3. Study sites and their environments

3.1 Introduction

In this chapter, detailed descriptions are given of the sites at which the study was carried out. Environmental data are also presented and compared among sites. Environmental similarity is an important assumption of the hypothesis of community-level convergence (see Chapter 1). On the basis of their environments sites that are well-matched in terms of particular parameters, or all parameters, are selected for particular attention in subsequent analyses.

3.2 Site descriptions

Seventeen study sites, encompassing four landmasses and ten regions, were established and sampled in the course of the study. Here, general features of the floristic composition, physical structure and environment of each site are described. The sites are listed under the landmass and region in which they occur. Each is identified by a two- or three-character code and a name. The code is based on the landmass (first letter), region (second letter, if more than one site was sampled in the same region), and a number, distinguishing different sites within a region or landmass. The name is based on a geographic feature at or near the study site. For example, ZS1 Ten Mile was one of three sites in the southern region (S) of New Zealand (Z), and was situated in a patch of forest known as Ten Mile Bush. In subsequent chapters, full site names are generally used in the text, while codes alone are presented in some tables and figures.

In the descriptions below, heights given for canopy trees are averages of the values obtained for a number of representative trees. Diameters at breast height (DBH) are averages among all canopy trees of a given species encountered within quadrats. Canopy trees are defined as individuals attaining more than 67% of mean canopy height (see Chapter 2). Familial affinities are given only at the first mention of a particular genus. Nomenclatural sources and conventions are described in Section 2.3.6. The reported species richness values are the numbers of vascular plant species encountered within all quadrats sampled. The number of quadrats sampled is also given for each site, as it varies from three to five, and would have some effect on the number of species observed over the whole site. Mean quadrat species richnesses for sites are given in Chapter 5 (Table 5.1).

LANDMASS: TASMANIA (T)

The three sites sampled in Tasmania broadly encompassed the geographic distribution of

Nothofagus cunninghamii there (Fig. 3.1). *N. cunninghamii* is the most important dominant species of lowland to montane cool temperate rainforest in Tasmania (Jarman *et al.* 1984). The other Tasmanian *Nothofagus* species, *N. gunnii*, is a deciduous shrub or small tree confined to a restricted range of subalpine habitats, and was not sampled, as the communities it forms are of a different kind to the tall, evergreen rainforests investigated by this study. The distribution, structure, composition and general features of the ecology of Tasmanian *Nothofagus*-dominated forests are described by Beadle (1981), Howard (1981), Jackson (1983), Busby (1984), Jarman *et al.* (1984), Hill (1982), Hill & Read (1984) and Read & Hill (1985, 1988).

Region: Northwest Tasmania

Site T1 Balfour, 41° 09' S, 144° 59' E. This site was situated on the crest of a gently-sloping ridge forming the southern boundary of the Balfour Forest Reserve, at an altitude of 190 m. The forest was dominated by mature *Nothofagus cunninghamii* at an average height of 23 m and DBH 67 cm. *Atherosperma moschatum* (Monimiaceae) and *Eucryphia lucida* (Eucryphiaceae) were also present, forming an irregular subcanopy. Other major component species were *Olearia argophylla* (Compositae), *Pittosporum bicolor* (Pittosporaceae) and the tree fern *Dicksonia antarctica* (Dicksoniaceae). Regeneration of *N. cunninghamii* occurred primarily within larger treefall gaps, where *A. moschatum* regeneration tended to be more conspicuous. Twenty-three vascular plant species occurred within the three quadrats sampled. Mean slope was 5° and aspect 180° S. The geology of the area comprises a volcano-sedimentary complex of Cambrian age, the Mt Read Volcanics (Department of Mines 1976). This formation is associated with soils of high fertility, and is the most characteristic geology for *Nothofagus*-dominated forest in Tasmania (Read & Hill 1988).

Region: Southwest Tasmania

Site T2 Anne, 42° 55' S, 146° 26' E. This site occupied a terrace on the northwest-facing slope of a ridge of Mt. Anne, *c.* 600 m asl. *Nothofagus cunninghamii* was the dominant species, attaining a height of 29 m and DBH 68 cm. *Atherosperma moschatum* formed a subcanopy locally, with *Eucryphia lucida*, *Anopterus glandulosus* (Escalloniaceae), *Anodapetalum biglandulosum* (Cunoniaceae) and *Dicksonia antarctica* forming a moderately dense understorey. *N. cunninghamii* regeneration was confined to treefall gaps. Species richness (three quadrats) was 21. Mean slope was 20° and aspect 345° N. The bedrock consists of Jurassic dolerite (Department of Mines 1976).

Region: Northeast Tasmania

Site T3 Mathinna, 41° 20' S, 147° 45' E. This study site was located on the Mathinna Plains, at an altitude of 800 m. *Nothofagus cunninghamii* formed a very even canopy at a height of *c.* 22 m. The canopy trees appeared to belong predominantly to one cohort, with mean DBH 36 cm. *Phyllocladus aspleniifolius* (Podocarpaceae) occurred occasionally in the canopy, while *Atherosperma moschatum* and *Tasmannia lanceolata* (Winteraceae) were the most prominent subcanopy trees. Tree ferns, *Dicksonia antarctica*, and metre-high tussocks of *Gahnia grandis* (Cyperaceae) dominated the otherwise sparse understorey: just 20 vascular species were observed within the five quadrats sampled. Slope averaged 5° with aspect 295° W. The presence of occasional sawn stumps suggests that selective logging has taken place on a minor scale in the past. Basement rocks are mudstones and sandstones of Permian age (Prickard 1980).

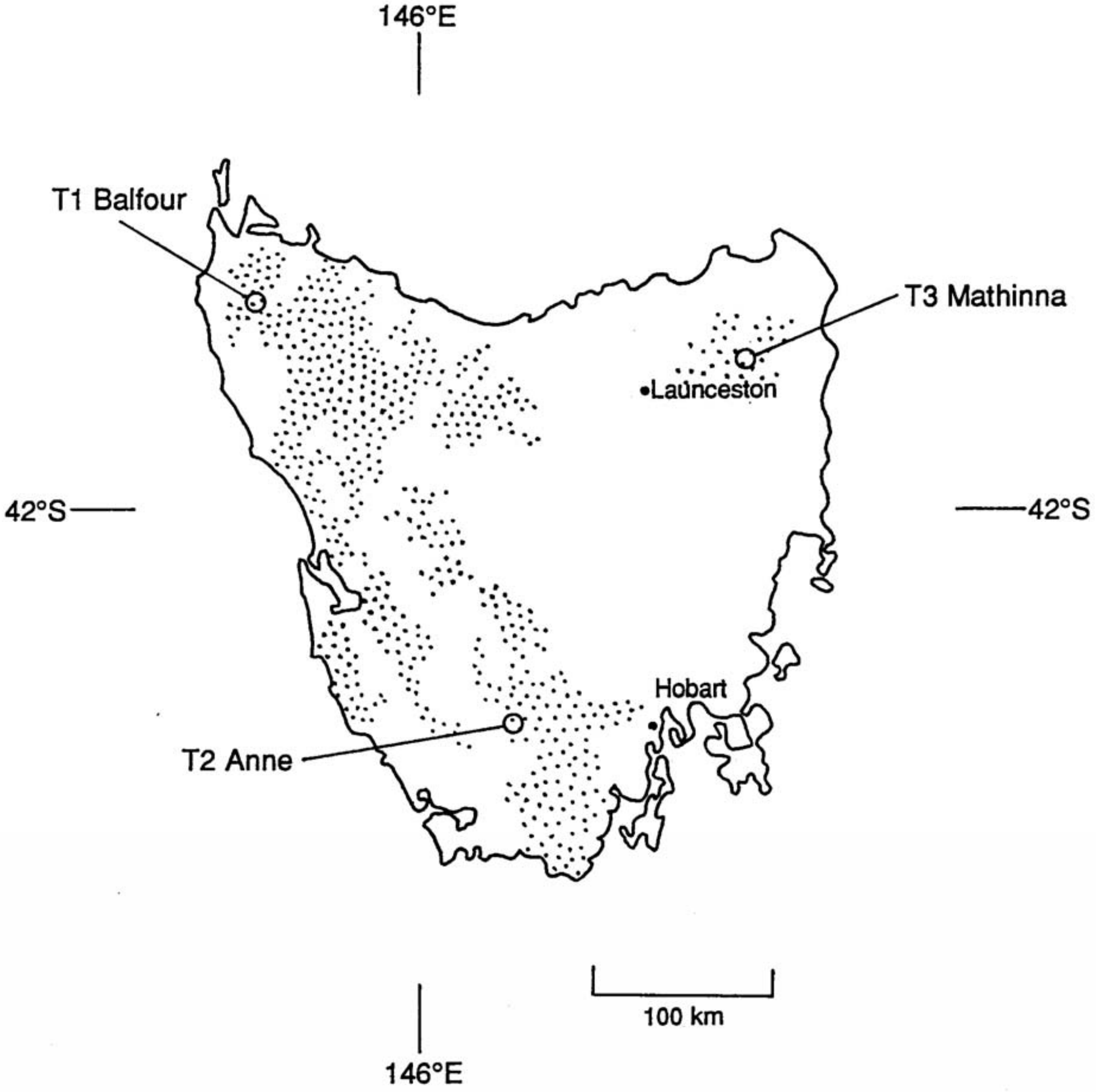

Fig. 3.1 Locations of study sites in Tasmania, showing (shading) the approximate distribution of *Nothofagus cunninghamii*-dominated rainforest (after Davies 1964).

