1

Introduction

Succession – nothing in plant, community or ecosystem ecology has been so elaborated by terminology, so much reviewed, and yet so much the centre of controversy.

(West, Shugart & Botkin, 1981: iv)

Nowhere can succession be studied more profitably than in the valley below the front of a large glacier.

(Ellenberg, 1988: 440)

1.1 Glacier forelands and simplicity

Ecologists, like all natural environmental scientists, must simplify in order to make progress. Simplification can take many forms. One approach is to seek a relatively simple landscape where it is possible to exclude, or at least significantly reduce, the effects of many of the interactions that occur in more complex landscapes. Although it is not possible to obtain perfect experimental control in such field laboratories (or microcosms), the approach enables a reduction in levels of interference. In this way it is possible to focus more clearly on the interactions and to progress towards a comprehensive understanding of the whole.

Glacier forelands are considered in this book as a unique type of field laboratory. A glacier foreland is the area of newly-formed landscape in front of a glacier, which was recently ice covered but has since been exposed by glacier retreat (Fig. 1.1). The term 'glacier foreland' is derived from the German *gletschervorfeld* (Kinzl, 1929) and was introduced into the English language by Beschel (1961). It is used here to define the land area exposed in historical times, since the glacier maximum of the 'Little Ice Age'. This is the glacier foreland *sensu stricto*, the glacier foreland in the narrow sense of Holzhauser (1982). Thus, the glacier foreland often forms a distinct zone of relatively bare terrain extending up to many kilometres from the margin of the glacier (Fig. 1.2). This recently-deglacierized zone (deglaciated by modern glaciers) should be distinguished from the more extensive and older landscapes deglaciated earlier in the Quaternary.

There are several fundamental advantages of using glacier forelands as field laboratories for ecological purposes. First, their restricted physical size

Fig. 1.1. Recently-deglaciated terrain, Storbreen glacier foreland, Jotunheimen, photographed in 1985. Bouldery terrain in the foreground (with moraine ridges) was deglaciated about 140 years ago.

facilitates comprehensive investigation. Second, with a relatively severe climatic environment, they support relatively simple ecosystems. Third, recently-deglaciated terrain has experienced only a short history of modification by changing natural environmental processes. Last, but by no means least, with increasing distance from a retreating glacier, a longer time period has been available for ecosystem development: hence, the pattern of ecosystems on the glacier foreland is commonly interpreted as a spatial representation of temporal change and as a vast natural experiment.

1.2 Ecology and primary succession

The first detailed study of glacier foreland ecology appears to have been made in the European Alps by Coaz (1887), who visited the Rhonegletscher in the summer of 1883. Coaz found *Saxifraga aizoides* growing on ground exposed from beneath the retreating glacier for less than three years. On progressively older terrain, more species were found, with a total of 70 species from 18 families on ground deglaciated for no more than 10 years, including 39 on the oldest terrain examined. Observations such as these, which indicate different species colonizing progressively older terrain, have inspired many ecologists with an interest in the time-dependent ecological process of primary succession. Other early studies

