3 METHODS

3.1 Introduction

In order to address the objectives of the study, the experimental design required the following data collection and analysis strategies:

(i) Using plot-based sampling along transects passing from old-growth eucalypt forest to warm temperate rainforest, record the abundance of all vascular plant species. Analyse the relationship between the boundary zone floristics and those of the adjacent vegetation communities. Identify whether the trend of changing diversity and abundance of species along the vegetation gradient is consistent with the trend found for other measured factors.

(ii) Measure tree stem and crown sizes in both the boundary zone and adjacent forest communities . Use these data as a surrogate for actual biomass and identify whether the biomass trend is consistent with the trend found for other measured factors.

(iii) Measure components of the microclimate in both the boundary zone and adjacent forest communities . Identify whether the microclimate trend is consistent with the trends found for other measured factors. Calculate the relative amounts of radiation reaching the forest canopies and apply these data, where appropriate and in conjunction with other macroclimatic data, to validate microclimatic or other data.

(iv) Measure the litterfall in both the boundary zone and adjacent forest communities . Analyse the litterfall by species contribution and relate the propagule input to the evaluation of boundary zone succession. Identify whether the trends in rates and quantities of litterfall are consistent with the trends found for other measured factors.

(v) Record evidence of disturbance and the trend in the percentage of plot area unoccupied by or unavailable to plants along the transects. Identify whether the trends in these data are consistent with the trends found for other measured factors.

3.2 Sampling and data collection

3.2.1 Sampling strategy

The usual strategy for ecological sampling in order to minimise bias and maximise analytical options, is to select sites at random or systematically within a stratification (Smartt and Grainger 1977). For this study, however, the location of the transects had to be controlled insofar as they were required to pass from WSF to WTRF. Gillison and Brewer (1985) demonstrated that random transects recover significantly less of the variation in vegetation than purposefully placed transects. Aerial photographic interpretation (API) was used for the coarse identification of vegetation types. Rainforest was defined as that vegetation association which had a closed canopy layer of trees none of which were pyrophytic sclerophyllous species (*i.e.* of the genera *Eucalyptus*, *Lophostemon* or *Syncarpia*) and the presence of any such species in the association was acceptable only if they were isolated emergents.

The need to minimise bias was met to the extent that site locations were determined from the photographs and not from the field. Sampling plots were sited in the WSF, the boundary zone and in the WTRF along straight line transects through those forest types. The elevation of transects was held constant within the 500 - 600 m range. Sample plots were 50 x 20 m orientated normally to the direction of each transect. Data recording was carried out systematically for each of the 10 x 10 m units, or deciplots, within the 50 x 20 m plots allowing the plots to be optionally analysed as 0.1 ha units or as reflexed belt transects (*conceptus novum*). This type of transect is one which doubles back in parallel to itself. It has a number of advantages. From an analytical point of view it provides a measure of the homogeneity of the sample plot and from a survey point of view it confirms the required sampling density for these forest types in future surveys. I argue that, because of the subjective (resulting from API determination) relative homogeneity of the site at which each plot is located, the statistical conundrum of auto-correlation (Cliff and Ord 1981; Legendre and Troussellier 1988) is relevant regardless of whether the data were collected from separate or contiguous plots within the patch. Data collection from contiguous units is more efficient and allows a higher level of precision in the time-consuming process of quantitative data acquisition.

3.2.2 Data collection

3.2.2.1 Existing data

The pre-existing data to which reference will be made in this dissertation include meteorological records, externally supplied aerial photographs and biological data pertaining to plant phenology and the range of dimensions for certain plant parts. The background meteorological data was recorded at the meteorological station at Byron Bay. Assistance with mapping of boundary distributions was obtained from a set of Shire-wide, 1:16000 colour aerial photographs previously commissioned by Byron Shire Council in 1984. Although these photographs were at a smaller scale than desired, they served to clarify photograph edge problems experienced with the larger scale set.

From the botanical literature a biological profile was obtained for a number of the species recorded. These data included reproductive strategy, fruiting frequency, seed volumes, seed dispersal strategy, seed morphology and seed viability. Other data compiled for each species related to competitive and survival strategies which included the capacity to produce a lignotuber or expand by root or coppice suckers, and leaf morphological data such as size, orientation and colour. These data were used to investigate whether the biologies of the plants of the transition zone were significantly different to those of the WSF and the WTRF.

3.2.2.2 Remotely sensed data

Observing the advice offered by Humphreys (1961) with respect to the season of the year and time of day, colour vertical aerial photographs of the study area were commissioned. The scale of these photographs was at 1:7600 (stereo pairs are shown in Plates 2-9) which enabled not only good delineation of the main assemblages and boundary types but also identification of the crowns of a number of the main species. From these photographs and those commissioned by Byron Shire Council, in conjunction with ground truthing, the distribution of associated canopy species and understorey species was described and mapped. The descriptions of these associations are presented in Chapter 4. Ground truthing also involved collection of data in order to map possible fire patterns and fire paths from fire evidence and topography. These data were to contribute to an assessment of the postulated distribution of the vegetation boundary types at the time of the last fire.

3.2.3 Field data methodology

Webb *et al.* (1967a, 1967b), in a major analytical study of rainforest floristics, evaluated the merit of total floristics data collection. They concluded (Webb *et al.* 1967b), after a comparative analysis of the classifications produced from the full data set and from selected subsets, that the understorey was independent of the canopy such that a physiognomic classification was able to be derived from the canopy species subset alone. However, for an intensive, localised study of this nature I determined that not only should full floristic surveys be conducted but also all data should be quantitative for the transects from WSF through the transition zone to rainforest in order to (a) establish vegetation trends, (b) evaluate the applicability of the conclusion of Webb *et al.* (1967b, that the disproportionate occurrences of single-site species made rainforest floristic classificatory work unreliable) to small-scale surveys and (c) assess the down-scale correlation of rank abundance or self-similarity in plant community structure (Collins and Glenn 1990).

Within each plot the data recorded included:

- the absolute abundance of every vascular plant species and also the singular non-vascular species, *Dawsonia superba*, because of its association with disturbed soil

- for all plants exceeding 3 m height, further data recorded included growth form, height, crown cover (width), crown depth, stem inclination, basal area
- the incidence of flowering and fruiting which was always noted in order to assess the reproductive vigour of the old-growth forests
- fire evidence by recording presence and severity of fire scars on trees, burnt logs and stags, bark charring, charcoal in litter and estimations of age classes of pyrophytic flora.
- the presence and count of dead plants identified to species where possible
- ground cover type represented by the percentages of ground cover made up of leaf litter or bare ground, exposed surface rocks and fallen and decaying logs
- physical site data comprising slope, position on slope, aspect and angle to the horizon for each of the cardinal compass points.

For all transects basic attributes measured included:

- width of the transition zone
- extent (in ha, and limited to the the parts that shared a common drainage area) of the WSF and WTRF at the ends of the transect.

For a subset of transects only, additional data included:

- soil samples from each plot
- litter collection traps (4 per plot)
- microclimate monitoring sites for each plot (throughfall was measured for all 7 transects)

3.3 Software

Various software tools have been utilised to analyse the data collected during this study and numerous computer programs were written to perform the specific analyses. All programs that receive and organise raw data were written in Lahey Fortran 77 (Lahey Computer Systems 1992) or S-PLUS (StatSci 1993) and those that are mentioned in the text are described in full in Appendix II. Some software packages or stand-alone programs have been used at various times including CANOCO (Ter Braak 1988) which is best for ordinations and biplots; PATN (Belbin 1993) which is an excellent all-round pattern analysis package that incorporates all the well-known association measures; and TWINSPAN. S-PLUS is a statistical and graphics programming package which is used for most of the graphics in this thesis. S-PLUS was also used to write all the software associated with the production of GAMs developed to model both the distribution of every species recorded and also the distribution of boundary types.