LANDMASS: MAINLAND AUSTRALIA (A)

In contrast to Tasmania, where *Nothofagus*-dominated rainforests are relatively abundant, *Nothofagus* has a very restricted and discontinuous distribution on mainland Australia. Both *N. cunninghamii*, which occurs at a number of localities in Victoria, and *N. moorei*, which is confined to a few isolated sites on the Great Dividing Range in northern New South Wales and southern Queensland, have probably suffered a marked contraction in their ranges as a result of decreasing rainfall in the late Palaeozoic (Hill 1994). *N. cunninghamii* rarely forms large pure stands in Victoria, but tends to occur as a codominant with *Eucalyptus* or *Acacia* species (Howard & Ashton 1978). For this reason, no Victorian sites were sampled. *N. moorei*, however, may occur as a sole canopy species, and sites dominated by this species were sampled at the southern end of its range, the Barrington Tops massif, and 200 km further north, in New England (Fig. 3.2).

Beadle (1981), Howard (1981) and Floyd (1990) describe the structure, distribution and floristic composition of *N. moorei*-dominated cool temperate rainforests. Turner (1976) has examined altitudinal gradients of texture (leaf size classes) as well as regeneration ecology in rainforest at Barrington Tops. Read & Hill (1985) investigated population size structures and regeneration of *N. moorei* at three localities, including Barrington Tops and New England.

Region: Hunter Valley, New South Wales

Site A1 Lumeah, 32° 07' S, 151° 25' E. Situated near Mt. Lumeah on the western flanks of the Barrington Tops massif, at an altitude of 930 m, this forest had a closed canopy of *Nothofagus moorei*. Canopy trees averaged 33 m in height, with DBH 80 cm. *Daphnandra* `sp. A' (Monimiaceae) also occurred at canopy level within the study site. Several other tree species made up a prominent subcanopy, including *Caldcluvia paniculosa* (Cunoniaceae), *Doryphora sassafras* (Monimiaceae), *Orites excelsa* (Proteaceae) and *Tristaniopsis collina* (Myrtaceae). The understorey was dominated by ferns, mainly *Lastreopsis decomposita* (Aspidiaceae) and *Diplazium australe* (Athyriaceae), while *Dicksonia antarctica* was associated with treefall gaps. Climbers, notably *Smilax australis* (Smilaceae) and *Palmeria scandens* (Monimiaceae), were prominent among the branches of trees. Species richness was 36 (five quadrats). Slope averaged 10° with aspect 250° W. Tertiary Basalts and Granites make up the bedrock in the area (David 1950).

Region: New England, New South Wales

Site A2 Cascades, 30° 30' S, 152° 25' E. This site was situated near The Cascades waterfall on an escarpment of the Great Dividing Range in New England National Park, altitude 1300 m.

Very mature *Nothofagus moorei* (height 28 m, DBH 71 cm) was emergent above a multispecific subcanopy including *Doryphora sassafras*, *Orites excelsa*, *Cryptocarya nova-anglica* (Lauraceae) and *Elaeocarpus holopetalus* (Elaeocarpaceae). Tree ferns, *Dicksonia antarctica*, and tussocks of *Lomandra* sp. (Xanthorrhoeaceae) were prominent in the understorey, while an unidentified graminoid (probably *Carex* sp.) was prominent within treefall gaps and patches in which thinning of the *Nothofagus* crowns permitted more light to reach the forest floor. Vascular species richness was 31 (five quadrats). Mean slope was 10°, aspect 160° S. Basement rocks in the area are Tertiary basalts and granites (David 1950).

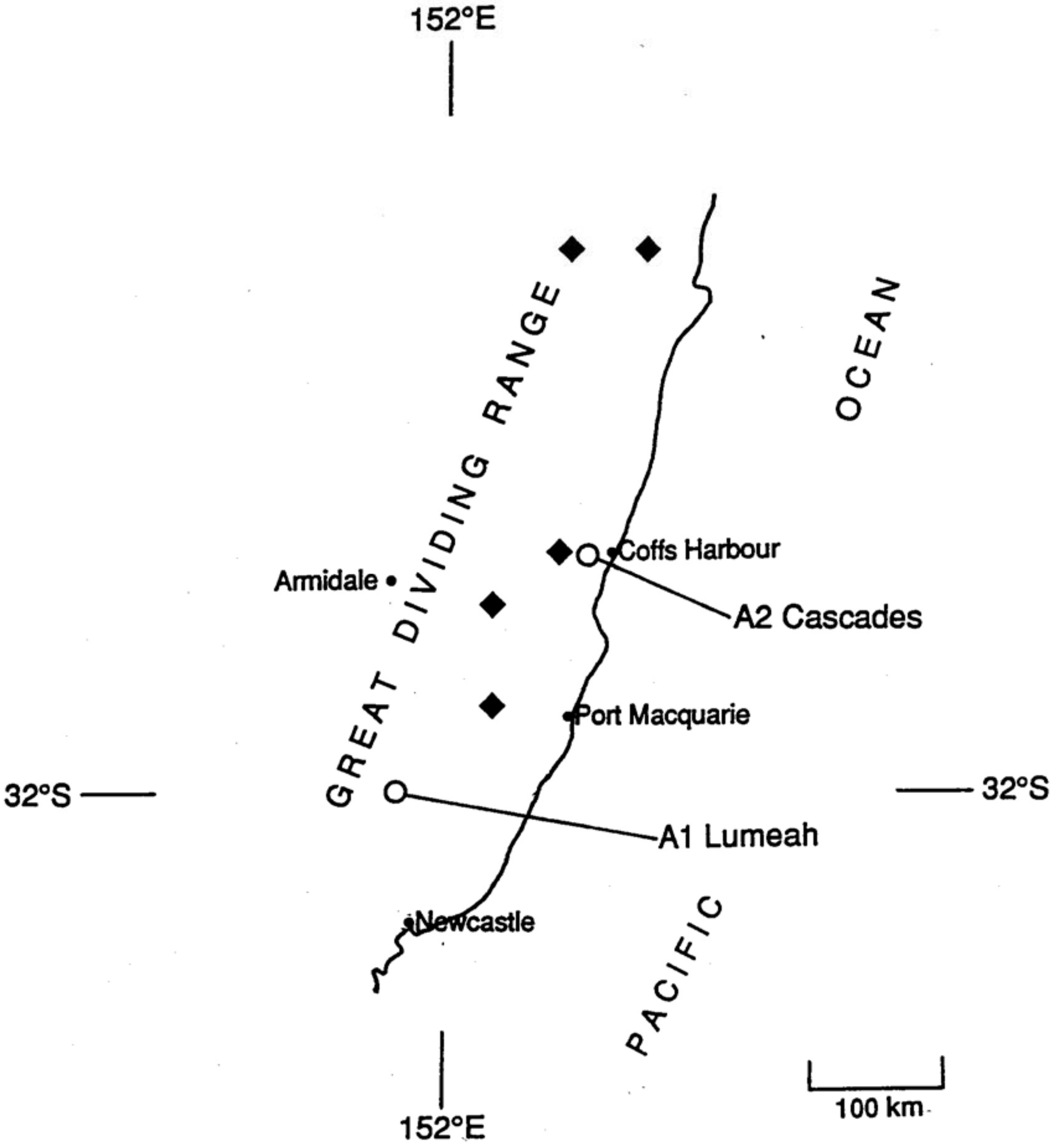

Fig. 3.2 Locations of study sites in New South Wales, Australia, showing (diamonds) additional *Nothofagus moorei* localities (after Floyd 1990; Williams & Bale 1993).

LANDMASS: NEW ZEALAND (Z)

The five New Zealand *Nothofagus* taxa generally occur as physiognomic dominants or codominants of evergreen rainforest that is the most abundant natural vegetation type in New Zealand (Wardle 1991). *N. fusca, N. menziesii* and *N. solandri* var. *cliffortioides* are the most common taxa, and often occur together, forming a pure or almost pure *Nothofagus* canopy (Wardle 1984). *N. truncata* and *N. solandri* var. *solandri* have more restricted distributions, and were not present at any of the eight study sites sampled in New Zealand. Three geographic regions were included in the study, broadly spanning the stronghold areas of *Nothofagus* forest in New Zealand (Fig. 3.3). Several individual sites were established in each region, to provide data suitable for comparisons at the local scale (see Chapters 1, 2).

