# 4 RESULTS

## 4.1 Plot-based floristics survey

### 4.1.1 Overview

The study area contained 248 vascular plant species belonging to 79 families identified in the plot-based survey while numerous others were noted in plant assemblages not surveyed. No analysis was undertaken on the extent to which the variation found in the distribution of species was also manifest in the pattern of family representation in the different environments but the work of Elsol and Clifford (1988) suggests that corresponding patterns would be likely.

The taxa were distributed across the vegetation types in a remarkably equitable fashion. The WSF samples recorded 215 species, the TZF samples recorded 238, and the WTRF samples (10 fewer than for the other two assemblages) resulted in 220 species recorded.

The diversity of each group was calculated using the Shannon-Weiner index and the bias inherent in this index (Magurran 1988) was eliminated by the use of the jackknife validation technique. The application of the jackknife for this purpose has been described by Adams and McClune (1979) and Heltshe and Forrester (1985). Confidence intervals were derived from the jackknifed pseudo diversity index values and, using the calculated variance in diversity for each forest type, a t-test allowed the diversities of each pair of forest types to be compared. All three formations were found to be highly significantly different from each other ($p < .001$) in terms of total floristic diversity. The summary diversity statistics are shown in Table 4.1.

### 4.1.2 Canopy patterns

#### 4.1.2.1 Wet sclerophyll forests

The canopy of wet sclerophyll forest can vary from being virtually continuous to one where a well-developed mid layer separates the

Table 4.1   Summary of diversity statistics for each vegetation type.   Data obtained from 7 transects and the species richness count is the accumulated total for all transects.

| Forest type | Samples | Species richness | Shannon index | Jackknifed index | 95% conf. |
|---|---|---|---|---|---|
| WSF | 70 | 215 | 2.10 | 2.11 | ± 0.26 |
| TZF | 70 | 238 | 2.12 | 2.13 | ± 0.32 |
| WTRF | 60 | 220 | 2.55 | 2.55 | ± 0.51 |

crowns of the canopy layer trees.   The canopies In the transects surveyed were essentially continuous and comprised of even-aged individuals of *E. pilularis*.   There was a minor component of younger individuals and other species.   The canopy individuals were, however, sufficiently distant from each other to allow prominent crown development, often up to 20 m in diameter (see Plate 2 where the WSF canopy is identified and individual crowns, hence packing density, are apparent).

A description of the canopy cannot be discussed without consideration of the structure of the vegetation.   Consequently, while these structural data will be presented and analysed in detail later in this Chapter some use will be made of them here.

A definition of the vertical depth of the canopy could not be presented in terms of height in metres as the canopy height varied depending on the situation.   At crests and along prominent ridge spurs canopy height tended not to exceed 35 m while at sheltered and, presumably, optimum sites canopies in WSF averaged 45 m with some individual trees exceeding 60 m.   The depth of the canopy and the height of the boundary between the mid-layer and the canopy also varied with these environmental factors.   The location of the canopy-mid-layer boundary was also confounded by the frequent incidence of emergents from the mid-layer.

The species comprising the canopy layer in WSF in the transects were *Eucalyptus pilularis* (the dominant tree), *E. campanulata* and *Syncarpia glomulifera*. Standing dead trees, known as stags, were present in most plots. A few species were present as minor components of the canopy and included *E. microcorys*, *E. gummifera* and *Acacia orites*. The mid-layer species, *Allocasuarina torulosa*, was often present in the lower portion of the canopy but in my view these individuals constituted mid-layer emergents because (a) they were atypical in that they represented much less than 1% of the total count for the trees of this species and (b) when this species does become the top canopy (in the event of treefall of the overstorey) it shows no capacity to secure this position from the competition of other species.

In order to identify the members of the canopy at each WSF plot, it was necessary to devise an objective technique to be applied to individuals based on their heights. The criteria developed were that canopy trees included any tree over 25 m high and which was a viable member of the canopy layer. As the recording of plants was conducted in 10 x 10 m units within each plot, a maximum of three trees within each recording unit could be regarded as canopy trees. This formula, therefore, excluded dead trees as well as *A. torulosa* and smaller specimens of some eucalypts.

Table 4.2 contains the results of this canopy qualification procedure. The interesting feature of these data is significant local displacement of *E. pilularis* by a group of species on transect 3; *S. glomulifera* on transect 4; and *E. campanulata* on transect 6. The index of dispersion (variance/mean) should be close to 1 for true random distribution and close to 7 for a maximally clumped distribution. At almost 2, the index suggests that, despite the API impression of this species comprising a virtually continuous canopy in the WSF, it has a slightly clumped, or variable, distribution.

4.1.2.2    Warm temperate rainforests

The canopy of the WTRF typically is much more even than the WSF (or other rainforest formations in the region) while not attaining the same

Table 4.2    Count of canopy individuals for each transect through WSF.  The species in parentheses are either regarded as lower layer emergents or were dead.  When relative variance >1, the species is tending to be clumped or underdispersed and when relative variance <1, the species is tending to be overdispersed.  For each transect, data were obtained from 10 deciplots.

| Species | Tran 1 | Tran 2 | Tran 3 | Tran 4 | Tran 5 | Tran 6 | Tran 7 | Mean | Var. |
|---|---|---|---|---|---|---|---|---|---|
| *Acacia orites* | - | - | 1 | - | - | - | - | 0.14 | 0.14 |
| (*Allocasuarina torulosa* ) | - | 2 | 2 | 5 | 3 | 1 | 3 | 2.29 | 2.57 |
| *Eucalyptus campanulata* | - | - | - | - | - | 3 | 3 | 0.86 | 2.14 |
| *Eucalyptus gummifera* | - | - | - | 1 | - | - | - | 0.14 | 0.14 |
| *Eucalyptus microcorys* | - | - | 1 | - | - | - | - | 0.14 | 0.14 |
| *Eucalyptus pilularis* | 11 | 9 | 3 | 3 | 5 | 2 | 7 | 5.72 | 11.57 |
| *Schizomeria ovata* | - | - | - | 1 | - | - | - | 0.14 | 0.14 |
| *Syncarpia glomulifera* | - | 1 | 4 | 6 | - | - | 3 | 1.72 | 5.67 |
| (Stags | 1 | 1 | 2 | - | - | 1 | -) | | |

height.  The incidence of emergents is low as is the incidence of canopy openings.  The canopy foliage occasionally includes a liane, although these can be considered as mid-layer emergents as the lianes of the WTRF typically do not form large woody stems and are generally restricted to the mid-layer.  In this study area the canopy ranged from 20 m to 35 m and only a single tree was recorded as exceeding 40 m. The rule for the identification of canopy individuals in WTRF was similar to that applied to the WSF data.  Trees were regarded as comprising the canopy if they exceeded a height of approximately 20 m and were viable member of the canopy layer.

For all transects a total of 25 canopy tree species was recorded.  This does not include 3 individual trees (2 on transect 5 and 1 on transect 6) which were not identified.  As in WSF, of the trees which formed the canopy, there was a number which I regarded as mid-layer emergents. These species included *Helicia ferruginea*, *Daphnandra tenuipes*, *Callicoma serratifolia* and *Neolitsea dealbata*.  The dominant species were *Ceratopetalum apetalum* and *Schizomeria ovata* while *Archontophoenix cunninghamiana*, *Acronychia suberosa*, *Orites excelsa*, *Cinnamomum oliveri*, *Sloanea woolsii*, *Stenocarpus salignus* and *Caldcluvia paniculosa* were present in most canopies.  On only one transect did *Ceratopetalum apetalum* and *Schizomeria ovata* occur as co-dominants and on only one transect was the canopy sufficiently

mixed that neither of these two species had been able to establish the typical marked numerical dominance which elsewhere identifies WTRF.

The extent to which the relationship between these two main species is one of forest succession, and can thereby be indicated by the overall floristic mix, or else a manifestation of the site environmental factors will be further discussed below. The WTRF is notable for the general absence, unlike the WSF, of standing dead trees as only one was noted in the canopy zone across all transects. This is presumed to be due to the less durable quality of the rainforest timbers in conjunction with the higher humidity which provides a more conducive environment for the populations of decay micro-organisms.

Table 4.3 shows the mix of canopy tree species for the WTRF sites. The species count per plot was higher than expected for WTRF varying from 6 on transect 3 to 14 on transect 1. The absence from the canopy plot data of typical canopy species of WTRF which were present in the area such as *Cryptocarya glaucescens* and *Doryphora sassafras* indicates that at least some species exhibit a marked non-random distribution through this forest type. Although an alternative possibility lies in the findings of Horne and Gwalter (1987) who reported that *Cryptocarya glaucescens* is much slower than *Ceratopetalum apetalum* at re-establishing itself as a canopy species after severe disturbance. It is possible that the floristic outcome of this slowness could persist long after other evidence of a severe disturbance has disappeared. The index of dispersion for *Ceratopetalum apetalum* is close to 6 which highlights the significant variation in the distribution of this species in the canopy even though it was common on all transects. The numbers of canopy trees in each plot may have relation with both disturbance history and the nature of the competition between the potential canopy trees and the lianes in the mid-layer. This point is pursued below where the structure of the forest is analysed.

4.1.2.3    Transition zone forests

The transition zone forests, as might be expected, share characteristics of both the WSF and WTRF. The canopy of the TZF typically has an overstorey of well-spaced, tall sclerophyllous trees but the rest of the

Table 4.3    Count of canopy individuals for each transect through WTRF.  The species in parentheses are regarded as lower layer emergents When relative variance >1, the canopy is tending to be clumped or underdispersed and when relative variance <1, the canopy is overdispersed.  For each transect data were obtained from 10 deciplots.

| Species | Tran 1 | Tran 2 | Tran 3 | Tran 4 | Tran 5 | Tran 6 | Mean | Var. |
|---|---|---|---|---|---|---|---|---|
| *Acacia orites* | - | 1 | - | - | 1 | - | 0.33 | 0.27 |
| *Acmena smithii* | - | - | - | 1 | - | - | 0.17 | 0.17 |
| *Acronychia suberosa* | 1 | 1 | - | - | 2 | - | 0.67 | 0.67 |
| *Archidendron grandiflorum* | 1 | - | - | 1 | - | - | 0.33 | 0.27 |
| *Archontophoenix cunninghamiana* | 2 | 2 | - | - | - | 6 | 1.67 | 5.47 |
| *Caldcluvia paniculosa* | - | 1 | 2 | 1 | 3 | - | 1.17 | 1.37 |
| *(Callicoma serratifolia)* | - | - | - | 1 | - | - | 0.17 | 0.17 |
| *Canarium australasicum* | 1 | - | - | - | - | - | 0.17 | 0.17 |
| *Ceratopetalum apetalum* | 15 | - | 10 | 2 | 9 | 22 | 9.67 | 66.67 |
| *Cinnamomum oliveri* | 2 | 1 | - | 3 | 1 | 1 | 1.33 | 1.07 |
| *(Daphnandra tenuipes)* | - | - | 1 | 1 | - | - | 0.33 | 0.27 |
| *Diospyros pentamera* | - | - | - | - | 1 | - | 0.17 | 0.17 |
| *Endiandra discolor* | 2 | - | - | - | - | - | 0.33 | 0.67 |
| *Halfordia kendack* | 3 | - | - | - | - | - | 0.50 | 1.50 |
| *(Helicia ferruginea)* | 1 | - | - | - | - | - | 0.17 | 0.17 |
| *Litsea reticulata* | - | - | - | 1 | - | 2 | 0.50 | 0.70 |
| *(Neolitsea dealbata)* | - | - | - | - | - | 1 | 0.17 | 0.17 |
| *Orites excelsa* | 1 | - | - | - | 1 | 2 | 0.67 | 0.67 |
| *Planchonella australis* | - | - | - | - | - | 1 | 0.17 | 0.17 |
| *Polyscias murrayi* | - | - | 2 | - | - | - | 0.33 | 0.67 |
| *Sarcopteryx stipata* | - | 1 | - | - | - | 2 | 0.50 | 0.70 |
| *Schizomeria ovata* | 2 | 8 | 5 | 4 | 2 | 1 | 3.67 | 6.67 |
| *Sloanea woollsii* | 2 | 1 | - | 1 | - | - | 0.67 | 0.67 |
| *Stenocarpus salignus* | 3 | - | 1 | 2 | - | - | 1.00 | 1.60 |
| *Syzygium luehmannii* | 3 | - | - | - | - | 1 | 0.67 | 1.47 |

canopy component varies from a  mixture of sclerophyllous and mesophyllous trees (e.g. Transects 1, 2 and 5) to one comprised mainly of mesophyllous species (e.g. Transects 3, 4 and 7) and to one where the remainder of the canopy is poorly developed such that the future canopy individuals are contained almost entirely within the mid-layer  (e.g. Transect 6).  The description of these canopy arrangements conventionally treats the tall sclerophyllous individuals as emergents from the main layer, but because the ecological processes and relationships of all the trees in the TZ are continuous with the community to which they are affiliated, I regard it more helpful to describe the canopy of the TZ as being two-tiered and this position will be further developed when the TZ forest structure is analysed below.

The height of the top canopy tier averaged 40 m with a range of 35 m to 45 m while some exceptional individuals attained nearly 60 m. The second tier averaged about 25 m in a range of 20 m to 30 m. The top tier is dominated by *Eucalyptus pilularis*, *Syncarpia glomulifera* and *Acacia orites* while *Allocasuarina torulosa* was occasionally represented indicating that greater heights are achievable by this species in this forest type. The lower tier included the sclerophyllous species in the top tier and the rainforest species were strongly represented by *Callicoma serratifolia* but also by *Schizomeria ovata* and *Ceratopetalum apetalum*. Table 4.4 contains the results of the recordings of the canopy tree species for the TZF. Of the 15 species 6 are pyrophytic sclerophyllous species. These results indicate a floristic richness of the transition zone canopy not present in north Queensland (note that Unwin (1989) found only three species above 6 m in the transition zone of which only one was a pyrophytic sclerophyllous species).

Table 4.4    Count of canopy individuals for each transect through TZF.
When relative variance >1, the canopy is tending to be clumped or underdispersed and when relative variance <1, the canopy is overdispersed. For each transect data were obtained from 10 deciplots.

| Species | Tran 1 | Tran 2 | Tran 3 | Tran 4 | Tran 5 | Tran 6 | Tran 7 | Mean | Var. |
|---|---|---|---|---|---|---|---|---|---|
| *Acacia orites* | 1 | 3 | 4 | 2 | 12 | 2 | 1 | 3.57 | 14.95 |
| *Allocasuarina torulosa* | 5 | 4 | 4 | 4 | 16 | - | 1 | 4.86 | 27.48 |
| *Austrobuxus swainii* | - | - | 1 | - | - | - | - | 0.14 | 0.14 |
| *Caldcluvia paniculosa* | - | - | - | - | - | - | 2 | 0.29 | 0.57 |
| *Callicoma serratifolia* | 2 | - | 5 | 30 | 8 | 5 | 10 | 8.57 | 92.62 |
| *Canarium australasicum* | 4 | - | - | - | - | - | - | 0.57 | 2.29 |
| *Ceratopetalum apetalum* | 11 | - | 1 | - | - | 2 | - | 2.00 | 13.14 |
| *Cinnamomum oliveri* | - | - | - | - | - | - | 1 | 0.14 | 0.14 |
| *Daviesia arborea* | - | - | - | - | - | 1 | - | 0.14 | 0.14 |
| *Eucalyptus gummifera* | 1 | - | - | - | - | - | - | 0.14 | 0.14 |
| *Eucalyptus pilularis* | 4 | 5 | 2 | 4 | 2 | 5 | 1 | 3.29 | 2.57 |
| *Litsea australis* | - | - | - | - | - | - | 2 | 0.29 | 0.57 |
| *Schizomeria ovata* | - | 3 | 5 | - | 1 | - | 1 | 1.43 | 3.62 |
| *Syncarpia glomulifera* | 2 | 8 | 3 | 2 | - | 1 | 7 | 3.29 | 9.24 |
| *Tristaniopsis collina* | 1 | - | - | - | - | - | - | 0.14 | 0.14 |
| (Stags | - | - | 2 | - | 2 | 1 | -) | | |

## 4.1.3    Mid-layer patterns

The canopy compositions of each forest type have been shown to be fairly consistent across all the transects. The extent of the floristic differences within each of those vegetation zones begins to be revealed with the examination of the species comprising the mid-layers on each transect. The mid-layer species included all plants (including lianes but excluding mid-layer epiphytes and parasites) which were over 3 m high but were not tall enough to be part of the canopy layer. A total of 116 species was recorded in this layer in the sample plots. They included 73 tree species, 20 liane species and 23 species represented by "emergent" understorey plants.

Rather than tabulate these results as for the canopy data, I will present them in the form of species accumulation curves. The use of these curves requires some initial cautionary comment. The shape of species accumulation curves and hence the projection of the curve beyond the number of sample units, is entirely a function of the sequence in which the units are grouped for curve plotting. By way of example, if some sites contain a number of species not recorded elsewhere and these sites are considered last when constructing the species accumulation curve, the projection will suggest that the curve is still rising and that further sampling is necessary to establish the shape of the curve. Whereas if those sites were considered at or near the commencement of the curve, it is more likely that the shape of the curve will underestimate the amount of sampling required.

The options, therefore, were to:
- write a computer program to optimise the organisation of the sites in such a way as to ensure that a desired shape was realised within the scope of the sites sampled;
- to use that same program to establish the two extreme shapes and hence settle for the mean shape;
- to rely on a random sequence of sites;
- to derive the curve from sites sequenced in the same order in which they were sampled; or
- to sequence the sites in some sensible way such as in decreasing order of total species recorded.

I decided to use the last of these alternatives because it was not biased by field decisions, it could not be regarded as delivering a contrived result and it was likely to produce a result consistent with field impressions.

The shape of these curves for mid-layer species in each vegetation zone are shown in Figs. 4.1-4.3. These figures show that, by sampling 100 m$^2$ units, most of the species richness in the WSF mid-layer is accounted for in about 20 samples and in the TZF by about 40 samples. The curve for the rainforest species (Fig. 4.3) is barely reaching an asymptote at 60 samples. This result suggests to me not simply that the WTRF is somewhat more floristically diverse than the other forest types but that there are multiple sub-canopy layers in the rainforest patches of the study area and these layers are floristically distinct. This suggestion will be evaluated by pattern analysis procedures below.

As with the interpretation of the species composition of the canopy layer, the mid-layer also contained some plants which were essentially "emergent" understorey species. Some of such species included *Dodonaea triquetra* and *Hovea longipes* in the WSF, *Cordyline petiolaris* in the TZF and *Linospadix monostachys* and *Cordyline rubra* in the WTRF. The average number of species per 0.1 ha plot recorded for the mid-layer increased from 15 in the WSF to 26 in the TZF to 43 in the WTRF. The breakdown of the distribution of the species along the vegetation gradient is presented in Section 4.1.6.

