2. Methodology for data collection

2.1 Introduction

In this chapter, the methodology adopted for the collection of data is described and justified. Under the heading `Rationale,' criteria for the choice of study sites are outlined. Parameters of a data set suitable for addressing the hypotheses proposed in Chapter 1 are developed with regard to practical constraints on sampling and laboratory measurement. Under the heading 'Methods,' procedures adopted for the selection of study sites, evaluation of site environmental parameters and collection and processing of species texture data are described.

2.2 Rationale

2.2.1 Site criteria

For the investigation of community-level convergence it is important that communities from similar environments be compared (see Chapter 1).

Nothofagus has a relatively restricted distribution with respect to major climate and soil factors. Disregarding alpine and subalpine communities, temperate-zone *Nothofagus*-dominated forests all occur within the `cool temperate or upper montane' bioclimatic zone, mean temperature of the warmest month (MTWM) *c.* 12.5-17.5 °C (Meurk 1984). The lower limit to rainfall is generally 600-1000 mm a year (Ash 1982) while competition with species dominating other forest types may impose an upper limit (Wardle 1970). In New Zealand and South America, *Nothofagus* tends to occur on soils that are relatively poor in major plant nutrients (Wardle 1984). In Tasmania and mainland Australia, *Nothofagus*-dominated forests may be associated with richer soils than other forest types, but nutrient levels are probably still comparable with those for *Nothofagus* forest in New Zealand and South America. *Nothofagus* typically grows on steeper slopes and is absent from permanently or seasonally waterlogged sites (Ash 1982).

In Australia and New Zealand, only evergreen *Nothofagus* species occur in lowland forest, but in South America there are deciduous forests dominated by *N. alpina, N. obliqua, N. pumilio* and (rarely as a forest dominant) *N. antarctica*. Deciduous trees impose substantial seasonal fluctuations in the light regime upon species growing beneath them, which would also have implications for temperature and water relations. There might be substantial microenvironmental spectra in deciduous and evergreen *Nothofagus*-dominated communities.

Tall, evergreen *Nothofagus*-dominated forest would thus represent an environmentally-restricted community type in which to seek community-level convergence. Fine control of environment would be achieved by choosing sites with similar climate and soils in different

regions. However, as temperature, rainfall and soil type vary largely independently, it might be difficult to control for all three of these parameters simultaneously. In general, climate is the most important feature controlling vegetation distribution, whereas within a climatic zone, other features such as soil type may be important (Woodward 1987). Therefore, the primary selection criterion for sites in this study was that they should have similar climates, while matching soil type (fertility) was a secondary criterion.

Climate will be affected by both latitude and altitude, temperature tending to decrease by approximately 1°C with a 150 m rise in altitude (Bureau of Meteorology 1975) and with latitude. The seasonal cycle of day-length also varies with latitude. Ideally, latitude should be standardised. Mainland Australian *Nothofagus moorei* forests occur at significantly lower latitudes than in the other temperate regions, but are restricted to high altitudes: temperatures, annual rainfall and dry season rainfall are comparable with other *Nothofagus* communities, for example, in Tasmania (Beadle 1981).

Aspect and slope have a pronounced effect on community composition and structure. North-facing slopes (in the southern hemisphere) receive more incident radiation than south-facing slopes and tend to be drier and warmer. Slope can influence water runoff, soil depth, and disturbance regimes. Shading effects of topography in narrow, steep-sided valleys can cause marked changes in light availability and temperature on a daily or seasonal basis. Restricting sites to shallow slopes would not only control the factors associated with slope, but would tend to eliminate major effects of aspect and topography as well.

In summary, close matching of the environments of different communities would be achieved if sampling were restricted to tall, evergreen *Nothofagus*-dominated forests with similar climates and, if possible, soils. Close matching would be further facilitated by standardising latitude, and choosing sites with shallow slopes.

2.2.2 Sampling data

To address the hypotheses of community structure proposed in Chapter 1, it is necessary to record several types of features of each community and its environment. Community-level convergence is sought in species richness and texture. A measure of species abundance is needed as a basis for weighting species in analyses. A record of the vertical structure of each community would allow analyses to focus on community subsets (vertical strata) within which species interactions might be concentrated (Wilson 1989; Pianka 1980). Finally, data are required to characterise features of the environment that might influence species responses, the operation of assembly rules and the likelihood of convergence between different communities.

Records of the number of species in each community are required to evaluate the hypothesis of community-level convergence in species richness. Comparisons are meaningful only when species richness is expressed with respect to the same sampling area (quadrat size) in different communities. This is because species richness increases in a non-linear way with area, and species-area curves can be different in different communities (Connor & McCoy 1979; Buys *et al.* 1994). For some statistical analysis, replicate data from within each community are required. Adequate degrees of freedom should be provided by sampling within five quadrats at each site.

TEXTURE

The texture of a community is composed of a virtually infinite number of species characters. An optimum data set for the investigation of community structure will comprise characters that are:

1. relatively easy to measure. If measurements of one sample can be made relatively quickly, more samples can be measured in a given period of time. This permits evaluation both of more characters, and more replicate samples for each character.
2. of *a priori* functional importance. Only functionally important characters are likely to reflect niche distribution patterns, the underlying patterns being tested.

Leaf characters are an obvious choice: leaves constitute the primary site of photosynthesis, and their structure and function have implications for gas exchange, water potential, nutrient and energy allocation, whole-plant architecture and growth, and interactions with other organisms (Givnish 1987). Consequently leaves (and their functional equivalents) would be subject to strong selection regimes and should closely reflect evolutionary outcomes of interactions both with the abiotic environment, and with other individuals and species. Phylogenetic history may influence the way characters evolve, occasionally producing different solutions to the same adaptive problems in different species. However, assuming that natural selection leads towards optimal form and function in relation to habitat factors, then for most species, morphology and physiology will reflect niche (Parkhurst & Loucks 1972).

Some plant species possess photosynthetic organs functionally equivalent to but not homologous with the typical angiosperm simple leaf (e.g. of *Nothofagus* spp.). Such organs could include leaflets, phyllodes, pinnae etc. in different species. To enable leaf characters of a range of species to be summed and compared meaningfully, measurements were applied to functionally-equivalent photosynthetic organs on different species. The general term `photosynthetic unit' (PSU) has been applied in previous studies to such functional `leaves' (Wilson *et al.* 1994; Smith *et al.* 1994). In the present study, the PSU is defined as the minimum mobile photosynthetic structure, i.e. the smallest unit for which some independent setting of

position and angle (e.g. to optimise light reception) is apparent. In the present study, all references to `leaves' will implicitly pertain to PSUs unless a more restricted meaning is implied by the context in which the reference is made.

