

Cambridge University Press

978-0-521-62309-4 - Plants at the Margin: Ecological Limits and Climate Change

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Excerpt

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Part I
The nature of marginal areas

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Fig. 1.1 A marginal population of mountain pine (*Pinus mugo*) colonizing stabilized scree slopes in the Vercors Regional National Park (France).

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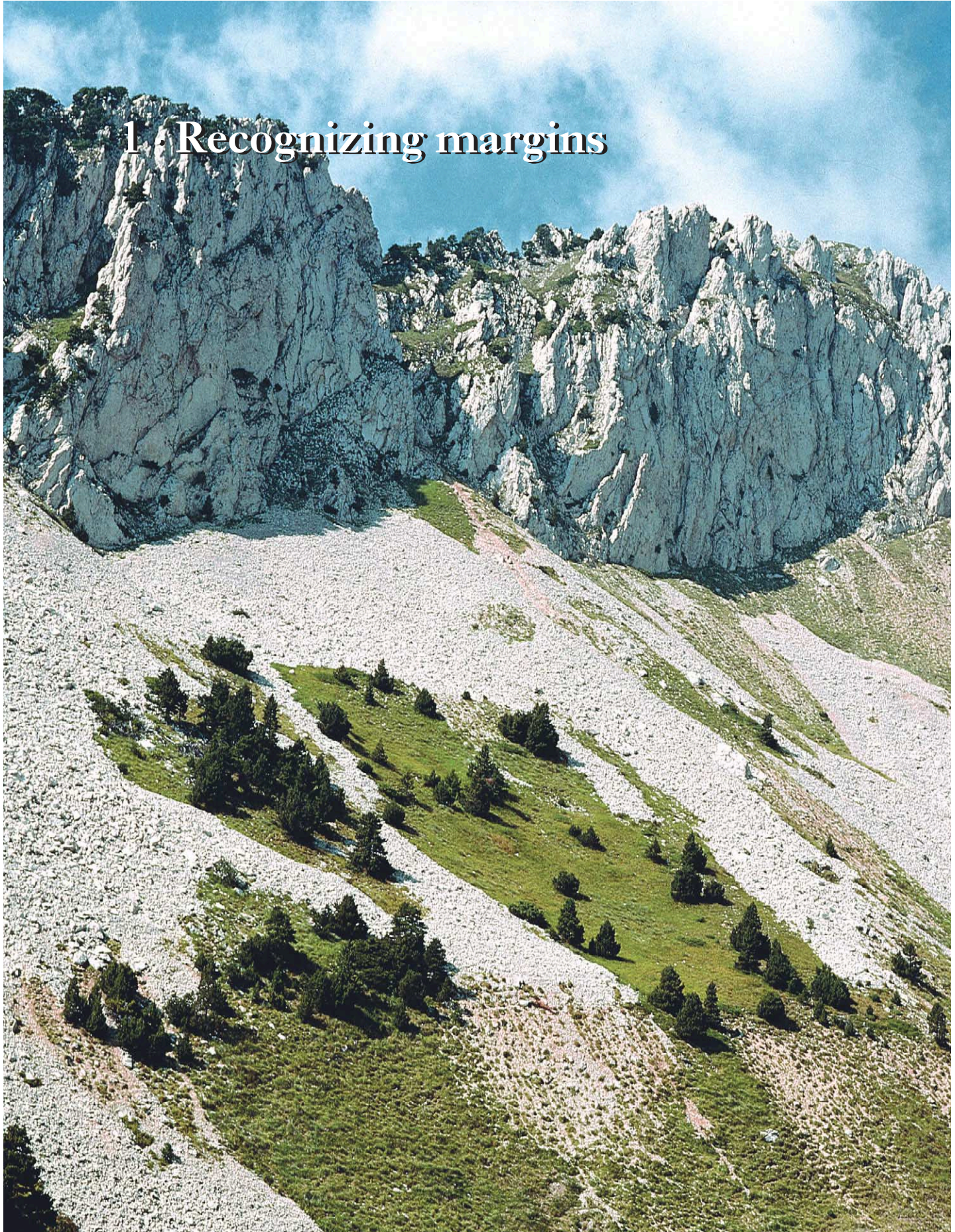
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1 Recognizing margins