Forest growth and succession in the boundary zone is modelled by a program called TREGRO which was written using a Monte Carlo procedure very closely based on JABOWA (Botkin *et al.* 1972). This is an application to which this class of model (gap replacement, boundary expansion) has not previously been subjected. A solar exposure model called SUNMAP calculates an index of the net insolation for each hectare in the study area. The amount of radiation received has, I believe, been underrated as a predictive variable for vegetation distribution. The values calculated by SUNMAP are used as an environmental variable for modelling of species and boundary distribution. The logic flow diagrams of all named original software are included in Appendix II.

3.4 Floristics survey methods

3.4.1 API and community-based data collection

API was used for a coarse identification of the canopy plant communities and their boundaries that were represented in the study area. Using three different sets of photographs, the scale of photography available ranged from 1:40000 (B&W prints, 1977) to 1:16000 (colour prints, 1984) and 1:10000 (colour slides, 1989). From the photographs the WSF was immediately separable from the WTRF by crown type and spacing. The WSF could be further divided into four main subgroups while the rainforest was clearly a mix of many species but two crown types were clearly especially common (see Plates 2 - 9 where floristic interpretations of stereo pairs of photographs are presented). The delineated subgroup formations were then identified by ground truthing.

In the process of ground truthing the API work, however, several WSF assemblages were recorded which did not abut with WTRF or if they did so it was only noted once and the connection was considered to be tenuous. These associations were separately recognised by the dominance of *Eucalyptus campanulata* above 600 m, *Acacia orites* on southern aspects above 600 m, *Eucalyptus resinifera* subsp. *hemilampra* on northern aspects above 600 m, *E. grandis-Lophostemon confertus* on the lower slopes below 500 m and the regionally uncommon *E. scias* subsp. *apoda* on rocky sites above 600 m. Dry sclerophyll forest, albeit with a well-developed understorey, occurred as *E. gummifera-E. signata* on exposed, shallow soils near escarpment edges. They were separated from WTRF by the major WSF community dominated by *E. pilularis* and, to a much lesser extent, *Syncarpia glomulifera*. Even though they were not further surveyed. and do not participate in the pattern analysis described below, the minor WSF communities nevertheless remain very interesting from a vegetation dynamics point of view. There are a number of questions to be answered about their distribution: are they the start of a new colonisation or are they the last remnants of an erstwhile wider distribution? is their physical environment unique, that is, are they occupying locations at which there is chance confluence of the components of their optimum resource niche? and, does their presence indicate an early seral stage of rainforest or another WSF type? These questions are in part answered by the modelling of canopy vegetation distribution over the study area but a complete answer awaits further study.

3.4.2 Field plot-based data collection

The transects, along which the plot sites for detailed vegetation sampling were sited, were selected on the basis of the API which identified the location of the rainforest patches and the surrounding TZF. The description of the placement and configuration of the plots was presented in section 3.2.1. The list of actual data collected is given in section 3.2.3. The data collection strategy was based on the recording of every plant, living or dead, in each plot. The recording of dead plants provided an insight to the natural population dynamics within each structural layer. Precedents for the recording of every plant had been set by European workers (see Mueller-Dombois and Ellenberg 1974) but also by Whittaker (1960). In Australia, most work on classifications, whether floristic or physiognomic, has been qualitative (i.e. using presence or absence data) such that there has not been any tradition of classification of quantitative plot data.

The plants recorded were limited to the vascular species with the single exception being the bryophyte, *Dawsonia superba*. This species is, locally, the most prominent of its order and, by sometimes attaining a height of 300 mm, it is easy to find and identify. The value of recording this species is that it grows almost exclusively on subsoils, that is, soils exposed typically by the disruption caused when trees are uprooted. The long persistence of this species provides a record of forest soil disturbance.

Field identification of rainforest trees sometimes presents virtually intractable problems. In the rainforest diversity literature, however, I found only Hubbell (1979) submitted for publication a dataset which included records of unidentified species. On occasions a tree trunk can be surrounded by mid layer vegetation to the extent that the canopy is completely obscured. At other times a tree may have a poorly developed crown which is so dominated by vine foliage that the leaves are not obtainable or even observable. In these, fortunately, rare instances in my situation, unless a determination could be made from a trunk blaze, the bole dimensions were recorded only. For the same reasons, the acquisition of quantitative data for canopy epiphytic and parasitic species and some lianes was impeded and consequently these data should be regarded as being under-represented.

At the ground layer, a number of plants were not identified either because they were insufficiently developed to attribute them to a species (determinations to genus or family levels were not regarded as adequate for pattern analysis) or else there was an inadequate amount of relevant plant parts for a confident identification to be made.

Specimens were taken for those plants for which adequate material was available for identification but for which the determination remained uncertain, and the names for these taxa were confirmed by the Queensland Herbarium staff. In total, just nine trees out of the nearly 6000 recorded and measured were not identified and an uncounted, but not significant, number of seedlings were not included among the hundreds of thousands that were identified. The collected data revealed one new plant taxon and range extensions for several others.

At each plot, any plant with height exceeding 3 m was treated as part of the tree domain and its height, basal area and crown dimensions were recorded accordingly. All other plants below 3 m were treated as representing the understorey domain. This approach was justified in several ways:

- In the WTRF, most seedlings of tree or potential tree species perish before they reach a height of 3 m. These individuals may spend up to 40 years waiting for a canopy gap to occur (A.G. Floyd pers. comm.). This means that the understorey layer has a permanent component of woody tree seedlings that will never grow taller than the shrubs or other woody plants that mature in that domain and, therefore, can be regarded as *bona fide* members of that stratum.

- Early field examination had revealed the frequent occurrence of individuals belonging to understorey genera such as *Linospadix, Cordyline, Acrotriche, Dodonaea* and *Cyathea* attaining heights well over 3 m. The inference was that these were either aged individuals which had benefited from a stability of resource and community or else they were occurring in locations which more closely approximated their optimal resource requirements. By setting the 3 m cut off for the understorey layer, the particular incidences of these tall understorey plants (which I will subsequently refer to as "understorey emergents" even though many are single-stemmed and tree-like) in the plots would be assured.

- By recording the physical dimensions of the individuals exceeding 3 m it was possible to undertake a comprehensive structural analysis of most of the forest without the "noise" of small plants dimensions.

Two species received special attention, however. The palm, *Archontophoenix cunninghamiana,* which epitomises the moist and shady environment of the rainforest, produces viable seed in such numbers that, in places, dense patches of 10 cm high seedlings of this species cover the rainforest floor to the exclusion of all other species. The number of these individuals which reach the stage of producing typical leaves is greatly reduced as is the subset of those which attain full growth. As this species is a gap-coloniser within rainforest, it was thought that recording the distribution of the incidence of this species at the seedling stage (cotyledon developed only), at the juvenile stage (typical leaves produced but stem still underdeveloped) and at the tree stage (woody stem developed) would assist with an understanding of the boundary dynamics.

Rose Maple, *Cryptocarya rigida*, unlike all of its congeners, is more common outside the rainforest and achieves its best development in and at the edges of moist sclerophyll forest where the transition to rainforest begins. The dynamics of this species were also considered potentially useful when predicting the nature of boundary floristics. Consequently, understorey layer counts made for this species were divided into size classes of <1 m, 1-2 m, and 2-3 m.