For many leaf characters, patterns of variation in relation to the environment have been documented. The existence of correlations between characters and environmental parameters attests to their functional significance, and many such relationships have been more closely investigated and underlying mechanisms identified. Although variation of characters with environmental parameters suggests a correlation with beta (gradient) niches, rather than alpha (resource) niches, which are of greater interest in this study, these two types of niches are related, especially for plants. For example, in the above-ground vertical structure of a forest there will be correlated gradients in several environmental (beta; e.g. temperature) and resource (alpha; e.g. light) gradients. Variation in a character (e.g. leaf specific weight) with height may (or may not) be fundamentally due to adaptation or plastic responses to only a subset of these gradients, but it may be a useful predictor for all of them.

Characters that satisfy criterion (2) above, and some functional relationships that have been hypothesised or demonstrated for them, are described below.

1. *Leaf size and shape* influence gas exchange and heat load through their effect on the thickness of the boundary layer of air of reduced velocity adjacent to the leaf surface (Taylor 1972; Givnish & Vermeij 1976; Grace 1977). Longer leaves of a given area will attract a narrower boundary layer. Similarly, lobation may significantly reduce boundary layer thickness with only a minor reduction in leaf area (Taylor 1972). Both among and within species, leaf size (area and width) tends to increase with increasing moisture and nutrient availability, and decrease with increasing irradiance (Givnish 1987). Positive relationships between mean leaf area and temperature among communities have been detected in temperate and tropical rainforests (Christophel & Greenwood 1989; Mackey 1993; Jordan & Hill 1994). There is evidence that small leaves may be advantageous in montane rainforests where reductions in root permeability at low soil temperatures can lead to physiological drought (Greller & Balasubramaniam 1988), while Woodward (1987) has suggested that mechanisms that provide protection against chilling and freezing injury to cell membranes may favour small leaves in cold climates.
2. *Leaf thickness* may be influenced by other aspects of leaf structure including mesophyll air space volume, cell size, the number of palisade cell layers, sclerophylly and succulence, which may reflect trade-offs in gas exchange, mechanical support and responses to herbivory (Björkman 1981; Gulmon & Chu 1981; Bongers & Popma 1988; Witkowski & Lamont 1991). Species tend to have thicker leaves in drier, nutrient-poorer and sunnier conditions (Loveless 1961, 1962; Beadle 1966; Grubb 1977; Medina 1984; Givnish 1987; Bongers & Popma 1988). A negative relationship between leaf thickness and nutrient availability is part

of a syndrome that has been labelled `oligotrophic xeromorphism' (Grubb 1977), which may arise through the optimisation of leaf morphology in the face of low plant nutrient levels and the energetic costs of absorbing scarce nutrients (Givnish 1984).

3. *Leaf succulence* (relative water content) may reflect osmoregulation mechanisms in plants of saline habitats (Kramer 1983) but more generally would be expected to reflect soil moisture status and humidity.
4. *Leaf specific weight* (SLW), the ratio of dry weight to area, reflects both leaf structure and photosynthetic capacity (Field & Mooney 1986) and can be a component of mathematical formulations of relative growth rate (Björkman 1981). It has been recommended as a character that may integrate the effects of canopy structure and light environment on leaf photosynthesis (Ellsworth & Reich 1993). Leaf specific weight tends to increase with irradiance and decrease with moisture and nutrient availability. It may also vary with temperature, herbivory and concentrations of atmospheric pollutants (Witkowski & Lamont 1991). A high leaf specific weight is characteristic of oligotrophic xeromorphy (see above).
5. *Leaf inclination* has implications for temperature load and light reception and may reflect leaf mechanical structure. Leaves tend to be more inclined from the horizontal at higher light intensities and lower moisture and nutrient availabilities (Sobrado & Medina 1980; Medina 1984; Givnish 1984; Hollinger 1989; Herbert & Nilson 1991). A tendency, both within and among species, and even on a single individual, for leaves to be more inclined in sunnier conditions has been explained as the result of an energetic trade-off of light reception against leaf thermal and gas exchange budgets (Givnish 1984; Hollinger 1989; Herbert & Nilson 1991).
6. *Leaf longevity* reflects a trade-off between two strategies for growth: production of `cheap' leaves which assimilate much carbon over a short period, permitting rapid growth, e.g. into light gaps or to the forest canopy; and production of more robust leaves, which photosynthesise at lower rates, but over an extended life-span (Reich *et al.* 1991). Longevity is associated with numerous leaf characters including specific weight, stomatal conductance, nitrogen and phosphorus content, net photosynthesis and support fraction (Reich *et al.* 1992).
7. *Support fraction*, is the ratio of non-leaf to total dry weight in terminal shoots. Support fraction is high in some species having divaricating stem architecture (Wilson *et al.* 1994), which is sometimes associated with long internodes and reductions in the size and number of leaves. Many understorey shrubs and juvenile trees in New Zealand exhibit divarication, which has been interpreted as an adaptation against herbivory by recently-extinct rattites (Greenwood & Atkinson 1977). Support fraction also reflects growth strategy, being correlated with leaf longevity (Reich *et al.* 1992).
8. *Stomatal density* on the abaxial surface is an important parameter governing gas exchange characteristics of leaves. Significant differences in stomatal density have been found among forest species differing in their regeneration ecology (Popma *et al.* 1992) and within species,

between sun and shade leaves (Bongers & Popma 1988).

9. *Mesophyll air space volume* influences diffusion of carbon dioxide from stomata to the sites of photosynthesis. It may limit photosynthetic rates in C_3 plants (Parkhurst 1986).
10. *Stomatal conductance* is a focus of the functional trade-off between carbon dioxide uptake and water loss. Stomatal conductance increases with increasing moisture availability and humidity (Givnish 1987), and with irradiance until heat load and/or leaf water potential become limiting (Cowan 1982, 1986). It is generally correlated with photosynthetic capacity (Field & Mooney 1986).
11. *Leaf absorptance* of photosynthetically-active radiation (PAR; 400-700 nm wavelength) has been shown to be related to leaf temperature and transpiration rate in plants of xeric environments (Ehleringer 1981) and to nitrogen content and photosynthetic capacity (Hollinger 1992).
12. *Mesophyll photosynthetic capacity* is the photosynthetic rate achieved under optimal conditions of temperature, humidity and carbon dioxide availability, and at saturating light intensity. Photosynthetic capacity tends to increase with increasing moisture and nutrient availability, and with irradiance (Björkman 1981; Ellsworth & Reich 1993). It is correlated with several other characters, including nitrogen content, stomatal conductance and (negatively) leaf specific weight (Reich & Walters 1994; Field & Mooney 1986; Evans 1989).
13. *Light compensation point*, i.e. the PAR level at which CO_2 production due to respiration balances photosynthesis, varies with photosynthetic capacity (Björkman 1981), tending to be lower in shade than in sun-associated plants, as well as in shade versus sun leaves of the same species or individuals (Bannister 1976).
14. *Leaf nitrogen and phosphorus content* are correlated with mesophyll photosynthetic capacity in C_3 plants (Field & Mooney 1986; Reich *et al.* 1991). Leaf nitrogen expressed on a dry weight basis has been shown to have utility as a proxy measure of photosynthetic capacity across many species (Field & Mooney 1986). This is probably a result of limitation of photosynthetic capacity by thylakoid and Calvin cycle proteins, which make up the majority of leaf nitrogen (Evans 1989).
15. *Leaf total chlorophyll content* is correlated with thylakoid nitrogen and leaf absorptance to PAR (Björkman 1981). Total chlorophyll is, however, a poor predictor of photosynthetic capacity. This is because thylakoid nitrogen declines as a proportion of total nitrogen in more sunlit, more fertile and moister environments (Evans 1989).
16. *Leaf chlorophyll* a/b *ratio* tends to decrease with irradiance (Boardman 1977; Björkman 1981; Chow *et al.* 1991; Dale & Causton 1992). This relation remains stable among different sun species, or shade species, and independent of other environmental factors, although different levels of response may exist between sun and shade species (Dale & Causton 1992).