1.1 DEFINING MARGINS

All species have limits to their distribution, and populations that demarcate margins demonstrate an end-point in adaptation to a changing environment. Margins are therefore of particular interest as they represent limits to survival that may alter with climatic change. Plants are ideally suited for the study of peripheral situations as their sedentary nature facilitates mapping and historical recording. Many plant atlases record limits to plant distribution both past and present (Hultén & Fries, 1986; Meusel & Jäger, 1992). Boundaries can also be observed between biomes (vegetation formations characterized by distinct life-forms) as in the latitudinal and altitudinal limits to tree growth. The interface between one vegetation type and another can vary as to whether it is abrupt and easily visible even at a distance (*limes convergens* or *ecotone*), as in the natural treelines of the *Nothofagus* forests in the Andes (Fig. 1.2), or whether it is diffuse, as one vegetation zone gradually merges into another (*limes divergens* or *ecocline*) as at the interface between the southern limits of the boreal forest and the northern limits of the deciduous broad-leaved forest. In this latter case, a more quantitative approach is needed for monitoring change, which may be ecologically just as significant as the movement of discrete boundaries (Fig. 1.3).

Significant plant migrations are to be expected as a response to climatic change. However, care is needed in distinguishing climate-induced changes from the current effects of widespread alterations in land use. Environmental change is likely to create diffuse boundaries as one community gradually replaces another but this can also result from changes in land use. Many alpine pastures are no longer grazed in summer with their former intensity and in many areas this has allowed a gradual uphill advance of tree cover even on steep mountain sides (Fig. 1.1).

In terms of plant distribution, living at the edge of any habitat or community poses the question: why do these plants grow there and no further? Numerous biological disciplines have applied their respective methods in the investigations of limits. Biogeography, demography, reproductive biology, physiology and genetics all provide cogent explanations as to why limits occur where they do. Each discipline is correct in its own particular way and can provide adequate answers to the questions that are asked. Whether or not the different

disciplines provide an answer as to a prime cause for any particular limit depends entirely on human perceptions of the problem. Where there are no geographical obstacles, physiological failure might be expected to account for the inability of a species to survive. On the other hand a geneticist might explain the boundary as due to a lack of variation and failure to adapt (see Section 2.2), or merely dismiss the importance of boundaries with the comment that ‘plants are static and it is their genes that migrate’. By contrast a demographer would claim that boundaries are no more than the place where recruitment finally fails to balance mortality. The recognition of boundaries can depend therefore in large measure on what the observer is capable of seeing.

Recognizing a margin and explaining the reasons for its existence are interconnected processes. What is observed as a margin can depend on the manner of observation. Life-forms present obvious boundaries that are immediately visible, as with treelines, or when rising water tables cause meadows to become marshes and bogs or changes in coastal topography cause dunes to give way to flood-prone dune slacks. Other boundaries may be discernible only when species or populations are examined in detail for morphological, demographic or genetic characteristics. Understanding the causes of these wide-ranging limits requires an equally comprehensive approach in recording the nature of variation in plant populations. The negative effect of warm winters on the carbon balance of certain arctic species can explain their southern limits, while their northern boundary is more likely to depend on the time available for growth and resource utilization rather than resource acquisition (see Section 5.6.2). Plants with adequate reserves and low resource demands may be able to survive a negative balance for many years and thus ensure continuance of peripheral populations during temporary episodes of climatic deterioration. The study of marginal areas therefore requires perceptive recording of relevant biogeographical data for matching with possible causes of limits to distribution from what is known about demography, physiological requirements and genetic variation.

1.2 MARGINS AND CLIMATE CHANGE

Despite varying concepts as to what constitutes a margin, boundaries provide an opportunity for observing



Fig. 1.2 *Limes convergens* as seen in two natural treelines in Patagonia at the frontier between Chile and Argentina ($40^{\circ} 30' S$; $70^{\circ} 50' W$). Below the snow-covered peaks can be seen an upper limit to tree survival with the deciduous southern beech (*Nothofagus pumilio*). Below is the upper limit for the evergreen *Nothofagus dombeyi*.

limits to plant survival. Consequently, it is the condition of plants at the approach to a boundary and how they may respond to environmental changes that provides much of the subject matter of this book.

