii* from different elevations in humid coastal or mountain areas and from a dry inland location (CV)

| Site | Altitude (m) | Mean thickness (mm, ±s.e.) | Number of samples | Significance |
|---|---|---|---|---|
| Humid sites | | | | |
| HR | 50 | 0.278±0.04 | 16 | HR/HT 0.016* |
| ME | 30 | 0.281±0.05 | 15 | ME/HT 0.028* |
| HT | 1,200 | 0.338±0.09 | 18 | |
| Dry site | | | | |
| CV | 830 | 0.335±0.05 | 15 | |

**Table 10.** Quantiative analysis of leaf cross sections in *Nothofagus menziesii* (relative units)

| Type | Low elevation (HR, 50 m) | | | Treeline (HT, 1,200 m) | | | Relative increase %, sign. |
|---|---|---|---|---|---|---|---|
| | mean | s.e. | *n* | mean | s.e. | *n* | |
| Thickness of outer wall of upper epidermis plus cuticle | 1.45 | 0.08 | 16 | 2.00 | 0.16 | 8 | +38** |
| Upper epidermis cell diameter | 2.21 | 0.09 | 16 | 2.86 | 0.09 | 7 | +29*** |
| Thickness of palisade mesophyll layer | 26.5 | 0.78 | 10 | 33.7 | 1.73 | 6 | +27*** |
| Thickness of sponge mesophyll layer | 20.6 | 1.00 | 10 | 25.4 | 1.54 | 5 | +23* |
| Lower epidermis cell diameter | 1.59 | 0.09 | 10 | 2.14 | 0.09 | 7 | +35*** |
| Thickness of outer wall of lower epidermis plus cuticle | 0.94 | 0.04 | 10 | 1.36 | 0.14 | 7 | +45* |

overall increase in thickness, the increase is most pronounced in the outer epidermal walls and cuticle.

These data show that costs in terms of structural matter per unit leaf area increase with elevation in all three life forms. The changes are least in trees and shrubs and greatest in the forbs.

### *Leaf nitrogen content*

Total leaf nitrogen content in the three studied plant life forms increases with altitude when expressed per unit leaf area. The increase amounts to 35% in *Nothofagus*, 59% in *Griselinia* , 65% in the ericaceous shrubs and 215% in the forbs when plants from the lowest and highest sites are compared (Table 8). Changes are much less on a dry weight basis within each groups of plants. This is particularly true for the trees. *Nothofagus* leaves from the principal sites contain 1.4 ± 0.1% N, *Griselinia* leaves contain 1.1 ± 0.05% N. In the ericaceous shrubs, N per unit dry weight varies between 0.95 ± 0.05% at the low sites and 1.14 ± 0.09% above tree line. In the *Ranunculus* species, only *R. sericophyllus* from 1,700 m (the highest site examined) deviates significantly from the rest (2.55% compared to 1.8 ± 0.4%).

Thus, the N-content shows an association with plant life form that is similar to that shown by other studied features; with trees exhibiting the smallest and forbs the largest changes within their range of occurance.

Additional data for the nitrogen content of leaves of *Nothofagus* are 1.73% (195 mmol m-2) from the edge of a grazed pasture at low elevation (MN), and 1.24% (160 mmol mm$^{-2}$) for a relict stand in arid Central Otago (CV). These are significantly higher, on a dry weight basis, than values from the principal study sites; but there is no difference in the N-content per unit area between the leaves from the pasture site (MN) and those from the timberline.

## Discussion

### *Interrelations between the observed leaf parameters*

The data obtained during this field study provide further support for various functional correlations between gas exchange parameters, nutritional status and structure of leaves that have received particular attention recently. Several authors have shown the existence of a close relationship between leaf conductance and photosynthetic CO2 uptake (Wong et al. 1979, Körner et al. 1979, Schulze and Hall 1982), and a close correlation between photosynthetic capacity and leaf nitrogen content has also been shown for many different plant species from various environments (references in DeJong 1982; Field et al. 1983; Medina 1984; Comstock and Ehleringer 1984). In the present study, there is an association of maximum leaf diffusive conductance with total leaf nitrogen content that would be expected from the above relationships (Fig. 3).

The relationship between maximum leaf conductance and nitrogen content appears to be markedly different in the studied species and life forms. This implies differences in nitrogen-use efficiency with respect to maximum epidermal conductance (which may correspond to photosynthetic capacity). *Nothofagus* appears the least and *Ranunculus* the most efficient. *Nothofagus* also shows the smallest gain in conductance for a given increase in nitrogen content, larger gains are shown by shrubs and the largest by herbs. This sequence (tree-shrub-herb) is also the sequence for decreasing leaf longevity and increasing specific leaf area among the studied species. Field and Mooney (1983) arrived at similar conclusions for the nitrogen-use efficiency of photosynthesis of aging leaves of a shrub from the Californian chaparral.