17. *Modular hierarchy* is the number of above-ground hierarchical levels that characterise species architecture. For example, many grasses and graminoids consist of tussocks comprising several tillers, in turn divided into a number of leaves — a modular hierarchy of 3. Modular hierarchy has been recommended as a functional character which provides a link between the ultimate photosynthetic organs (leafs, leaflets, pinnae etc.) and their organisation and density (Wilson *et al.* 1994).

Not all of these characters satisfy criterion (1) above, the requirement that the characters should be straightforward to measure. Fortunately, the existence of robust correlations among many characters means that several can be omitted without significant loss of information, as justified below.

Measurement of photosynthetic capacity and light compensation point should ideally be done *in situ* and would require the use of an elaborate apparatus, for example, an infrared gas analyser (Bannister 1976). Among the many vascular species occurring in most *Nothofagus*-dominated communities this would be highly impractical. Furthermore, because conditions within the chamber in which foliage is enclosed for measurement are highly artificial, results are not always repeatable between different implementations (Chapman 1976). This would pose a problem for a study such as the present one, for which laboratory analyses must be done in several different geographical locations. Stomatal conductance is likewise inconvenient to measure, requiring a specialised apparatus. Photosynthetic capacity, light compensation point and stomatal conductance would be relatively strongly intercorrelated, all being related to light reception (Björkman 1981; Field & Mooney 1986). Leaf nitrogen content is known to be a good predictor of photosynthetic capacity, at least for C_3 plants (Field & Mooney 1986). This implies that leaf nitrogen content — which is more practical to measure — could be used instead of photosynthetic capacity, light compensation point and stomatal conductance, as a proxy variable for light niches.

Characters concerning the microscopic structure of leaves are time-consuming to measure because of the detailed preparation involved. Characters of this kind — stomatal density and mesophyll air space volume — would be expected to represent adaptations to CO_2 uptake and diffusion. Leaf size and shape characteristics should show similar relations (Givnish 1984), but have the advantage that they are more practical to measure. Therefore, microscopic characters were not included in texture as it was evaluated in this study.

Direct measurement of leaf longevity would require monitoring of plants in the field over a period of up to several years (the life-span of the longest-lived leaves). In the present study, however, most sites could be visited only once. Leaf longevity is associated with several characters (leaf specific weight, nitrogen and phosphorus content, support fraction; Reich *et al.* 1992) for which `snapshot' measurements are possible. Consequently, leaf longevity was not included in the present study.

Leaf absorptance to PAR has emerged as a useful predictor of photosynthetic capacity in some recent studies (Hollinger 1989, 1992). However, photosynthetic capacity is even more strongly predictable from leaf nitrogen content (Field & Mooney 1986), while optical measurements, which must be performed on fresh foliage, require a specialised apparatus. No advantage was seen in quantifying both leaf nitrogen and leaf absorptance to PAR. Therefore, nitrogen content alone was measured.

Modular hierarchy, though readily determined for some species (e.g. tussock-forming grasses and graminoids), is not clearly apparent for many growth forms of plants, including many shrubs and trees. It is doubtful whether a given modular hierarchy corresponds to any particular niche or niche axis (for example, a modular hierarchy of 3 might be shared by a grass, a fern and a canopy tree). It was therefore not included in the evaluation of community texture.

Following elimination of characters from the above list that are either impractical to measure, or would duplicate the role of other — more easily measured — characters as proxies for species niches, 12 characters remain. These have the advantages that can be measured relatively quickly and accurately, yet are likely to be functionally important, reflecting major aspects of species niches. The characters are listed in Section 2.3.5.

Sampling of heteroblastic species and canopy trees

For some species, adult and juvenile forms may exhibit significant differences in their morphology, implying that they have a different niche. This is notably the case in the New Zealand flora, for which heteroblasty (morphological and physiological differences between adults and juveniles of the same species) is characteristic (Gould 1993). Differences between juvenile and adult niche are also likely to be pronounced for canopy trees. In terms of the model for community structure developed in Chapter 1, it is the niches, rather than species *per se*, that are important in producing community structure. Therefore, juvenile and adult forms were sampled separately for canopy species, and for species in which distinct differences between juvenile and adult morphology were apparent.

SPECIES ABUNDANCE

Whether community texture in terms of a particular character (texture variate) is expressed as an index (e.g. mean among species) or as a distribution (e.g. in frequency classes), it is desirable that species of greater abundance be weighted more heavily than minor ones in evaluating it. This is because abundant species will have more effect on each other than species of low abundance, and so are more likely to exhibit non-random patterns (e.g. in their characters) which might indicate community structure (James & Boeklen 1984). A measure of species abundance is a suitable weighting factor. Photosynthetic biomass, the total dry weight of PSUs, has been recommended

(Werger & Ellenbroek 1978) as it will be correlated with production, a logical measure of a species' contribution to ecosystem functioning (e.g. nutrient cycling) and of its effect on other species. It is the only `snapshot' measure of production that can be used for all species (basal area, a useful correlate for trees, can not be meaningfully determined for many shrubs and herbs [Bonham 1989]). Photosynthetic biomass is more meaningful functionally than cover or frequency estimates, which tend to weight minor species, such as scrambling ground-layer herbs, at the expense of major ones, such as canopy trees (Smith *et al.* 1994).

Photosynthetic biomass for a species in a given area (quadrat) is the product of PSU density and mean PSU dry weight. PSU density may be determined by hierarchical enumeration of subsamples (Wilson *et al.* 1994). This is the least subjective practical method available for quantifying species abundance in terms of foliage density for large numbers of species, particularly those of high stature. Although this method has a subjective component when applied to species which do not conform to a strict modular hierarchy, values can be `transformed down' (e.g. by taking the square root) to give weighting factors in which the subjective factor is less important, certainly less so than in purely subjective measures such as percentage cover.