Comparisons between geographically different areas need to be made with caution. Although some boundaries such as treelines and scrub zones may appear similar, and contain species with comparable functional types, they may have geographically different evolutionary and ecological histories and be controlled by diverse environmental factors. Isomorphism – the occurrence of similar forms in unrelated taxonomic groups – is common in plants. It can therefore be dangerous to make global generalizations without careful examination. Even within a single biome, boundary positions may differ in their response to climate change.

In the interface between the arctic tundra and the boreal forest (see Chapter 5), the intuitive prediction would suggest that the tundra will retreat and the boreal forest should expand in response to climatic warming. However, in Alaska, the treeline is currently at its most northerly Holocene extent, while

in north-eastern Canada there has been a retreat since the mid Holocene (Edwards & Barker, 1994). A forest retreat southwards (see Section 5.3.1) has been observed in the Siberian Lowlands (Kremenetski *et al.*, 1998). In Finland an inland rather than a northward migration of the bulrush (*Typha latifolia*; Fig. 1.4) has been attributed to reduced ice cover rather than just warmer temperatures at higher latitudes (Erkamo, 1956).

Some well-defined communities contain groups of species sharing a common boundary (e.g. salt marshes and wetlands; Figs. 1.5–1.6). In these cases it is possible to define such specific plant communities in terms of their present-day species composition. Nevertheless, in terms of geological time these assemblages are only temporary, and species and population aggregations have no biological permanence. The late-glacial floras of Great Britain and Denmark and Russia consisted of communities which contained species which are now dispersed as plants of tundra, steppe, mountains and dunes. In the same way, the northern European forests during the Holocene had an ever-changing species composition (Huntley, 1990).



Fig. 1.3 *Limes divergens* as seen in autumn in northern Vermont, USA showing deciduous trees gradually interspersing and replacing coniferous forest.

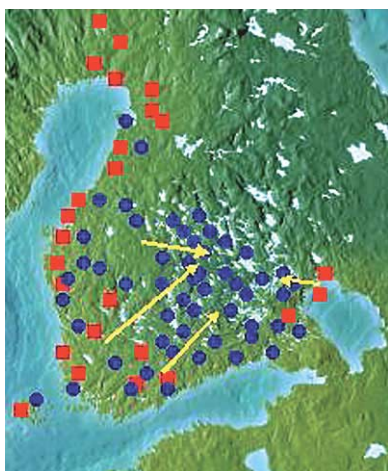


Fig. 1.4 Eastward spread of *Typha latifolia* in Finland 1900–50. Symbols: red, at or before 1900; blue, new records 1926–50. (Adapted from Erkamo, 1956.)

Species survival in peripheral regions is not controlled merely by the impact of average probability of adverse climatic conditions. Survival is also profoundly affected by competition from other species and by the frequency of extreme events, such as drought, flooding, freezing and disturbance. These periodic events, sometimes measured in terms of decades or centuries, can create a complicated pattern for limits to plant existence both geographically and at a microsite level. Marked differences can also be found between populations of the same species. One of the most widespread and ancient of arctic flowering plants is the early flowering purple saxifrage (*Saxifraga oppositifolia*; see Section 6.4.2). Plants of this species from the High Arctic (Spitsbergen) can be deprived of oxygen for months when encased in ice and yet survive. Such a well-developed tolerance of anoxia is not found in more southerly populations of this species (Crawford *et al.*, 1994).



Fig. 1.5 Community limits imposed by a regular flooding regime. A very distinct boundary is visible between the non-flooded dune vegetation and the upper limit of flooding in a salt marsh marked by a zone of *Suaeda vera* near Romney, south-east England.

Boundaries can also be found at a local level, particularly in regions with marked seasonal variations in climate. Many local factors modify the degree of exposure of plants to the adverse season with the result that boundaries can be found in relation to topography, geology, and soil type. Changes in bedrock, particularly at outcrops of chemically basic rocks such as limestone can produce an abrupt boundary that extends over considerable distances (Fig. 1.7). Flooding frequency and depth is also a powerful discriminator between plant communities and creates easily visible boundaries (Figs. 1.5–1.7).