Comparative diversity statistics were calculated for the mid-layers of each forest type. The measurements of species distribution, *viz.* richness, evenness and diversity, for the forest mid-layers have been calculated and are shown in Figs. 4.4-4.6. The richness statistic shows that the WSF mid-layer has a consistent species count of usually 4 to 7 species per 100 m$^2$ sample. The TZF mid-layer is more variable. Although most of the samples contained 3 to 8 species there were several with more than 10 and they ranged up to 17. The WTRF is still more variable with as few as 3 to as many as 32 species in the midlayer of a 100 m$^2$ sample.
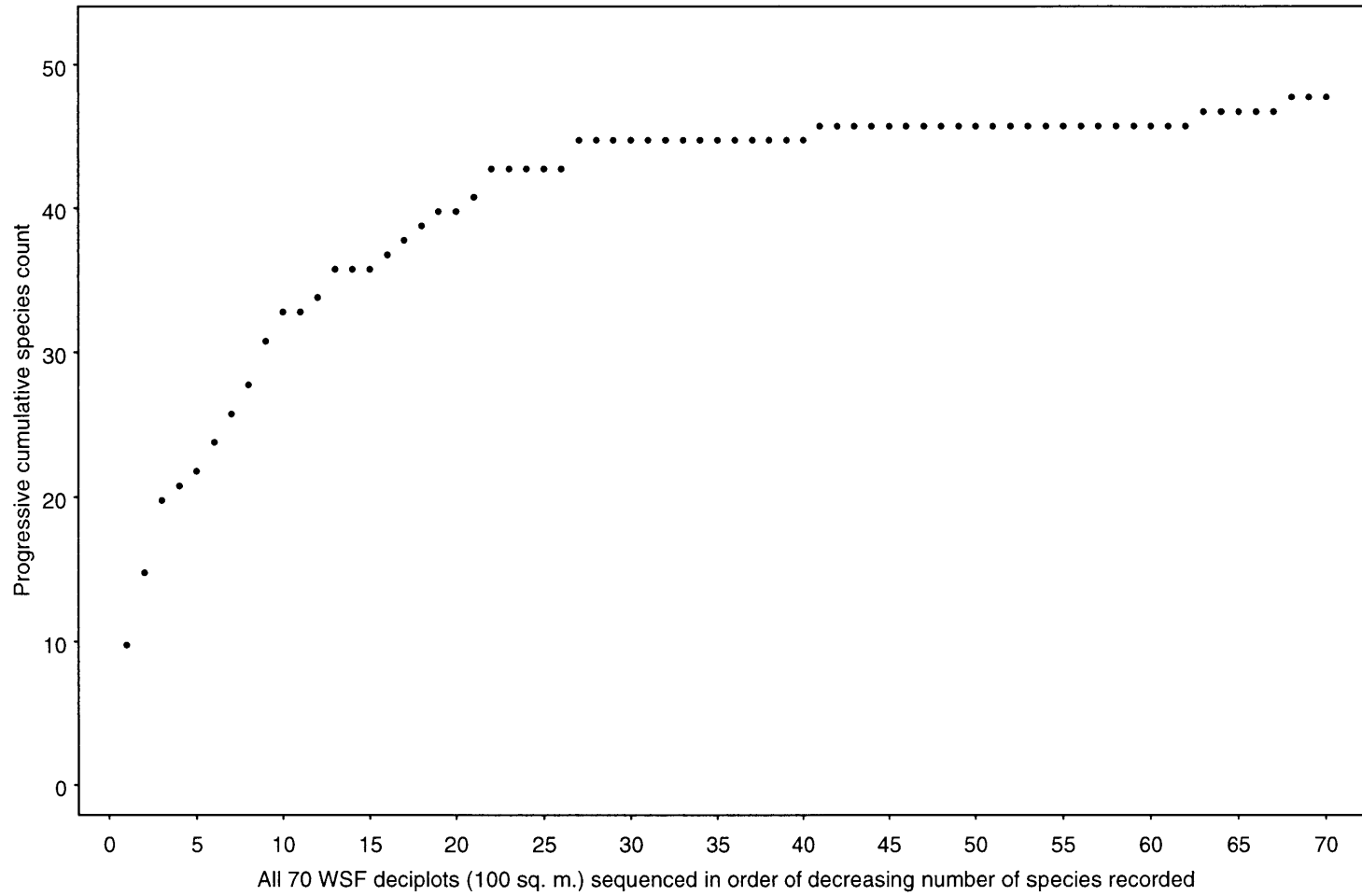
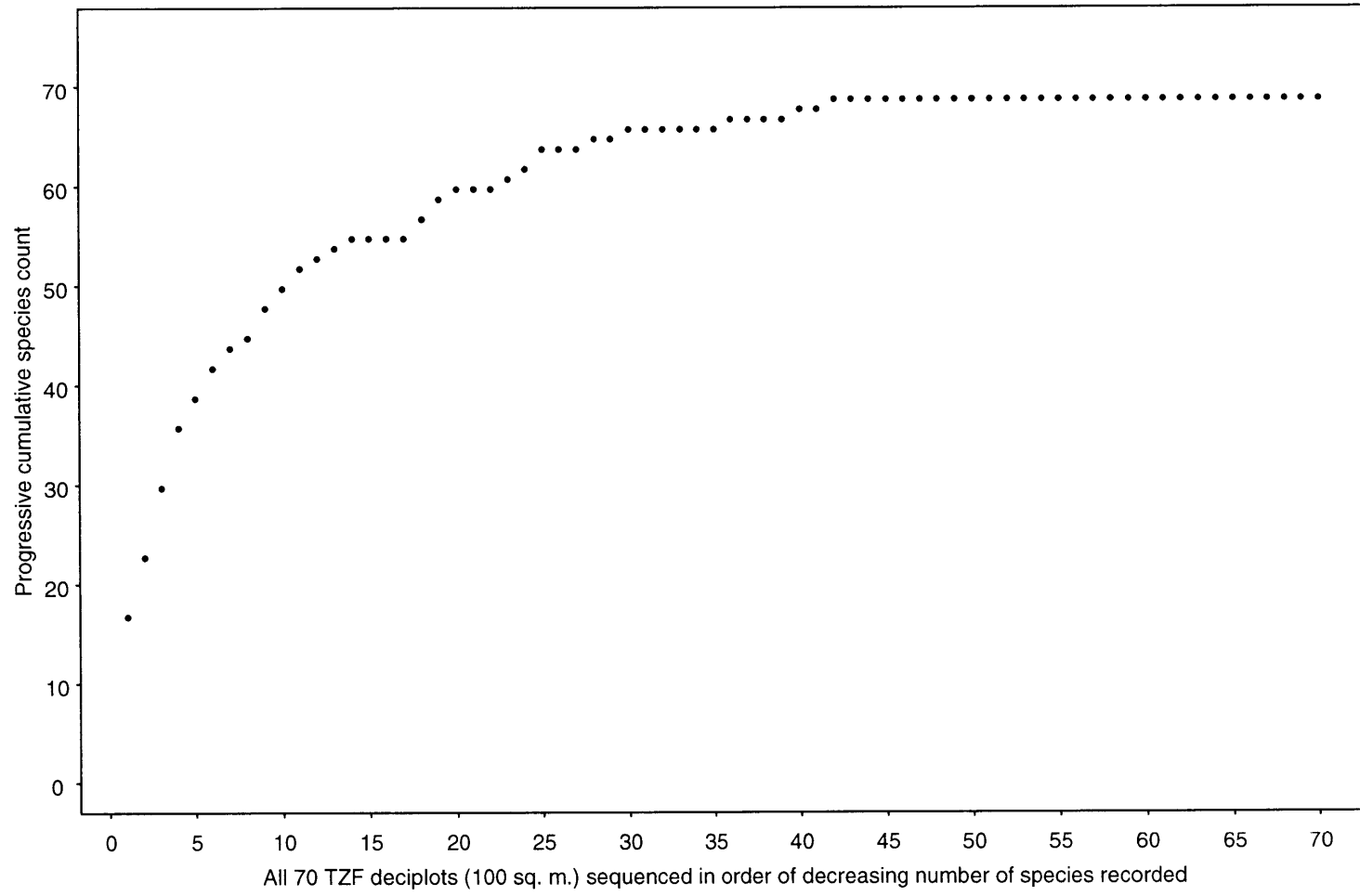Figure 4.1  Accumulation of species with repeated survey in the mid-layer of WSF

Figure 4.2   Accumulation of species with repeated survey in the mid-layer of TZF
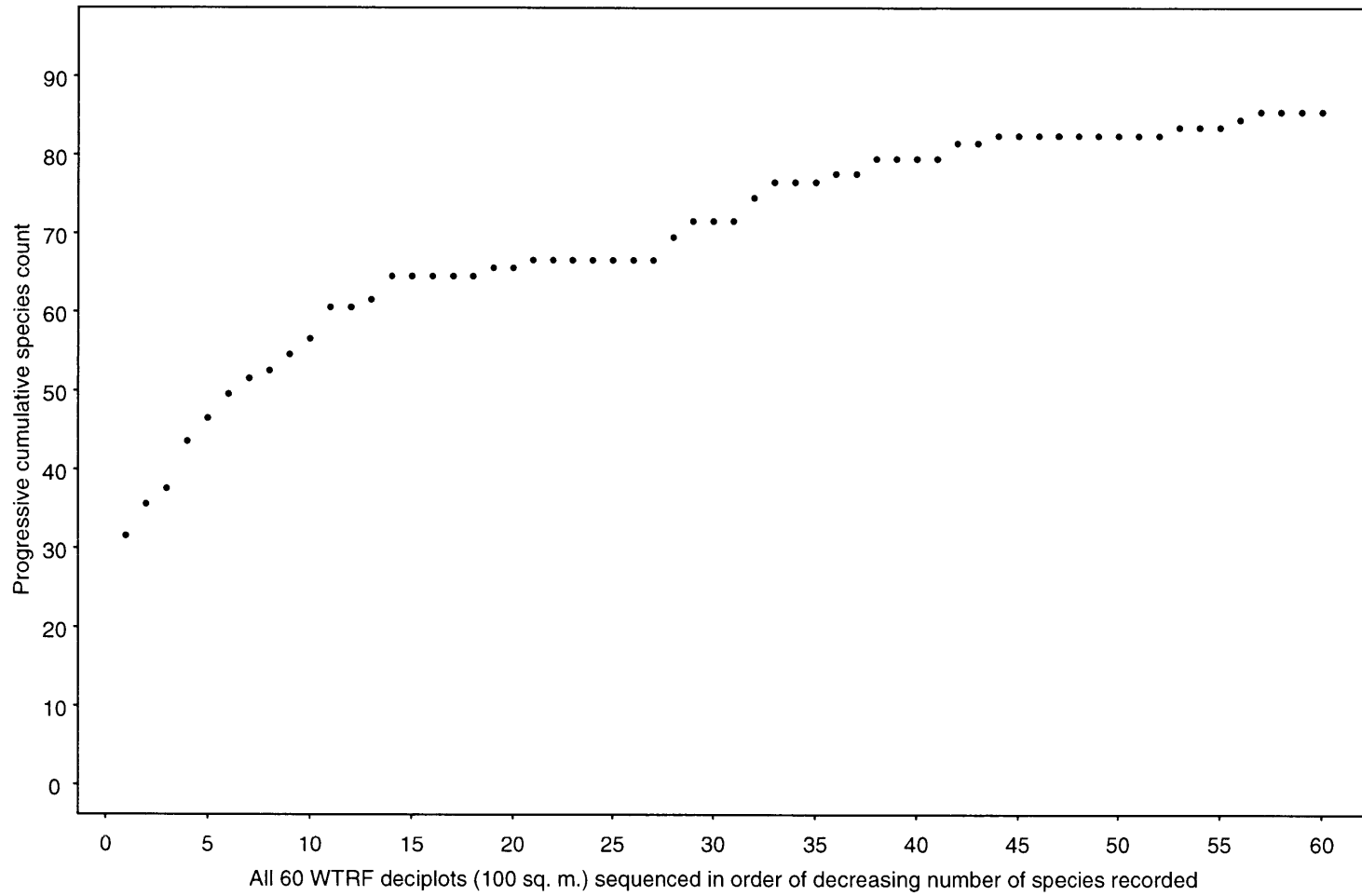
Figure 4.3   Accumulation of species with repeated survey in the mid-layer of WTRF
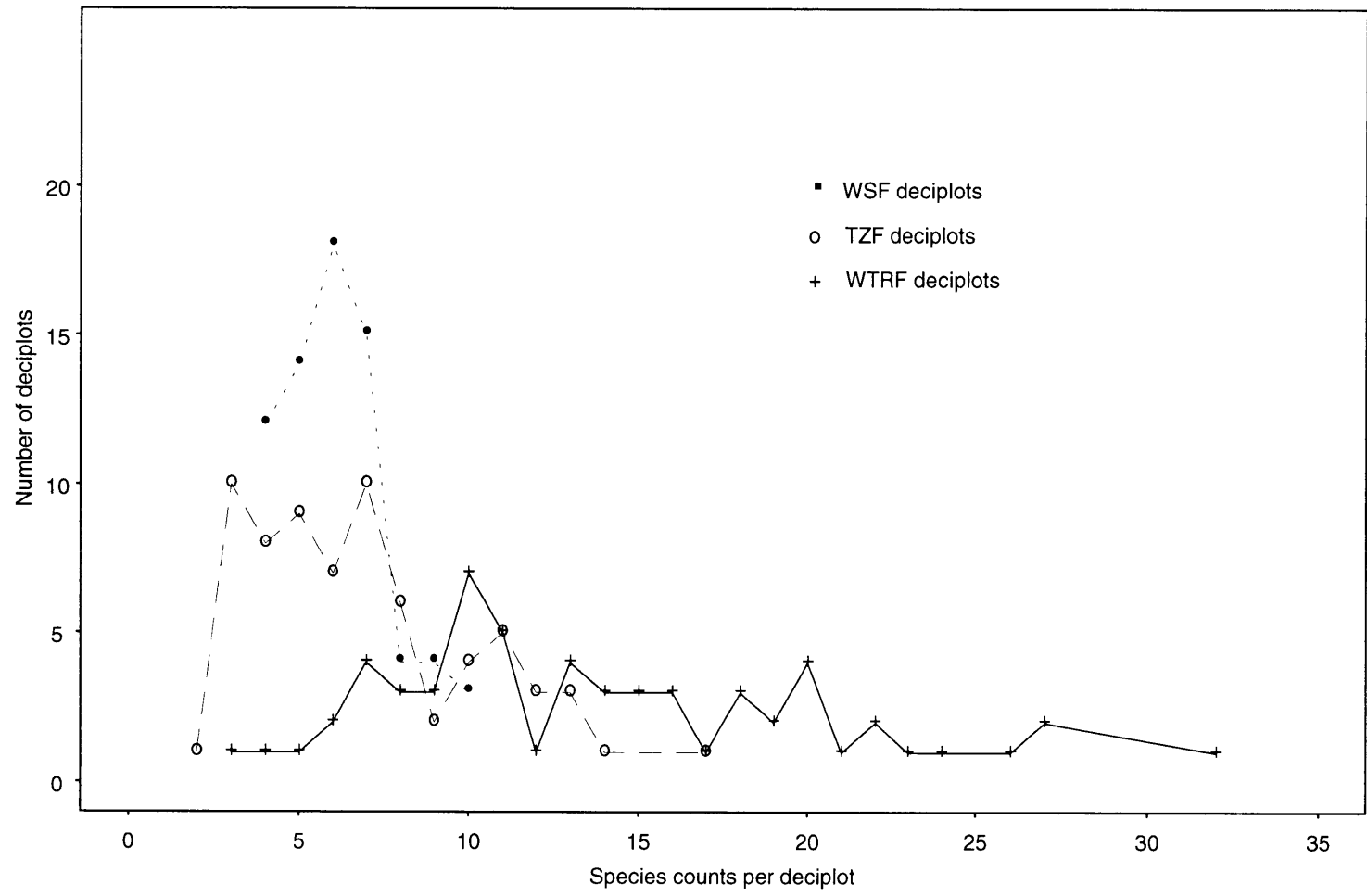
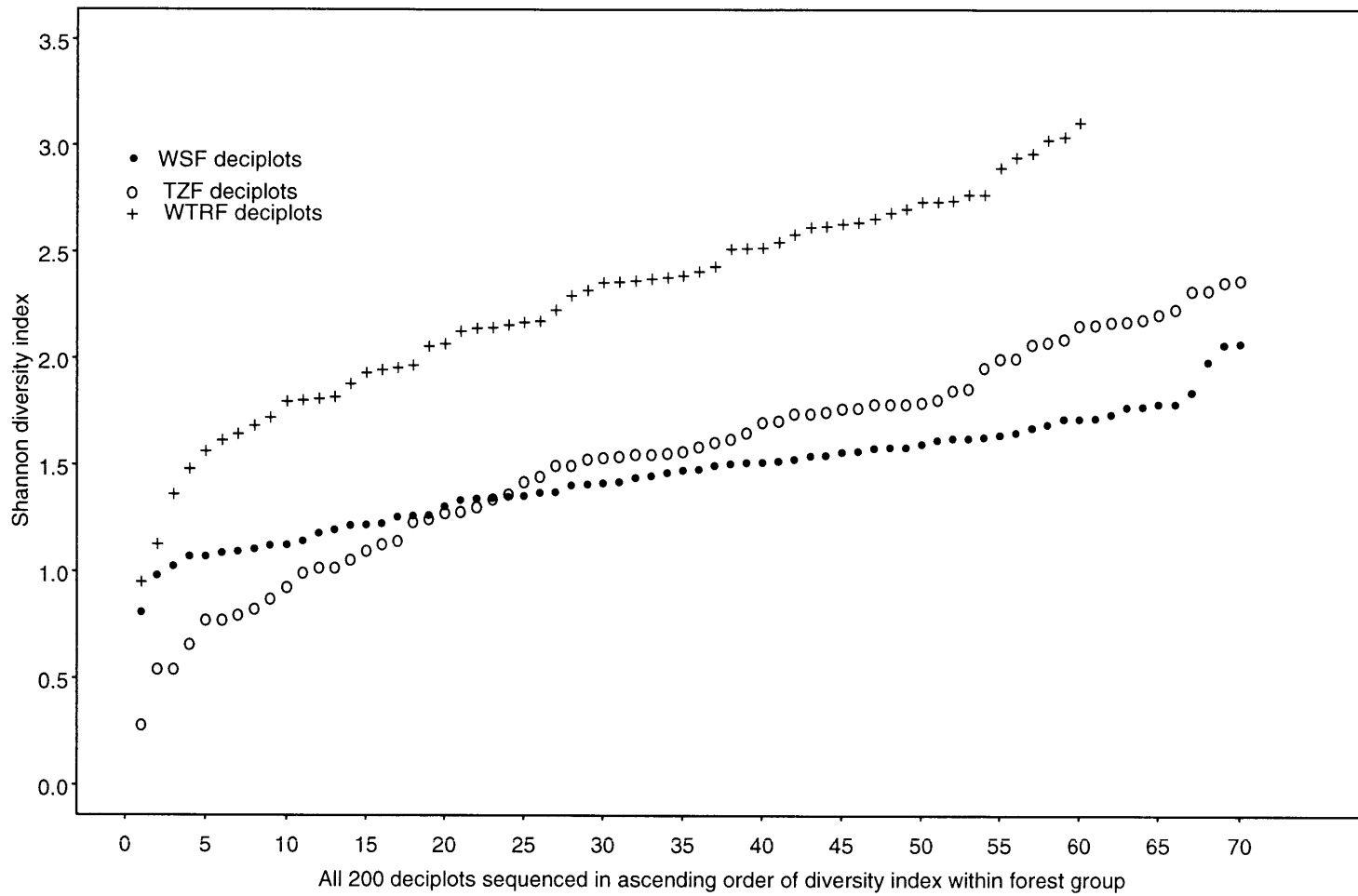Figure 4.4   Species richness in the mid-layer in each forest type