VERTICAL STRUCTURE

Information relevant to the vertical structure of communities is needed to enable comparisons to focus on vertical zones (strata, or height guilds [Chapter 10]), where reciprocal species interactions are likely to be concentrated. Precise measurements at vertical scales above a few metres are difficult to make as well as time consuming, but some information would be provided by estimating the proportion of PSUs of each species occurring in each of several height classes within quadrats.

ENVIRONMENTAL PARAMETERS

Environmental data are required to characterise abiotic influences on species responses, the operation of assembly rules and the likelihood of convergence between different communities.

Climate

The principal climatic constraints limiting the distribution of particular plant functional types are summer warmth requirements, winter cold limits and drought limits (Woodward 1987). Biologically-important differences in climate among communities would therefore be in terms of these factors, which may be characterised by the mean temperature of the warmest month, mean minimum temperature for the coldest month, annual rainfall and rainfall in the driest quarter. All these parameters would potentially vary from year to year, so long-term averages are to be

preferred.

Soils

For soil parameters, as for species chararacters, the explanatory value of each parameter must be weighed against time, cost and practical constraints in collecting it. The existence of strict restrictions on the importation of soil samples in New Zealand decreed that soil analyses had to be performed in the country in which samples were obtained, an additional practical constraint.

The soil nutrients most often limiting for plants are nitrogen, phosphorus and potassium (Salisbury & Ross 1985). Therefore, concentrations of these elements were determined to characterise soil nutrient status. Further parameters that are readily measured include pH, which is useful as a general measure reflecting soil aeration (and therefore drainage) and nutrient status (Russell 1950), and soil organic content, which is related to ion exchange capacity and may reflect nutrient availability, particularly of nitrogen (Russell 1950).

Light regime

An important aspect of the environment of the forest understorey is the irradiance regime. Because of shading by canopy trees, only a fraction of the sunlight incident at canopy level reaches the understorey. Light quality in the understorey will also be affected by preferential absorption of red and blue wavelengths by canopy trees (Salisbury & Ross 1985). Both effects result in a marked reduction in the amount of photosynthetically-active radiation available to understorey species. Light attenuation by the canopy, or its inverse, the proportion of light transmitted, is therefore an important parameter of the environment as it is perceived by the majority of species.

Ideally, measurements of canopy light transmittance should be standardised with respect to cloud conditions. In sunny conditions light fluxes are highly directional. This results in greater spatial and temporal variation in light intensity, in part because the `averaging' effect of scattering by foliage is reduced (Salminen *et al.* 1983). Therefore, it would be preferable to measure canopy light transmission consistently under overcast conditions.

2.2.3 Study site design

The size and structure of the study sites in which data are collected will influence the suitability of the data for addressing the hypotheses.

The smallest scale at which community-level convergence is likely to be detectable is that of the local community (see section 1.5). A local community would include several plant neighbourhoods, and would be large enough to accomodate microenvironmental (and associated

floristic) variation. A neighbourhood comprises a single individual and its immediate neighbours (Aarssen 1992), perhaps 5-6 individuals for adult *Nothofagus*. A single neighbourhood would seem appropriate as a basic sampling unit, and so the area 20 × 20 m was chosen for sampling quadrats. This area is small enough to be sampled efficiently (noticing all species, and estimating their abundance with tolerable accuracy) and in a reasonable amount of time. It is comparable to the sizes of quadrat that have previously been used to sample in forest (e.g. Foster 1988; Tonteri *et al.* 1990; Hättenschwiler & Körner 1995). A neighbourhood is also the area in which most direct species interactions would occur (Aarssen 1992) and so is a suitable scale at which to record species richness, one of the community properties for which assembly rules are predicted and sought.

Nothofagus-dominated forests exhibit a considerable amount of spatial heterogeneity, both as a result of microtopographic variation, and the presence of treefall gaps with associated differences in microenvironment and composition. To accomodate some of the spatial heterogeneity, and to obtain the replicate values for species richness needed for analyses, several (usually five) neighbourhood-scale quadrats were sampled at each site.

PSU densities need to be determined (by definition) on a per-area basis, and so were obtained within quadrats. All plants that appeared to be rooted within a quadrat were sampled, i.e. their PSU densities determined. In comparison with shoot presence, this had the advantage that the composition of quadrats could be precisely determined at ground level (with the exception of epiphytes, which are not rooted at ground level): projection of quadrats into higher strata is difficult in forest (Bycroft *et al.* 1993).

Most texture characters exhibit significant variation within species. Consequently a relatively large number of replicate samples (PSUs, shoots etc) are required in order to obtain an accurate estimate of the population mean for each species. Many species will be relatively rare within quadrats, but be represented more often in the whole study site (comprising several quadrats). Since the quadrats were taken to be representative of the whole study area, species samples for the evaluation of texture were taken from anywhere within the sampling area, and not necessarily only from the quadrats in which the species were recorded.

2.2.4 Seasonality considerations

Seasonal fluctuations in texture are to be expected, both with respect to species characters, and PSU densities. Leaf area index (LAI, the ratio of total leaf area to ground area within a sampling unit) may vary substantially between winter and summer, even in evergreen forest. Leaf concentrations of nitrogen and phosphorus would be expected to increase in summer, when translocation from woody tissues to the new shoots and buds occurs (Kramer & Kozlowski 1979), while various physical characters (e.g. succulence) would vary with leaf age, which would also have a seasonal component. To avoid bias due to seasonal variation in species characters

and PSU densities, all sites would ideally be sampled at approximately the same time of year.

2.3 Methods

2.3.1 Selection of sites

Sampling sites were sought in Tasmania, mainland Australia (`Australia,' for brevity), New Zealand and South America. These four regions are referred to as `landmasses' throughout this report. In comparison to the other landmasses, a greater number of study sites was established in New Zealand. This was in order to be able to focus on questions of community structure at the local and regional scales. In Tasmania, Australia and South America the principal aim in selecting sites was to encompass a range of tall, evergreen *Nothofagus*-dominated communities representative for each landmass. Locational, floristic and environmental data for each of the 17 study sites are presented in Chapter 3.

All sites comprised tall mature forest (average canopy height 30 m or more) dominated (at least 90% canopy cover) by one or more evergreen species of *Nothofagus*. Standardisation of climate to Meurk's (1984) `cool temperate or upper montane' bioclimatic zone (MTWM *c.* 12.5-17.5°C) was achieved by adjusting latitude and altitude, remaining within the latitudinal range 42 ± 3 °S in all landmasses except Australia (where *Nothofagus moorei* forest has a scattered montane distribution from *c.* 25 °S to 32 °S). Areas with particularly infertile soils (for example, over precambrian quartzite in Tasmania) were avoided. Steep terrain (>15° slope) and areas with impeded drainage were likewise avoided, as were narrow valleys in which shading by surrounding topography could be significant. Where slope was not negligible, southerly aspects were chosen if possible. Areas subject to human disturbance were avoided, and a buffer zone of at least 50 m was maintained, separating study sites from tracks, roads and other areas of human disturbance, as well as from sizeable natural clearings.