Several species including mainly *Tmesipteris ovata, Fieldia australis* and *Macroglena caudata* occur as epiphytes on the two main tree ferns of the area, *Cyathea australis* and *C. leichhardtiana.* These epiphytes occurred with irregular densities, in numbers too large to conveniently count and on a substrate which had a different distribution to that of the remaining flora. Consequently, they were recorded as present or absent for each tree fern stem.

3.4.3 Modelling species spatial distribution

3.4.3.1 Database of environmental variables

The study area was divided into a grid of 1 ha cells and a range of environmental variables was evaluated for each cell. For each cell that included a transect plot the environmental variables for that cell were able to be linked with the plant species recorded for the plot. For each cell that was located in a transition zone, the attributes of that transition were also able to be linked with the environmental variables for that cell. The collection of cell values for any particular environmental variable constituted a "surface". For each variable these surfaces were able to function as spatial predictors for both individual species and boundary types.

The availability of the predictor surfaces facilitated the use of generalised additive modelling as described in Chapter 2. GAMs were able to identify the extent to which the environmental variation explained the distribution of the species. The credibility of models predicting species distribution based on highly localised data is problematic and I noted the caution issued by Webb *et al.* (1972) to workers in such situations.

The abiotic variables available for incorporation into the predictive models were:

- angle of slope;
- slope type (see explanation Chapter 1);
- length of slope;
- position of the cell in the slope sequence (a percentage whereby 100% indicated a crest and 0% indicated the base of a slope);
- aspect (converted to a radial function of range 0 to 1 such that 355° was very similar to 5°, and 170° was very similar to 190° (unfortunately this strategy also meant that 90° modelled similarly to 270° which the radiation study (see Section 3.6.7 below) subsequently showed to be incorrect);
- amount of direct insolation before noon and after noon;
- angle to the horizon along the aspect bearing;
- angle to the horizon in the direction of the equinox sunrise;

- angle to the horizon in the direction of the equinox sunset;
- dominant forest type (if two forest types were significantly present within a cell then both types were recorded);
- probability of surface rocks;
- disturbance (described in Section 3.5.3 below and derived from fire evidence, dead plants and logs);
- size of the tract of the dominant vegetation of the cell contained in the same drainage area as the cell (if two vegetation types were significantly present within a cell then the sizes of both tracts were recorded against the cell); and
- in the event of a cell including a boundary zone then the attributes of that boundary zone were recorded for the cell.

One of the banes of logistic regression models is the presence of collinearities (or correlations) among the independent variables. The incidence of collinearity between variables is signalled by the presence of large estimated standard errors and inflated or nonsensical predictions. Avoidance of collinear variables being included in statistical models is, therefore, a highly desirable feature of the model building process. The possibility of collinearity between variables is normally dealt with by inspection of the data and removal of selected offending variables. The subsequent variable selection for species models then proceeds with access only to the remaining variables. That procedure is a satisfactory method for handling collinearity but particular models may suffer in those instances when the deleted variable would have been included in those models had it been retained in preference for the variable which was. It was, therefore, considered important to allow all variables, correlated or not, to advance to the stepwise selection process and leave it to the selection algorithm to ensure that two correlated variables were not included in any model. In this way the most appropriate variables would be included in each model. The procedure employed for evaluating collinearity involves tests which are performed in three different ways: between continuous variables; between continuous and categorical variables; and between categorical variables.

The test for collinearity between two continuous variables is a straight forward calculation of the correlation index. The test for collinearity between a continuous and a categorical variable is performed by first obtaining the total mean squares for the continuous variable and next aggregating the sum of squares of the continuous variable for each level of the categorical variable. The latter value is divided by the degrees of freedom (variable length minus number of categorical levels). The correlation is then unity minus the dividend of the last value calculated and the total mean squares.

The test for collinearity between pairs of categorical variables is obtained by using correspondence analysis. Correspondence analysis uses matrix algebra and proceeds by first scaling the rows and columns of a table, comprised of the two factor variables, by the square root of diagonal matrices derived from the row and column means. It then takes the first non-trivial solution from the singular value decomposition of the table as the correlation index. The technique used is described and illustrated by Venables and Ripley (1994, p 321).

Once having obtained the correlation indices for all combinations of variables, the program then decided which variables should be regarded as collinear. The strategy was to use a blanket threshold value of 0.6 above which pairs of variables were regarded as collinear and below which they were not. The program did, however, examine near misses and if there were some near misses that were distinctly separated from the cluster of genuinely non-correlated pairs, then those were also treated as if correlated.

3.4.3.2 Model construction

The model construction process involved a stepwise selection and rejection of variables until the optimum combination of the available variables was found. The optimum model was that model which resulted in the best fit of a GAM to the species-environment data. This process is now described in greater detail.

The selection of a close approximation to the optimum model was dealt with somewhat empirically. It was not possible to evaluate every possible model for a species but it was possible to evaluate every possible model comprised of predictors which were found to have a significant relationship to the biological data. Various provisions and tests were performed at the outset in order to find the best set of potential explanatory variables and the best form of those predictors. By "form" I mean the complexity of the permitted relationship between species data and predictor data, in terms of the degrees of freedom of a curve depicting that relationship. For GAMs, linear terms for continuous environmental variables (e.g. slope angle) were not permitted and instead the appropriate curve complexity was arrived at by selecting the degrees of freedom (df) for each term from a range of two to four. The df of a term is usefully viewed as a continuous scale for combining variable selection and smoothing parameter selection. This strategy follows Hastie and Tibshirani (1990 p259-60) who wrote that it is not enough to select which terms to include in a model, it is necessary to select how smooth they should be.

For each species the initial exploratory tests involved the evaluation of all possible univariate models. Any form of a variable which did not significantly ($p < 0.15$) reduce the null deviance was discarded permanently. The null deviance is the deviance of a model built on the distribution of the species data alone without any consideration of environmental or other variables. In general, the deviance is a measure of the closeness of fit of a model to the data from which it was derived such that the lower the deviance the better the fit (see Hastie and Tibshirani 1990 for details). If no univariate models significantly ($p < 0.15$) improved the null fit then a null model would have resulted. A null model for a species would have prevented it from being considered for the subsequent classification of species. In the event of correlation between two variables being encountered by the model building program, the variable which better reduced the null deviance proceeded to the next stage whereas the other variable took no further part in the model.

After the initial stage of evaluation of univariate models, the main forward and backward stepwise variable selection process began with a pool of independently distributed variables and each represented by a single form. The starting model was the univariate model that achieved the most significant reduction in the null deviance.

Each of the other variables was added in turn to the starting model to derive a series of bivariate models. Again, the bivariate model that achieved the most significant ($p < 0.15$) reduction in the deviance of the starting model (i.e. the univariate model) became the new interim model. A similar process produced the best trivariate model whereupon backward stepwise selection was invoked to determine whether a bivariate model comprised of the most recently added variable and either of the two already included significantly ($p < 0.20$) reduced the deviance of the trivariate model. If so, that particular bivariate model became the new interim model otherwise the trivariate model entered a new cycle where a fourth variable was tested for addition on the same basis as on previous cycles. After each new addition, backward selection was performed to explore whether it was possible to revert to a simpler model. When four variables were in the model or when no other variable significantly reduced the deviance of the interim model, further selection ceased.

Of fundamental importance was the test by which variables were added to or removed from a model. In a stepwise selection procedure developed by the author for New South Wales National Parks and Wildlife Service, variables were added if the reduction in deviance was significant at the $p < 0.05$ significance level (NSW NPWS 1994). Experimentation undertaken during this study suggested that the significance test should be less stringent and in the range of $p < 0.15$ to $p < 0.20$ without necessarily leading to over-fitting.