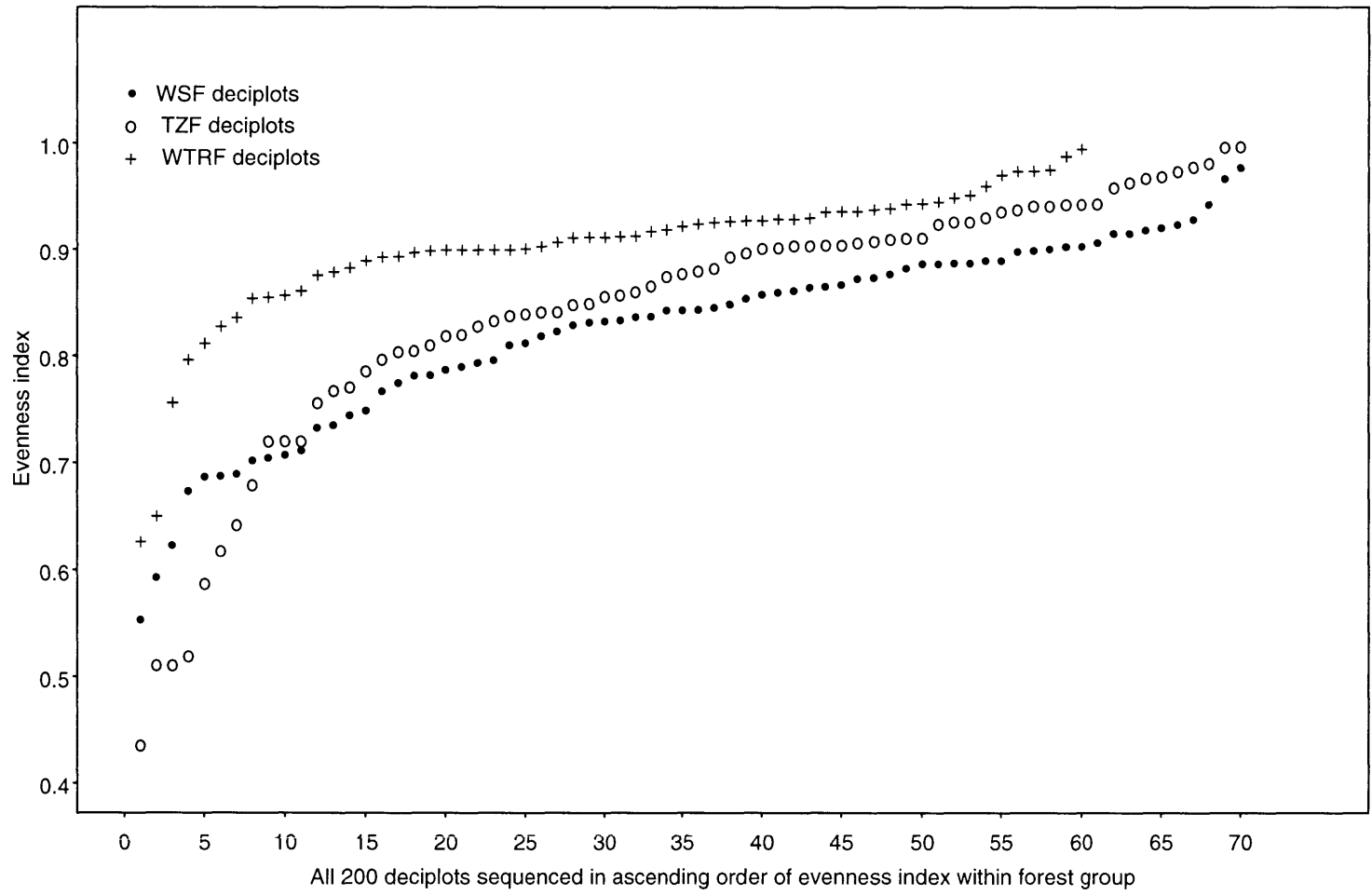Figure 4.5   Range of species diversity in the mid-layer in each forest type

Figure 4.6   Range of species evenness in the mid-layer in each forest type

Table 4.5   Summary of diversity statistics for the mid-layer. Data were obtained from 7 transects and the species count is the accumulated total for all transects.

| Forest type | Species richness | Species evenness | Shannon index | Jackknifed index | 95% conf |
|---|---|---|---|---|---|
| WSF | 47 | 0.599 | 2.27 | 2.31 | ± 0.16 |
| TZF | 68 | 0.805 | 3.32 | 3.40 | ± 0.13 |
| WTRF | 85 | 0.831 | 3.64 | 3.69 | ± 0.07 |

The diversity indices (see Table 4.5) for each sample area (Fig. 4.5) provide a good example of how, in some situations, richness and diversity are closely related.  While it is true that the diversity index differs by being influenced by the underlying species abundance distribution, the correlations between the two indices were $r=0.81$ (WSF), $r=0.89$ (TZF) and $r=0.91$ (WTRF).  For both indices, the range of WSF values is completely contained within the range of TZF values and the WTRF values significantly exceed the values for either of the other two forest types.  The low diversity indices for the WSF sites reflect the usually comparatively lower richness of this layer in this forest type.  Although the Shannon index takes into account species evenness, it is still possible to take this further and calculate the ratio of the observed diversity to the maximum diversity possible (where all species are equally abundant) and apply the result as a measure of sample evenness.  This procedure was applied to the data in Fig. 4.5 and the results are shown in Fig. 4.6.  If the extremes of the distributions are ignored, the patterns revealed in Fig. 4.6 indicate a constancy in the evenness relations between the three vegetation types.  The evenness indices for WSF are depressed by the large numbers of, particularly, *Allocasuarina torulosa* but also *Cryptocarya rigida* and sometimes *Elaeocarpus reticulatus* and *Persoonia media* in relation to the comparatively low numbers of other mid-layer species.

4.1.4      Understorey layer patterns

The understorey layer was defined above in the broadest sense as incorporating all those plants up to 3 m in height regardless of their

situation. That is, the group includes epiphytes, lithophytes and mistletoes as well as the ground rooted species and potentially temporary members such as canopy tree seedlings. The species range from prostrate herbs such as *Viola hederacea* to large, bushy and sprawling shrubs such as *Acrotriche aggregata.* A total of 239 species was recorded in this category of which 26 were only recorded in WSF, 28 only in TZF and 18 only in WTRF. Of the remaining 167 species, 34 occurred in WSF and TZF, 40 occurred in TZF and WTRF, while 90 were recorded in all vegetation zones.

Three species (*Davallia pyxidata, Dendrobium monophyllum* and *Microsorum scandens*) were found in WSF and WTRF without any records for the TZF. These were all rare species (see raw data in Appendix I) each with only a single record in WSF. It is probable that with further sampling, those species would be recorded in the TZF or else their affiliation with the WTRF would be confirmed. For the purposes of the analysis I have included them in the group that was found in all vegetation zones. The final figures for species richness of the understorey layer for all three zones in the study area are then 153 for WSF, 151 for WTRF and 192 for TZF. Of interest are the proportions of these counts which are "permanent" or "genuine" members of this stratum as opposed to the proportion of potentially "transitory" members. That is, how rich are these understorey layers if we disregard the component that represents the potential canopy and mid-layer species? Table 4.6 provides the answer to this question showing that the count of genuine understorey species is very high for all forest types. The actual ratio of transitories to genuines is lowest in the WSF and gradually increases along the vegetation gradient indicating that the suitability of conditions for establishment of genuine shrub and herb species is declining. The one obvious change along the gradient is the concomitant decrease in ground light levels and I presume that this is the dominating factor. The results of the analysis of the crown structure of the canopy layer presented in Section 4.2 contribute further to this presumption.

An interesting aspect of the understorey species data is the absence of annuals and terrestrial orchids. Although terrestrial orchids were occasionally encountered outside the plots, the absence of annuals was

Table 4.6.    The separation of "genuine" understorey species from
              "transitory" understorey species for each forest type.

| plant group | WSF | TZF | WTRF |
|---|---|---|---|
| potential canopy trees | 46 | 66 | 58 |
| potential canopy vines | 4 | 6 | 6 |
| potential mid-layer trees | 14 | 21 | 14 |
| total transitory species | 64 | 93 | 78 |
| understorey woody plants | 21 | 24 | 13 |
| scramblers | 24 | 30 | 29 |
| herbs, grasses, ferns | 30 | 32 | 21 |
| epiphytes, mistletoes | 14 | 13 | 10 |
| total genuine species | 89 | 99 | 73 |

noted across the study area.   In conjunction with the trivial component
of exotic species, this paucity of r-selected species indicates a general
ecological stability or robustness of the mature forest ecosystem.
The summary diversity statistics for the understorey layer for each
forest type are shown by Table 4.7 and will be discussed in terms of the
Figures 4.7-4.12.

The shapes of the species accumulation curve for each zone are depicted
in Figures 4.7-4.9.   The progression of these curves are such that they
are all still, albeit slowly, rising at the extremity.   This characteristic
reflects the consequence of chance germination successes and the
heterogeneity of micro-scale habitat conditions in all forest types.   The
slopes of the curves, however, indicate a similar trend outcome to the
mid-layer curves.   That is, about 30 100 $m^2$ samples will capture most
of the species complement of WSF, about 40 samples are required for
the TZF and about 60 samples will establish the species range in the
WTRF.

 The WTRF has the lowest total understorey species count but requires
the most number of samples to find them.   This indicates a significant
non-random distribution of understorey species in the rainforest
patches in the study area.   An alternative explanation that the 100 $m^2$
samples are too small is not supported when the data are considered in
terms of the 0.1 ha plots.   The species accumulation graph for the latter
group illustrated by Figure 4.9 is a much steeper curve than those for

The y-axis is labelled "Progressive cumulative species count" with values 40, 60, 80, 100, 120, 140, 160.

The x-axis is labelled "All 70 WSF deciplots sequenced in order of decreasing number of species recorded" with values 0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70.
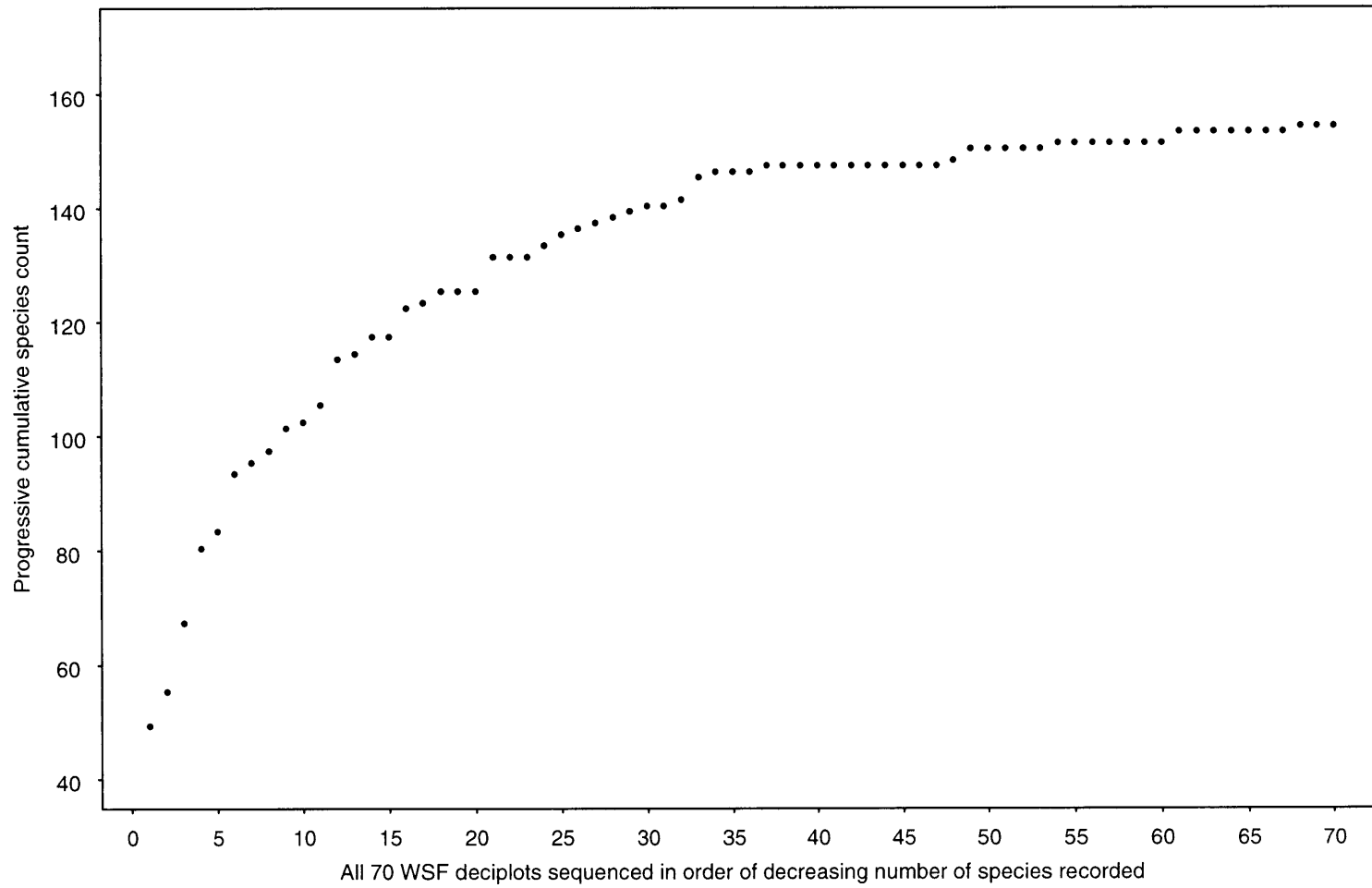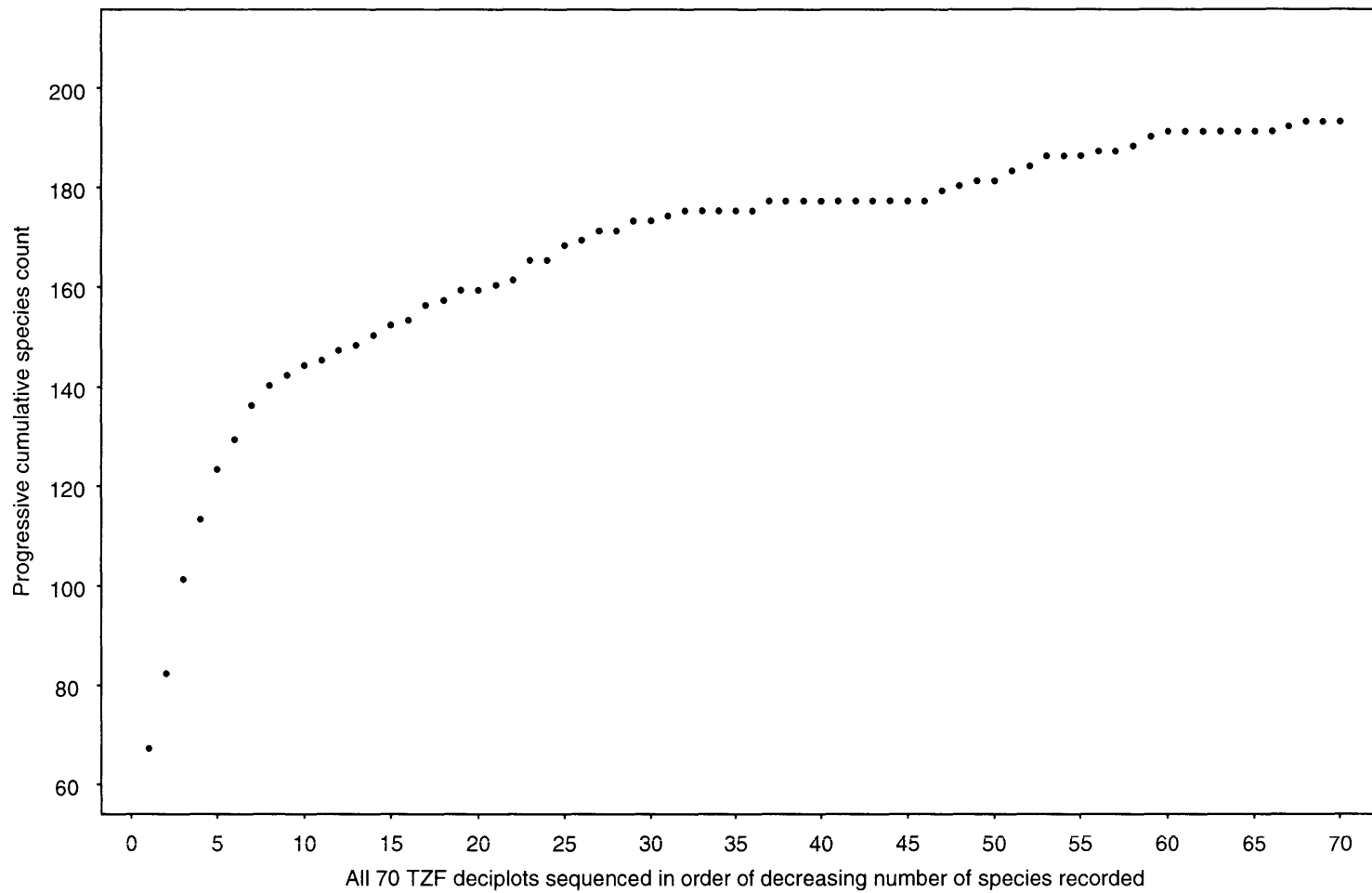
Figure 4.7   Accumulation of species with repeated survey in the understorey of WSF