2.3.2 Field sampling

To standardise with respect to seasonal effects on texture, most sampling was done from the last month of spring (November) until the first month of Autumn (March). However, this could not be achieved for all sites and, in particular, mainland Australian sites were sampled at the beginning of spring (September-October) while some collections in southern New Zealand were made in late autumn (April-May).

STUDY SITE LAYOUT

Sampling was carried out within a 100 × 200 m study area at each site, the long axis being aligned perpendicular to the prevailing slope (where applicable) to ensure that elevation effects within the study area would be negligible. To avoid subjectivity in the choice of sampling area, its exact position was randomised within a 200 × 400 m area where possible. Five (occasionally, when available sampling time was limited, three or four) 20 × 20 m quadrats were located within the study area by stratified randomisation. As it was intended to sample only closed forest, quadrats were repositioned (to a different random point within the study area) if a canopy opening covered more than one-third of their area.

QUADRAT SAMPLING

In each quadrat, shoot presence of all vascular plant species was recorded. PSU densities were determined for each species present by hierarchical enumeration of subsamples. This method of counting PSUs was applied in different ways for different types of species. In the case of functional types having a distinct modular hierarchy (e.g. many graminoids, which have tussocks divided into tillers, in turn divided into individual leaves), the average number of PSUs in first-order modules was determined, then the number of first-order modules in second-order modules, and so on, finally estimating the number of highest-order modules rooted in the entire quadrat. At each level, values were obtained for several modules, on different individuals if possible, to ensure that the mean for that level was as accurate as possible. The average numbers of units at each level for a species were multiplied together and divided by quadrat area (400 m^2) to determine its PSU density in the quadrat. In the case of species lacking a distinct modular hierarchy a similar protocol was followed, but modules were defined arbitrarily. Binoculars were used to facilitate enumeration of PSUs for canopy trees. All PSUs of all individuals rooted (or appearing to be rooted) in the quadrat, and only those individuals, were included in the density estimates. To determine whether epiphytic species not rooted at ground level appeared to occur within the quadrat, quadrats were projected visually upwards. Adult and juvenile forms of heteroblastic species, as well as seedlings (0-2 m), saplings and subcanopy individuals (2 m to 67% of mean canopy height), and canopy individuals (above 67% of mean canopy height) of canopy species, were treated as separate entities for the purposes of PSU density estimation and texture sampling (see below).

As a record of the vertical distribution of each species, the proportion of its PSUs occurring in each of the following height classes within the quadrat was estimated visually: 0-0.3 m; 0.3-1 m; 1-2 m; 2-5 m; 5-10 m; 10-20 m; 20-30 m; 30-40 m.

The height of a representative canopy individual of each canopy species (as defined above) present in the quadrat was determined using a clinometer. Diameters at breast height

(DBH) were recorded for all canopy individuals using a diameter measuring tape. Breast height was taken at 1.6 m above ground level, except for buttressed trees, for which measurements were made just above the buttress. Soil samples were taken from the upper mineral horizon at three random points within each quadrat, and bulked to give one sample of *c.* 1 kg, representative for the quadrat. In Argentina only, soil samples from all quadrats at each site were bulked to give one sample per site. Mean slope across the quadrat (nearest 5°) was estimated using an Abney level, and aspect (nearest 5°) determined with a magnetic compass. Obvious features of the vegetation structure, composition and microtopography were noted.

CANOPY LIGHT TRANSMISSION

To determine the proportion of incident light transmitted by the forest canopy above each quadrat, sampling of PAR quantum flux was done in the open and beneath the forest canopy. Using an electronic quantum photometer (LiCor LI-185B and similar), a light measurement was made at 2 m above ground level in an open area (e.g. large clearing or field) near the study site, at which trees and surrounding topography would have little influence on light levels. Measurements were then made at 1 m above ground level at 10 random points within each quadrat at the study site, a 1 m rule being used to position the quantum sensor at the appropriate height. A second value was then obtained in the open. At one Chilean (SC2 Antillanca) and one Argentinian site (SA2 Gutierrez), quadrat light measurements were made at 2 m as well as 1 m above ground level. This was because a dense layer of bamboo (*Chusquea* spp.) in the understorey would have reduced light levels at 1 m height significantly. Whenever possible, light transmission measurements were made at midday ±1 hr (standard time) in stable overcast conditions. At several sites, however, sampling had to be done during full sunshine. Sunflecks were avoided in these conditions. Sampling was completed as quickly as possible to avoid error due to changes in light intensity during the measurement period.

TEXTURE SAMPLING

To evaluate community texture, shoot samples were collected for each species (or entity: see above) encountered within quadrats at each study site. Where the same species occurred in more than one quadrat at a particular site, only one collection was made. However, separate collections were made at each site regardless of whether some species had been sampled elsewhere (except in the case of occasional missing values; see below). Samples were sought within the whole study site, not just within quadrats.

PSU inclination was measured *in situ* to the nearest 5° using an Abney level or clinometer. Inclination measurements were independent of whether PSUs were erect or pendent, and independent of the position of the midrib. For each species 10 representative PSUs were

measured, from different individuals if possible.

For the evaluation of chlorophyll characters, single PSUs (or, in the case of species with very small PSUs, several PSUs) were collected from 10 different individuals of each species, or occasionally fewer if the species was of low abundance, endangered or had exceptionally large leaves. Damaged, diseased or moribund foliage, as well as new foliage not fully developed, was avoided.

To evaluate all other texture characters, 10 terminal shoots were collected from different plants if possible. The number of plants and/or shoots sampled was reduced (to the largest number practicable) in the following cases.

1. For canopy trees (mainly *Nothofagus* spp.) sampling was exceptionally time-consuming (see below). Therefore, only three trees of each species were sampled at most sites. However, three to four terminal shoots were taken from each tree, generally yielding a total of 10 samples.
2. For rare or obscure species less than 10 individuals were sampled if that number could not be found within the study area, or if collection of the full complement of samples might have placed the persistence of the local population in jeopardy. In the case of North Island New Zealand sites (ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements) only one terminal shoot (to a maximum of five leaves) was allowed to be taken for mistletoe species at each site.
3. For species with exceptionally large leaves (e.g. *Cordyline indivisa*, whose mean leaf area at ZN1 Ohakune was 483 cm^2) as much foliage as practicable was taken.