A considerable body of literature on the ecology of New Zealand *Nothofagus*-dominated forests exists, and only a representative sample is cited here. Wardle (1984) deals with the distribution and composition of the forests in some detail, also discussing regeneration dynamics, the roles of consumer organisms in *Nothofagus* ecology, and effects of exotic herbivores. Population dynamics and regeneration ecology have been examined for *N. fusca* by June & Ogden (1975, 1978); for *N. solandri* by Wardle (1970); for *N. menziesii* by Wardle (1980) and Stewart (1986); and for mixed *N. fusca*-*N. menziesii* forests (including that at site ZC2 Station, see below) by Stewart & Rose (1990) and Stewart *et al.* (1991). Succession and the role of disturbance in *Nothofagus* ecology was investigated by Jane (1986) and Mark *et al.* (1989), while Jane (1994) and Allen *et al.* (1994) examined effects of introduced herbivores on stand structure. Bycroft *et al.* (1993), Smith *et al.* (1994) and Wilson *et al.* (1995) have sought community structure in New Zealand *Nothofagus*-dominated forests using various approaches.

Region: Southern New Zealand (ZS)

Site ZS1 Ten Mile, 45° 17' S, 167° 48' E. This site was part of the Ten Mile Bush, a stand of *Nothofagus solandri* forest by the eastern shore of Lake Te Anau, altitude 220 m. The dominant canopy trees are ascribed to *N. solandri* var. *cliffortioides* by Wardle (1984). Their mean height and DBH were 29 m and 45 cm, respectively. *N. menziesii* also reached canopy height occasionally. A scattered small tree stratum included *Myrsine australis* (Myrsinaceae), *M. divaricata*, and *Pseudopanax crassifolius* (Araliaceae), while the well-developed shrub layer was dominated by *Neomyrtus pedunculata* (Myrtaceae) and *Coprosma* spp. (Rubiaceae). Dense regeneration of both *Nothofagus* species occurred under treefall gaps and minor canopy openings. The forest floor was characterised by luxuriant bryophyte cover, possibly reflecting somewhat poor drainage associated with the very gentle slope (5°). Thirty-three vascular plant species were observed within the five quadrats sampled. Aspect averaged 230° SW. Surface geology consists of recent gravels and till of glacial origin (New Zealand Geological Survey 1972).

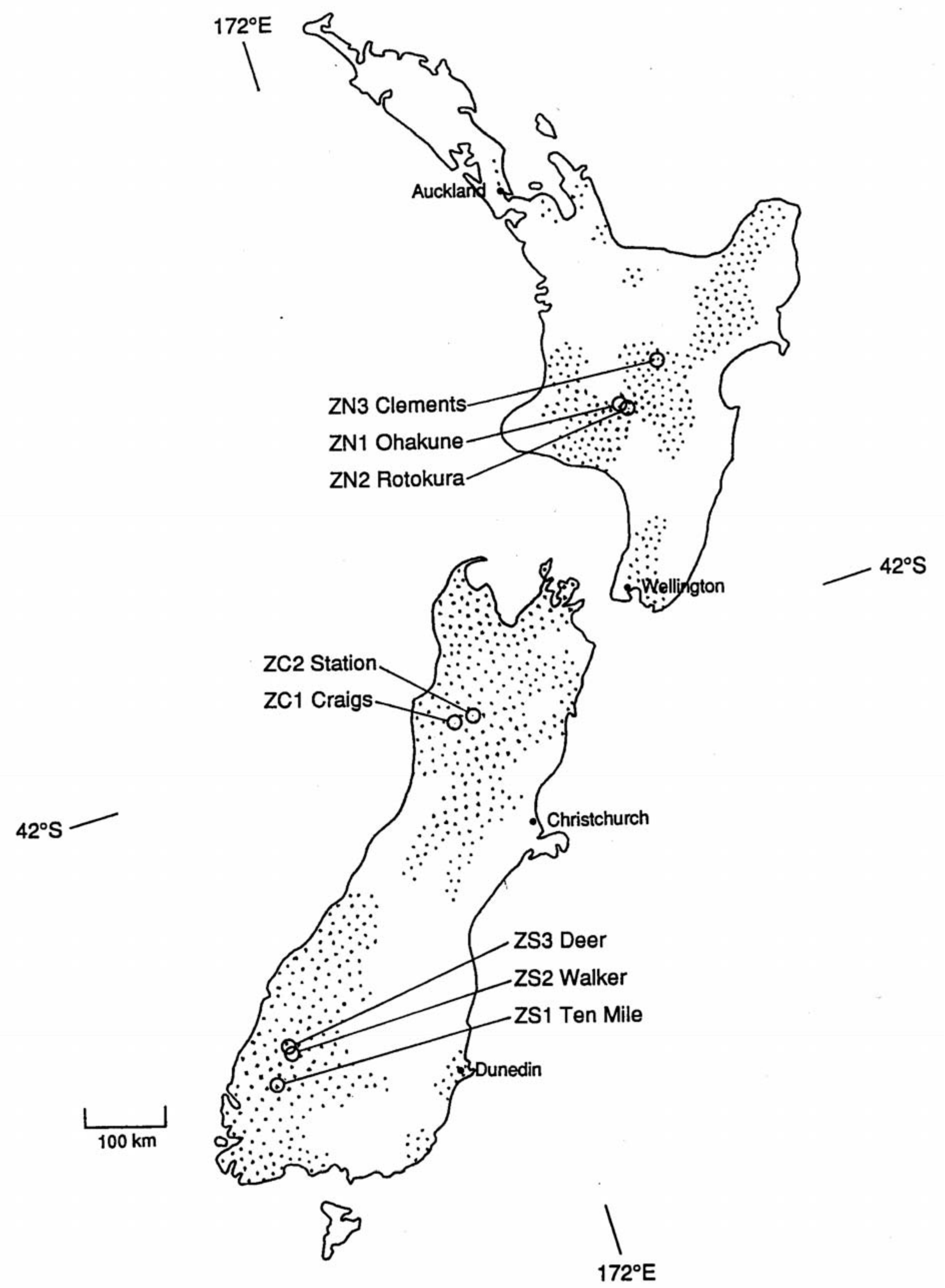

Fig. 3.3 Locations of study sites in New Zealand, showing (shading) the approximate distribution of *Nothofagus*-dominated forests (after Wardle 1984).

Site ZS2 Walker, 45° 07' S, 167° 57' E. Situated near Walker Creek, on terraces above the Eglinton River, 335 m asl, this site was dominated by tall, multi-aged *Nothofagus fusca* (height 33 m, DBH 77 cm), with *N. menziesii* also present as a subcanopy or, occasionally, canopy tree. Small trees, including *Pseudowintera colorata* (Winteraceae), *Griselinia littoralis* (Griseliniaceae) and *Carpodetus serratus* (Escalloniaceae), were associated mainly with canopy openings. A dense shrub and juvenile tree layer (*Coprosma* spp., *Neomyrtus pedunculata*, *Pseudopanax* spp.) attained maximum density and diversity in treefall gaps, although *N. pedunculata* was most conspicuous beneath the closed canopy. Advance growth (very low seedlings) of *N. fusca* was ubiquitous at ground level. Ferns, notably *Polystichum vestitum* (Aspidiaceae) and *Blechnum* spp. (Blechnaceae), and tussocks of *Microlaena avennacea* (Graminiae), were associated mainly with ephemeral watercourses. Species richness was 36 (five quadrats). Slope averaged 20°, aspect 250° W. The bedrock consists of upper Mesozoic (probably Devonian) diorite, quartz diorite, granodiorite or granophyre (New Zealand Geological Survey 1972).

Site ZS3 Deer, 44° 59' S, 168° 00' E. This study site, near Deer Flat, was located within a *Nothofagus menziesii*-dominated community associated with gravelly river fans in the base of the Eglinton River valley, altitude 370 m. Within the study area *N. menziesii* (height 29 m, DBH 42 cm), formed an almost pure canopy except for occasional individuals of *N. fusca*, which grew on elevated ground with deeper soils. A well-developed shrub layer, dominated by *Coprosma* spp., was present, while dense regeneration of *N. menziesii* occurred mainly beneath canopy openings. A large fern, *Polystichum vestitum*, formed the principal ground cover over much of the study site. Twenty-six species occurred within the five quadrats sampled. Mean slope was 5°, aspect 200° S. Basement geology consists of Permian volcanics (New Zealand Geological Survey 1972), but alluvial deposits were present at the ground surface and probably extended to a considerable depth.

