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.

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.

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

(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...
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...