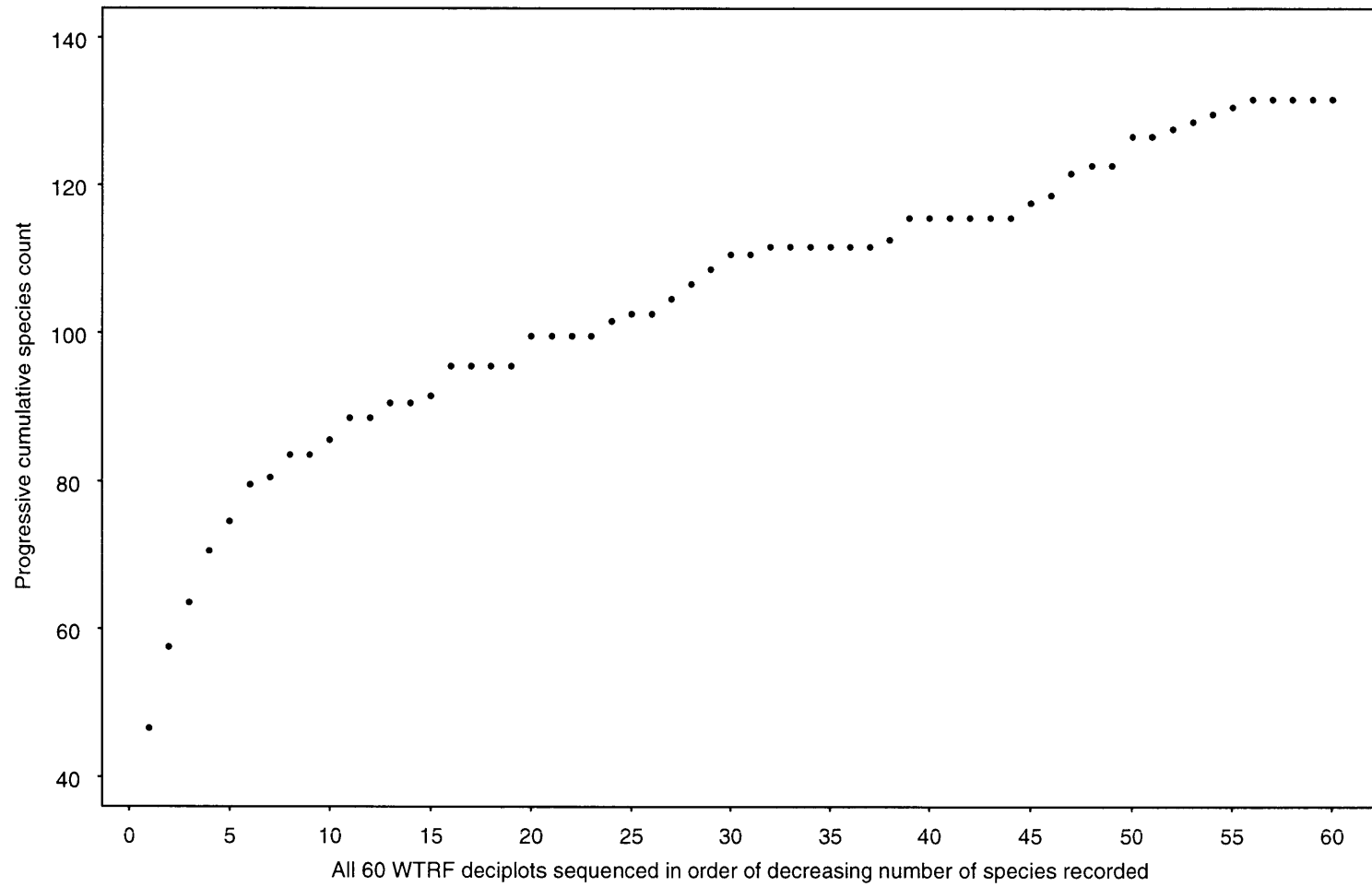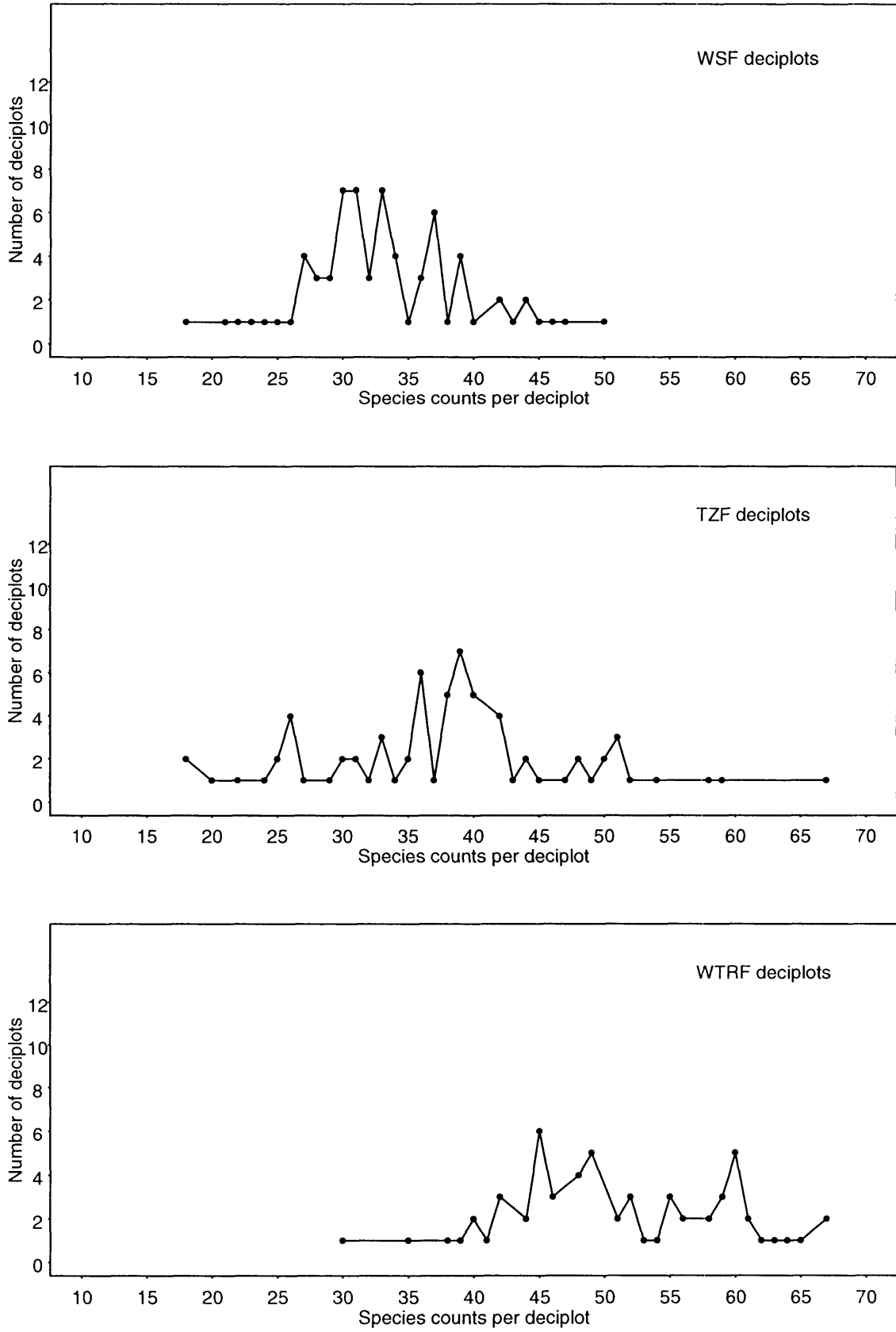Figure 4.8   Accumulation of species with repeated survey in the understorey of TZF

Figure 4.9   Accumulation of species with repeated survey in the understorey of WTRF

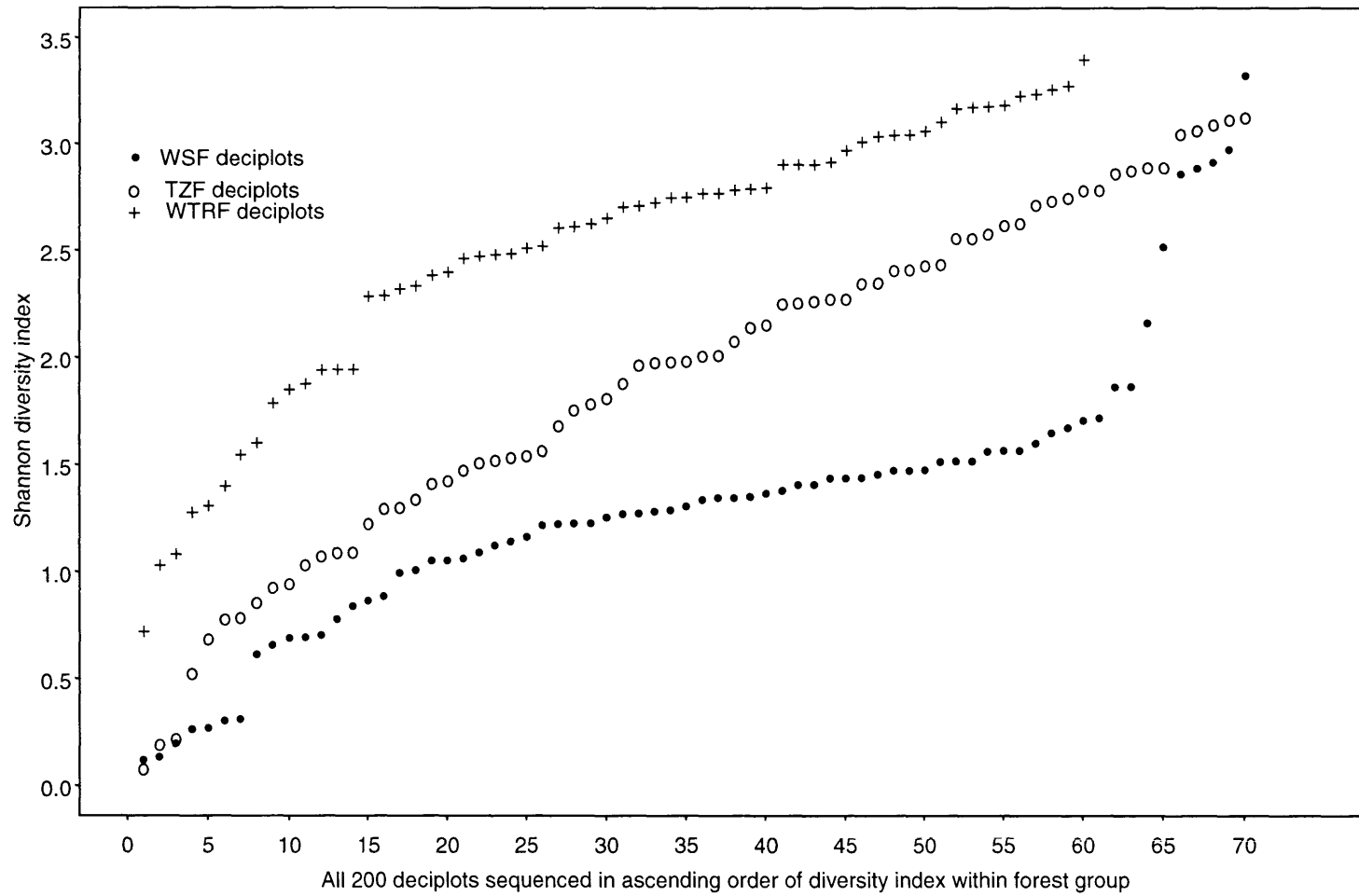Figure 4.10   Species richness in the understorey of each forest type

Figure 4.11   Range of species diversity in the understorey of each forest type
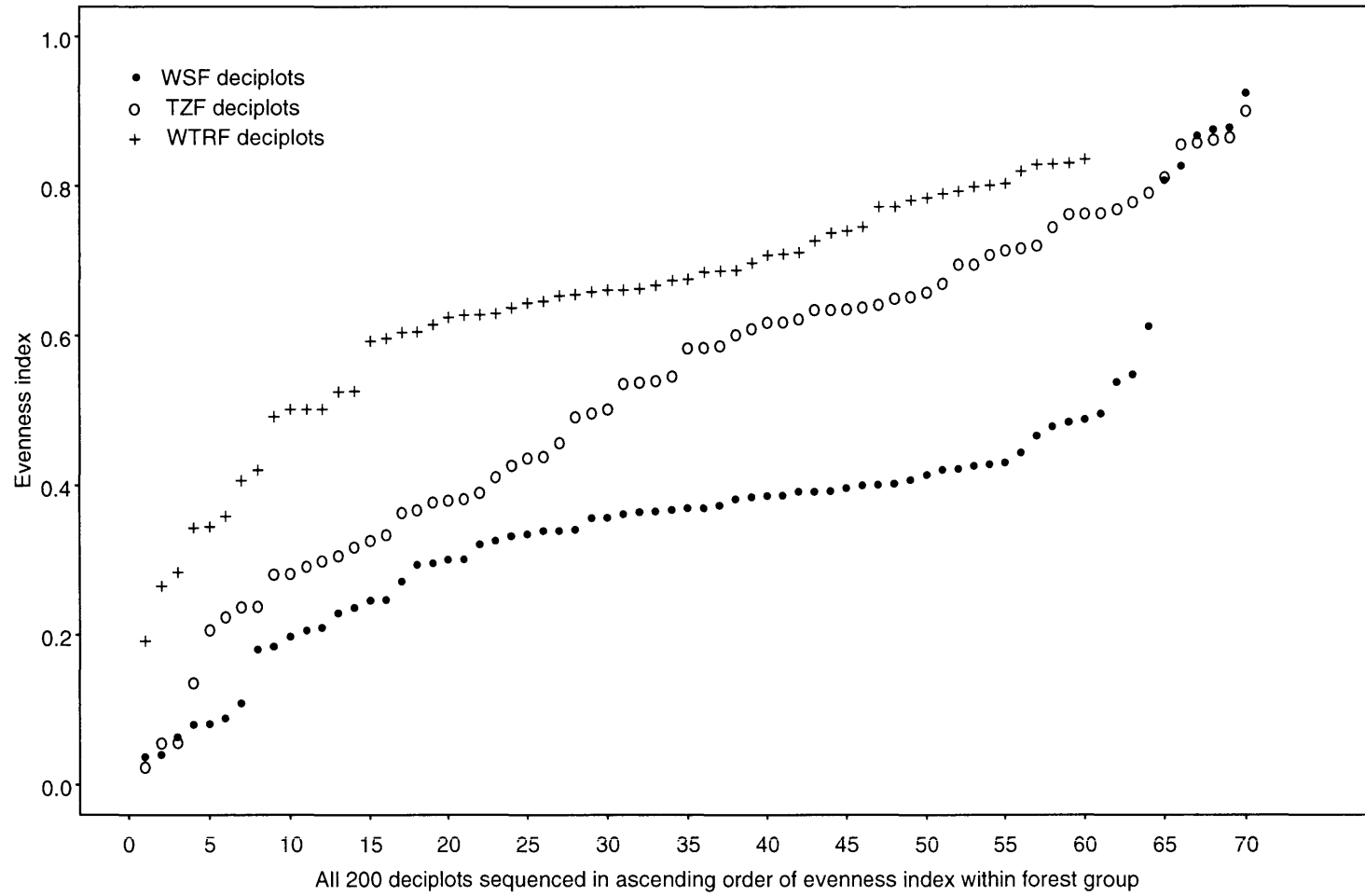
Figure 4.12   Range of species evenness in the understorey of each forest type

Table 4.7    Summary of diversity statistics for the understorey. Data were obtained from 7 transects and the species count is the accumulated total for all transects.

| Forest type | Species richness | Species evenness | Shannon index | Jackknifed index | 95% conf |
|---|---|---|---|---|---|
| WSF | 153 | 0.343 | 1.71 | 1.73 | ± 0.24 |
| TZF | 192 | 0.356 | 1.89 | 1.87 | ± 0.54 |
| WTRF | 151 | 0.617 | 3.08 | 3.10 | ± 0.24 |

WSF and TZF which confirms the patchiness of the understorey species distribution in the WTRF. This point will be pursued in the pattern analysis of Section 4.1.9.1.

As indicated above, potential emigrants from the understorey represent the majority of species recorded in this layer in the WTRF. However, because many of those species are able to persist in this layer for sometimes 40 or 50 years (A.G. Floyd pers. comm.), they may make a longterm contribution to both the floristic diversity and structural complexity of the understorey layer. The mechanisms which control either their growth out of the understorey layer or their death within it are still very much uncertain (Adam 1992).

The comparison of the understorey layer species richness for all samples is shown in Figure 4.10. There is much greater overlap in the data for these layers than shown in Fig. 4.4 for the mid-layers. Nevertheless, the WSF can still be seen to average about 30-35 species per sample which increases to about 40 species in the TZF and to over 50 species in the WTRF. The average understorey species richness for the transition zone samples compares favourably with the results for north Queensland. Unwin (1989), using sample subplots of 25 x 12.5 m (more than 3 times the area of my deciplots), averaged about 60 understorey species per transition zone subplot. The understorey results confirm the canopy and mid-layer indication that in northern N.S.W. the transition zone, when compared to the respective adjacent

rainforests and sclerophyll forests, is floristically more complex than its counterpart in north Queensland.

The diversity and evenness of the sample areas (Figs. 4.11, 4.12) clearly reflect the impact of the domination of WSF by sedges and ferns, and occasionally grasses, by depressing these indices with respect to the other forest types. The occasional dominance of a TZF sample by sedges has led to the lowering of the net indices for evenness and diversity for this forest type as a whole (see Table 4.7) but when considered individually, the diversity of the TZF sample areas show a far greater affinity with the rainforest than with the wet sclerophyll forest. The deception of the Shannon index is revealed in these Figures, however, because not only do the number of species in the WTRF exceed the TZF but so do their abundances. In other words, the TZF, despite a lower species richness than the WTRF, has a very similar range of indices to that of the WTRF due to fewer of its species complement being "rare" in the samples.