Region: Central New Zealand (ZC)

Site ZC1 Craigs, 42° 14' S, 171° 57' E. This site, near Craigs Clearing, was representative of the luxuriant rainforest characteristic of the humid western watersheds of the Southern Alps (Wardle 1984). *Nothofagus fusca* (height 28 m, DBH 43 cm) was the dominant species with *N. menziesii* (height 25 m, DBH 45 cm) forming a secondary canopy and subcanopy component. Both species were very mature and canopy openings due to fallen trees were a prominent feature of the forest. The small tree stratum included *Aristotelia serrata* (Elaeocarpaceae), *Fuchsia excorticata* (Onagraceae), *Carpodetus serratus* and *Pseudopanax crassifolius*. The shrub layer was characterised by *Pseudowintera colorata*, *Neomyrtus pedunculata* and *Coprosma* spp., while tree ferns (*Dicksonia fibrosa*) were associated with canopy gaps. A diversity of pteridophytes, notably *Leptopteris superba* (Osmundaceae), *Cyathea colensoi* (Cyatheaceae), *Polystichum vestitum* and *Blechnum* spp., occurred at ground level, as well as tussocks of *Microlaena avennacea* and *Astelia nervosa* (Liliaceae). Epiphytic ferns, especially *Hymenophyllum* spp. (Hymenophyllaceae), were abundant. Little regeneration of *N. fusca* was observed, although seedlings and saplings of *N. menziesii* were abundant beneath canopy gaps. The climber *Muehlenbeckia australis* (Polygonaceae) was relatively common. Species richness (five quadrats) was 47. Slope averaged 10°, aspect 250° W. There was some evidence that nearby forest had been overcut in the past. Underlying geology consists of granite, granodiorite, quartz diorite, diorite or aptite of upper Mesozoic age, and is overlain by recent glacial deposits (New Zealand Geological Survey 1972).

Site ZC2 Station, 42° 12' S, 172° 15' E. Located in a rainshadow zone, the Maruia River valley, at an altitude of 410 m, this site contrasted markedly in structure and composition with its neighbour, described above. *Nothofagus fusca* (height 31 m, DBH 79 cm) and *N. menziesii* (height 27 m, DBH 20 cm) dominated a fairly closed canopy, *N. fusca* accounting for some 75% of total canopy cover. The understorey was sparse, mainly comprising the shrub *Neomyrtus pedunculata* and scattered individuals of *Pseudopanax crassifolius*, *Myrsine divaricata* and *Coprosma* spp. *Pseudowintera colorata* and *Griselinia littoralis* occurred beside a watercourse (Station Creek) which flowed past the study site. Regeneration of both canopy species was present at a moderate density. Fewer vascular plant species (22 species in five quadrats) were observed than at any of the other New Zealand sites sampled. The study site had negligible slope and aspect. Bedrock in the area consists of lower Quaternary marine sediments (New Zealand Geological Survey 1972), overlain by alluvial sand and silt at the study site (Stewart *et al.* 1991).

Region: Northern New Zealand (ZN)

Site ZN1 Ohakune, 39° 22' S, 175° 28' E. This site was located on a terrace at 840 m altitude on the southern slopes of Mt. Ruapehu, an intermittently active volcano. The canopy was more-or-less equally dominated by *Nothofagus solandri* var. *cliffortioides* (height 23 m, DBH 48 cm) and *N. menziesii* (height 23 m, DBH 40 cm). A single adult individual of *N. fusca* (height 16 m, DBH 30 cm) was also observed within the study area. The forest was characterised by a complex structure and high diversity of vascular taxa (63 species in five quadrats). Small tree or subcanopy species present included *Nestigis cunninghamii* (Oleaceae), *Carpodetus serratus*, *Pseudowintera colorata*, *Prumnopitys ferruginea* (Podocarpaceae) and *Podocarpus cunninghamii* (Podocarpaceae). Important shrubs were *Coprosma* spp., *Pseudopanax anomalus*, *Neomyrtus pedunculata* and *Elaeocarpus hookerianus* (Elaeocarpaceae). Pteridophytes were conspicuous both at ground-level (e.g. *Leptopteris superba*, *Polystichum vestitum*, *Blechnum* spp. and a tree fern, *Cyathea smithii*) and as epiphytes (*Asplenium flaccidum* [Aspleniaceae], *Phymatosorus diversifolius* [Polypodiaceae], *Hymenophyllum* spp.). Several angiosperms were present as epiphytes, including *Astelia nervosa* and *Cordyline indivisa* (Agavaceae), as well as the climbers *Clematis paniculata* (Ranunculaceae), *Parsonsia capsularis* (Apocynaceae) and *Rubus schmidelioides* (Rosaceae). *Microlaena avennacea* formed the predominant ground cover. *Nothofagus solandri* and *N. menziesii* showed good regeneration in gaps, but there were few seedlings of *N. fusca*. Slope and aspect were negligible. Quaternary volcanic deposits characterise the geology (Riddolls 1987).

Site ZN2 Rotokura, 39° 26' S, 175° 30' E. Situated near Lake Rotokura at the base of Mt. Ruapehu to the south, altitude 680 m, this site had the highest species richness of any examined in the course of the study, a total of 65 species in five quadrats. Dominant species were *Nothofagus fusca*, which attained a height of 28 m and DBH 33 cm, and accounted for some 80% of total canopy cover; and *N. menziesii* (height 27 m, DBH 72 cm, 20% cover). An irregular understorey of small or juvenile tree species included *Carpodetus serratus*, *Aristotelia serrata*, *Pseudowintera colorata*, *Knightia excelsa* (Proteaceae) and *Prumnopitys ferruginea*. Tree ferns — *Dicksonia squarrosa*, *D. fibrosa*, *Cyathea smithii* and *C. dealbata* — formed a prominent layer in some parts of the site. Small-leaved shrubs (e.g. *Coprosma* spp., *Neomyrtus pedunculata*) were less prominent than at other New Zealand sites. One individual of the exotic shrub *Rubus fruticosus* was observed. The ground stratum was dominated by the ferns *Blechnum discolor* and *B. fluviatile* and the grass *Microlaena avennacea*. Epiphytes (e.g. *Asplenium* spp., *Hymenophyllum* spp., *Astelia nervosa*) and climbers (e.g. *Rubus schmidelioides*, *Parsonsia capsularis*) were relatively abundant. Moderate regeneration of *Nothofagus menziesii* and *N. fusca* was associated mainly with treefall gaps. Slope and aspect were negligible. A single sawn stump attested to overcutting of the forest in the past. Recent lahar constitutes the surface geology (Riddolls 1987), as at the neighbouring Ohakune site.

Site ZN3 Clements, 38° 58' S, 176° 10' E. This site was located off Clements Mill Road, on undulating ground on the western slopes of the Kaimanawa Range, at an altitude of 740 m. Codominant in the canopy were *Nothofagus fusca* (height 32 m, DBH 71 cm) and *N. menziesii* (height 27 m, DBH 72 cm). Canopy density was relatively variable, with numerous gaps, containing abundant regeneration of both *Nothofagus* species, being present. There were few trees below canopy level, but the shrub stratum was locally dense. The most abundant shrub species were *Neomyrtus pedunculata*, *Pseudowintera colorata* and *Coprosma* spp. Tree ferns, *Cyathea smithii* and *Dicksonia squarrosa* were common in patches, while ground cover consisted mainly of mosses, bare litter or, locally, the fern *Blechnum discolor*. Fifty-five species were observed within the five quadrats sampled. Slope averaged 5°, aspect 250° W. Lower Quaternary marine sediments comprise the predominant geology in the area (Riddolls 1987).

LANDMASS: SOUTH AMERICA (S)

In South America, *Nothofagus* is distributed from 33°S to the southern tip of the continent, at 56°S. It occurs predominantly west of the Andes (i.e. in Chile), but locally also on the slopes and foothills of the Andes to the east, in Argentina (Donoso 1993). Of the nine or ten taxa described only three — the closely related *N. dombeyi*, *N. nitida* and *N. betuloides* — are evergreen. All three species may be dominants of temperate rainforest in the Valdivia province (*c.* 41°S) of southern central Chile, while *N. dombeyi* occurs at corresponding latitudes in northwest Patagonia, Argentina. Two study sites were established in each of these regions, one, dominated by *N. nitida*, on the Chilean Coastal Range; the others, dominated by *N. dombeyi*, on the western slopes and eastern foothills of the Andes (Fig. 3.4). A marked rainfall gradient exists from west to east across the Andes, and the three Andean communities might be expected to show corresponding differences in structure and composition. Ecological differences between the Andes and the Coastal Range have been attributed to enhanced disturbance regimes in the Andes, where volcanic eruptions, landslides and earthquakes are common (Veblen *et al.* 1981).

Donoso (1993) summarises the extensive Spanish-language literature on the structure, composition and dynamics of South American *Nothofagus*-dominated forests. Veblen *et al.* (1983) have reviewed the floristics and distribution of temperate evergreen forests in Chile and Argentina. Veblen and colleagues have also investigated stand establishment, population dynamics and interspecific interactions within various *Nothofagus*-dominated communities in Chile (Veblen *et al.* 1977a,b, 1981, 1989; Veblen 1979, 1985, 1989; Robertus *et al.* 1993) and Argentina (Veblen & Lorenz 1987; Veblen 1989; Veblen *et al.* 1989; Robertus *et al.* 1993).