A terminal shoot was defined as:

1. an entire tiller, for grasses and graminoids;
2. an ultimate shoot for most trees, shrubs, ferns and forbs; for consistency, the shoot was severed just below the lowest PSU remaining attached to the main axis;
3. a segment including at least 10 true leaves for certain climbing or scrambling species with persistent leaves.

In all cases, foliage not fully developed was detached from samples collected. Care was taken to sample from the upper surface or outer canopy of all plants, including trees. At most sites, a pole pruner was used to access outer canopy foliage of understorey trees, while a specially-developed canopy sampling apparatus, described below, was used to retrieve foliage of canopy trees.

APPARATUS FOR TEXTURE SAMPLING OF CANOPY TREES

Foliage samples were obtained from canopy trees using a bow-and-arrow-based apparatus developed by R. Gympel, A.J. Watkins and the author for use in the present study. A fishing reel wound with standard (12 lb breaking strain) nylon fishing line was attached to the bow. One end of the fishing line was tied to a lead-weighted arrow. To collect a foliage sample, the arrow was propelled near-vertically across the outer branches of a target tree, uncoiling the fishing line and draping it across the tree. The fishing line was then detached from the arrow and tied to one end of a 50 m length of 1.8 mm braided polyester line, at the other end of which was a 50 cm length of flexible saw wire (multi-stranded embriotic wire, designed for the amputation of bovine horns), followed by a further 50 m of braided line. The line and saw were then drawn over a branch by winding the fishing line back onto its reel, and the branch was sawn down by drawing alternately on the two ends of the line. The apparatus was used successfully at all sites sampled in this study, and was found effective to a height of approximately 40 m.

2.3.3 Climate parameters

For each site, values of the following climate parameters were obtained: 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). Mean minimum temperatures for the coldest month, thought preferable to MTCM in characterising absolute winter cold limits, could not be obtained for South American sites. However, MTCM should be strongly correlated and was therefore used instead. For Tasmania, mainland Australia and New Zealand, climate data were obtained using the climate estimation procedures of the computer program BIOCLIM (Nix 1986; Mitchell 1991; Orr 1993). BIOCLIM interpolates among locations for which climate data are available, taking account of the position and altitude of the target point (Hutchinson 1984). This represents the best method of estimating climate for localities distant from climate recording stations. Climate data for Chilean and Argentinian sites were estimated from published records (Almeyda & Saez 1958; Anon. 1964; Putney 1970; Dimitri 1972; Veblen & Schlegel 1982), with mathematical correction for altitude and location where necessary.

2.3.4 Laboratory measurement

SOIL PARAMETERS

The soil parameters evaluated for each site were total nitrogen, phosphorus and potassium, pH and organic content. It was endeavoured to standardise extraction methods for all sites, to ensure

that data would be comparable. However, due to limited facilities in some of the regions visited in the course of the study, complete standardisation could not always be achieved. Analysis methods for extractions also varied, although presumably this would affect the precision of results, not their absolute values. Some analyses were performed by, or with the assistance of, staff of specialist laboratories, as follows: Soil and Plant Laboratory, Department of Primary Industry Tasmania (DPI); Forestry Department, Australian National University (ANU); Soil Fertility Service, New Zealand Pastoral Agriculture Research Institute (NZPARI); Laboratorio de Nutrición y Suelos Forestales, Instituto de Silvicultura, Universidad Austral de Chile (UAC) and Estactión Experimental Regional Agropecuaria Bariloche, Instituto Nacional de Tecnología Agropecuaria (INTA). In the following discussion, each organisation is referred to by its abbreviated code, shown in parentheses above.

Except in Argentina, where a single measurement was made on bulked soil samples from each of the two sites, separate values for each parameter were obtained for each quadrat sampled. For mainland Australian soils only, samples were also replicated at the analysis stage, three values being obtained for each quadrat from the same field sample and averaged. This was intended to improve the accuracy of overall values for each quadrat.

Descriptions of analytical methods below are from Allen (1989) unless otherwise indicated. Exact methods adopted by commercial laboratories may have differed in detail from the regimes described here in some cases.

Nitrogen

Nitrogen and phosphorus analyses were carried out by DPI (Tasmania); ANU (Australia); NZPARI (New Zealand); UAC (Chile) and INTA (Argentina). In Tasmania, Chile and Argentina, nitrogen was extracted using a Kjeldahl procedure. In this method, samples are digested under heat in concentrated sulphuric acid in the presence of a selenium, copper or mercury catalyst. This converts soil nitrates, nitrates and insoluble organic nitrogen compounds to ammonium (Allen 1989). In New Zealand and Australia a variation on the Kjeldahl procedure was adopted, including hydrogen peroxide is the digestion mixture. This had the advantage that phosphorus concentrations could be determined from the same digest (see below).

In Tasmania and Australia nitrogen concentrations in digests were measured by means of an automated colorimetric (indophenol blue) procedure. Ammonium in the soil extract is oxidised by sodium hypochlorate. A subsequent reaction with sodium salicylate imparts a blue colour to the solution, whose concentration, measured by spectrophotometry (absorptance at 660 nm), is proportional to the amount of nitrogen present. In Chile and Argentina, a distillation and titration method was used. Ammonium is distilled from the soil digest and received by a hydrochloric or sulphuric acid solution of known concentration, raising its pH. Titration, for example against sodium hydroxide in the presence of an indicator (phenolphthalene), allows the

ammonium-nitrogen concentration of the original solution to be determined (R. Grez, *unpublished*). An automated variation on this method was used by NZPARI to analyse New Zealand soils.

Phosphorus

In New Zealand and Australia, phosphorus was extracted simultaneously with nitrogen using a modified Kjeldahl procedure, as described above. In Tasmania, soils were digested under heat in concentrated nitric and perchloric acids (see `Potassium' below). In Argentina, Truog's extraction procedure was used. More soluble phosphate compounds, as well as free phosphate ions adsorbed to exchange sites in the soil are released by a dilute, buffered sulphuric acid solution. The amount of phosphorus extracted by this procedure is intermediate between total soil phosphorus and the ambient amount available for uptake by plants (Allen 1989). The values obtained cannot be compared on an equal basis with the total phosphorus values obtained at other sites.

In Tasmania, determination was done using an inductively coupled argon plasma (ICP) spectrophotometer (Jakubowski & Stuewer 1994). In Australia, New Zealand and Argentina a molybdenum blue procedure (automated, except in Argentina) was used. Dissolved phosphate in the soil extract is coupled with a molybdate reagent and a reductant (either stannous chloride or ascorbic acid) giving a blue colour whose intensity, measured by spectrophotometry (absorptance 700 nm), can be used to calculate the amount of phosphorus extracted.

Due to unforseen laboratory problems, no phosphorus values were obtained for Chilean sites.