## 4.1.5     Canopy indicator species

The canopy of the WSF in the study area is represented by discrete, almost monospecific, communities such that it becomes a tautology to describe a set of indicator species for this formation. The more helpful indicator in terms of WSF canopy classification is the stand density. This variable is a component of vegetation structure and its treatment will be discussed in relation to vegetation structure below. Nevertheless, simple significance tests can be applied to the plot-based canopy data to test for non-random affinities which may exist between the various species recorded in the canopy of the WSF as well as the canopies of the other two forest formations.

Table 4.8 shows the result of applying a Chi-squared test of association to the data in Tables 4.2-4.4. These ratings show the canopy of the TZF as being significantly comprised of two prominent members of the rainforest canopy, *Ceratopetalum apetalum* and *Schizomeria ovata* as well as three significant members of the WSF canopy, *Eucalyptus pilularis, Syncarpia glomulifera* and the mid-layer emergent, *Allocasuarina torulosa.* The transition zone canopy also includes a

Table 4.8    Indications of the significance of the association of each species with the canopy layer(s) in which it was recorded.  Significant at p < 0.1 (*), p < 0.05 (**) and p < 0.01 (***).    ns is not significant.

| Species | WSF | TZF | WTRF |
|---|---|---|---|
| *Acacia orites* | ns | * * * | ns |
| *Acmena smithii* | | | ns |
| *Acronychia suberosa* | | | * * * |
| *Allocasuarina torulosa* | * | * * * | |
| *Archidendron grandiflorum* | | | * |
| *Archontophoenix cunninghamiana* | | | * * * |
| *Austrobuxus swainii* | | ns | |
| *Caldcluvia paniculosa* | | ns | * * * |
| *Callicoma serratifolia* | | * * * | ns |
| *Canarium australasicum* | | * | ns |
| *Ceratopetalum apetalum* | | * | * * * |
| *Cinnamomum oliveri* | | ns | * * * |
| *Daphnandra tenuipes* | | | * |
| *Daviesia arborea* | | ns | |
| *Diospyros pentamera* | | | ns |
| *Endiandra discolor* | | | * |
| *Eucalyptus campanulata* | * * * | | |
| *Eucalyptus gummifera* | ns | ns | |
| *Eucalyptus microcorys* | ns | | |
| *Eucalyptus pilularis* | * * * | * * | |
| *Halfordia kendack* | | | * * |
| *Helicia ferruginea* | | | ns |
| *Litsea australis* | | ns | |
| *Litsea reticulata* | | | * * |
| *Neolitsea dealbata* | | | ns |
| *Orites excelsa* | | | * * * |
| *Planchonella australis* | | | ns |
| *Polyscias murrayi* | | | * |
| *Sarcopteryx stipata* | | | * * |
| *Schizomeria ovata* | ns | * | * * * |
| *Sloanea woollsii* | | | * * * |
| *Stenocarpus salignus* | | | * * * |
| *Syncarpia glomulifera* | * * | * * * | |
| *Syzygium luehmannii* | | | * * * |
| *Tristaniopsis collina* | | ns | |
| Stags | * | * | |

significant representation by three species, *Acacia orites*, *Callicoma serratifolia* and *Canarium australasicum*, which are not significantly present in the canopy of the other forest types.  The number of tall standing dead trees is significant in both the WSF and TZF canopies and this point has relevance to the interpretation of the results of structural analysis and the community dynamics of these forest types. The relative complexity of the WTRF canopy is indicated by the significant association with that forest type of 17 species.

## 4.1.6     Mid-layer  indicator  species

A total of 47 species occurred in the mid-layer of the WSF, 68 in the mid-layer of the TZF and 85 in the mid-layer of the WTRF.  Before any pattern analysis is performed on the mid-layer data it is possible to make some preliminary assessments of the potential for any particular species to be regarded as an indicator species for a mid-layer community within the WSF formation.  Tables 4.9-4.11 contain the net records for 17, 10 and 42 species which exhibit either a high constancy of  association with WSF, TZF and WTRF respectively or else their distribution suggests an affiliation with that association.  Four species, *Acmena smithii*, *Austrobuxus swainii*, *Cissus hypoglauca* and *Schizomeria ovata*  are all well represented in the mid-layer of each vegetation type and the allocation of their proper position in the vegetation gradient is left to the results of the pattern analysis.

Table 4.9     Summary of plot-based observations for species recorded in the mid-layer of WSF which appear to have potential as indicators for a mid-layer community within the WSF.  All observations are from the mid-layer stratum only.

| Species | WSF obs. | TZF obs. | WTRF obs. |
|---|---|---|---|
| *Acacia orites* | 8 | - | - |
| *Acrotriche aggregata* | 11 | 6 | - |
| *Allocasuarina torulosa* | 549 | 72 | - |
| *Archirhodomyrtus  beckleri* | 18 | - | 5 |
| *Cryptocarya  microneura* | 4 | - | - |
| *Cryptocarya  rigida* | 326 | 58 | - |
| *Daviesia arborea* | 16 | 4 | - |
| *Dodonaea triquetra* | 3 | - | - |
| *Elaeocarpus reticulata* | 148 | 41 | - |
| *Eucalyptus campanulata* | 4 | - | - |
| *Eucalyptus pilularis* | 18 | - | - |
| *Hakea salicifolia* | 9 | 8 | - |
| *Hovea longipes* | 6 | - | - |
| *Leptospermum micrantha* | 12 | - | - |
| *Persoonia media* | 113 | 18 | 2 |
| *Phebalium squameum* | 4 | - | - |
| *Syncarpia glomulifera* | 103 | 13 | - |

Table 4.10    Summary of plot-based observations for species recorded in the mid-layer of TZF which appear to have potential as indicators for a mid-layer community within the TZF. All observations are from the mid-layer stratum only.

| Species | WSF obs. | TZF obs. | WTRF obs. |
|---|---|---|---|
| *Cissus sterculifolia* | - | 7 | - |
| *Callicoma serratifolia* | 41 | 170 | 8 |
| *Duboisia myoporoides* | 4 | 7 | 2 |
| *Geissois benthamiana* | - | 3 | 1 |
| *Geitonoplesium cymosum* | 2 | 63 | 28 |
| *Litsea reticulata* | - | 3 | - |
| *Melicope hayesii* | 15 | 35 | 12 |
| *Pittosporum undulatum* | 2 | 3 | - |
| *Smilax glyciphylla* | 1 | 18 | 5 |
| *Syzygium oleosum* | - | 4 | 2 |

## 4.1.7    Understorey indicator species

The validity of describing an understorey species as an indicator for any particular assemblage depends not only on its presence in that assemblage but also on the frequency of incidence and the fidelity or evenness of its distribution within the assemblage. For example, a species may be represented in all vegetation types but numerically far stronger in one than in others such that its level of abundance is the appropriate measure of its capacity to be treated as an indicator. The other aspect to consider is evenness. If a species occurs sparsely throughout an assemblage it can be regarded as a superior indicator to one which occasionally occurs in large numbers.

Consequently, it was necessary to have an abundance result for each species. Some species occasionally occurred in great profusion such that it was impractical to count the individuals. In this situation the area occupied was measured and a conversion factor applied to the areal figure. The species concerned and their conversion factors are shown in Table 4.12.

The result of the data collection of understorey species revealed a similarity of species richness for the WSF and WTRF while the TZF was found to be more species rich than either of the adjoining vegetation types. In terms of shared species there was a 58% affinity between the

Table 4.11   Summary of plot-based observations for species recorded in the mid-layer of WTRF which appear to have potential as indicators for a mid-layer community within the WTRF. All observations are from the mid-layer stratum only.

| Species | WSF obs. | TZF obs. | WTRF obs. |
|---|---|---|---|
| *Acmena hemilampra* | - | 4 | 7 |
| *Acronychia suberosa* | - | 12 | 24 |
| *Anopterus macleayanus* | - | 4 | 40 |
| *Archidendron grandiflorum* | - | - | 8 |
| *Archontophoenix cunninghamiana* | - | 60 | 122 |
| *Austromyrtus* sp. A | - | 1 | 7 |
| *Beilschmiedia elliptica* | - | - | 9 |
| *Caesalpinia scortechinii* | - | - | 5 |
| *Caldcluvia paniculosa* | 4 | 12 | 52 |
| *Canarium australasicum* | - | 2 | 4 |
| *Ceratopetalum apetalum* | 4 | 130 | 122 |
| *Cinnamomum oliveri* | 2 | 52 | 120 |
| *Cryptocarya glaucescens* | - | 1 | 8 |
| *Cryptocarya meissneriana* | 2 | 54 | 78 |
| *Cyathea australis* | 1 | 5 | 5 |
| *Cyathea leichhardtiana* | - | 6 | 48 |
| *Daphnandra tenuipes* | - | 17 | 87 |
| *Denhamia celastroides* | - | 1 | 6 |
| *Doryphora sassafras* | - | - | 6 |
| *Flagellaria indica* | - | 16 | 107 |
| *Halfordia kendack* | - | 1 | 11 |
| *Helicia ferruginea* | - | - | 65 |
| *Linospadix monostachys* | - | 1 | 46 |
| *Melodinus acutiflorus* | 2 | 16 | 52 |
| *Melodinus australis* | - | 5 | 32 |
| *Neolitsea dealbata* | - | 13 | 50 |
| *Notelaea longifolia* | - | 1 | 24 |
| *Pandorea pandorana* | - | - | 7 |
| *Parsonsia fulva* | - | 4 | 15 |
| *Planchonella australis* | - | - | 9 |
| *Psychotria simmondsiana* | - | - | 11 |
| *Randia benthamiana* | - | 13 | 108 |
| *Sarcopteryx stipata* | 2 | 19 | 67 |
| *Sloanea woollsii* | 1 | 1 | 15 |
| *Smilax australis* | 1 | 4 | 4 |
| *Stenocarpus salignus* | 1 | - | 22 |
| *Symplocos bauerlenii* | - | 5 | 56 |
| *Syzygium hodgkinsoniae* | - | - | 6 |
| *Syzygium luehmannii* | - | 2 | 5 |
| *Triunia youngiana* | - | - | 6 |
| *Uromyrtus australis* | - | - | 5 |
| *Wilkiea huegeliana* | - | 7 | 54 |

Table 4.12    Area (1 m$^2$) to abundance conversion values for those species which were normally or occasionally recorded in terms of m$^2$.

| Species | count per m$^2$ |
|---|---|
| *Adiantum hispidulum* | 80 |
| *Blechnum cartilagineum* | 50 |
| *Calamus muelleri* | 50 |
| *Cissus hypoglauca* | 20 |
| *Dawsonia superba* | 250 |
| *Dianella caerulea* | 50 |
| *Entolasia stricta* | 500 |
| *Exocarya scleroides* | 75 |
| *Gahnia aspera* | 25 |
| *Gahnia insignis* | 350 |
| *Helmholtzia glaberrima* | 10 |
| *Hibbertia dentata* | 25 |
| *Kreysigia multiflora* | 100 |
| *Lepidosperma elatius* | 25 |
| *Lepidosperma laterale* | 100 |
| *Lepidosperma urophorum* | 500 |
| *Lomandra longifolia* | 35 |
| *Patersonia glabrata* | 50 |
| *Petermannia cirrosa* | 50 |
| *Schoenus melanostachys* | 500 |
| *Sticherus lobatus* | 50 |
| *Viola hederacea* | 50 |

WSF and the TZF and a 62% affinity between the WTRF and TZF.

Identification of understorey indicator species for any of the forest types was somewhat problematical. No species met the requirements of being distributed evenly across and being exclusive to a particular formation. Also there was no understorey species that could confidently be regarded as a TZF indicator species although 22 of the 25 records for the Broad-leaved Palm Lily (*Cordyline petiolaris*) were recorded for the TZF. There were several WSF understorey species which were distributed patchily through the understorey with just a few records for TZF and another set of species which were similarly patchily distributed through the WTRF and were recorded rarely in the TZF. The list of these potential indicator species and their respective affinities are presented in Tables 4.13 and 4.14.

Table 4.13    Summary of plot-based observations for species recorded in the understorey layer of WSF which appear to have potential as indicators for an understorey community within the WSF.  All observations are from the understorey stratum only.

| Species | WSF obs. | Deciplots | TZF obs. | Deciplots |
|---|---|---|---|---|
| Lomatia silaifolia | 145 | 22 | 5 | 2 |
| Patersonia glabrata | 1238 | 40 | 4 | 2 |
| Polyscias sambucifolia | 325 | 43 | 19 | 6 |
| Pteridium esculentum | 108 | 35 | 4 | 3 |
| Xanthorrhoea latifolia | 133 | 34 | - | - |

Table 4.14    Summary of plot-based observations for species recorded in the understorey layer of WTRF which appear to have potential as indicators for an understorey community within the WTRF.  All observations are from the understorey stratum only.

| Species | WTRF obs. | Deciplots | TZF obs. | Deciplots |
|---|---|---|---|---|
| Blechnum patersonii | 2192 | 21 | - | - |
| Citriobatus pauciflorus | 145 | 22 | 5 | 2 |
| Denhamia celastroides | 44 | 22 | 10 | 3 |
| Helmholtzia glaberrima | 281 | 16 | - | - |

## 4.1.8    Foliage discolouration

Of the 249 species (248 vascular and one non-vascular) recorded in the plot-based survey, 21 exhibited a very obvious characteristic of white or very pale dorsal, or abaxial, leaf surfaces.  A further three species which possessed this characteristic were noted outside the plots.  Of this group (sensu lato), 16 were either exclusive to, or else achieved most prominence in the TZF, while six  were in the WSF and two were mainly in the WTRF.  The 16 TZF species are generally mesophyllous and have taxonomic affinities with rainforest species.  This suggests that they have evolved from the rainforest community by developing a method for coping with increased levels of light and greater potential water stress.

It has been suggested that the prevalent feature among WSF plants, sclerophylly, was developed primarily as an adaptation to low fertility

substrates (Beadle 1966) and that the capacity of this characteristic to contribute to the management of water stress was a secondary consequential advantage. It could be that the greater incidence of the trait of pale abaxial leaf surfaces (which are variably due to a covering of white or colourless hairs, or waxes, or simply an epidermal layer of cells lacking chlorophyll) among the TZF species indicates an alternative strategy to sclerophylly enabling transitional species to manage the microclimatic regime of the TZF. The hairs could serve to enhance the boundary layer close to the leaf surface thereby reducing water loss while the reflective capacity of the "paleness" could act as a mechanism to manage photosynthetic rates.

The fact that there were six members of the WSF plots which have also evolved this feature is supportive of the hypothesis while one of the rainforest species concerned was a member of the Proteaceae, a family which has a long and well-documented history of adaptive radiation to non-rainforest situations (White 1986). It may be that this particular species is evolving a capacity to succeed in the transition zone as many confamilial species have successfully done in epochs past. Unfortunately, the evaluation of this hypothesis requires substantial ecophysiological investigation which is beyond the domain of this study.

## 4.1.9      Floristics   analysis

### 4.1.9.1    Classification  of  species  and  sites

All the classifications of sites were subject to my cluster analysis validation program CLUANVAL and the results are shown in Figures. 4.13-4.15. The production of these classifications depended on, firstly, the completion of a preliminary classification of the plots and, secondly, on the production of predictive models for the distribution of all species in the study area. The detail of the models produced is described below. CLUANVAL indicates which branches in the hierarchy are in doubt  and the truncations to the hierarchy suggested by CLUANVAL are indicated by dotted lines in Figures 4.13 - 4.15. CLUANVAL looks for any species for which the 95% confidence range about the probability that it will occur in the environment described by one branch of a fusion does not overlap with the 95% confidence about
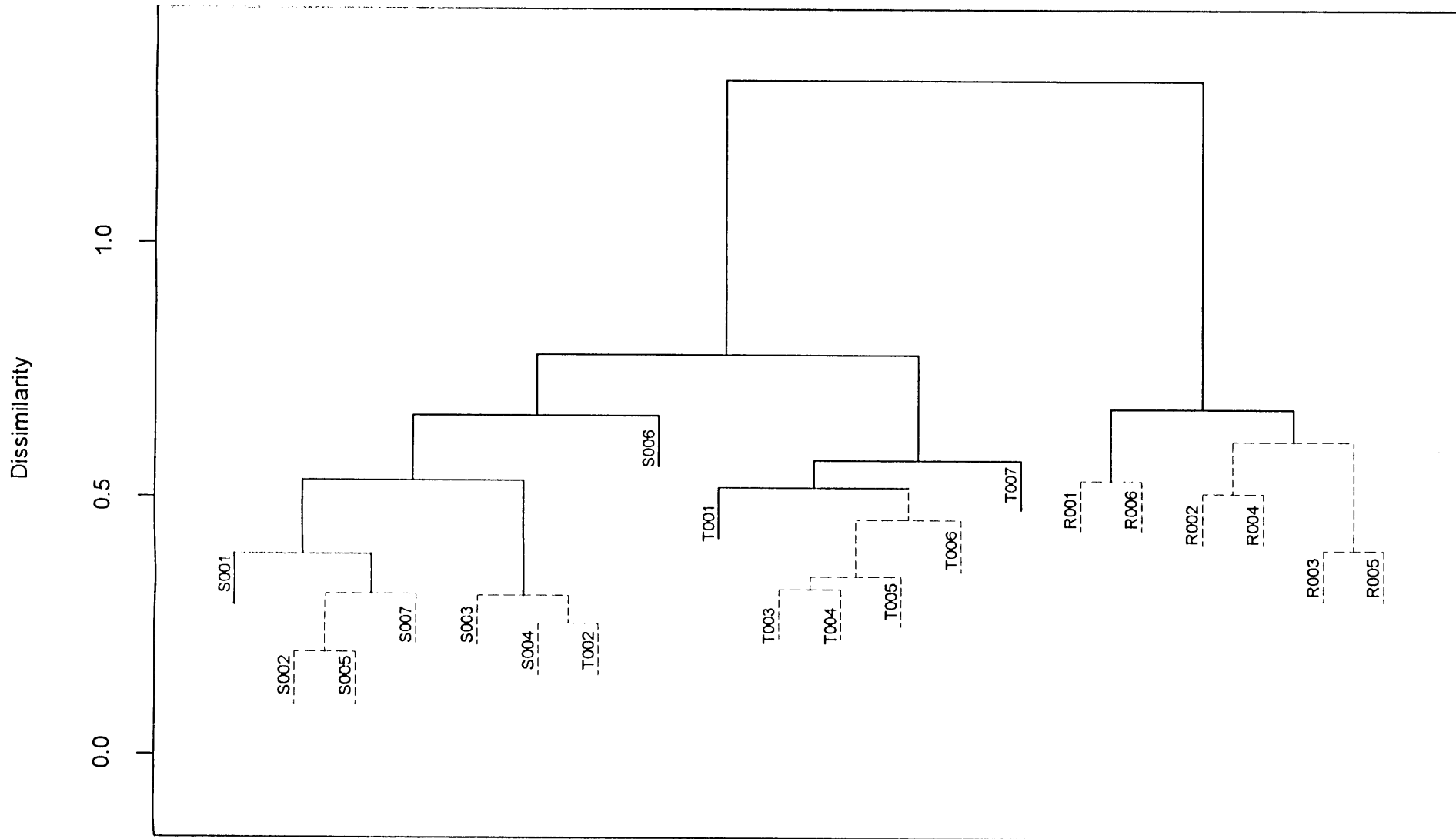
Figure 4.13   Classification of transect plots using canopy species