Region: Valdivia, Chile (SC)

Site SC1 Pelada, 40° 12' S, 73° 26' W. This site was located at 945 m asl on top of the Cordillera Pelada, a section of the range of hills that flanks the west coast of Chile from Santiago southward to Puerto Montt. The dominant species was *Nothofagus nitida*[1], which was predominantly even-aged with a height of 20 m and mean DBH 38 cm. Stem density was extremely high, with an average of 28 canopy *N. nitida* individuals occurring in each 20 × 20 m quadrat. A few apparently older individuals with DBH up to 86 cm were present in one part of the study site. *Podocarpus nubigena* and *Saxegothaea conspicua* (both Podocarpaceae) were present as subcanopy trees, as were smaller trees and shrubs, *Laurelia philippiana* (Monimiaceae), *Amomyrtus luma* (Myrtaceae) and *Myrceugenia chrysocarpa* (Myrtaceae). *Chusquea quila* (Gramineae), a species of bamboo, was present in locally-dense thickets to a

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[1] Although taken to be *N. nitida* on the basis of the leaf morphology of the canopy individuals sampled, regeneration in the area has a leaf morphology more suggestive of a hybrid between *N. nitida* and closely-related *N. betuloides* which is present nearby (C. Ramirez, *personal communication*).

height of 2-3 metres. An understorey of *Chusquea* spp. is characteristic of *Nothofagus*-dominated forests in southern central Chile (Veblen *et al.* 1977a). Ground cover included several shrub species, e.g. *Ugni candollei* (Myrtaceae), *Drimys winteri* (Winteraceae) and *Desfontainea spinosa* (Desfontaineaceae); and ferns, *Blechnum magellanicum* and *Lophosoria quadripinnata* (Lophosoriaceae). Species richness was 27 (four quadrats). Slope averaged 15°, aspect 210° SW. There was evidence of small-scale harvesting of trees and dead wood in the vicinity of the study site. Bedrock in the area consists of schist, slate, quartzite and other metamorphics of Palaeozoic age (Rojas & Subiabre 1991).

Site SC2 Antillanca, 40° 47' S, 72° 15' W. This site was located 5 km west of the township of Antillanca on the western slopes of the Andes, altitude *c.* 800 m. The dominant species was taken to be *Nothofagus dombeyi*[2], with average height 28 m and DBH 75 cm. A distinct subcanopy of *Saxegothaea conspicua* was present over much of the site, with bamboos *Chusquea culeou* and *C. uliginosa* forming an extremely dense understorey up to a height of 2-3 m. A number of low shrub species, for example, *Drimys winteri* var. *andina*, *Maytenus magellanica* (Celastraceae) and *Pernettya mucronata* (Ericaceae) were present at minor densities. *Hymenophyllum* spp. were abundant as epiphytes growing on tree trunks. Regeneration of *N. dombeyi* was limited to a few seedlings growing on fallen logs. Thirty-three vascular plant species were observed within the five quadrats sampled. Microtopography was quite variable and locally steep; average slope was 15°, aspect 245° SW. The geology consists of Tertiary volcanics overlain by recent volcanic ash and glacial deposits (Rojas & Subiabre 1991).

Region: Northwest Patagonia, Argentina (SA)

Site SA1 Quetrihué, 40° 51' S, 71° 37' W. Situated at the southern end of Peninsula Quetrihué, near the shore of Lake Nahuel Huapi, altitude 770 m, this site was unusual among *Nothofagus*-dominated forests in the region in lacking a bamboo understorey. The canopy trees were *N. dombeyi* (height 40 m; DBH 91 cm). A conifer, *Austrocedrus chilensis* (Cupressaceae) was also present, occasionally reaching canopy height within the study area. Common understorey trees or tall shrubs were *Luma apiculata* (Myrtaceae) and *Aristotelia chilensis*, the latter forming a distinct layer up to 3-4 m height, superficially reminiscent of that of *Chusquea* spp. within other forests in the area. Several low shrub species were present at minor densities, including *Berberis darwinii* (Berberidaceae), *Maytenus chubutensis* and *Schinus patagonicus* (Anacardiaceae). Larger canopy gaps were characterised by dense seedling and sapling growth of *N. dombeyi*.

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[2] The closely-related species *N. betuloides* dominates montane forest a few km further up the Antillanca Valley (Veblen 1979). The two species are difficult to distinguish morphologically, and the canopy trees at the site could be a hybrid, or even pure *N. betuloides* (C. Ramirez, *personal communication*).

Species richness was 25 (three quadrats). Slope and aspect were negligible across the study site. Tertiary and Quaternary andesitic volcanic ashes characterise the local geology (Veblen *et al.* 1989).

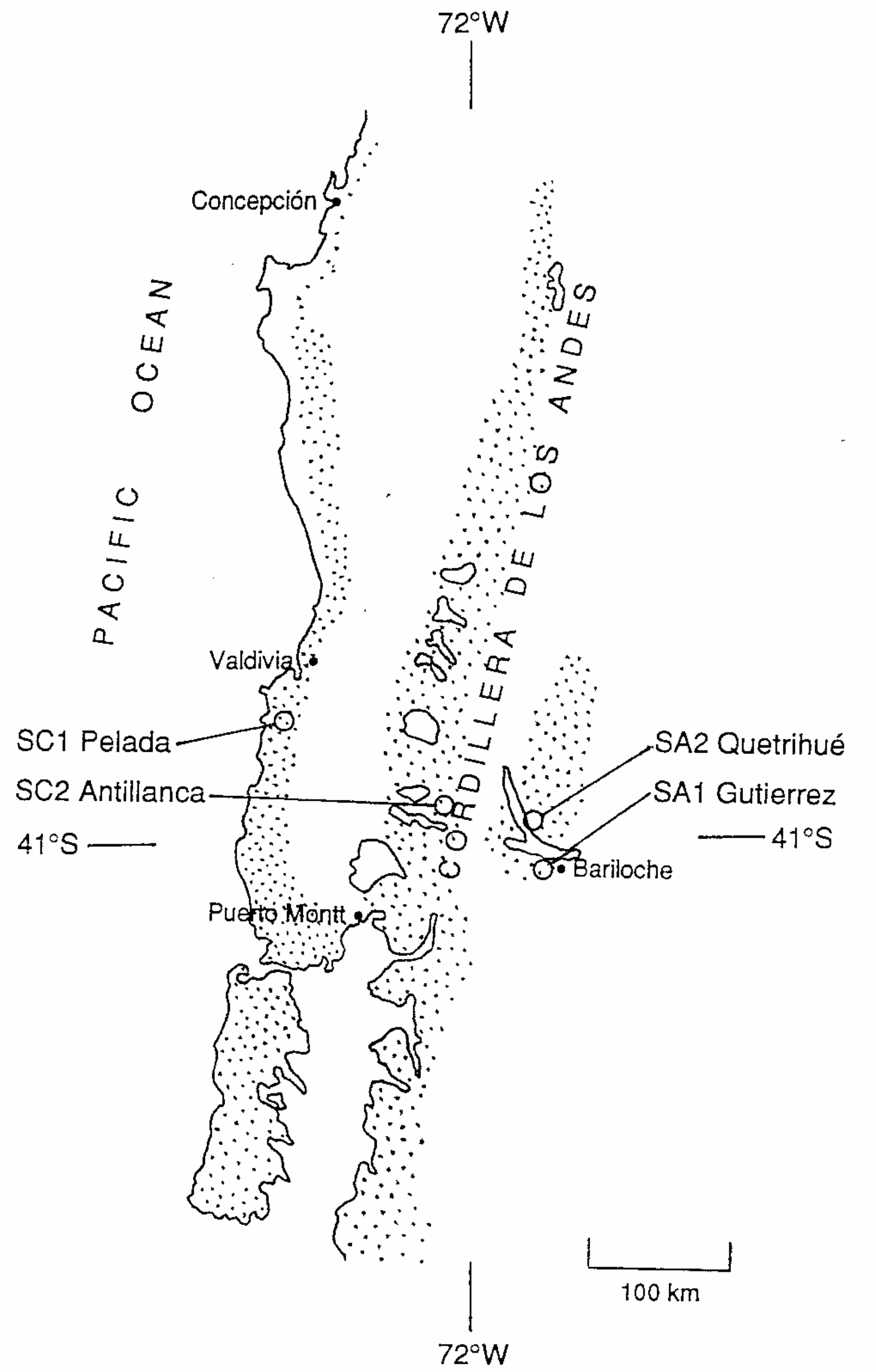

Fig. 3.4 Locations of study sites in South America, showing (shading) the approximate distribution of *Nothofagus betuloides, N. dombeyi* and *N. nitida* in southern central Chile and northwest Patagonia, Argentina (after Donoso 1993).