Potassium

Analyses for total potassium, pH and organic content were carried out by DPI (Tasmania); UAC (Chile) and INTA (Argentina). For New Zealand and Australian sites, potassium analyses were done by the author; in Australia, with the assistance of ANU staff. Except in Argentina, extractions were done in a heated 3:1 mixture (volume basis) of concentrated nitric and perchloric acids. In Argentina extraction was done in nitric acid.

Determination of potassium concentration in extracts was by automated atomic-absorption spectrophotometry (Australia) or flame photometry (New Zealand, Chile, Argentina).

pH

Measurements of pH were done in distilled water using a pH meter. For New Zealand and Australian samples, a mixture of *c.* 5 g soil and 25 ml distilled water, shaken for 1 hr, was used.

Organic content

Organic content was estimated by loss-on-ignition at 500°C for 10 hr, except in Chile and Argentina, where a Walkley-Black carbon extraction procedure was used. Soil carbon is oxidised under heat by potassium dichromate in concentrated sulphuric acid. The resultant solution is titrated against ferrous ammonium sulphate in the presence of an indicator (diphenylamine) to determine the amount of carbon present. The chemical extraction method was considered to give a more reliable estimate of organic content for the volcanic ash-derived soils that prevail at the South American sites (R. Grez, *personal communication*). The two methods have been shown to produce an acceptable correspondence (Allen 1989).

SPECIES CHARACTERS

To ensure maintenance of field turgor, field samples were stored in plastic bags and, if possible, refrigerated (at *c.* 4°C) until laboratory measurements and drying were carried out. Storage time was kept to a minimum (generally less than two weeks). However, samples were found to remain fresh for up to two weeks if refrigerated immediately after collection.

PSU chlorophyll content

Chlorophyll *a* and *b* content were determined using a method adapted from Moran & Porath (1980), Moran (1982) and Inskeep & Bloom (1985) by A.J. Watkins, S.J. Clarke and the author. Leaf samples collected in the field were divided into three (occasionally two or one) replicate samples for each species. For each replicate, approximately 30 mg of macerated leaf material was introduced into a glass container. The container was weighed (1 mg precision) before and after addition of the leaf sample and the difference (the weight of the sample) recorded. Containers used were 10 ml screw-top test tubes (central and southern New Zealand sites), 10 ml soil vials (Tasmania) or 20 ml soil vials (northern New Zealand, Australia and South America). Larger glass containers (capacity *c.* 50 ml) were used for a small number of samples in Argentina. The data obtained from these were inconsistent with values elsewhere and were not used. 5 ml (for some sites, 4 ml) of N,N-dimethylformamide (DMF), retrieved with a pipette, were added to the container, the container was sealed, sheathed in aluminium foil to inhibit the entry of light, and stored, refrigerated at *c.* 4°C, for a period of 3-14 days. The resultant chlorophyll solution was analysed by spectrophotometry for absorptance in 1 cm cuvettes at wavelengths 647 nm and 664.5 nm, callibrating (to 0 absorptance) with fresh DMF. Formulae for determining chlorophyll *a* and *b* concentrations from the absorptance values are given in Section 2.3.4.

For Chilean sites, chlorophyll concentrations were measured by staff of the Laboratorio

de Nutrición y Suelos Forestales, Instituto de Silvicultura, Universidad Austral de Chile.

Species physical characters

For each terminal shoot sample, all leaves were detached, counted and weighed. Mean PSU fresh weight (nearest mg) for the sample was calculated and recorded. Petioles (or functional equivalents) were treated as stem, not leaf. Fresh leaves were placed with their respective stems in folded sheets of absorbent paper or newspaper, marked with a code identifying the species, replicate number, and the number of PSUs in the sample. Multiple sheets were then placed in a plant press, interleaved with corrugated aluminium sheets or corrugated cardboard to ensure adequate ventilation, and dried. Drying was achieved over incandescent light bulbs (southern and central New Zealand sites), in a drying oven at *c.* 45°C (northern New Zealand, Tasmania and South America) or in a fan-forced oven specialised for the drying of herbarium specimens (Australia). Prior to pressing, thickness was determined for one randomly selected PSU from each terminal shoot, or more than one PSU if fewer than 10 samples had been collected, giving 10 values for most species. PSU thickness was measured with a micrometer (precision 0.01 mm), avoiding the midrib (or prominent nerves of some graminoids, e.g. *Astelia* spp.) but taking no account of other veins.

Once dry, PSUs from each sample were reweighed to determine mean PSU dry weight. Dried stems were also weighed. Replicate samples for each species were pooled and 10 PSUs were selected at random for further measurements. In the case of species for which 10 or fewer PSUs had been collected, no random selection was made and all PSUs were used. PSU length and (maximum) width were determined using a ruler (nearest mm), and area using a scanning leaf area meter (LiCor Model 3100) or, for leaves narrower then 2 mm, by counting the number of 1 × 1 mm grid squares intersected by the PSU under transparent graph paper. Area was recorded to a precision of 1 mm^2. Length was defined as the length of a straight-line between ends of the midrib, while width was the largest distance between leaf margins perpendicular to the axis along which length was measured.

PSU nitrogen and phosphorus content

To determine PSU nitrogen and phosphorus concentrations, all dried PSU samples were pooled for each species and ground finely using a rotary grinder. Ground material was processed by staff of the Forestry Department, Australian National University. A Kjeldahl extraction was carried out (Allen 1989) and total nitrogen and phosphorus content (dry weight basis) determined by auto analysis.

2.3.5 Calculation of texture variates

MAIN CALCULATIONS

Texture was evaluated in terms of the following species characters (characters for which no units are shown are dimensionless):

1. PSU area (cm^2);
2. PSU shape;
3. PSU lobation;
4. PSU thickness (mm);
5. PSU succulence;
6. PSU specific weight ($g\ cm^{-2}$);
7. PSU inclination (°);
8. Support fraction;
9. PSU nitrogen content (% dry weight);
10. PSU phosphorus content (% dry weight);
11. Total PSU chlorophyll content (% dry weight);
12. PSU chlorophyll *a/b* ratio.

Chlorophyll characters

For each replicate, PSU chlorophyll *a* (c_a) and *b* (c_b) concentrations were calculated as a percentage of leaf dry weight using the following formulae (Inskeep & Bloom 1985):

$$c_a = \frac{v.F}{f.D}(12.7\,a_{664.5} - 2.79\,a_{647}) \times 10^{-4}$$

$$c_b = \frac{v.F}{f.D}(20.7\,a_{647} - 4.62\,a_{664.5}) \times 10^{-4}$$

where f = weight of leaf sample (g);
v = volume of DMF added (ml);
a_{647} = absorptance at 647 nm;
$a_{664.5}$ = absorptance at 664.5 nm;
F = mean species PSU fresh weight (g) (see below);
D = mean species PSU dry weight (g) (see below).