Association measure is Bray-Curtis and clustering uses an unweighted pair group mathematical averaging algorithm. The dotted lines indicate the fusions in the hierarchy which the CLUANVAL algorithm calculated were unreliable. Site codes beginning with "S" are WSF, "T" are TZF and "R" are WTRF.
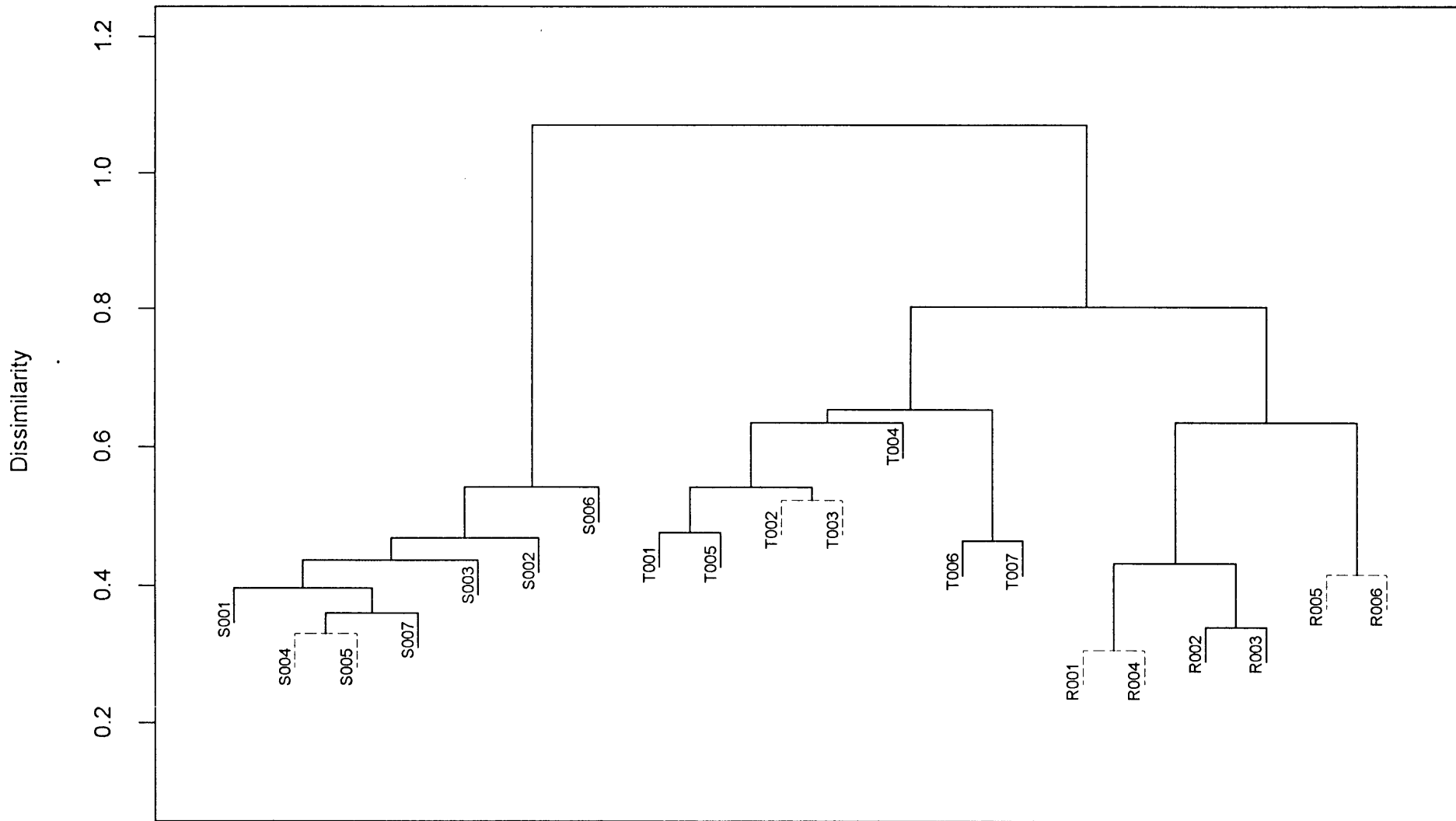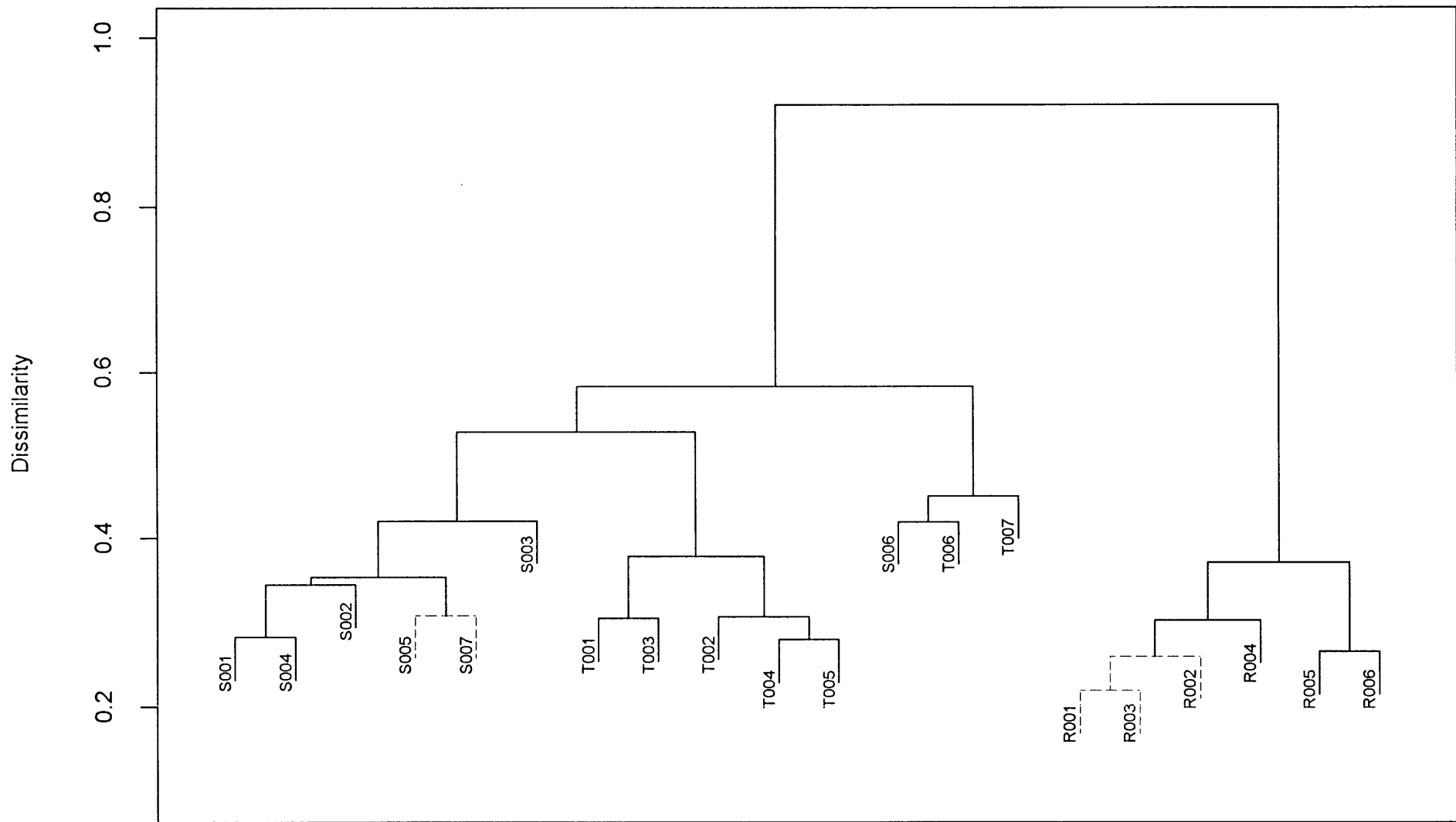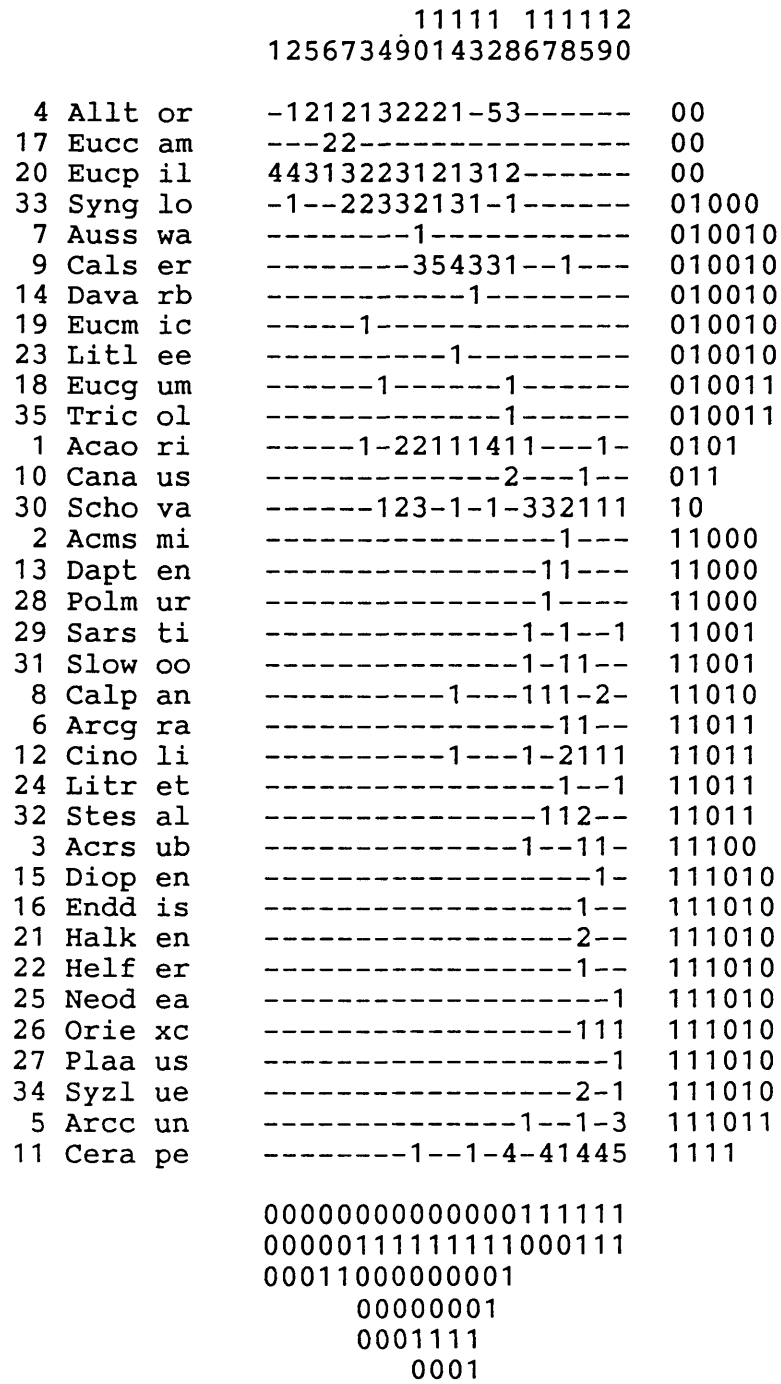
Figure 4.14   Classification of transect plots using mid-layer species

Association measure is Bray-Curtis and clustering uses an unweighted pair group mathematical averaging algorithm. The dotted lines indicate the fusions in the hierarchy which the CLUANVAL algorithm calculated were unreliable. Site codes beginning with "S" are WSF, "T" are TZF and "R" are WTRF.

Figure 4.15   Classification of transect plots using understorey species
Association measure is Bray-Curtis and clustering uses an unweighted pair group mathematical averaging algorithm.
The dotted lines indicate the fusions in the hierarchy which the CLUANVAL algorithm calculated were unreliable.
Site codes beginning with "S" are WSF, "T" are TZF and "R" are WTRF.

```
                              11111 111112
                       12567349014328678590

    4 Allt or       -1212132221-53------   00
   17 Eucc am       ---22---------------   00
   20 Eucp il       44313223121312------   00
   33 Syng lo       -1--22332131-1------   01000
    7 Auss wa       --------1----------   010010
    9 Cals er       --------354331--1---   010010
   14 Dava rb       -----------1--------   010010
   19 Eucm ic       -----1-------------   010010
   23 Litl ee       ----------1---------   010010
   18 Eucg um       ------1------1------   010011
   35 Tric ol       -------------1------   010011
    1 Acao ri       -----1-22111411---1-   0101
   10 Cana us       -------------2---1--   011
   30 Scho va       ------123-1-1-332111   10
    2 Acms mi       ----------------1---   11000
   13 Dapt en       ---------------11---   11000
   28 Polm ur       ---------------1----   11000
   29 Sars ti       --------------1-1--1   11001
   31 Slow oo       --------------1-11--   11001
    8 Calp an       ----------1---111-2-   11010
    6 Arcg ra       ----------------11--   11011
   12 Cino li       ----------1---1-2111   11011
   24 Litr et       -----------------1--1   11011
   32 Stes al       ---------------112--   11011
    3 Acrs ub       ---------------1--11-   11100
   15 Diop en       ------------------1-   111010
   16 Endd is       ------------------1--   111010
   21 Halk en       ------------------2--   111010
   22 Helf er       ------------------1--   111010
   25 Neod ea       ------------------1   111010
   26 Orie xc       -----------------111   111010
   27 Plaa us       ------------------1   111010
   34 Syzl ue       -----------------2-1   111010
    5 Arcc un       --------------1--1-3   111011
   11 Cera pe       --------1--1-4-41445   1111

                 00000000000000111111
                 000001111111111000111
                 00011000000001
                     00000001
                     0001111
                      0001
```

Figure 4.16    TWINSPAN classification of transect plots and canopy species. The plot shows the species codes to the left and the site numbers (1 to 20) along the top. The data are scaled abundances where 1 is rare and 5 is very common. The classification of sites appears at the bottom where the 0s and the 1s indicate how the sites were dfivided at each fusion. Splitting was terminated for classes of three or fewer members. The truncated hierarchical classification of the canopy trees appears on the right. This classification is significantly different from those appearing in Figures 4.13 and 4.17.

the probability that it will occur in the environment described by the other branch. Whenever a single species is found which satisfies this criterion then the fusion is regarded as significant and the algorithm proceeds down the hierarchy to the next fusion. The software used for the preliminary classification is PATN v. 3.6 (Belbin 1993).

For comparison with the PATN output, alternative classifications were performed using the popular TWINSPAN (Hill 1979). The output for the dual classification of sites x canopy species using that program is shown as Fig. 4.16. The TWINSPAN classification is similar to Fig. 4.13 only at the first division which separates rainforest sites from the rest. Thereafter, the TWINSPAN result becomes increasingly unreliable. This dissimilarity was not confirmed statistically although the ideas of both Strauss (1982) and the two-way contingency tables of Digby and Kempton (1987) in this situation were noted. I chose to test my classification somewhat pragmatically by preparing a parallel classification of sites based on my assessment rules, i.e., species richness, species evenness and total abundance of individuals.

### 4.1.9.2 Interpretation of classification

The first classification was the comparatively simple one of transects based on canopy species alone. Fig. 4.13 shows the that the sites readily split into the three expected groups based on the distribution of canopy species. The initial classification grouped the transition zone plot from transect 2 with the WSF plots which reflects the prominence of WSF canopy species in the TZF for that transect. The validation of this classification based on the confidence of the predictions for the component species which emanated from the distribution models, resulted in several fusions in the hierarchy being treated as unreliable.

The modelled confidences for the occurrence of each species at each site were derived from generalised additive models which are described in Section 4.1.10. The approach presented here to reduce classification error is still experimental and the variables used to produce the models were essentially those that were available, but the preliminary results are encouraging. In the cases where sites were classified using only the mid-layer or understorey species, because there were many more

species, it was expected that there would be fewer adjustments to the PATN-derived classifications of sites. Figures 4.14 and 4.15 show this to be so, yet still there is evidence that even these simple dendrograms for 20 sites still incorporate significant error.

The results of the three classifications (Figs. 4.13-4.15) show the important result that at each stratum the three vegetations are floristically distinct. This result is important because it means that the TZF situations are recognizable regardless of the variations in their size and physical setting and despite the floristic differences between all of the TZF transects. The understorey classification (Fig. 4.15) shows the WSF site 6 being grouped with the TZF sites. This site differed from the other WSF sites in that it lacked the significant component of a grass/sedge/fern sward. The scattered shrubs and tree seedlings gave it a similar structure to the typical TZF understorey. WSF site 6 was also shown as distinct from the other WSF sites in Fig. 4.13. This is due to the prominence of *Eucalyptus campanulata* in the canopy.

The classification of canopy species (Fig. 4.17) is an excellent portrayal of the relationships of the species insofar as it closely resembles impressions noted in the field. The classification was performed by PATN and it is notable for the significantly different placements of *Syncarpia glomulifera*, *Eucalyptus campanulata* and *Ceratopetalum apetalum*, as well as several of the minor canopy species, as compared with the TWINSPAN result in Fig. 4.16. Fig. 4.17 shows the grouping of the WSF species to the left, gradually fusing with uncommon TZF species, then the main TZF species which all have rainforest affinities, and finally the large group of rainforest species.