Hosmer and Lemeshow (1989) had previously suggested that $p < 0.15$ for addition and $p < 0.20$ for removal ought to be reliable thresholds in stepwise model building. A lot of work is currently being published in this area which generally confirms that the most suitable significance levels for logistic regression models is in the range $p < 0.15$ to $p < 0.20$. Consequently, the thresholds used by Hosmer and Lemeshow (1989) were adopted for this algorithm. The use of jackknifing for model validation revealed that over-fitting could still be avoided with this more relaxed constraint and the probability of finding the optimum model was greatly improved.

Using this procedure with the given set of environmental variables, the resulting models included variables which provided distinctive and recognisable associations for many species. The statistical validity of any particular variable was not evaluated.

These models were able to predict the association between the distribution of each species and the environmental variables available for modelling. There were insufficient data in terms of climatic variables and geographic spread of the samples to suggest whether there are any limits to the distribution of any of the vegetation associations to which the modelled species have allegiance. Similarly, the models cannot be used to indicate the likely existence of apparent concentrations of resource availability. Models which used data concerning the distribution of boundary types are, however, able to predict the association of boundaries with certain environmental variables and consequently can be used to indicate the limits to boundary type distribution.

3.4.4 Vegetation classification

3.4.4.1 Classification objectives and evaluation criteria

The prime purpose of the species modelling stage was not so much to predict the distribution of species in the study area but to use the error of the predicted distributions to demonstrate the possibilities of my CLUANVAL strategy for validating classifications of environments or sites.

The CLUANVAL algorithm developed for the classification of the vegetation data applies a stopping rule based on the 95 % confidence range for the model predictions for the occurrence of each species at the sites being classified. This rule has the advantage that, although being uniformly applied to all nodes in a putative classification, the value of the stopping parameter at each node is determined by the error associated only with that data which contribute to the construction of that node. This enables branches of the classification to be truncated at various distances from the root node. [This algorithm was developed from an idea originally mooted by Dr S. Ferrier of the New South Wales National Parks and Wildlife Service].

The application of the stopping rule was as follows. The PATN package was used to obtain an initial classification of sites. The detail of this procedure is described in the following Section. The programs within PATN leave a comprehensive trail of information files which enables a great deal of further exploration of the relationships in the data. For each dendrogram produced by PATN, the relevant available files include the the matrix of ultrametric distances, the group (or node branch) to which each class belongs and the group fusion sequence. Using the latter file, CLUANVAL tests the prediction confidence range for each species against all the sites which participated in each fusion. If for any species the range of 95% prediction confidence limits for the occurrence in sites on one side of the fusion did not overlap with the range of confidence limits for sites on the other side of the fusion, then the fusion was accepted by CLUANVAL. When a fusion was rejected as being unreliable, all its daughter fusions were automatically discarded as well. The program worked systematically down the hierarchy of fusions until all fusions had been discarded or accepted. Its findings enabled the adjustments to be made to the dendrograms as shown.

My purpose was to derive a classification which applied to that vegetation occurring along the vegetation gradient from WSF to WTRF in this study area. Separate classifications for both species and sites were produced for each vegetation stratum. Co-classified sites were expected to have general uniformity of floristic composition, species richness, species evenness and total abundance of individuals. For the classification of species, similar rules applied such that species with the same shaped distribution curve, albeit with differing amplitudes reflecting differing abundances, were expected to be co-classified. The classes had to make good ecological sense and they had to be able to be sensibly represented by a dendrogram. The classification results ultimately had to be able to contribute to the development of a theory regarding the distribution of the vegetation along the gradient.

3.4.4.2 Classification measures and mechanisms

A classification requires three main decisions. First, in what form are the data to be presented for classification; second, which technique among the family of classification techniques, will be utilised; and third, what measure of association will be applied to the data. As indicated above, this analysis is to be based on quantitative data. The range of abundances among species recorded, particularly within the understorey stratum, is very large. Consequently the abundances were transformed to a logarithmic scale. This enabled the very common species to make a strong contribution to the classification while a contribution from the rare species was still possible. This strategy is in line with the spirit, at least, of the hierarchical continuum theory.

The classification technique for sites was hierarchical, as was that for species, at least for the analysis of the species in the canopy and mid-layer. In the case of the classification of the understorey layer, the species count, at well over 200, is somewhat cumbersome for an hierarchical approach. Gauch (1982) also makes the point that there are problems associated with the communication and assimilation of the results of a hierarchical classification of a large data set. I did note that suggestions have been proposed which deal with such problems (e.g. van der Maarel *et al.* 1987). Their solution involved the clustering of sub-clusters to reduce complexity, but this approach effectively throws away specific biological relationships and compounds errors already present in the sub-clusters.

The hierarchical classifications are agglomerative because (a) the PATN program, FUSE which performs hierarchical classification, provides a file containing the group fusing sequence which is required by CLUANVAL and (b) the files are sufficiently small to balance the theoretical advantages of divisive classification. The agglomerative algorithm is polythetic, that is, all the data at each node participate in the decision to fuse or not to fuse. The non-hierarchical approach applied to the understorey stratum utilises a serial optimization of the group structure.

The choice of dissimilarity measure always requires careful consideration and there is a large literature available for consultation on this subject (e.g. Clifford and Stephenson 1975; Orlóci 1978; Faith 1983; Gower 1986; Faith *et al.* 1987). Belbin (1993) includes 17 options some of which are further optionalized. On the basis of the results of the reviews just cited, I decided to use the familiar Bray-Curtis (Bray and Curtis 1957) association measure for classification of sites because it is robust, well-tested and widely utilised. For species classification I was pleased with preliminary test results resulting from Austin and Belbin's (1982) Two-Step, which has been included as an option in PATN, in which the first step produces an asymmetric matrix (i.e. the relationship between species A and B is not assumed to be the same as between B and A) of species relationships using the Bray-Curtis measure and the second step derives a new symmetric matrix in which the similarity of any two species becomes based on the prior-evaluated similarity and differences of their responses to the other species.

To summarise, hierarchical agglomerative classifications were performed on the sites and canopy and mid-layer species using Belbin's (1993) ASO and FUSE (within PATN) and his non-hierarchical classification (ALOC) was applied to the understorey layer species.

3.5 Vegetation structure survey methods

3.5.1 Introduction

In this study, three main aspects of the structure of each forest zone were to be investigated. These were: firstly the variety in the prevalence of growth forms represented among the forest flora, secondly the variation in the arrangement in space of these forms and thirdly, the variation in the physical dimensions of the components of each form. The purpose of these three lines of investigation were to evaluate the objectives listed in the opening chapter. That is, identify and quantify any structural differences between the three forest zones; identify the variation in forest structure within the transition zone samples; and use the transitional zone structure data to assess the stability, or current dynamic, of the transitional zone in the study area.

3.5.2 Structural dimensions

The actual dimensions of the overstorey of a forest provide the clues to the nature of the forest substructure. Oke (1987) wrote that the stand architectures in the forest exert considerable influence over microclimatic processes and of central interest is the vertical variation of foliage density. As a surrogate for Oke's (1987) parameter I chose to measure the distribution of crown depths and their cross-sectional area for all plants at least 3 m high and each species was given a crown density factor rating of low, medium or high. This enabled the construction of a profile of the forest structure types, and the layers within those types, based on crown depth homogeneity.

When standing in the highly productive forests of north-east New South Wales, it is usually possible to discern a number of putative forest layers beyond the standard three-layer model. At ground level there is almost always a herb layer which is overtopped by a shrub layer. The shrub layer may be comprised of a mix of tall and low shrubs the exact make up of which may alternatively give the impression of two layers within the shrub zone or else simply a single broad shrub zone. Beyond the shrub zone it may be possible to describe an emerging tree zone comprising a mix of young canopy and mid-layer species. There is typically a well-developed mid-layer and sometimes there is a distinct sub-canopy layer comprising a different set of species to those of the canopy.