From c_a and c_b, total chlorophyll c_t and chlorophyll *a/b* ratio $c_{a/b}$ could be calculated:

$$c_t = c_a + c_b$$

$$c_{a/b} = \frac{c_a}{c_b}$$

Physical characters

PSU shape (*h*) was calculated as the ratio of PSU length to width, i.e.

$$h = \frac{l}{w}$$

where l = PSU length (mm);
w = PSU width (mm).

Lobation (*b*) was determined for each replicate using the formula:

$$b = \frac{\pi . l . w}{a} \times 10^{-2}$$

where π = 3.14159... (the ratio of the circumference to the diameter of a circle);
a = PSU area (cm^2).

This formula expresses the ratio of the area of an ellipse with the same length and width as the sample PSU, to the area of the PSU itself. It will give the value 1 for a perfectly elliptical leaf, tending to give larger values for increasingly divided leaves, although undivided non-elliptical leaves may also yield values greater than 1.

PSU succulence (*u*) for each replicate was calculated as:

$$u = \frac{f}{d}$$

where f = mean PSU fresh weight (g);
d = mean PSU dry weight (g);

Support fraction (*s*) was determined for each replicate using the formula:

$$s = \frac{\sum z}{\sum d + \sum z}$$

where Σd = total dry weight of PSUs in terminal shoot (g);
Σz = total dry weight of stems in terminal shoot (g).

Species means for each character were obtained by averaging replicate values (no means had to

be calculated for PSU nitrogen or phosphorus concentrations, as only one value was obtained for each species). Prior to calculation of species means, replicate values were graphed to look for extreme values that might represent measurement or calculation errors. Where a calculation error was found, the calculation was repeated. Where a measurement error was suspected, the replicate value was discarded.

PSU specific weight (*M*) for each species was calculated as:

$$M = \frac{A}{D}$$

where A = species mean PSU area (cm^2);
D = species mean PSU dry weight (g).

TRANSFORMATIONS OF TEXTURE VARIATES

Statistical tests for skewness and kurtosis were carried out to determine whether texture variates (comprising species means for all characters from all sites) were distributed normally. A normal distribution is assumed by some parametric tests (employed in Chapter 4) and is desirable for the randomisation and bootstrap tests performed elsewhere in this study, so that test statistic values are not affected disproportionately by species with extreme character values. Tests for normality were performed with the Teddybear computer program (Wilson 1975). Variates that departed materially from a normal distribution were transformed to improve normality (Table 2.1). Only the transformed variates were used in subsequent analyses.

Table 2.1 Transformations applied to each texture variate. The expression shown gives the transformed value from a raw species character value, *x*. ln=natural logarithm; $\sin^{-1}$=arcsine.

Texture variate	Transformation expression
PSU area	$\ln x$
PSU shape	$\ln x$
PSU lobation	$\ln x$
PSU thickness	$\ln x$
PSU succulence	$\ln x$
PSU specific weight	$\ln x$
PSU inclination	$\ln x$
support fraction	$\sin^{-1} x$
PSU nitrogen content	$\sin^{-1} 0.01x$
PSU phosphorus content	$\sin^{-1} 0.01x$
total PSU chlorophyll content	$\ln x$
PSU chlorophyll *a/b* ratio	x

TREATMENT OF MISSING VALUES

Community structure is expected to arise as a result of a network of interactions, potentially among all species in a community or guild (see Chapter 1). Consequently, community structure might be reflected in the characters of all species present. Analyses seeking structure in community texture might therefore be weakened by the omission of some species from texture.

Missing species character values arose occasionally where an obscure species was found during initial survey of a quadrat, but could not be located again; where samples were damaged or became moribund due to unavoidable prolonged storage and there was no opportunity to collect replacement samples; where seedling, subcanopy/saping and/or canopy samples of canopy species were inadvertently mingled and could not be reliably distinguished *post hoc*; or where a measurement procedure yielded unreliable results.

Where missing values occurred, priority was given to revisiting the initial site, or another, similar, site, and collecting replacement samples. If collection of further samples was not possible, values for the same species from the nearest available site were used.

In rare cases, no substitute values from the same species were available. This problem arose only in respect of 10 species from sites in Chile and Argentina, for which reliable chlorophyll values could not be obtained due to unforseen laboratory problems, and for one New Zealand species (*Alepis flavida*, at ZS1 Ten Mile) for which chlorophyll solutions could not be analysed due to interference with the chlorophyll absorption peaks by other dissolved substances. To obtain estimates for total chlorophyll and chlorophyll *a/b* ratio for these species, linear models expressing these variates as combinations of the remaining 10 derived texture variates were obtained by multiple regression. All species from all sites for which there were no missing values (583 species) were used to calculate the regression models. Transformed variates were used. For each equation, a step-down procedure was performed, interatively dropping and adding terms, to find a combination including only those terms that materially influenced the mean square of the residuals (a measure of the goodness-of-fit of the regression to the observed data). This procedure results in the exclusion of parameters that do not contribute to the predictive power of the model. The resultant, `step-down,' equations are shown below (all variables transformed as in Table 2.1):

$$C_{a/b} = 0.0541H + 0.1444M - 0.2309I + 0.556S - 4.974N + 36.16P + 3.267$$

$$C_{t} = 0.3668U - 0.3126M + 1.218N - 2.6979$$

where C_t = total PSU chlorophyll content;
$C_{a/b}$ = PSU chlorophyll *a/b* ratio;
H = PSU shape;
U = PSU succulence;
M = PSU specific weight;

I = PSU inclination;
S = support fraction;
N = PSU nitrogen content;
P = PSU phosphorus content.

Fitted to the data used for the regression, the first equation has relatively poor predictive power, accounting for 29% of the variation in $C_{a/b}$. The second equation is more powerful, explaining 56% of the variation in C_t. Using these equations, values were calculated for the 11 species with missing values for total chlorophyll and chlorophyll *a/b*. Multiple regression was performed with the Genstat 5 computer program (Genstat 5 Committee 1987). All estimated or substituted species character values are indicated in the summarised texture data set, presented in Appendix A.

2.3.6 Nomenclature

Taxonomic nomenclature in this study follows Curtis (1963, 1967), Curtis & Morris (1975), Jones & Clemesha (1980) and Jarman *et al.* (1984) (Tasmania); Jones & Clemesha (1980) and Harden (1990) (Australia); Allan (1961), Moore & Edgar (1970), Brownsey *et al.* (1985) and Connor & Edgar (1987) (New Zealand); Marticorena & Quezada (1985) (Chile); and Diem (1943) and Correa (1971) (Argentina). In the case of a small number of taxa, family, genus or species designations differ between regions. In these cases, conventions adopted in New Zealand (references cited above) were observed.

2.3.7 Analyses

Analyses seeking evidence for community structure are described in Chapters 6-11. Except where otherwise acknowledged, all statistical analyses were performed using computer programs written by the author in the C++ programming language.