The separate classifications of the sample areas within each forest type (Figs. 4.18-4.20) revealed a level of heterogeneity among transects which was not apparent in the field. It was expected that there would be considerable similarity between the sample areas of the transects. The sample areas were submitted to the classifying algorithm in sample area code order, and it is not clear to what extent that has influenced the result. The trend of the classifications, however, matches field impressions. The trend shows that the rainforest patches are markedly
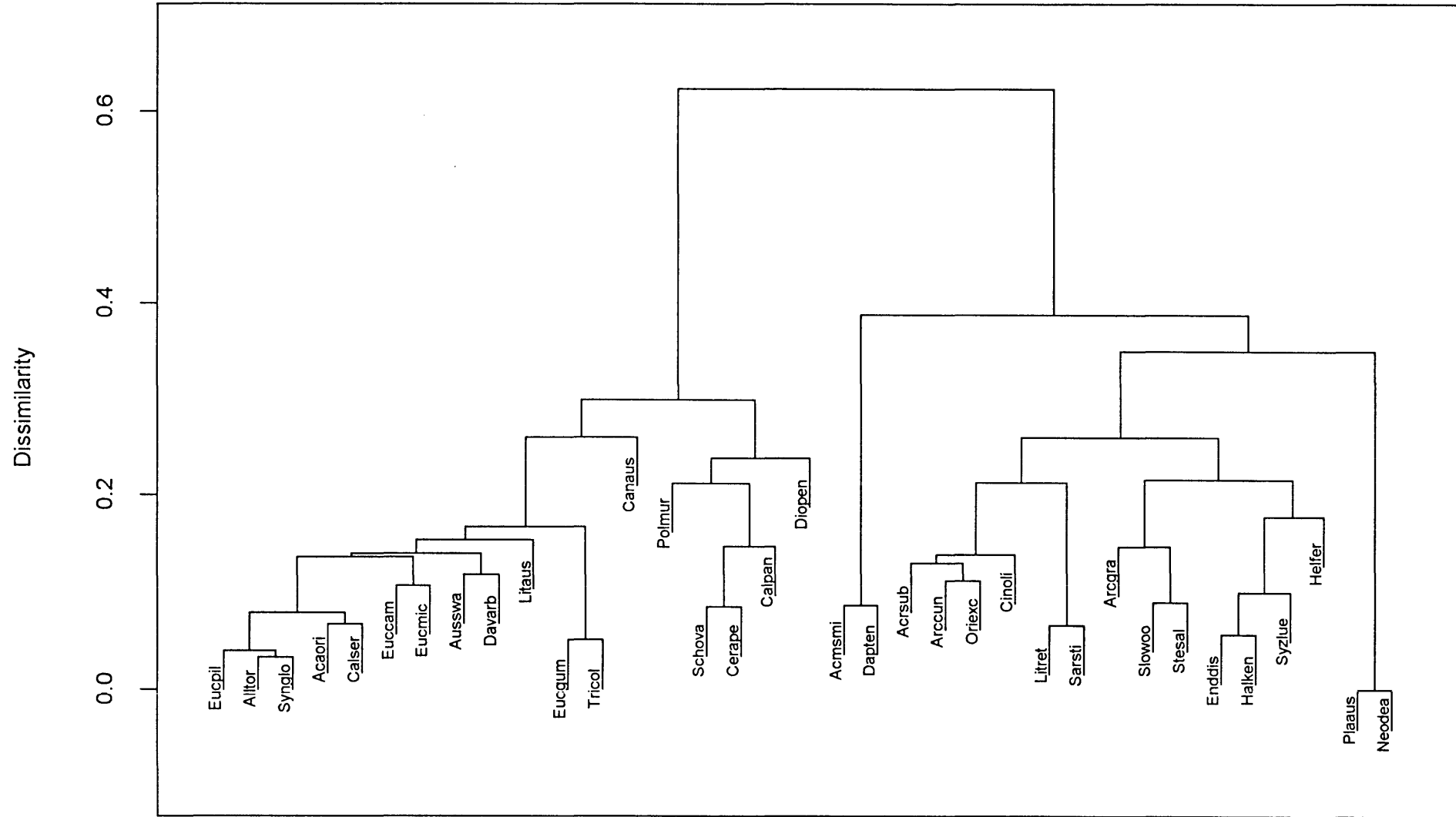
Figure 4.17   Classification of canopy species occurring in the transects.
Association measure is Two Step and clustering uses an unweighted pair group mathematical averaging algorithm.
Species codes are a concatenation of the first three letters from the genus and from the specific epithet.
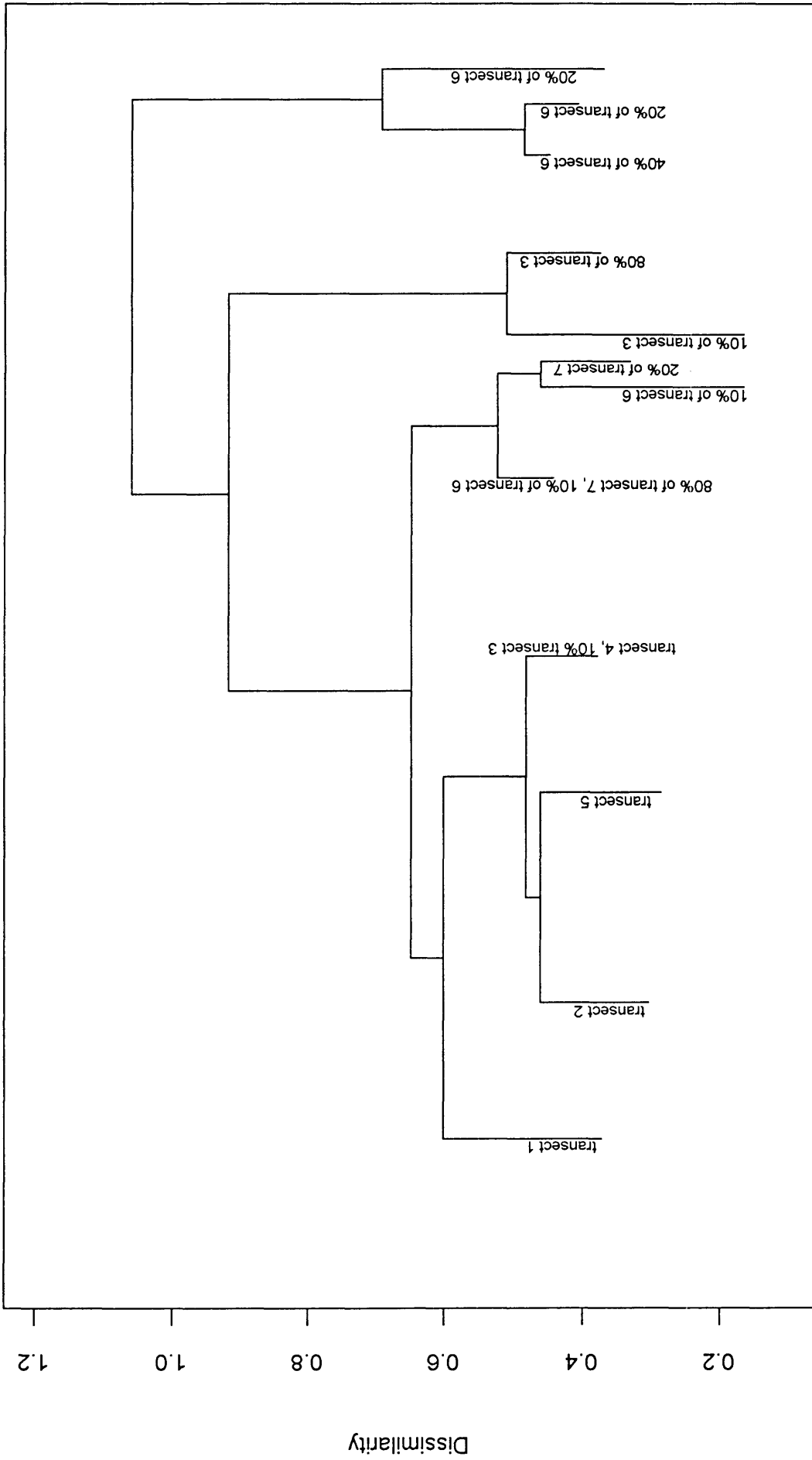
Figure 4.18  Classification of sample areas in WSF.
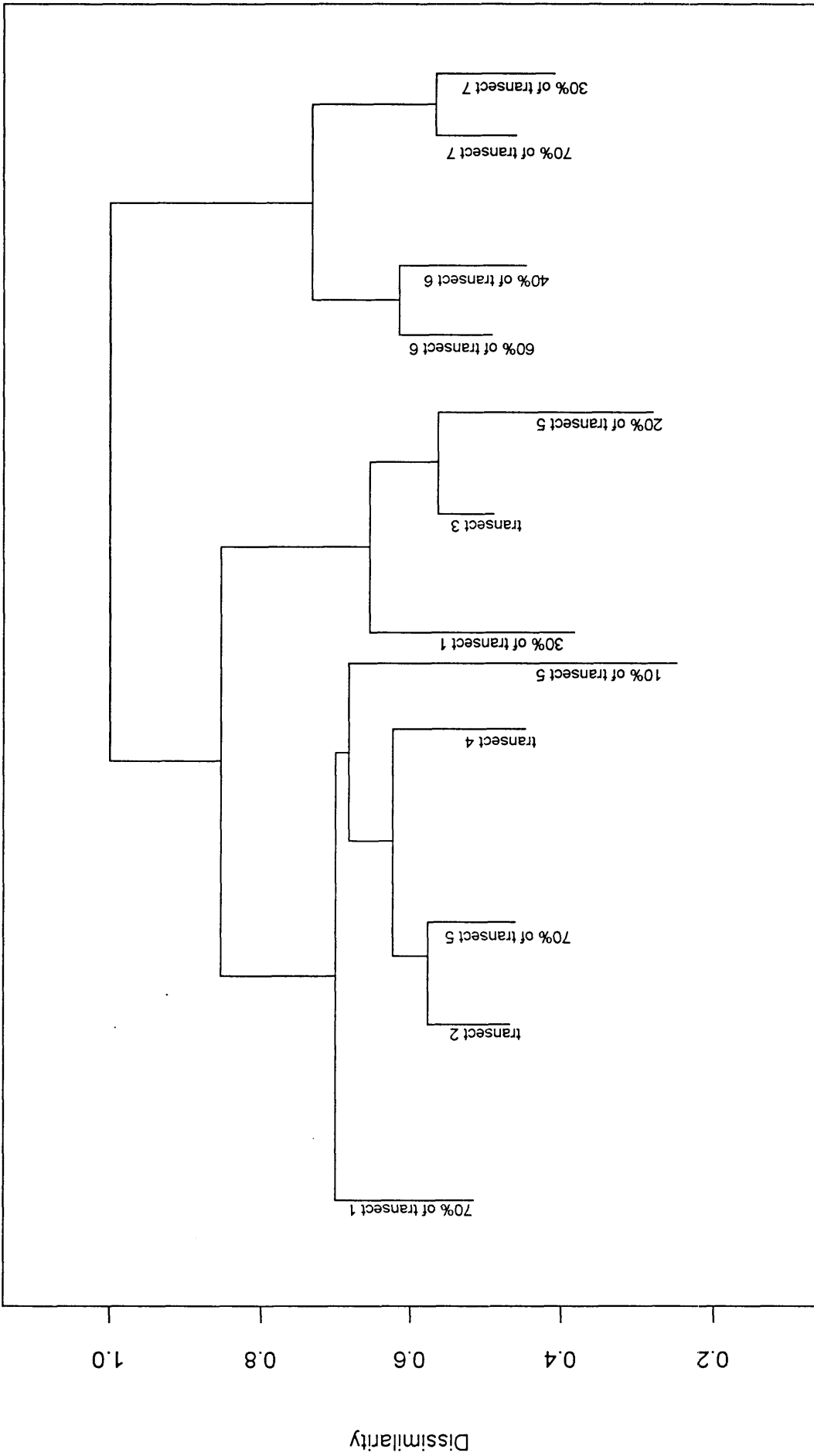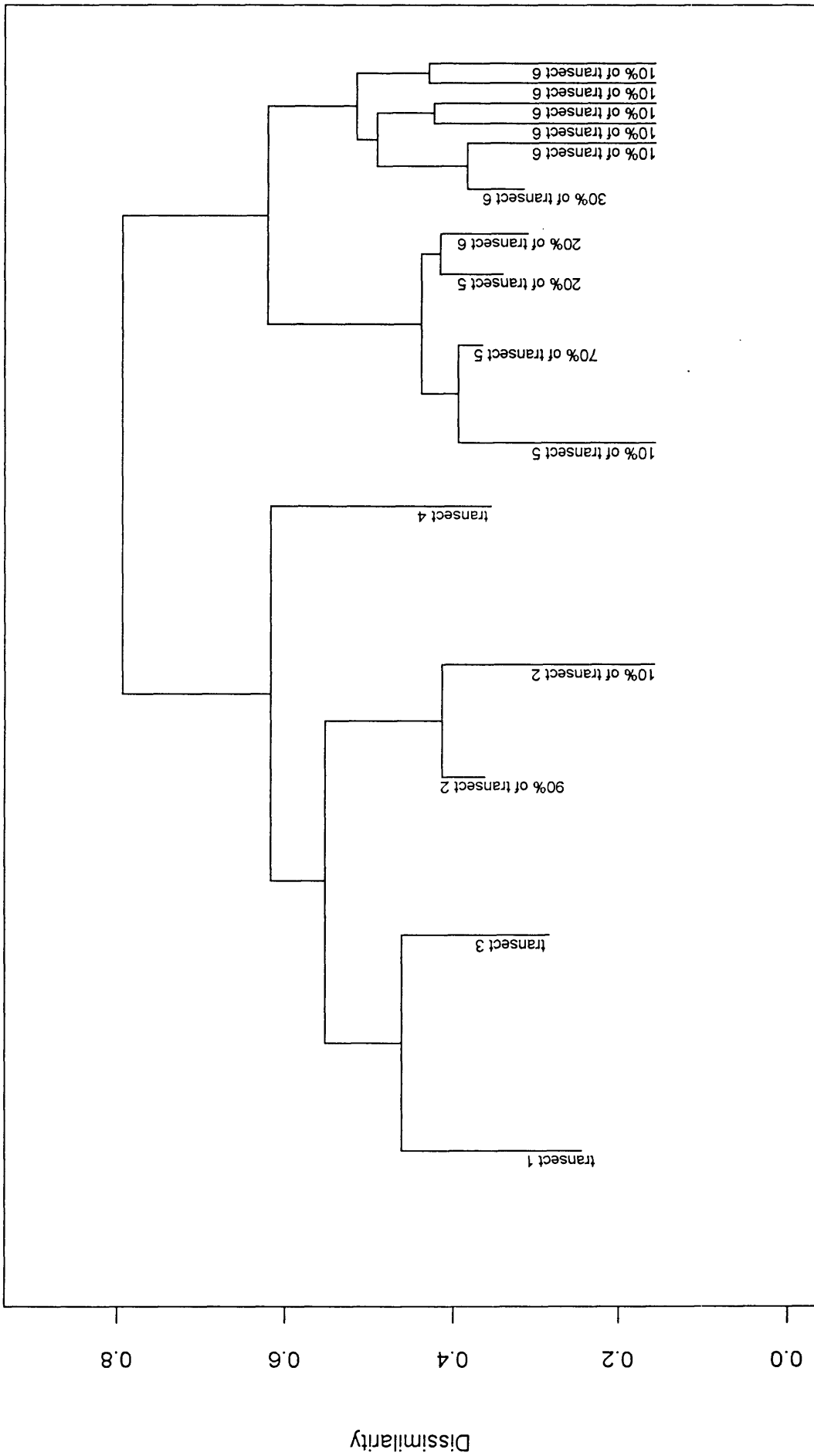Association measure is Bray-Curtis and clustering uses an unweighted pair group mathematical averaging algorithm.

Figure 4.19   Classification of sample areas in TZF.
Association measure is Bray-Curtis and clustering uses an unweighted pair group mathematical averaging algorithm.

Figure 4.20  Classification of sample areas in WTRF.
Association measure is Bray-Curtis and clustering uses an unweighted pair group mathematical averaging algorithm.

heterogeneous, the transition zone patches somewhat less so and the the wet sclerophyll forest were the least heterogeneous with several sample areas showing similarity with those from another transect.

In Section 3.4.2, I referred to the special data collection for *Archontophoenix cunninghamiana* and *Cryptocarya rigida*. The results of this investigation are shown in Table 4.15. The two species have population densities and forest type affiliations which are unique amongst the species sampled. From Table 4.15, the sizes of the standard deviations indicate immediately the patchiness of even the most typical of species for these forests. The microclimate of the rainforest suits the germination requirements of *A.cunninghamiana* but the ratio of juvenile plants to seedlings is very low in that forest type. This low ratio is presumed to be due to competition with other plants. There was no evidence that the seedlings were being predated by either vertebrates or invertebrates. The species clearly experiences severe intra-specific competition as many seedlings can be densely clumped together in a space with might permit perhaps two mature specimens to eventually occupy. Competition from other plant species comes in the form of overshadowing. *A.cunninghamiana* seedlings are not able to persist at, or not far beyond, the cotyledon stage for many years waiting for ideal growth conditions, as are many of the other trees of the rainforest. They need access to, at least, intermittent, elevated light levels to develop. There are two ways in which that development is suppressed by other species in the WTRF. The first is the obvious one in which the canopy is closed and remains so in the critical early years of the seedlings life. The second mechanism perhaps has to do with the morphology of the cotyledon of *A.cunninghamiana*. The seedlings appear to be less resilient to the rain of litter than are the taller seedlings of the other tree species. The litter tends to lie on the seedlings severely reducing their access to light. Seedlings buried under the influx of dying leaves resulting from the broken limb of an overhanging tree commonly perish. The reduced understorey competition of the transition zone (in terms of the numbers of plants, not species, in the understorey layer), in conjunction with a more open canopy, allows a much higher percentage of seedlings to reach the juvenile stage of development.

Once having established as juveniles, the species is more likely to reach

Table 4.15    Distribution of size classes across the three forest types of
two indicator species, *Archontophoenix cunninghamiana* and
*Cryptocarya rigida*. Figures are densities per 0.1 ha. The
standard deviation is shown in brackets (n = 7)

| | WSF | | TZF | | WTRF | |
|---|---|---|---|---|---|---|
| *A. cunninghamiana* | | | | | | |
| trees | | 0 | 8.57 | (9.43) | 22 | (19.2) |
| juveniles | 3.86 | (5.87) | 58.71 | (57.53) | 61.6 | (36.94) |
| seedlings | 85.14 | (41.13) | 325.57 | (181.7) | 1040.67 | (1060.9) |
| | | | | | | |
| *C. rigida* | | | | | | |
| trees | 46.57 | (36.25) | 8.29 | (9.72) | 0 | |
| saplings 2m-3m | 64.57 | (18.16) | 28.14 | (21.22) | 0 | |
| saplings 1m-2m | 68.86 | (29.91) | 80.57 | (53.3) | 0 | |
| seedlings | 137.57 | (72.3) | 165.86 | (107.99) | 0.17 | (0.41) |

tree status in the rainforest than in the transition zone.    The reduced
and variable   moisture status of the transition zone is presumed to not
meet the requirements of mature specimens of *A.cunninghamiana.* and
this situation is exacerbated by the WSF.   The hostility of the WSF
environment for this species is indicated by the pattern of its
occurrences in the WSF transects.   In that forest type *A.cunninghamiana*
manages to find a significant number of suitable germination sites but
only a very small percentage of the seedlings proceed to the juvenile
stage and none at all occurs as a tree.