1.3 LIMITS TO DISTRIBUTION

In many demographic studies, edge effects or boundaries have traditionally been regarded as merely ‘nuisances’. Nevertheless, they can be modelled and investigated for the dynamic properties of populations at the edge of their distribution. Such studies can be used to provide graphic demonstrations that the distribution patterns of individuals at population edges have distinctive properties due to the influence of space on population margins. Processes occurring at the margin of populations are likely to have an influence

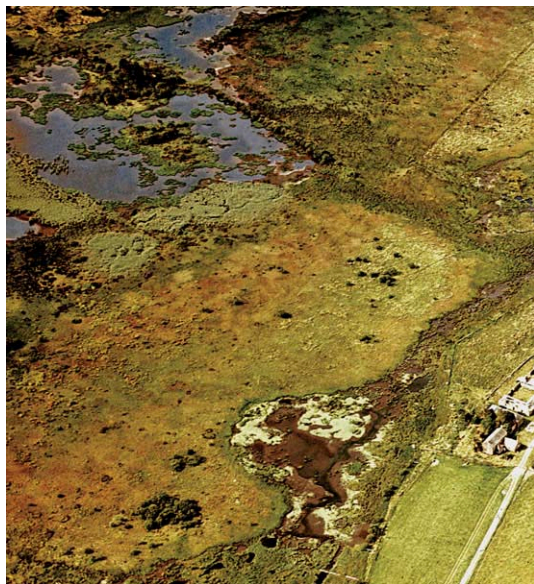


Fig. 1.6 Aerial view of wetland plant community zonation. Boundaries between plant communities on the shores of Loch of Kinnordy, Angus, as photographed in 1969. (Photo J. K. S. St Joseph.)

on the extension and distribution, particularly when populations are small and localized (Antonovics *et al.*, 2001).

1.3.1 Physiological boundaries

Figure 1.8 is an attempt to divide the physiological limitations to species distribution into a number of discrete categories. Physiological requirements for plant survival are considered under the heading of resource availability, which involves biological properties and can therefore be separated from purely physical limits to viability such as heat and cold tolerance. As modelling studies suggest, individuals at the margins of populations may be exposed to special spatial features resulting from a different relationship with their neighbours which can be influenced by a variety of factors including seed production, pollen dispersal, gene flow and the availability of potential sites for establishment (Antonovics *et al.*, 2001). The margin is also a region where environments oscillate. For sedentary organisms, particularly if they require

several years to develop before they can reproduce, this poses a particular problem. First and foremost, the long-term survival of individuals will depend on their physiological capacity to survive in a fluctuating environment.

Whatever their location in a population, be it marginal or at the core, all individuals if they are to survive have to attain a positive carbon balance and secure adequate supplies of nutrients, light, and water. This does not have to be steady-state existence. For some species access to certain resources can be interrupted for prolonged periods without causing any serious injury. Consequently, in the study of limits to distribution, particular attention has to be paid to the timing of environmental stresses and the frequencies of extreme events. Ultimately, the survival of any individual or population is related to the relative resource needs of the species in question as compared with their competitors. This, however, cannot be observed in any one growing season. Short-term experiments (e.g. 3–4 years), which can include raising the ambient temperature with shelters or giving additional nutrients, therefore have limited value. Species that succeed in capturing resources to the detriment of a less vigorous competitor, in what for these dominant plants may have been a series of favourable growing years, may ultimately be excluded from the habitat if they cannot survive at other times when resource levels are reduced. The species with the smaller demand may have therefore a greater long-term viability (Section 3.6.2).

1.3.2 Resource availability

In ecophysiological studies it is often considered desirable to have some common unit for assessing the relative viability of plant populations as they approach limits to their distribution. Given that plants may be limited by different resource deficiencies at various stages in their life cycle, carbon balance is commonly used as an appropriate currency for measuring success in resource acquisition as it is the investment of carbon that makes possible the acquisition of all other plant resources. In recent years the acquisition of resources as affected by environmental factors has been much studied, possibly because carbon acquisition either in individual plants or whole communities is readily monitored by recording carbon dioxide flux from



Fig. 1.7 Boundary zone marking the interface between limestone and acid Torridonian sandstone in the Scottish north-west Highlands. View looking north to Elphin with cliffs of Durness limestone on the right (east) supporting a calcicole flora that contrasts with the bog and acid mountain vegetation of the Torridonian sandstone and Lewisian gneiss lying to the north-west.

individual leaves, whole plants, or even forest canopies (Lee *et al.*, 1998). In this approach, limits to plant distribution can be viewed in terms of carbon balance with the potential theoretical physiological limit for any species or community being reached only when carbon

gain is no longer greater than expenditure. Current interest in climate change and the desire to be able to predict through modelling future limits to plant distribution makes the use of a general metabolic currency, such as carbon, a potentially attractive proposition.