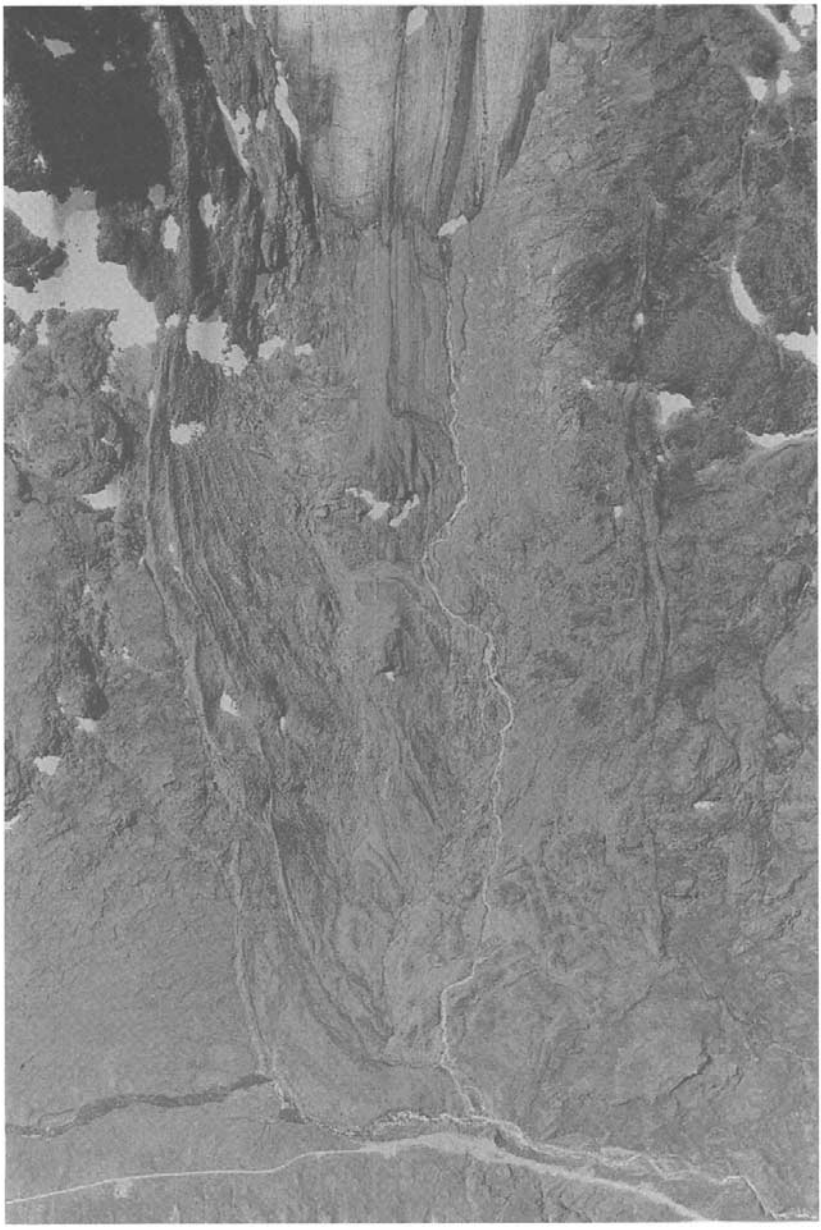

Fig. 1.2. Vertical aerial photograph of the Storbreen glacier foreland, Jotunheimen, southern Norway (Widerøe's Flyveselskap A.S., 1968). The outermost of the prominent sequence of end-moraine ridges, which extends about 1.5 km from the glacier snout, defines the glacier foreland boundary and indicates the position of the glacier about A.D. 1750. See also Fig. 2.4.

include those in the European Alps (Lüdi, 1921, 1945; Frey, 1922; Braun-Blanquet & Jenny, 1926; Negri, 1934, 1936; Friedel, 1934, 1937, 1938; Oechslin, 1935), the Pyrenees (Davy de Virville, 1929), North America (Butters, 1914; Cooper, 1916, 1923a–c, 1931, 1939) and Scandinavia (Fægri, 1933). More recently, research has intensified, and other aspects of ecosystem development (particularly soils) have been investigated.

Succession, the complex of processes producing gradual, directional changes in the species composition and structure of ecosystems, is commonly encountered, yet it is far from fully understood. Indeed, Cooper (1926), a pioneer in the study of the ecology of recently-deglaciated terrain in North America, proposed that the universality of change should be regarded as a fundamental fact of ecology. Today, a variety of largely unsubstantiated succession theories remain one of the basic conceptual underpinnings of the subject (McIntosh, 1981, 1985; Miles, 1987). A recent survey of opinion amongst members of the British Ecological Society has revealed that succession is regarded as the most important ecological concept after that of the ecosystem itself (Cherrett, 1989).

There is also a continuing and increasing practical interest in succession and related concepts of stability, especially in the context of human-induced primary and secondary succession, land restoration and conservation (Bradshaw & Chadwick, 1980; Cairns, 1980; Jordan, Gilpin & Aber, 1987; Salzberg, Fredriksson & Webber, 1987; Luken, 1990). Even though succession is of fundamental importance, it is only rarely amenable to conventional observation and experimentation because its timescale (10–10^3 years) is too long. Primary succession, whereby a newly-formed land surface devoid of life is colonized and develops a new ecosystem, generally operates over a longer time period than the related process of secondary succession. The latter is initiated from at least a vestige of an existing ecosystem, tends to proceed at a faster rate, and may differ qualitatively from primary succession. Thus sites and methodologies which permit the detailed investigation of succession in general and of primary succession in particular are essential to the advancement of both pure and applied ecology.