Site SA2 Gutierrez, 41° 11' S, 71° 25' W. This site was located by Lago Gutierrez at an altitude of 810 m. An apparently even-aged stand of *Nothofagus dombeyi* (height 29 m, DBH 54 cm) formed the forest canopy. *Austrocedrus chilensis* was present occasionally as a subcanopy tree, and there was a dense understorey of bamboo, *Chusquea culeou*. Scattered low shrubs included *Berberis darwinii*, *Schinus patagonicus* and *Maytenus chubutensis*. Ground cover consisted primarily of forbs, *Osmorhiza chilensis* (Apiaceae), *Baccharis* aff. *salicifolia* (Asteraceae) and *Alstroemeria aurea* (Alstroemeriaceae). *Vicia nigricans* (Fabaceae) was relatively common twined among the branches of shrubs. Species richness was 15 (three quadrats), the lowest encountered in the present study. Mean slope was 10°, aspect 106° E. Volcanic ash comprises the surface geology in the area (L. Sancholuz, *personal communication*).

3.3 Comparison of site environments

An important assumption of the hypothesis of community-level convergence is that the communities being compared occur in similar environments (Orians & Paine 1983). It is not clear how great an environmental difference would be needed before a tendency towards convergence, due to overdispersion of species niches by the action of assembly rules, would be balanced by a tendency towards divergence, caused by species adaptations to different physical environments (see Section 1.5). If convergence can not be shown statistically, this could mean that there were no assembly rules, but, alternatively, it could mean that the communities were too dissimilar environmentally for convergence to be detectable, even if assembly rules did apply. While the possibility of convergence can therefore never be rejected with complete confidence (Barbour & Minnich 1990; Keeley 1992), it may be deemed unlikely if no convergence can be shown, even for communities that are very closely matched in their environmental parameters, i.e. that would seem to fulfil this assumption of the convergence hypothesis.

Community-level convergence might be expected to occur both among sites within a local area, or among disjunct sites, for example, on different landmasses. Floristic overlap is likely to be very low between landmasses, which is a technical advantage for statistical tests for convergence, which must focus on the species that are not in common between communities (see Section 6.2). However, convergence may be more difficult to demonstrate among landmasses, because the likelihood that the sites being compared have similar environments would tend to be lower.

In the following analysis, the 17 study sites are compared in terms of the major environmental parameters measured, to identify the sites, regions and landmasses for which the assumption of environmental similarity appears most likely to be met. Particular attention is given to the identification of environmentally-matched sites from different landmasses, since environmental differences are more likely to confound convergence at the landmass, than at the local, level. In subsequent chapters, this information is used to focus comparisons on communities that are most likely to possess the preconditions to exhibit community-level convergence.

METHODS

Environmental data

The environmental data compiled for each site were climate parameters (mean temperature of the warmest month [MTWM], mean temperature of the coldest month [MTCM], mean annual temperature [MAT], annual rainfall [AR] and rainfall in the driest quarter [RDQ]), soil parameters (total potassium [K], nitrogen [N], phosphorus [P], pH and organic content [OC]) and proportional canopy light transmittance. Methods by which these data were acquired are described in Section 2.3.

Analysis

To aid in the comparison of sites, principal component analysis (PCA) was carried out on the environmental parameters. PCA provides a means of concentrating the shared variation in a number of intercorrelated variables within a smaller number of uncorrelated ones, the principal components (PCs). The PCs are linear combinations of the original variables, uncorrelated with respect to the data supplied, and in rank order of the proportion of the total sample variance they explain (Manly 1994). Separate PCAs were carried out for climate data (five variates) and soil data (four variates). Phosphorus was not included in the soil PCA because no values were obtained for Chilean sites, and values for Argentina were not comparable with those obtained elsewhere (see Section 2.3.4). Variables were standardised (mean 0, standard deviation 1) prior to analysis, to ensure that they would be weighted equally in generating PCs. For both analyses, each PC with an eigenvalue ≥1 was used, while remaining PCs (which would explain less variation than one of the original variables) were ignored.

Varimax factor rotation of climate and soil PCs was performed, to attempt to improve interpretability of the derived variables. Axes of the chosen PCs were `rotated' in abstract space, such that the variance of the squares of the loadings (linear coefficients on the original variables) of the new (rotated) axes was maximised. This means that, for each axis (factor), the absolute values of the loadings of some variables are maximised relative to the other variables. This can improve interpretability of the factors, which will be more more closely related to variables with large loadings than small ones. The disadvantage of factor analysis is that the rank order of explained variation in the original PCs may be lost (Manly 1994). Factor rotation did not significantly improve interpretability for the climate or soil data. Consequently, unrotated axes (the original PCs) are presented below.

PCA and factor rotation were performed with the Genstat statistical program (Genstat 5 committee 1987).

RESULTS

Climate

Climate data for each of the 17 sites are presented in Table 3.1.

Table 3.1 Climate parameter values for all study sites, showing means among sites. MTWM=mean temperature of warmest month; MTCM=mean temperature of coldest month; MAT=mean annual temperature; AR=annual rainfall; RDQ=rainfall for driest quarter. Site codes are given in Section 3.2.

Site	MTWM (°C)	MTCM (°C)	MAT (°C)	AR (mm)	RDQ (mm)
T1	15.9	7.8	11.3	1570	230
T2	13.1	4.3	8.3	1790	330
T3	13.3	3.3	8.1	1730	270
A1	18.4	5.0	12.2	1120	250
A2	17.0	5.9	11.3	1460	270
ZS1	14.6	4.2	9.7	1210	270
ZS2	14.4	3.8	9.4	1680	360
ZS3	14.4	3.7	9.3	2400	490
ZC1	15.5	4.2	10.0	2510	510
ZC2	15.3	4.2	9.8	2080	410
ZN1	13.2	3.6	8.5	1880	360
ZN2	14.5	4.6	9.7	1250	240
ZN3	14.8	4.3	9.6	1510	320
SC1	15.0	7.9	11.3	4000	460
SC2	12.3	3.5	7.8	4970	130
SA1	13.5	6.0	10.2	1650	140
SA2	12.5	6.5	10.3	1090	100
mean	14.6	4.9	9.8	1990	300

Loadings and percentage variation explained by the first three principal components (PC1, PC2, PC3) based on the five climate variables, are given in Table 3.2. The fourth and fifth PCs had eigenvalues <1 and were therefore not used. The loadings for each PC are the linear coefficients on the original variables from which PC scores are calculated. The importance of each variable in defining the PC is thus given by the magnitude of its loading (which is a Pearson *r* correlation coefficient between the base variable and the PC). PC1 is most strongly correlated with MAT and MTWM, and so may be interpreted as representing primarily temperature. PC2 is strongly related to dry-season rainfall (RDQ), while PC3 corresponds to both total rainfall (AR) and winter temperatures (MTCM). Site coordinates in three-dimensional space defined by the climate PCs are shown in Fig. 3.5. Sites whose coordinates fall close together are relatively similar in terms of the climate parameters measured. The figure is interpreted below.

Table 3.2 Loadings used to calculate principal components (PCs) from climate variables (see Table 3.1), and percentage of variation explained by each PC. Loadings >0.5 are shown in bold type.

Variate	Loading		
	PC1	PC2	PC3
MTWM	**0.54**	0.36	0.17
MTCM	0.47	-0.29	**-0.52**
MAT	**0.64**	0.01	-0.11
AR	-0.26	0.24	**-0.82**
RDQ	0.00	**0.85**	-0.02
% variation explained	47	25	20