Figure 4 shows that there is a correlation between the amounts of nitrogen and dry matter per unit leaf area. Such trends have also been found by Khan and Tsunoda (1970), Yoshida and Coronel (1976), Mooney et al. (1978), Mooney (1983), Medina (1984), Körner and Cochrane (1985) and others.

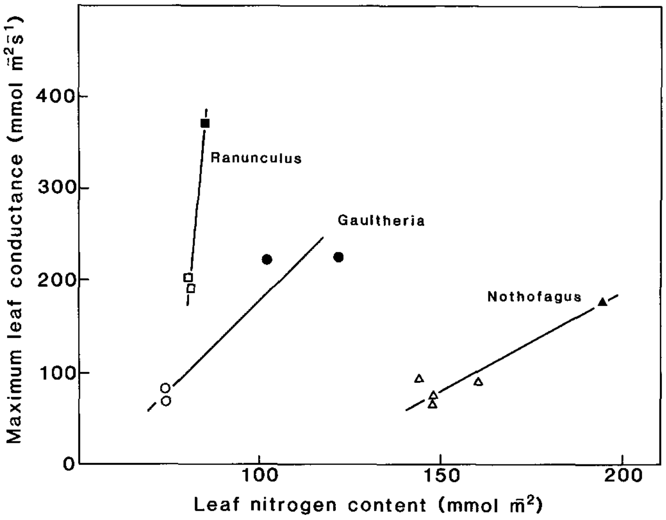

**Fig. 3.** The relation between maximum leaf diffusive conductance and leaf nitrogen content for the three studied life forms. Open symbols indicate data from low elevation, closed symbols indicate values from the highest studied elevation where both these parameters have been measured (1,100–1,200 m)

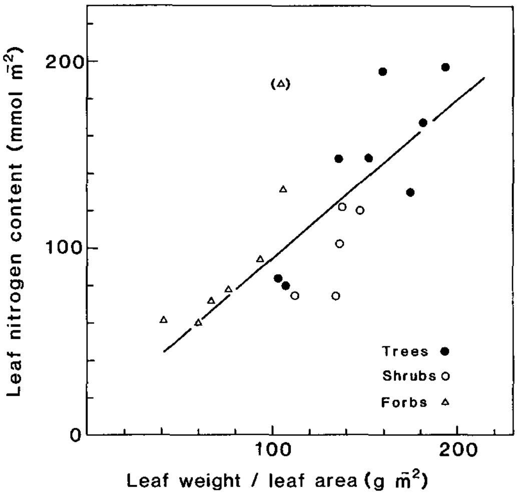

**Fig. 4.** The relation between the inverse of specific leaf area (1/SLA) and leaf nitrogen content in the three studied plant life forms. [N] = 10.5 + 0.84 (1/SLA) r = 0.84

It appears, therefore, that the relationships obtained for native plants from the humid mountains of New Zealand are basically similar to those observed in plants with leaves of varied sclerophylly or longevity from a range of contrasting environments (e.g. mediterranean or semi-arid shrublands, tropical forests and grassland, or even agricultural crops). Hence the altitudinal variation of the leaf characteristics described in this paper reflects functional patterns that are apparently widely distributed in nature.

### *The altitudinal variation of structure and function of leaves in different mountain environments*

Distinct altitudinally-related changes in a number of physiological and anatomical characteristics of leaves have been shown to exist in plants from the mountains of New Zealand. As elevation increases, leaf size and specific leaf area decrease, whereas stomatal conductance, nitrogen content