The potential of glacier forelands for the study of primary succession and related aspects of ecosystem development was appreciated only when observations of these sites were made with the aid of an appropriate methodology. By substituting space for time, Coaz (1887) and later workers realized that increasing distance from the margin of a retreating glacier could be interpreted as representing a temporal sequence (chronosequence) in ecosystem development. Combined with absolute dating of terrain age,

quantitative rates of change can also be inferred. However, this methodology of space-for-time substitution is based on some largely untested assumptions and is not without limitations (Pickett, 1988). The aim of this book is therefore to review not only the available information on the ecology of recently-deglaciated terrain and its relevance to concepts and theories of succession but also the methodology used. The remainder of this chapter provides an introduction to this methodology and to the distinctive approach adopted in this book.

1.3 Space-for-time substitution (chronosequences)

The most influential research on the ecology of recently-deglaciated terrain, at least in the Anglo-American literature, has undoubtedly been that from Glacier Bay, Alaska, where a series of studies on plant succession was pioneered by Cooper (Cooper, 1923a–c, 1931, 1939). Utilising a well-documented record of glacier retreat, three major vegetation types (pioneer community, willow–alder thicket and spruce forest) were recognized, and a successional scheme has been elaborated to include up to eight intergrading successional stages (Lawrence, 1958; Decker, 1966; Reiners, Worley & Lawrence, 1971; see section 5.1.1). The research of Crocker & Major (1955) in particular is widely cited, even in textbooks (e.g. Krebs, 1985; Kershaw & Looney, 1985; Colinvaux, 1986; Begon, Harper & Townsend, 1990), as they link vegetation changes to soil development and thereby provide evidence of a mechanism for succession. For example, they suggest that soil acidification and nitrogen accumulation under Sitka alder (*Alnus crispa*) precede the invasion of Sitka spruce (*Picea sitchensis*). The reaction of alder on the soil, which facilitates invasion by spruce (cf. the facilitation model of Connell & Slatyer (1977), is invoked as the mechanism of change. Thus the research at Glacier Bay has been interpreted as supporting the classical view of vegetation-controlled or autogenic succession (Tansley, 1935), driven by reaction mechanisms (Clements, 1928) (but see section 6.1.4).

Most ecologists have interpreted the vegetation patterns on recently-deglaciated terrain in much the same way, though few have provided good evidence for mechanisms of change. Nevertheless, valuable data have been collected during studies in many different parts of the world. These data together constitute one of the main sources of empirical information on primary succession and soil development. However, the chronosequence methodology employed in most of this research has been rather restrictive.

The concept of a chronosequence as a spatial representation of a

temporal sequence has been systematized by Jenny (1941, 1946) in the context of soil development. A similar concept and systematization in the context of vegetation succession forms part of Major's (1955) functional factorial approach to plant ecology (see also Perring, 1958; Jenik, 1986), and the concept has since been extended to ecosystem development (Olsson, 1958; Jenny, 1961, 1980). Chronosequences are spatial sequences in which environmental factors other than time are assumed to be unimportant, either because they are invariant or because they are relatively ineffective.

In front of a retreating glacier, the time factor is obviously a major control on spatial patterns in the vegetation and soils. Immediately after deglaciation the terrain is normally viewed as being devoid of living organisms (but see section 6.1.4). The ecosystems developed on older ground probably began from a broadly similar state. Selection of comparable sites (in terms of climate, parent material, relief, etc.) for the description and analysis of chronosequences reduces the effect of environmental factors other than time. In addition, the time factor can often be quantified quite precisely in terms of terrain age. A chronosequence, however, is not identical to a successional sequence at a single site. Environmental factors vary to some extent between sites in a chronosequence (and through time at particular sites) and terrain age does not always correspond precisely with the time elapsed since deglaciation.

1.4 Geoecology (landscape ecology)

Although the objective of most research has been to describe chronosequences and, more recently, to define chronofunctions quantitatively, many observations and results suggest that an interpretation of the ecology of recently-deglaciated terrain merely in terms of chronosequences is an oversimplification. Even Coaz (1887: 11) recognizes the importance of such factors as snow and avalanches, cold winds, shifting glacial meltwater streams and torrential rains as effective influences on the vegetation. Similarly, later workers have recognized this problem. For example, where vegetation maps have been produced they do not show a simple vegetation zonation corresponding to the pattern of deglaciation (Friedel, 1938; Richard, 1968; Jochimsen, 1970, Matthews, 1979a). Such maps demonstrate a complex mosaic of communities (see section 5.3.1). They also suggest the need for a broader perspective for studies of the ecology of recently-deglaciated terrain. Such a perspective is provided by geoecology (landscape ecology).