The vegetation floristics analysis in this dissertation, in terms of vertical stratification, is based on a generalised three-layer scenario (i.e. canopy, mid-layer and understorey) for all forest types in the study area. For the purposes of the floristics analysis that generalisation was apposite. For structural analysis, however, the range, definition and identification of forest layers can be pursued with a greater precision.

It was thought that an objective examination of the plant height data might support that working hypothesis which emanated from the field impressions of the existence of identifiable vegetation sub-layers in the forest. Further, it was suggested in Chapter 2, that the gross evaluation of crown structure variation in the main forest types might also lead to the identification of vegetation layers. The relevant data collected included not only the height of plants but also, where appropriate, the width and depth of the crown.

Working from crown depths might identify layers but the extent to which crowns overlap in the vertical plane may tend to confound the location of layer boundaries. Similarly, working from a list of plant heights alone does not necessarily identify layers as layer heights (particularly tree layers) tend to vary with the variation in canopy height. Terborgh's (1985) model suggests that layer heights are controlled ultimately by the canopy height and regularity. These problems were overcome by concatenating a series of 0.01 ha "snapshots" of the forest profile. It was reasoned that if sub-layers were present in the forest structure, they should be apparent in such a two-dimensional representation of the forest. The selected area of the snapshots for layer assessment was important. Clearly, if too large an area had been chosen, the plot of the sorted heights of all the plants in the sample would appear as a continuum from the lowest to the highest plant. Therefore the area needed to be small such that the variation in local canopy height and regularity are minimised.

The presence of layers and their positions was determined by recording the height of all plants for which crown details were obtained. The extent to which these plants dominated the soil-borne resources was approximated by measuring the basal area of those same plants. Localised responses were noted with the recording of degree of lean and the incidence of multi-stemming. The measured variables included three of Küchler's (1988) categories of growth form: leaf characteristics, plant height and crown coverage. The role of leaf characteristics is complex and I considered only the impact of leaf shading which was incorporated in the crown density factor.

3.5.3 Acquisition of structural data

All structural data were plot-based and were obtained at the same time as the recording of the species abundances. Structural measurements were taken only from those plants which were 3 m or more in height. The 3 m level was estimated by eye. All measurements were obtained using a Suunto clinometer, a 50 m tape measure and a diameter tape measure. For each plant, the dbh and crown width, the lean and multi-stemming (if present) were recorded directly. The presence of fire scars or residual burn marks on the bole was also noted at this time.

After a visual inspection of the shape of the crown, a line approximating the average width was selected and the distance between the vertical projections of the extremities of that line was recorded as crown width. A ground position was then selected from where the top and bottom of the crown were both visible. In a number of instances in WTRF clear views of the crown were not possible. In these instances the crown location could be inferred from the characteristics of adjacent crowns. When the extremities of the crown were located, the angle from the observer to these points was read from the clinometer. Depending of the observer's situation three different sets of readings were taken. In the simplest case, if these readings were taken on flat ground, then the horizontal distance from the observer's eye to the tree was recorded. If, as was more often the case, the observer was on sloping ground, the distance from the observer's eye to the base of the tree was recorded and the clinometer provided the angle between that line and the horizontal. A third possibility occurred when the base of the tree was not in view the distance was measured to the lowest part that was in view and the distance from that point on the trunk to the ground was measured separately.

The height and basal diameter of all dead trees were also measured. There will be no attempt to analyse the dead trees or dead shrubs by species because, although the field notation did ascribe a species name to many of them, in a significant number of cases the identification was uncertain. Therefore dead trees and shrubs will be treated as two aggregated entities. The site physical data recorded which pertained to the current structure included the amount of litter exposed (i.e. ground not occupied by the understorey) and the amount of ground occupied by fallen logs.

In order to incorporate a disturbance factor into the structural models specific data pertinent to disturbance were collected. For each sample unit, the abundances of fallen logs and standing dead plants were recorded and any evidence of fires having occurred in the life of the current vegetation which might have contributed to boundary maintenance or movement was also noted.

3.5.4 Organisation of structural data

The organisation of the structural data was performed at the time of data entry to the database. For each tree, height and crown depth were calculated as soon as the field data for that individual were entered. In the field data sheets, a code was recorded against each tree to indicate which of the three possible measurement situations described in Section 4.2.1 had been encountered. At the time of data entry that field code was then used to determine which of the set of equations below was applied to the recorded measurements.

(i) For level ground:

$$\text{tree height} = d \tan a + r$$
$$\text{crown depth} = d (\tan a - \tan b)$$

(ii) For sloping ground (tree base visible):

$$\text{tree height} = d \tan a \cos q - d \sin q$$
$$\text{crown depth} = d \cos q (\tan a - \tan b)$$

(iii) For sloping ground (tree base not visible):

$$\text{tree height} = e + d \tan a \cos q - d \sin q$$
$$\text{crown depth} = d \cos q (\tan a - \tan b)$$

where a = angle from eye to top of tree
b = angle from eye to base of crown (may be negative)
d = (i) horizontal. distance from eye to tree
(ii) distance from eye to base of tree
(iii) distance from eye to lowest part of tree
e = distance from lowest visible point to base of tree

q = (ii) angle from eye to base of tree (may be negative)
(iii) angle from eye to lowest part of tree (may be negative)
r = distance from eye to ground

Packing density was recorded for each 100 m^2 area within each plot. The average and the predicted range (95%) of stems and basal area (m^2 ha^{-1}) for each species and for each formation were calculated at the conclusion of the data entry procedure. For the calculation of the crown packing arrangements, an assumption was made for all species that the measured crown width (the average maximum width) was expressed by a horizontal plane located at the vertical centre of the crown and an ellipse function was used to model the crown taper above and below the centre plane. This meant that for the purposes of calculating crown packing, crown overlap was not permitted at the plane but was enabled above and below the plane.

In the understorey layer, some species occasionally occurred in great profusion such that it was impractical to count the individuals. In this situation the area occupied was measured in m^2 and an area/species conversion factor applied to the areal figure. The species concerned and their conversion factors are shown in Table 4.12.

3.6 Microclimate data collection methods

3.6.1 Introduction

The purpose of the microclimate measurements conducted in this study was to evaluate the notion that not only do microclimates vary from the open forest through the transition zone forest to the closed forest, but that this variation represents a gradient and this gradient exists in both monthly and seasonal (and by inference, daily) time scales. The shape of this gradient influences the subsequent discussions where I examine the presumed distribution of species along this microclimate gradient (Chauvin 1967). Of the critical microclimate components, the two measured were air temperature and humidity as these two were considered most likely to provide rewarding insights to the vegetation gradient. These components were monitored and analyzed against background intensity and periodicity data for rainfall, cloud cover and wind. Both of these factors reach their maxima near the ground (but not *at* the ground). This is because of the high proportion of the remnant incident solar energy is absorbed at ground level causing the temperature to rise and in the forest a large amount of heat energy is exchanged close to the ground in the humidity-raising processes of condensation, transpiration and evaporation.