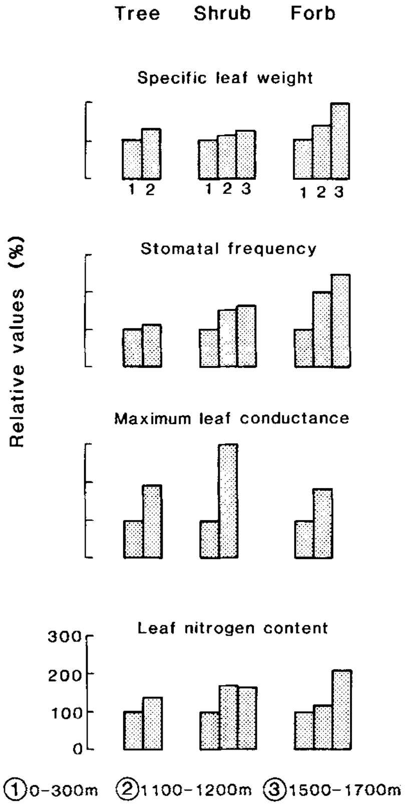

**Fig. 5.** Summary of results. Values for 0–300 m altitude are set equal to 100%. "Specific leaf weight" = 1/SLA

per unit leaf area, stomatal frequency and leaf thickness all increase. Figure 5 summarizes these results. The same basic trends have been observed in other mountain areas of the temperate zone, namely the Central Alps of Europe (Bonnier 1980; Wagner 1892; Körner and Mayr 1981), the Snowy Mountains of SE Australia (Körner and Cochrane 1985) and N-American mountains (anatomical data of Mooney and Johnson 1965; Masters 1978; Ch. Körner unpublished work). However, the changes found in New Zealand are larger than elsewhere.

These large changes in leaf characteristics with altitude may be merely a reflection of the more rapid changes of temperature and, possibly, the effective amount of light intercepted by the leaf, that seem to occur in New Zealand. The absence of microclimatic data allows no more precise explanation than this. Woodward (1983), however, describes similar steep elevational gradients in leaf characteristics in the humid oceanic environment of the Scottish mountains.

The study in New Guinea (Körner et al. 1983) allowed a critical evaluation of the importance of light: a strong decrease of the daily sum of photosynthetically active radiation with altitude was coupled with decreasing leaf conductance and stomatal index, the opposite to what is found in mountains where radiation increases with altitude, as was observed here, and in the European and Australian Alps.

Similarily, the present study allows a critical evaluation of the importance of moisture for the expression of "alpine" leaf features. It appears that changes in leaf characteristics with altitude are greater where the supply of soil moisture is unrestricted. Consequently water supply cannot be the factor responsible for the induction of leaf modifications such as the high diffusive conductances, stomatal frequency, and nitrogen contents found at high elevation. Other studies have also shown that a continuously unrestricted water supply is not a prerequisite for either high stomatal frequency or stomata occurrence on the upper leaf surface; to some extent even the opposite may be true (Mott et al. 1982; Körner et al. 1983).

On theoretical grounds, Schulze (1980) assumed that nutrient status may be a decisive factor in determining growth and photosynthesis at high altitudes, providing a parallel with the arctic tundra, where the nutrient supply of plants is subject to severe constraints (Tieszen 1978). However, the high nitrogen contents per unit leaf area that were found in all three studied life forms, indicate that the low rates of mineralization and nitrogen fixation found in soils at high altitude (Rehder and Schäfer 1978; Haselwandter et al. 1983) do not necessarily lead to assimilative organs that suffer from nutrient deficiency. This is in accordance with the review by Chapin (1980), which concludes that plants from infertile habitats may respond to nutrient stress by maintaining higher concentrations through either luxury consumption and/or reduced growth.

Increased leaf nitrogen contents at the timberline have also been found for the introduced *Pinus contorta* in the Craigieburn Range of the South Island of New Zealand (Nordmeyer 1980), for *Eucalyptus pauciflora* in the Snowy Mountains of Australia (Körner and Cochrane 1985), and for *Picea abies* in the Austrian Alps (Ehrhardt 1961). A recent survey of mineral contents in 55 herbaceous plant species also revealed a significantly higher nitrogen and phosphate content in populations at about 3,000 m as opposed to 600 m in the Austrian Alps (Körner and U. Renhardt, unpublished data). Relatively high nitrogen and phosphate concentrations in leaves of plants from the nival zone are also reported by Haselwandter et al. (1983). Leaf nitrogen contents in plants from alpine habitats appear to be generally higher than in those from the arctic tundra (Wielgolaski et al. 1975; Tieszen 1978) if similar leaf types and life forms are compared.

It seems that total leaf area is controlled so that nutrient content is optimal for the given light and temperature regime. Field (1983) showed that the optimal nitrogen content of leaves for CO2-uptake in creases with increasing photosynthetically active radiation. Apart from its temperature dependency, the potential for photosynthesis to acclimate to high light levels is also strongly dependent on nitrogen content (Osmond 1983). As the total light received tends to increase with elevation in mountains of the temperate zone, including those of New Zealand, and daytime leaf temperatures, particularly in low vegetation, can be quite high even in the alpine zone, high photosynthetic activity is a real possibility at high elevations.

Yet, some species and life forms from moderately high elevations typically function at low levels of leaf nitrogen; e.g. ericaceous dwarf shrubs in the European Alps (Larcher 1977, Rehder and Schäfer 1978), sclerophyllous trees in New Guinea (Grubb 1977), and snow tussocks in New Zealand (Greer 1984). Accordingly, available data for photosynthetic capacity in these dwarf shrubs and tussock grasses show rather low values, (Larcher 1977; Mark 1975; Greer 1984).