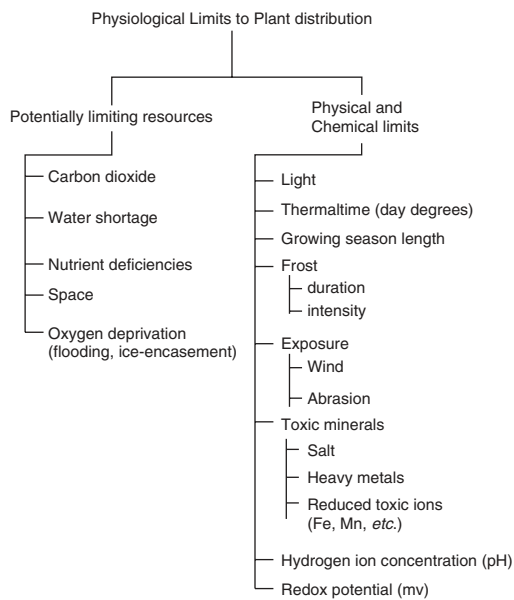


Fig. 1.8 A selection of physiological factors that can impose limits on plant distribution.

If such a generally applicable method could be found to monitor energy resources it might serve to detect potential carbohydrate impoverishment before the plants in question showed any other signs of decline in viability.

In some cases it is possible to demonstrate a relationship between carbon balance and limits to distribution and physiological viability. Drought and cold both reduce the potential for carbon acquisition. In addition, certain stressful environmental situations can further deplete carbon reserves by causing an increase in carbohydrate consumption. The depletion of carbohydrate reserves by high respiratory activity at warm temperatures has often been suggested as a factor that limits the southward extension of northern species (Mooney & Billings, 1965; Stewart & Bannister, 1973). Various case histories relating plant distribution to carbon balance are discussed in Chapter 3. Although in certain cases carbon starvation is associated with failure to survive it is not a universal method that can be applied crudely to all plant forms in any situation for determining their distribution limits as there is remarkably little evidence that carbon starvation is the primary cause for either woody or herbaceous species failure at the cold end of their ecological distribution.

The most thoroughly examined aspects of the ecology of plants in relation to temperature are the altitudinal and latitudinal limits for the survival of trees. Many studies have sought to determine whether or not the low temperature regimes of high latitudes and altitudes cause trees to come into a carbon balance deficit. Physiologically, this would appear a simple and logical explanation of the effect of low temperatures on tree survival. It might be expected that as woody plants devote a considerable part of their resources to the formation of non-productive trunks and stems they may be unable to support such a growth strategy when growing seasons are cool and short. However, an extensive worldwide study of the carbon balance in trees at their upper altitudinal boundaries has shown the converse, namely, that tree growth near the timberline is not limited by carbon supply (Fig. 1.9) and that it is more probable that it is sink activity and its direct control by the environment that restricts biomass production of trees under current ambient carbon dioxide concentrations (Körner, 2003).

A worldwide study looking at numerous thermal indicators found that a growing season mean soil temperature of 6–7 °C provided the best generalized indicator of montane treelines from the tropics to the boreal zone (Körner & Paulsen, 2004). The soil temperature provides an approximate indicator of thermal conditions at the treeline and suggests that an edaphic thermal summation of growing season conditions could replace the older Köppen's Rule that the limit to tree growth coincided with the 10 °C isotherm of the warmest month of the year (Fig. 1.10). This modification from a measurement indicating maximum warmth to a temperature mean for the entire growing season reflects a realization that the altitudinal limits to tree growth are not directly related to the ability to make a net carbon gain. Instead, the treeline is more likely to be related to the length of growing season that is needed for the production and development of new tissues (Körner, 1999). However, in any discussion between cause and effect it is necessary to remember that mean temperatures do not exist in nature and therefore should be considered merely as indicators and not causal factors. The same is true for mean soil temperatures (Holtmeier, 2003).

Although overall carbon starvation is not a feature of large woody plants at their upper limits of distribution, it is nevertheless possible that certain organs