3.6.2 Temperature

Ideally, temperature in the forest microclimate should be recorded as a profile from above the canopy to ground level. There are three broad zones of temperature change along this profile. These zones are (i) from above the canopy to within the canopy, (ii) from within the canopy to below the canopy and (iii) from below the canopy to the ground. It was not feasible to measure the upper two zones and it was decided that the temperature range in the lower zone could be approximated by measuring at ground level and at 1.5 m. The temperature gradient of this lower zone from wet sclerophyll forest to warm temperate rainforest was then measured from three points of view. Maximum-minimum thermometers were positioned at ground level (at the surface of the litter layer) and at 1.5 m above the ground and a hygrothermograph, which was used to record the pattern of temperature change, was placed next to the ground level thermometer but under a protective shelter (Plate 16). Since it is known that microclimate varies with position with respect to any openings in the forest (Lee 1978; Turton 1991), care was taken to ensure that when locating all equipment at the centre of each plot that the vegetation was representative of the surrounding forest.

The thermometers were designed such that their sensors were protected from direct sunlight. This feature is important because thermometers have relatively large sensors which themselves absorb solar radiation thereby affecting the temperature of the space being measured (Unwin 1978). The effect of direct and indirect radiation is the main source of error with mercury thermometers. If the incoming radiation exceeds the outgoing radiation (as is generally the case during the day), the sensor will be above air temperature. The reverse situation occurs during the night. This source of error is reduced by shielding the sensors from exogenous radiation but in such a way that allowed air movement past the sensors (Unwin 1980).

In order for precise readings to be made with confidence it was necessary for the thermometers to be accurate. They were therefore calibrated in the laboratory before the experiment began. Calibration was achieved by placing each thermometer next to one that had been found to match the output of a laboratory temperature data logger. Any differences were noted on a diurnal hourly basis for three days. This period was required to confirm whether consistent variations between the thermometers existed. The field readings were subsequently adjusted by the amount of these recorded variances.

The high-level thermometers were initially fixed to wooden stakes but it was soon noticed that forest birds, particularly yellow robins *Eopsaltria australis* , used these stakes for perches during feeding forays and the force of their landing impact shook the posts and thermometers such that the maximum and minimum markers were dislodged. The thermometers were subsequently repositioned by fitting them to the trunks of trees. They were still used as supports by some birds such as the white-throated tree-creeper *Cormobates leucophaea* but the markers were not affected. Early readings suggested that despite the shielding around the sensors they might still be reacting to sunflecks. The thermometers were then repositioned to ensure that sunfleck activity was not a factor for consideration. These various adjustments shortened the period of reliable data. The consequence was that maximum and minimum temperatures were recorded weekly for 20 months which incorporated two summers and two winters.

Temperature data were also provided for each zone by the hygrothermographs. The sensors for the units were at a height of 75 mm above ground level such that different results were anticipated to the thermometer sensors set at ground level (Unwin 1978). The advantages of the hygrothermograms vis-a-vis the thermometers was

Plate 16. A hygrothermograph in recording position under its protective shelter

that they provided (a) a continuous record of temperature fluctuation; (b) showed the extent to which the extremes of temperatures for each zone were not synchronized; and (c) the lag of extremes behind the times of solar extremes. From the hygrothermograms not only were periodic minima and maxima available but I could also calculate a much more accurate average temperature relationship between the separate zones.

3.6.3 Humidity

Humidity was regarded as a useful measure of the extent to which the canopy was closed to external drying effects. Two Izuzu electronic Thermo-hygrographs and one Micromech mechanical Hygrothermograph were placed on bare ground as close as possible to the centre of the ecotone and each of the adjacent vegetation patches on the transect. A small shelter was erected above each unit to protect it from direct sunshine, rain, hail and falling branches (Plate 16).

Hygrothermographs are not generally regarded as being accurate to more than about 5% (according to MacHattie (1958) average error for a well-adjusted unit is ±3.5% for relative humidity) even provided an allowance is made for the effect of temperature. When calibrated correctly at 15°C they will read 10% low at 38°C and 10% high at -6°C (Unwin 1980). Accordingly, the units were carefully calibrated against an electronic data logger for both accuracy and sensitivity before being taken to the field sites.

The hygrothermographs were read on a weekly basis but as the two battery-powered units could run on an optional 31-day cycle, it was sometimes necessary to take advantage of that feature. In those instances, data from the mechanical unit, which could only run for 10 days, and which was positioned in the transitional zone plot, were lost. The extent to which data were lost is discernable from the gaps in the graphs comprising Fig. 2.16. Each hygrothermograph was removed for retesting once during the recording period. Reliable data were recorded for 16 months.

3.6.4 Rainfall

In North Queensland high annual average rainfall levels have been shown by Ash (1988) to allow rainforest to prosper on soils that would otherwise be nutritionally inadequate. Young and McDonald (1987) have noted that rainforest rarely persists in southern Queensland where rainfall is below 800 mm. Similarly, Floyd (1989) describes the low rainfall limit for dry rainforest in northern New South Wales as 600 mm. There appears to be, therefore, an annual rainfall threshold below which, no matter how fertile the soil, rainforest will not occur. Rainfall, therefore, has a bearing on the distribution of the rainforest in the region.

Significant and consistent rainfall variation across the gradient (if it occurred at all) was regarded as being too small to be measured by the equipment used, especially as the transects along the gradients rarely exceeded 200 m. Any confidence in such a variation, if found, would have been undermined by the innate problems of accurately recording rainfall in forest conditions. It was therefore decided that, for any one transect, only one gauge would be used to record the throughflow (direct fall and leaf drip). Notwithstanding that only one gauge was used for each transect, some comparisons might still be made concerning the amount of interception (that amount of rainfall retained on plant surfaces and subsequently evaporated) and stemflow for closed forest as opposed to open forest and the transition zone forest on the basis of the tree species present, their density and the characteristics and dimensions of the tree crowns.

Each gauge was comprised of a 250 mm capacity plastic beaker containing a 25 mm capacity graduated flask. Rainfall is intercepted by a funnel which directs the water to the graduated flask from which it overflows to the beaker. The funnels in these gauges are, unfortunately, inclined to be dislodged during heavy rain. This is because it is sometimes easier for the air being displaced from the beaker to lift the funnel than it is to force a way through the water entering from the flask. This problem was overcome by drilling a hole through the side of the beaker just below the funnel. I noted that a number of other ancillary techniques have been employed to maximise accuracy of rain gauges such as the addition of paraffin to prevent evaporation (Lamb 1985), nylon wool placed in the mouth to prevent litter ingress (Kimmins 1973) or chloroform added to prevent algal colonisation (Likens *et al.* 1967) but none of these were employed in this study.

The gauges were all deliberately positioned on the edge of the TZF plot toward the WSF where the throughfall was expected to be intermediate between that for the WSF canopy and the WTRF canopy. By this method, the rain data would most closely represent the average throughfall for the transect. I noted that Lee (1978), reported that rainfall in forest openings tends to exceed the "true" amount but I nevertheless placed my gauges clear of overhanging understorey plants.

The gauges were mounted on wooden stakes at about 1.5 m above the ground with the top of the funnel horizontal (Plate 17). A seventh gauge was set up outside the forest in an area of no trees which provided a guide to the proportion of the rainfall which could be attributed to interception and stemflow. The gauges were read on a variable timetable. Because of their design, these gauges have minimal losses from evaporation such that during the dry season they were emptied monthly. At other times the gauges were read whenever the amount of rainfall was such that they were in danger of overflowing before the end of the month. The gauges were routinely read whenever the sites were visited regardless of the time of the month.

3.6.5 Wind

Wind makes an important general contribution to the structure of the old-growth forest. Canopy height on ridges and exposed spurs is reduced sometimes by up to half the optimum height for that particular species mix. Wind also effects foliar morphology by reducing leaf size and in some cases increasing scleromorphy. Jones (1983) attributes these consequences to the impact wind has on a plant's water status resulting from an increased evaporation rate associated with exposure to wind. Wind also causes the shaking and sometimes felling of dead branches and old trees.