The term 'landscape ecology' was first used by the German geographer C. Troll, who later coined the term 'geoecology' to include not only the study of ecosystems but also all the phenomena and interacting processes of the natural (and cultural) landscape (Troll, 1939a, b, 1971, 1972). Although landscape ecology has been recently rediscovered in America (e.g. Risser, Karr & Forman, 1984; Forman & Godron, 1986; Urban, O'Neill & Shugart, 1987), the concept of landscape (German: *landschaft*) and the principles of geoecology (landscape ecology) have a long tradition in Europe (Naveh & Lieberman, 1984; Schreiber, 1990). Geoecology shares common ground with the study of ecosystems and has an even closer relationship with the Soviet field of biogeocoenology (Sukachev & Dylis, 1964). However, the concept of landscape differs from that of ecosystem in giving greater emphasis to spatial organization on the Earth's surface and to the interaction of ecological processes within a broader framework of environmental processes. The emphasis given to spatial organization of the landscape has been termed the horizontal (geographical) aspect of geoecology; the vertical (biological–ecological) aspect emphasizes functional interrelationships at particular sites (Troll, 1971). Both aspects are necessary to obtain a comprehensive understanding of any landscape.

From the viewpoint of geoecology, ecosystem succession in front of a retreating glacier is clearly part of the developing landscape – or landscape succession (Troll, 1963) – in which plant life changes together with the animals, the soil and the abiotic environment. The thesis that newly-developing ecosystems in front of retreating glaciers can be fully understood only when viewed as part of the developing landscape is examined further in this book. The geoecological approach that has been developed aims to provide a more comprehensive, integrated and interdisciplinary treatment of the ecology of recently-deglaciated terrain than has been attempted before. The areas in front of retreating glaciers are particularly appropriate for such a holistic approach because of the almost unique opportunity to define an accurate timescale.

2

The nature of the timescale

The ecological significance of recently-deglaciated terrain depends in large measure on the existence of a timescale. It is appropriate, therefore, that the nature and limitations of the timescale be fully assessed.

Few landscapes exist where even the relative age of the land surface exhibits a simple pattern or can be established with any certainty. Distance from the margin of a retreating glacier is exceptional in that it is directly related to terrain age and therefore represents an index of relative age. Because glacier retreat rates are rarely constant, however, the relationship between distance and time is non-linear and more information is necessary to obtain absolute (numerical) age estimates. Derivation of an absolute timescale requires an observed history of glacier variations or the application of dating techniques. A full understanding of the nature and limitations of the timescale therefore demands an appreciation of the extent and timing of glacier variations, the range and accuracy of available dating techniques, and their interaction in the context of specific glacier forelands.

2.1 Glacier variations

The size of a glacier depends essentially on the balance between winter accumulation and summer ablation and is therefore determined by climate (Meier, 1965; Andrews, 1975; Porter, 1981a). For a given climatic environment an equilibrium size and an equilibrium profile may be considered (Fig. 2.1a). The equilibrium profile is maintained by the flow of ice from areas of net accumulation to areas of net ablation. This condition theoretically pertains after a number of years with a similar climate and is characterized by a stationary ice margin. However, because of climatic variability and change the ice margin, particularly at the glacier terminus, is rarely stationary.

Although the relationship between climatic change and glacier variations is not simple (Meier, 1965; Paterson, 1981; Sutherland, 1984; Oerle-