When plants from different mountain regions of the globe are compared, the most consistent changes with altitude are in specific leaf area. Except for some plant species with scale leaves from very high locations (e.g. above 4,000 m in New Guinea) and succulents, specific leaf area tends to decline with altitude (Grubb 1977; Körner et al. 1983; Woodward 1983). The data for *Nothofagus* indicate that increased thickness of cell walls and of the palisade layer are the reasons for its decline in SLA. Similar anatomical changes have been observed in *Eucalyptus* (Körner and Cochrane 1985) and in *Rhododendron* in New Guinea (Körner et al. 1983) and had been described even in the last century by Bonnier (1890) and Wagner (1892) for a number of dwarf shrubs and forbs of the European Alps.

The fact that the number and distribution of stomata in the two cosmopolitian weeds do not follow the same altitudinal trends that were observed in the largely native *Ranunculus spp.* may be explained by higher light interception in their lowland microhabitats and the smaller elevational range studied. These species were usually found only in disturbed, sparsely vegetated, open locations. Similarly, no altitudinal changes in stomatal characteristics have been obtained for another ruderal species, *Tussilago farfara*, in the Austrian Alps (Ch. Körner, unpublished data).

The high stomatal numbers and the high abundance of adaxial stomata that were found in the tiny *Ranunculus* plants from heavily grazed pastures or mown lawns at low elevation, may be related to the various specific local disturbances leading to restricted growth and increased light availability. Similarly, a study in subalpine sheep pastures in the Central Caucasus by Nachuzrisvili and Körner (1982, and unpublished data) showed increased stomatal frequency and maximum leaf conductance as compared to non grazed plots. Furthermore, Scheel (1979) showed that if plants of *Vaccinium myrtillus* of lowland origin were exposed to high light intensities as their leaves were unfolding, they produced the stomatal densities and distributions that were normally associated with plants from timberline.

In conclusion, the results of this study support the view that the changes in maximum leaf conductance and related anatomical features that occur with altitude are largely controlled by light climate, and are strongly related to life form. Such a conclusion could be verified if comparable data were obtained for arid or semi- arid mountain ranges where water stress might override light effects. The data from Central Otago indicate such a possibility. The dominance of a light effect under conditions where moisture stress is not seriously limiting, appears highly functional, if light interception – and not temperature – is the major factor limiting the photosynthetic CO2-uptake of alpine plants during the snow-free period (cf. Körner 1982). As light conditions are not the same in all mountains, these characteristics also do not alter in a uniform manner. In contrast, uniform changes in leaf structure (namely specific leaf area and its related anatomy) with elevation have been found in all transects studied sofar: these are probably related to the altitudinal temperature gradient. Such a temperature-related interpretation of leaf structure would also explain the physiognomic convergence between arctic and alpine plants (Billings and Mooney 1968).

There is evidence that low temperatures alone can induce decreases in specific leaf area (e.g. Noble 1980, Wardlaw et al. 1983). Studies of short term growth dynamics in the European Alps, using linear variable differential transducers, indicate that growth processes (at least extension growth) of alpine plants are far more temperature dependent than their photosynthetic responses (F.I. Woodward and Ch. Körner, unpublished data). This highlights the importance of detailed growth-analytical investigations for the understanding of the developmental processes at high altitude.

### *Comparison of life forms*

When the variability of any of the investigated parameters within the three different life forms is considered, trees are found to be the least variable and forbs the most variable, with shrubs holding an intermediate position.

None of the three life forms shows any signs of increased nutrient deficiency with increasing altitude (as judged from leaf nitrogen content). As the investigated herbaceous plants showed the most pronounced altitudinal increase of nitrogen in their leaves, they would be expected to be most successful in utilizing the higher quantum supply at high elevation for carbon fixation. Following Schulze's (1980) considerations this is to be expected, as herbaceous plants may invest all excess carbohydrate in root growth, whereas the other two life forms support a large body of wood, which also effectively dilutes the concentration of acquired nutrients.

However, it is not only the higher proportion of photosynthetically active tissue that enables herbaceous plants to maintain a positive carbon balance high above the treeline. There is also a microclimatic effect that simply provides a more favourable temperature regime for small and prostrate plants and which is not necessarily linked to any patterns of carbon allocation that are associated with a particular growth from.

It may be concluded from the results of this study that the higher potential for modification observed in the leaves of the herbaceous plants is a major factor in their success at very high elevations. It is possible that the lack of large amounts of supporting tissue facilitates this higher adaptibility.

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