Wind data were sought to provide background insights to the

Plate 17. Typical positioning of rain gauge at the edge of the transition zone plot. Plot boundary marking tape can be seen in the foreground.

environmental conditions which had prevailed during the period of both litterfall and rainfall data collection. These insights were taken into account when calculating the litterfall rates within the respective vegetation zones and for particular species. Higher wind speeds also reduced the throughfall and lead to underestimates of the rainfall. These data, therefore, were only acquired for the 14 months of validated litter collection. The data were supplied by the Bureau of Meteorology as recorded by its station at Byron Bay. At that station, the lighthouse, recordings of wind velocity (in knots) and direction were taken every 3 hours, except for midnight. As the study area is just 27 km from, and in direct line of sight of the lighthouse, the data have credibility, although the light breezes recorded at the station would have no relevance for the forest. The main prevailing winds at the station, however, can reasonably be expected to have also occurred at the study area. The program WINDIN (Appendix II) was used to organise the wind data.

3.6.6 Cloud cover

Cloud cover data from the Byron Bay station were also supplied by the Bureau of Meteorology. These data were also recorded every three hours. For the purposes of evaluating cloud cover in terms of its impact on sunlight and temperature, only the diurnal readings were of interest. The cloud cover had been scored from zero (sky completely free of cloud) to 8 (100% cloud cover) and the zone of observance was from horizon to horizon.

For these data to be applicable, it was necessary to adjust the data from the horizon to horizon form to an estimation of the cloud in the vicinity of the study area. To do this some assumptions and approximations were made. Firstly, it was assumed that the cloud cover for the period of study was not significantly atypical for the recording station. This assumption seems reasonable as Hoyt (1978) found that, for the United States, annual cloud cover variation amounted to just 4%. Secondly, a preliminary assumption was made that the cloud cover was evenly spread across the dome of observation. However, from personal observations the amount of cloud over the mountainous region greatly exceeds that over open country. From the view of the recording station (see Fig. 1.1), only 25% of the horizon is occupied by mountainous terrain while the remainder is comprised of undulating low country (25%) and the Pacific Ocean (50%). Therefore, for the purposes of modelling solar radiation levels for the mountainous area, the adjustment to the cloud scales for the general region was as follows:

given values:	0	1	2	3	4	5	6	7	8
adjusted values:	0	1	2	4	6	7	7	8	8

3.6.7 Radiation

Very little attention has been given to the potential impact of insolation differences within an ecosystem on the distribution of plant assemblages and the nature of their boundaries. Lee and Sypolt (1974) noted that in the classification of forest site potential there have been three general assumptions :

1. that sun-facing slopes are drier,
2. that soil moisture deficits limit growth on those sites and
3. that certain species are better adapted to compete on these sites.

Their findings indicated that characteristic growth differences that occur with aspect appear to be attributable to certain radiation and thermal regimes that directly affect the physiological processes of trees. Consequently, they argue that thermally induced plant water stress magnitudes are the best way to delineate sites - not whether they are moist or wet.

In order to model the impact of solar radiation on the distribution of the two main vegetation types and the variation in the nature of the boundaries, a typical geographic information system (GIS) for the area was established. The level of precision for the system required that the study area be divided into 600 x 1 ha cells and to each cell was ascribed the average slope, aspect, latitude, longitude, and horizon angles at the position of sunrise and sunset for mid-winter and mid-summer. Layers for other variables were also included in the GIS to be used subsequently for the modelling and prediction of the distribution of boundary types.

The computer program, SUNMAP (Appendix II), was written to evaluate the hours of sunlight per year that each cell received. SUNMAP calculates this value for each cell for each day and adjusts the value by the amount of cloud cover, by the nature of the horizon as viewed from that cell and by the approximation of diffuse radiation. SUNMAP utilises the formulae of Spencer (1971), Bugler (1975) and Muhammad (1983). It reads the GIS containing the topographical and locational data as well as a file containing the cloud data for the study area and systematically calculates the annual insolation for each cell in the landscape. The calculated radiation values were returned to the GIS for later application of statistical analysis of the affinities of the boundary types.

Other computer programs have been written to achieve similar results (e.g. Nunez 1980; Doley 1982; Nikolov and Zeller 1992) but they all either rely on approximations made to simplify the algorithm or else they do not take into account one of more critical factors such as surrounding horizon, diffuse radiation or cloud behaviour. Nor have such models been extended by the inclusion of canopy and wind characteristics such that they could predict the type and amounts of radiation actually reaching the understorey.

When two cells receive the same amount of direct or indirect radiation this does not necessarily mean that similar vegetation will be likely. The impact of radiation is asymmetric in that the radiative heat received in the morning is mainly used to dry soil and plant surfaces and it is not until the afternoon that most of it is used for heating the soil. Given this variation in soil temperature it should be reasonable to assume that different vegetations are likely to be supported by eastern and western aspects. The results of SUNMAP will be reviewed in terms of this proposition.

3.7 Litterfall data methods

3.7.1 Data collection

The objective of the litterfall investigation was to measure the input of litter, including propagules, by species and across the range of forest types. The first outcome was to establish whether the different floristics and growth structure of the transition zone, as identified by the data analysis results in Chapter 4, correlate with a differing litterfall regime in the transition forest. The second outcome was to establish if there *is* a significantly different rate of litterfall in the transition zone, whether it can be said that the characteristics of the litterfall have an impact on the nature of the transition zone.

All the papers referred to in Chapter 2 which reported results of litterfall studies, also described the type or range of equipment used. A wide range of equipment is described therein. The design used for the litterfall traps in this experiment is in the same class as those used by a high proportion of other investigators. Each trap was based on a circular metal frame of doubled 8 gauge wire (approx. 6.4 mm) enclosing a space of 1 m^2. A conical net of 75% shademesh (the 25% was comprised of mesh holes about 2 x 0.5 mm) was attached to a canvas hem around its perimeter and the circular frame was fed into the hem. The base of the net was left unstitched leaving a hole of about 250 mm in diameter. When the trap was in position the hole was folded and clamped to prevent the loss of any material and when the time came to empty the trap, the clamps were removed, the fold was opened, and the contents of the net were dropped through the exposed hole into a plastic bag which was then immediately sealed, labelled, dated and packed with the other trap collections into backpacks. Each trap frame was permanently supported by three sufficiently stout timber stakes such the traps were capable of withstanding everything except a falling tree or very large limb. The traps stood about 500 mm above ground level at the centre of the trap but as the frames were horizontal, on very steep sites the height was set such that the upslope side of the frame was never closer than 200 mm to the ground. This restriction was necessary to limit the likelihood of any litter thrown up during upslope foraging activities of lyrebirds *Menura albertii* and scrub turkeys

Alectura lathami actually landing in the trap. These birds are vigorous foragers and their scratchings can easily propel litter a metre or more. The trap height and shape were designed to ensure that trapped litter could not blow out and to prevent or discourage entry by the variety of large forest fauna in the study area. The traps were robust enough to withstand the weight of a possum or large forest bird without temporary or permanent distortion. Because of the rugged terrain and forest fauna it was impossible to implement Birk's (1979) recommendation that the traps be placed directly on the ground.