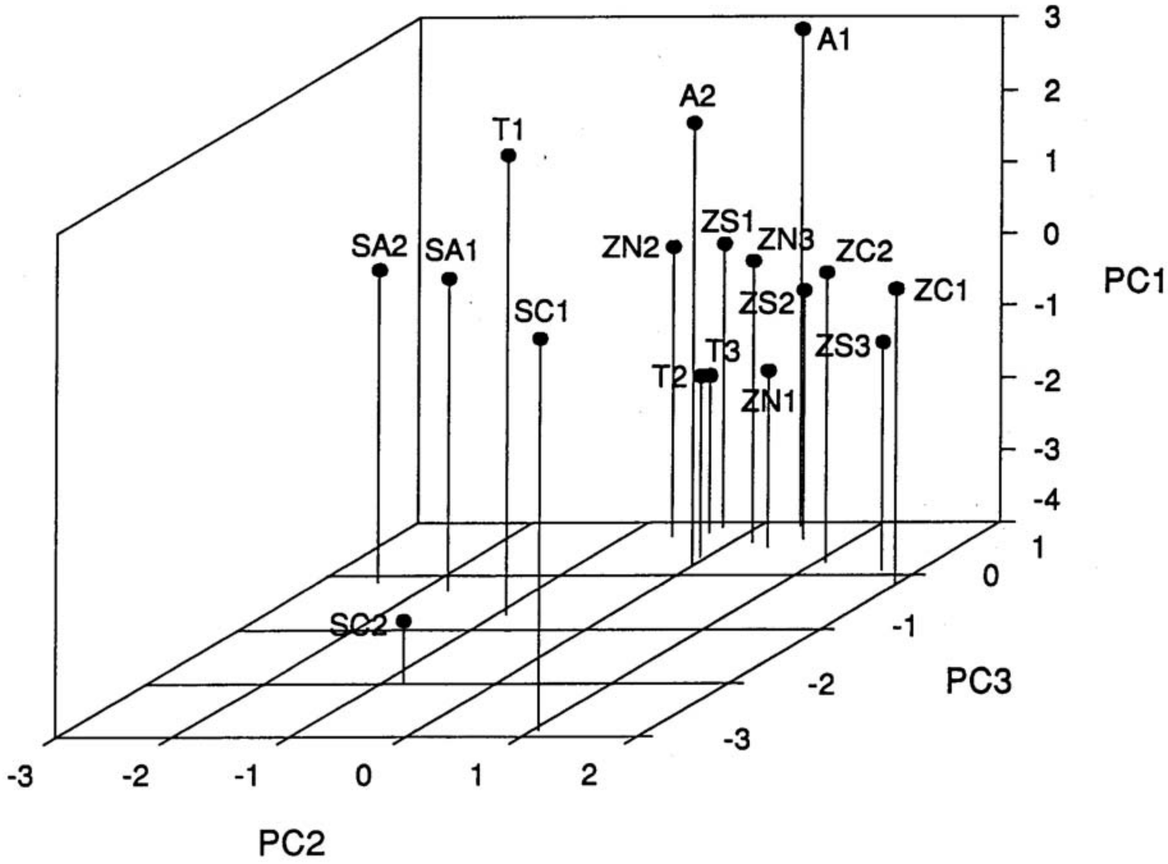

Fig. 3.5 Site scores on the first three axes of a principal component ordination of study sites based on five climate variables (see Table 3.1). Site codes (shown beside each point) are given in Section 3.2.

Soils

Soil data for the study sites are given in Table 3.3.

Table 3.3 Soil parameter values for all study sites, showing mean among sites. Site codes are given in Section 3.2. P values for sites SA1 and SA2 were obtained by a different method and are indicative only. Mean P is calculated from sites T1 to ZN3 only.

Site	Total K (ppm)	Total N (ppm)	Total P (ppm)	pH	Organic content (%)
T1	1400	2500	480	5.3	25
T2	1350	4800	420	4.7	33
T3	2900	2300	260	4.0	15
A1	1440	1000	2250	4.8	36
A2	730	800	890	4.5	31
ZS1	460	1700	180	4.6	13
ZS2	670	3300	980	4.9	15
ZS3	750	4500	740	5.2	18
ZC1	880	3600	700	4.7	15
ZC2	920	1800	420	4.2	10
ZN1	410	5400	420	5.4	22
ZN2	410	6700	520	5.4	26
ZN3	400	3100	340	5.4	18
SC1	210	3000	-	3.8	9
SC2	230	4700	-	4.9	14
SA1	80	4100	(50)	6.4	15
SA2	90	3200	(70)	6.7	11
mean	780	3300	660	5.0	19

Loadings and percentage variation explained by the first two principal components (PC1, PC2) derived from four soil variables, are given in Table 3.4. The third and fourth PCs had eigenvalues <1 and were therefore not used. PC1 summarises variation in three variables, K, N and pH, while PC2 is primarily related to the remaining variable, organic content. Site coordinates in soil PC space are shown in Fig. 3.6, which is discussed below. Soil P is shown separately, for the sites for which P measurements were made (Fig. 3.7).

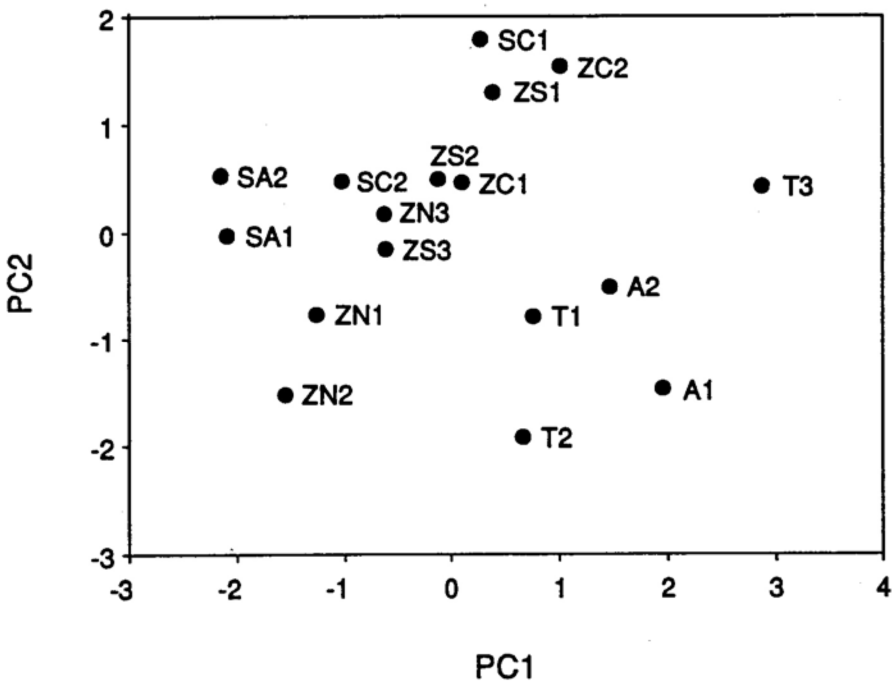

Fig. 3.6 Site scores on the first two axes of a principal component ordination of study sites based on four soil variables (see Table 3.3; P not included in the ordination). Format as for Fig. 3.5.

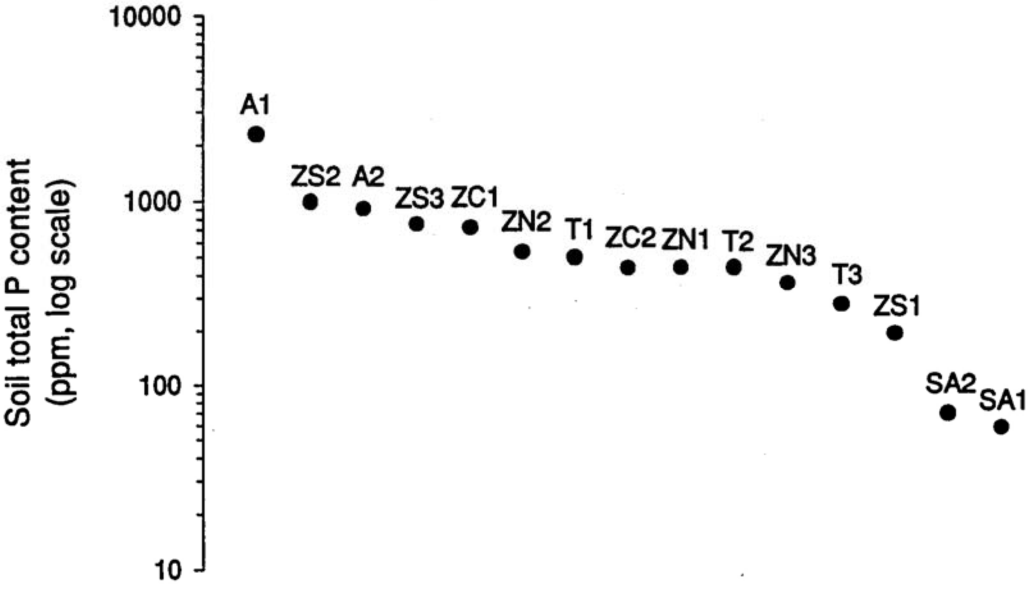

Fig. 3.7 Soil phosphorus concentrations (log scale) at study sites. All values are total P except for SA1 and SA2, which were obtained by a different method and may be interpreted as available P (see Section 2.3.4). Format as for Fig. 3.5.

Table 3.4 Loadings used to calculate principal components (PCs) from soil variables (see Table 3.3), and percentage of variation explained by each PC. OC=organic content. Format as for Table 3.2.

Variate	Loading	
	PC1	PC2
K N pH OC	**0.61** **-0.50** **-0.57** 0.22	-0.22 -0.33 -0.28 **-0.88**
% variation explained	46	27

Light transmittance

As anticipated, differences in light flux conditions during measurement appeared to affect canopy light transmittance values (Table 3.5). Measurements made in direct light (sunny) conditions were significantly lower than those made in diffuse light (cloudy) conditions (*P*<0.001; one-tailed *t*-test on ln-transformed site means for `sunny' versus `cloudy' sites). Only sites measured in similar light conditions can be compared. Values are presented separately for `sunny' and `cloudy' sites in Fig. 3.8, which is discussed below. Note that no light transmittance measurements were made for T2 Anne.