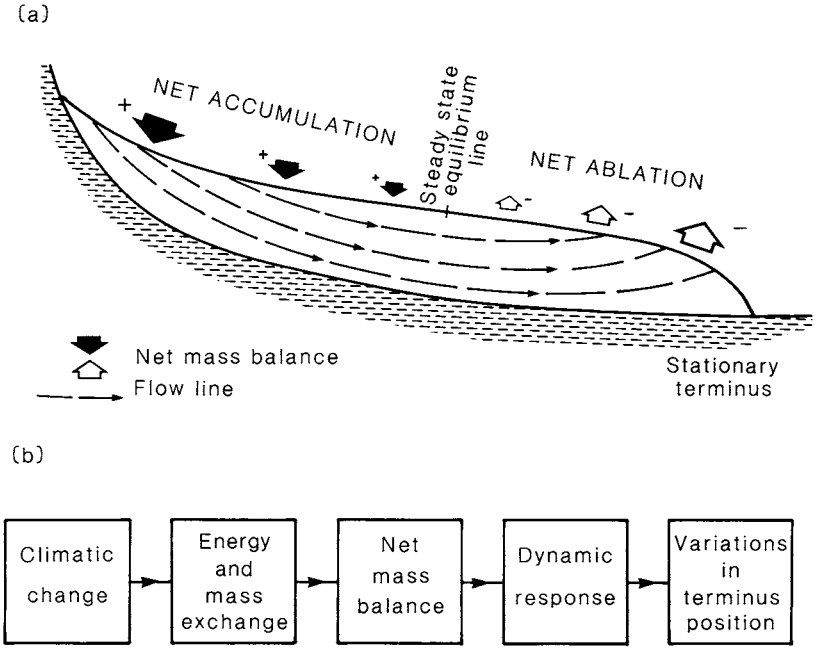

Fig. 2.1. Some theoretical aspects of the relationship of a glacier to climate: (a) mass balance and ice flow of a glacier in steady-state equilibrium with climate (from Sugden & John, 1976); (b) the dynamic response of a glacier to climatic variation (from Meier, 1965).

mans, 1989), it may be envisaged as a chain of distinct processes (Fig. 2.1b). A change in climate alters the local mass and energy exchange processes at the surface of the glacier, which produce changes in accumulation and/or ablation and hence net mass balance. The gain or loss of mass determines the dynamic response of the glacier, generally resulting in a change in glacier thickness and the rate of flow, an adjusted surface profile and an advance or retreat of the terminus. Complications include the existence of negative (damping) and positive (amplifying) feedback relationships, varying response times (the period during which adjustment to a mass balance change occurs), and varying lag times (the interval between maximum or minimum mass balance and maximum or minimum terminal position). Factors such as the size, surface slope and thermal characteristics of the glacier are effective influences. For example, response times for small glaciers generally vary from several years to decades; for large glaciers and ice sheets, values of hundreds or even thousands of years have been calculated (Paterson, 1981).

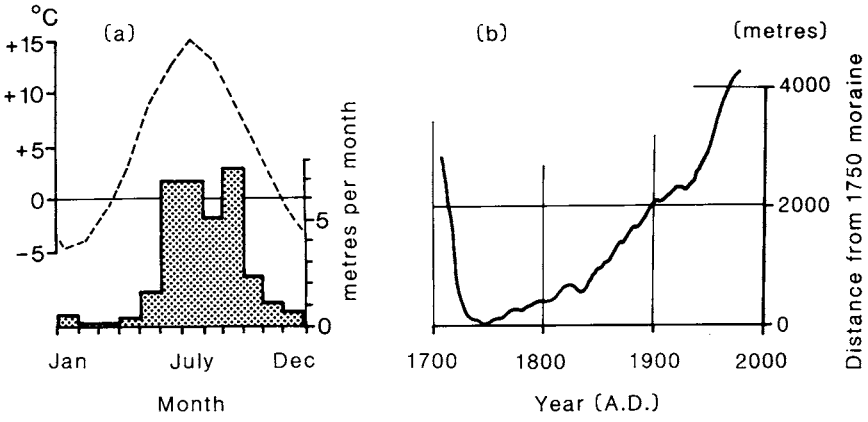

Fig. 2.2. Short- and long-term advance and retreat of the terminus of Nigardsbreen, southern Norway: (a) mean monthly variations, October 1935 to July 1947 (during a period of rapid glacier retreat) compared with mean monthly temperatures at Fjærland (from Fægri, 1950); (b) longer-term variations since A.D. 1710, based on annual measurements and documentary sources, and including a major advance followed by a major recession (from Østrem, Liestøl & Wold, 1976).

Variations in the position of the glacier terminus are only partly determined by the dynamic response of the glacier to changes in mass balance described above. Major advances and retreats can be explained in such terms but minor glacier fluctuations often demonstrate a more direct and immediate response to seasonal and annual climatic fluctuations. Consider the equilibrium profile in Fig. 2.1a. The position of the glacier terminus depends on the ice velocity and the rate of ablation. The glacier advances when the former exceeds the latter and retreats when the reverse case is true. It would be expected, therefore, that a glacier in equilibrium with climate might advance in winter, when the terminus is snow covered, and retreat in summer, when ablation is at a maximum. In a year with above average ablation (as would occur, for example, in an abnormally warm summer or in a year with reduced winter snowfall) the summer retreat might be accentuated (Fig. 2.2a) and in a year with below average ablation the summer retreat would be less. Similarly, a run of years with reduced ablation might produce a short-term glacier advance during a period when the long-term dynamic response of the glacier is to retreat (Fig. 2.2b). Thus, for glaciers that are responsive to these direct seasonal and annual climatic fluctuations, ratchet-like advances and retreats can be envisaged.

The seasonal, annual and longer-term advance or retreat of a glacier