The traps were placed on two transects with four traps placed in each of the WSF, TZF and WTRF formations resulting in 24 traps overall, equivalent to a density of 40 traps per ha. Various authors have recommended a range of trap densities, but, as Richards and Charley (1977) point out, the selected density should depend on the variance of the litter components of interest. From their experience, leaf litter is far more variable than branch litter and hence requires a greater trap density. Originally, the traps were planned to be randomly placed in permanent positions within each vegetation plot. Some other workers (e.g. Attiwill *et al.* 1978; Turnbull and Madden 1986) employed Wilm's (1946) technique of randomly relocating some of the traps after each collection but none found any statistical advantage in this approach. The strategy was that the positions for each trap within any plot were exactly calculated by dividing the plot into 1000 x 1 m^2 units and a random number generator was then used to allocate four trap sites within the 1000 units. When the traps were placed in this way, more than half were either clumped, situated under sheltering shrubs such as low tree ferns or right at the base of a large tree such that it was obvious that the overall results were going to be distorted. To return to the random number generator seemed too much like orchestrating the results so I decided to place the traps on a grid pattern such that they were evenly spaced across each plot (a strategy for which Orlóci (1978) provides justification).

In the event of material straddling the trap (e.g. a tree branch, treefern frond or palm frond) the overhanging components of the material were sawn off *in situ* and the collectable section broken into easily transportable pieces. All material which fell into or onto a litter trap was collected for subsequent classification regardless of its size. The traps were in place for fourteen months and were not dislodged by large falling limbs and apparently not misshapen, displaced or otherwise disturbed by forest animals. Consequently, the results have a high level of reliability. The only litter components about which there is any uncertainty with respect to the results are seeds and fruits. The forest ground-foraging eastern whipbird *Psophodes olivaceus* was twice flushed from inside a trap suggesting that (although this species is not a frugivore) occasionally some small fruits may have been removed by forest birds. The possibility of small seed removal by ants was accepted but never observed. The design of the traps enabled efficient air drying such that there was never any evidence of actual rotting of litter. Further, the shape of the traps allowed the copious leaf fall to act as a further filter against loss of the very fine material.

3.7.2 Data processing

The traps were emptied on the same date each month but occasionally poor weather conditions caused a delay of one or two days. This variability was overcome by deriving an average daily catch for the period and extrapolating that to a monthly figure on the basis of 30.4 days to the month. Annual accession values were then obtain by summing the monthly values. A similar approach was used by Birk (1979). Litter was collected from the 24 traps for a period of fourteen months from October 1990 to November 1991.

Of the fourteen months' data, the first two months were used to develop sorting skills and obtain familiarity with the range of species represented and thus the number of categories that were to be anticipated from the subsequent twelve month survey period. The development of identification skills of dry leaves and seeds was important particularly for separating those species for which the dry-condition colour were very similar. Fast leaf sorting is made much easier if identification can be made on colour alone. The main purpose of the learning stage was to ensure that all subsequent material sorting was correct. One consequence of the learning period was the discovery that mistletoes may have been under-represented in the plot-based species counts. That is, mistletoe leaves were collected in plots for which the species had not been observed. Counting small mistletoes had presented similar problems to those already described for small epiphytes. It was not possible to make any adjustment, however, to the mistletoe species abundance data used in the analyses of Chapter 4.

The litter samples were occasionally collected in a wet condition in which case they were carefully air-dried prior to sorting. The contents of each trap were sorted into the five classes of leaves and leaf parts (including petioles), woody parts (which included branch wood, twigs and bark), fruits, flowers and comminuted residue (which included minute leaf parts, minute woody pieces, insect frass and insect parts, possum faeces, pollen grains and dust). Green leaves and green leaf parts were not distinguished from dead leaf material. In order to study the litter variation in the transition zone, it was essential to examine the contribution to the litter made not only by the overstorey and understorey but also by the species which had affinities with any of the three forest types. Consequently, all leaves, flowers and fruits were separated into species groups while an extra leaf group was allocated for "miscellaneous species" which included instances where a species was represented by just one or two leaves or else when there was insufficient leaf material to be sure of a determination.

Although initially attempted, it became impractical to try to identify the species of all woody pieces. Also, the adult leaves and leaf parts of *Eucalyptus pilularis* and *E. campanulata* were too similar in the dead state to allow instant determination such that it was necessary to aggregate the data for these species, about 90% of which would have been attributable to *E. pilularis*. Consequently, the fruit capsules of these two species, although identifiable, were also aggregated. In another instance, an assistant sorter found considerable difficulty with rapid separation of the leaves of *Daviesia arborea* and *Acacia orites* such that where they co-occurred (at four traps) the leaf data for these two species have been combined.

After sorting, each collection was dried in a forced draught oven at 68°C for three days (larger woody parts were left for up to two weeks at this temperature) after which they were immediately weighed in grams to one decimal point. All weights presented in the results are therefore referring to dry weight. Sorting was undertaken prior to drying because, once dried, the leaves become quite crisp and are easily broken up with handling. I noted that some other researchers (e.g. McColl 1966; Lowman 1988; Thomas *et al.* 1992) chose to dry their litter before sorting. I cannot recommend this sequence of procedure, not only because of likely damage to the material but the delay due to the sorting process allows the dried material to take up moisture before weighing.

3.8 TREGRO - a model of boundary canopy floristics

One of the outcomes intended from the intensive study of the floristics and structure of the transition zone was the possibility of modelling these two aspects of vegetation survey. Accordingly, I derived my own version, called TREGRO, of the earlier version of the widely-applied Monte Carlo forest simulator called JABOWA (Botkin *et al.* 1972; JABOWA II is specified in Botkin 1993). TREGRO delivered predictions for growth and change of floristics mix in a nominated forest using a range of input data which describes the forest environment and the attributes of the key species. TREGRO was employed to characterise the nature of the competition at the edge of the eucalypt forest by investigating the floristic stability of the boundary canopy community. The task of the simulation in this study was to model longterm change in the canopy of the transition zone in the continued absence of environmental perturbation.

TREGRO embodies a number of assumptions which both enhance and detract from the reliability of the output. It assumes that each species has an optimal growth curve which is derived from expected maximum age and size; growth rate is proportional to that part of photosynthate production which contributes to manufacture of vegetative tissue; growth rate is reduced by sub-optimal conditions of light, temperature, water and soil conditions; each species has certain intrinsic life history characteristics such that it can be assigned to a seral class; tree species ultimately compete for light and their respective capacity to do so allows them to be placed in separate tolerance classes; trees must keep growing to survive; and climatic extremes have a greater impact on forest processes than mean climatic conditions. The establishment, growth and death of each tree is controlled by both deterministic, intrinsic stand variables (e.g. shading and crowding) and stochastic environmental variables (e.g. temperature and moisture conditions). A full description of the model strategy is provided by Botkin (1993).

For the purposes of simulating the future dynamics of the transition zone canopy, the thirteen most common, or ecologically significant, species which were recorded in the canopy and mid-layer strata were selected. The model required essential life history data for these species and the sources used were Boland *et al.* (1984) and Floyd (1989). Local climatic variables including rainfall, temperature and insolation were those obtained during this study. The range of equations for calculation of growth, climatic and environmental conditions are from Botkin *et al.* (1972) or references therein.

3.9 Modelling boundary-environment associations

As explained earlier, the study area was divided into a grid of 1 ha cells. For each cell, a range of environmental data was either available or calculable. These variables were then used to contribute to the development of predictive models for boundary distribution. Of interest was whether the diffuse boundaries were located in different environments from the sharply defined boundaries hence indicating that boundary type is a response to the environmental variation more than perhaps it is to historical factors. The procedure was to develop a Generalized Additive Model, as had been previously done for the vegetation, for each boundary type.

The set of variables available for each cell have been listed in Section 3.4.3.1 above.

The remaining variables were subjected to a forward and backward stepwise selection procedure (Chambers and Hastie 1992) in which each combination of variables using alternative smoothing settings was evaluated according to whether it significantly reduced the model deviance. The procedure was the same as that described for species models in Section 3.4.3.2 above.