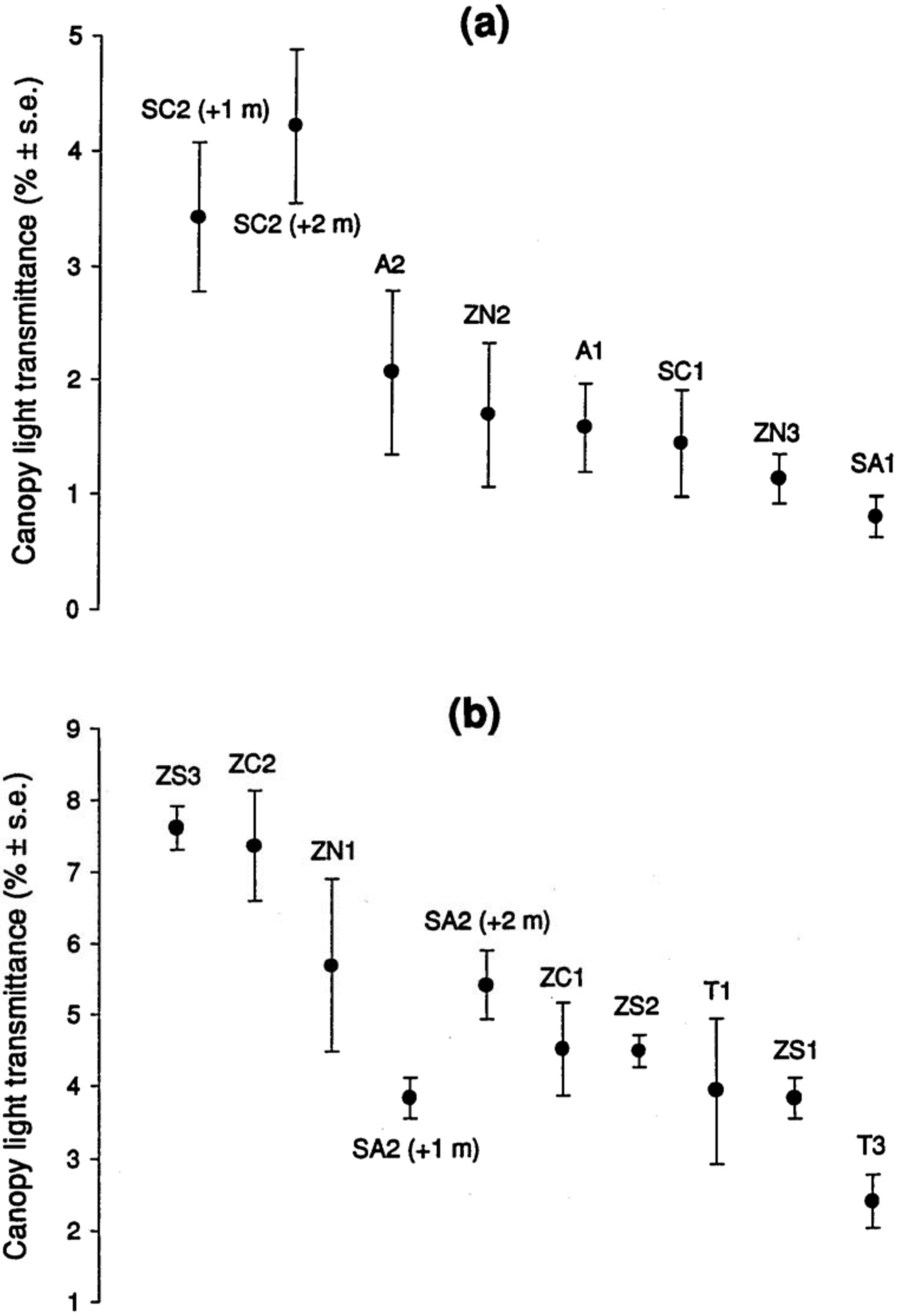

Fig. 3.8 Mean canopy light transmittance (% of incident light at canopy level) for **(a)** sites measured during diffuse light (cloudy) conditions; **(b)** sites measured during direct light (sunny) conditions. Standard error bars ($\sigma/\sqrt{n}$; σ=standard deviation of quadrat mean values; n=number of quadrats sampled) are shown. Values measured at 1 m and 2 m above ground level are shown for sites SA2 and SC2; for all other sites, values are for 1 m above ground level.

Table 3.5 Mean canopy light transmittance (% of incident light at canopy level) for study sites, showing light conditions during sampling and means among sites for `cloudy' and `sunny' sampling conditions. Values measured at 1 m and 2 m above ground level are shown for sites SA2 and SC2; for all other sites, values are for 1 m above ground level.

Sampling conditions	Site	Transmittance (%)
cloudy	T1	3.9
	T3	2.3
	ZS1	3.7
	ZS2	4.4
	ZS3	7.6
	ZC1	4.5
	ZC2	7.3
	ZN1	5.7
	SA2 (+1m)	3.8
	SA2 (+2m)	5.4
	Mean*	5.0
sunny	A1	1.6
	A2	2.1
	ZN2	1.7
	ZN3	1.1
	SC1	1.4
	SC2 (+1m)	3.4
	SC2 (+2m)	4.2
	SA1	0.8
	Mean*	1.8

*Based on values at +2m only for SA2 and SC2.

DISCUSSION

Environmental variation among landmasses, regions and sites

In terms of both climate (Fig. 3.5; Table 3.1) and soils (Figs. 3.6, 3.7; Table 3.3) sites on the same landmass tend to be more similar to each other than to sites on other landmasses, demonstating that there may be systematic environmental differences between the landmasses. In particular, the eight New Zealand sites have rather similar scores on all three climate PCs, as well as on soil PC2. There are no clear differences in environments between the northern, central and southern regions of New Zealand. Two of the three Tasmanian sites, T2 Anne and T3 Mathinna, are very similar climatically and have relatively similar soils, although the third, T1 Balfour, experiences higher temperatures, placing it some distance away in climate space. The two Australian sites, A1 Lumeah and A2 Cascades, are relatively closely-matched in terms of both climate and soils. Argentinian sites SA1 Quetrihué and SA2 Gutierrez have similar climates and soils, but differ markedly from the Chilean sites, which experience considerably higher rainfall and (for SC2 Antillanca) low temperatures. The Chilean sites themselves differ markedly in climate, temperature and summer rainfall.

Understorey light climates, on the other hand, show no simple geographic patterns (Fig. 3.8; Table 3.5). For example, light transmittance (as measured in cloudy conditions) varies from 3.7% to 7.6% in southern New Zealand, while values in Argentina (SA2), Tasmania (T1), northern New Zealand (ZN1) and central New Zealand (ZC1, ZC2) are intermediate between these extremes.

Among the landmasses, Tasmania and New Zealand appear to be the most similar, at least in terms of climate, two Tasmanian sites, T2 Anne and T3 Mathinna, having quite similar values on PC2 (dry season rainfall) and PC3 (annual rainfall and winter temperatures) to most New Zealand sites, although PC1 (temperature) values are somewhat lower. Soil parameters tend to match for PC2 (organic content) but are somewhat higher for PC1 primarily due to higher K concentrations in the Tasmanian soils. Soil P values in Tasmania are comparable with the northern New Zealand sites. At the level of individual sites, T3 Mathinna and ZN1 Ohakune have similar climates, but rather different soils. Understorey light conditions may also be rather different at the two sites, light transmittance at Mathinna being less than half that at Ohakune. T2 Anne and Ohakune, however, are very similar climatically, and also have rather similar soils, their dissimilarity on soil PC1 being mainly due to different potassium concentrations. A comparison with respect to canopy light transmittance cannot be done, since no values were obtained for Anne.

Australian sites A1 Lumeah and A2 Cascades are exceptional both in terms of temperatures (high values on climate PC1) and soils (high values on soil PC1 associated with low N, but high P, concentrations). However, Cascades is relatively close to the Tasmanian site T1 Balfour in climate space, at least on PC1 (which accounts for almost 50% of variation in the climate parameters), and these two sites also have relatively similar soils. Comparison of these sites in terms of canopy light transmittance is not possible, as measurements were made in different light flux conditions at the two sites.

South American sites tend to be dissimilar from the other regions climatically, primarily due to differences in the amount of rainfall (especially Chile) and the seasonality of rainfall (Argentina). In terms of soils, Chilean sites have low K content and low pH, although N content is comparable with New Zealand and Tasmania; Argentinian soils are more alkaline than those of other regions and appear to be deficient in potassium. However, SA1 Quetrihué and ZN2 Rotokura experience relatively similar climates, and are only moderately dissimilar in terms of soils (though no comparison can be made for phosphorus) and light regimes.

Identification of environmentally-matched communities

The above observations suggest several between-site, between-region and between-landmass comparisons that are more likely to reveal community-level convergence than others, because the communities concerned have relatively similar values for major environmental parameters.

At the landmass scale, New Zealand and Tasmania appear to be more closely matched than any other pair of the landmasses sampled. Between regions within a landmass, the northern, and particularly the southern and central regions of New Zealand exhibit little overall environmental dissimilarity. Tasmanian sites Anne and Mathinna are also closely matched, as are the Lumeah and Cascades on mainland Australia. Environmental variation among sites at the local level is generally low, with the exception of Chilean sites Pelada and Antillanca.

Best-matched sites from different landmasses are Anne (Tasmania) and Ohakune (New Zealand); Quetrihué (Argentina) and Rotokura (New Zealand); and Balfour (Tasmania) and Cascades (Australia).

Particular attention will be focused on these comparisons in interpreting the results of tests seeking community-level convergence in Chapters 6-10.