*Cryptocarya rigida*  displays a very different response.  From a
rainforest ancestry this species has evolved an adaptation to lower
moisture and higher light environments.   It is now most plentiful in the
WSF and there was only one instance of this species occurring in a
rainforest sample.   The highest density of seedlings for this species
was found in the TZF but the high standard deviation for that density
(see Table 4.13) indicates that its distribution was more patchy than in
the WSF.   Once having obtained small sapling size, this species has very
high rates of progression to the larger growth size classes.   In the TZF,
however,   this species experiences successively deteriorating chances
of progressing to the next size class.

## 4.1.10    Predictive species models

The response of the main indicator species to the variables used in the modelling process is very interesting and three key species are presented, one from each of the forest types.  The question of interest is:  to what environmental factors do the species show sensitivity?  The three models with the upper and lower 95% confidence intervals are presented as Figures 4.21-4.23.  Taking each one in turn, Fig. 4.21 shows the response of *E. pilularis* to the variables found to be most significant in the modelling process.  The most important variable was the dominant vegetation at the site (Fig. 4.21a).  There were no records for *E. pilularis* at WTRF sites so this variable was able to explain much of the variation in the data.  The response to aspect (Fig. 4.21b) predicts a clear association with the sunnier, northern aspects while the slight flattening of the other end of the curve is due to the few sample units on southeast- or southwest-facing spurs.  The relationship of *E. pilularis* with rocky sites (Fig. 4.21c) is complicated by one deciplot at which about 15% of the surface comprised exposed rock.  The extent to which that one site is contradictory is indicated by the widening confidence intervals at the upper end of the curve.  Normally, this species, while flourishing on lower fertility sites, is not associated with rocky situations.  The association with annual hours of direct afternoon radiation (Fig. 4.21d) shows that *E. pilularis* does not grow at those sites maximally exposed to afternoon sunshine.  These sites in the study area are occupied by *E. campanulata* on the highest points of the plateau and by *E. gummifera* and *E. signata* elsewhere.  Nor does it grow at those sites which are sheltered from afternoon sunshine which are predominantly occupied by WTRF.

One of the main TZF species, *Callicoma serratifolia*, is shown in Fig. 4.22.  This species exhibited a definite association with locations obtaining most of their annual direct radiation before noon (Fig. 4.22a).  The outlier group showing up on the plot are due to the precision of the environmental grid used for modelling.  This grid was defined using 1 ha cells which meant that the values for the cell were averages for the whole of the cell.  The outlying group of sites containing *C. serratifolia* were, in fact on deciplots experiencing greater morning radiation than the cell as a whole.  The selection of aspect (Fig. 4.22b) for the model
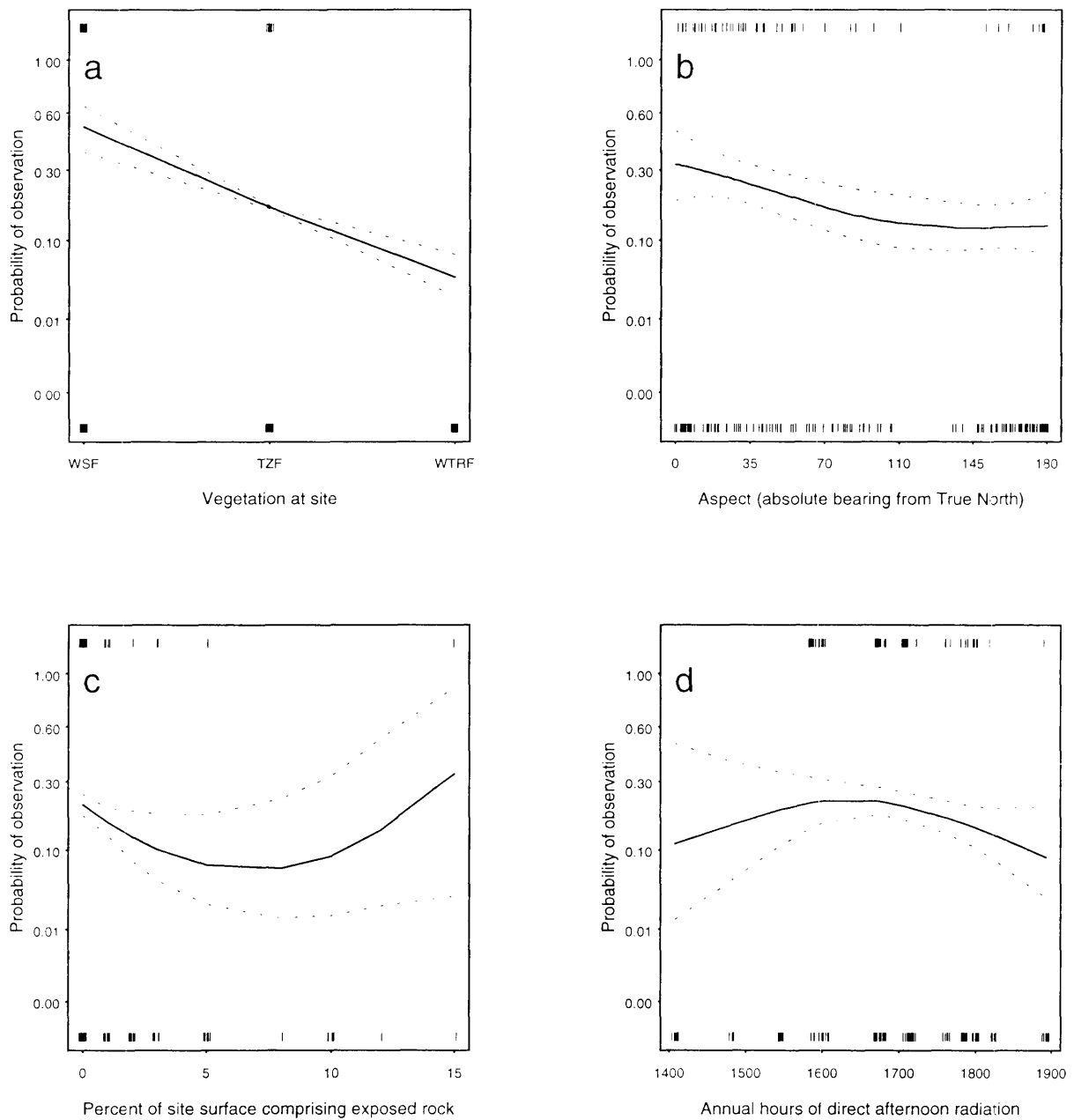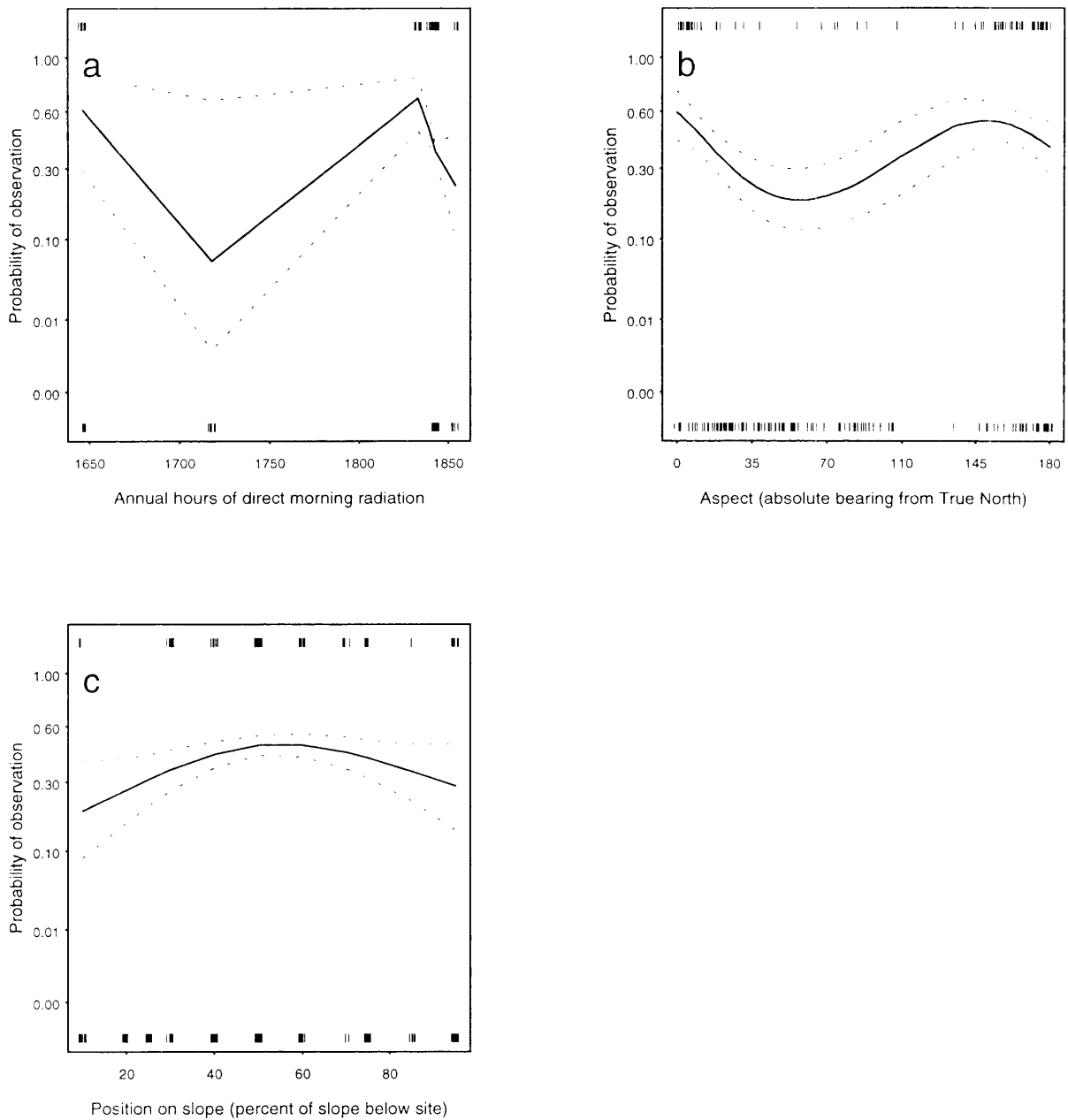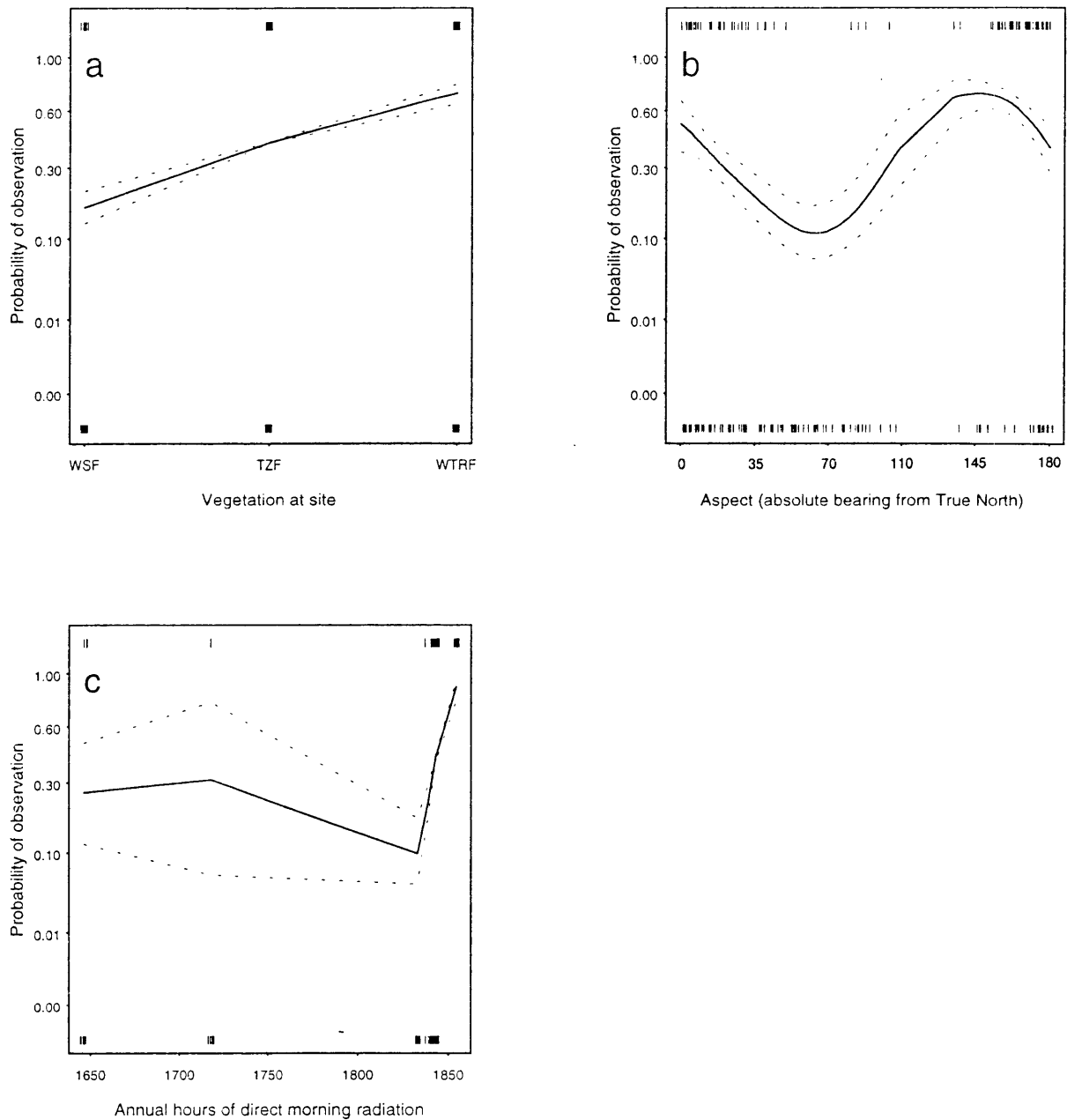
Figure 4.21    The relationships between the data and the variables selected for the GAM constructed to model the distribution of *Eucalyptus pilularis* in the study area.   The solid lines are the model predictions and the dotted lines are the 95% confidence limits around the predictions.   The probability of observation at a 0.01 ha site is scaled in order to accentuate the nature of the low probability region.   The markings along the top of the plots show the positive observations and those along the base of the plots show the negative observations. The individual plots are in the order of importance to the model and are discussed more fully in the text.

Figure 4.22    The relationships between the data and the variables selected for the GAM constructed to model the distribution of *Callicoma serratifolia* in the study area.   The solid lines are the model predictions and the dotted lines are the 95% confidence limits around the predictions.   The probability of observation at a 0.01 ha site is scaled in order to accentuate the nature of the low probability region.   The markings along the top of the plots show the positive observations and those along the base of the plots show the negative observations. The individual plots are in the order of importance to the model and are discussed more fully in the text.

reflected the distribution of survey transects. This species was widespread from northerly to southerly aspects experiencing predominantly morning sunshine. More data in the middle aspect range may have negated the importance of this variable. This species typically occupies a middle position on the slope (Fig. 4.22c) especially on slopes where a point of inflection occurs as in a type "1" slope (see Table 1.1).

The last model presented in Fig. 4.23, is that for *C. apetalum*, the most prominent rainforest tree species. The most important variable was vegetation type (Fig. 4.23a). This species was predominantly recorded in WTRF with many records in TZF and a few seedlings found in WSF. The straight line representation of this relationship is expected but the slope is reduced by the dominance at some WTRF sites of *Schizomeria ovata* which excluded *C. apetalum*. This species shows strong associations with southern facing aspects (Fig. 4.23b, cf. Fig. 4.21 for *E. pilularis* ) but apparently southeast facing sites because there is an association with sites which receive high levels of morning sunshine (Fig. 4.23c). The same comments about the precision of the grid made in reference to the modelled response to morning radiation for *C. serratifolia* also apply to Fig. 4.23c.

Figure 4.23    The relationships between the data and the variables
selected for the GAM constructed to model the distribution
of *Ceratopetalum apetalum* in the study area. The solid lines
are the model predictions and the dotted lines are the 95%
confidence limits around the predictions. The probability of
observation at a 0.01 ha site is scaled in order to accentuate
the nature of the low probability region. The markings along
the top of the plots show the positive observations and those
along the base of the plots show the negative observations.
The individual plots are in the order of importance to the
model and are discussed more fully in the text.

## 4.2 Vegetation structure survey

### 4.2.1 Growth forms

The growth forms of plants recorded in the sample areas were split into 12 categories. These were:

Field code        Description

| | |
|---|---|
| T | tree |
| V | canopy liane |
| P | palm tree |
| R | small-tree (includes small trees, aged treeferns and "emergent shrubs") |
| S | understorey woody plant (includes tree seedlings) |
| C | understorey climber or scrambler |
| F | ground fern (includes young treeferns) |
| H | herb (includes sedges and undifferentiated palm seedlings) |
| G | grass |
| E | epiphyte |
| L | lithophyte |
| M | mistletoe |

In order to describe structure it made sense to allow some species to be members of more than one group. Essentially, the incidence of multiple group membership applied to those plants that either exhibited morphological variation with age or else had the capacity to persist in a particular height stage for extended periods. For example, some species, notably the palms, germinate readily in all habitats but in WSF only rarely survive beyond the production of their first seedling leaf. Thus palm seedlings were treated as herbs until they were tall enough to have established the typical palm appearance whereupon I treated them as understorey woody plants and those that were tall enough were included with the small trees. Similarly, young treeferns were treated initially as ground ferns but once the trunk had developed I placed them in the understorey woody plants group while some were sufficiently tall to be grouped with the small trees.

Juvenile trees were treated as understorey woody plants. There were several justifications for this approach. Firstly, as mentioned above, many tree seedlings never succeed in growing out of the understorey layer. Secondly, at the time of recording, their contribution to forest structure is not as a tree but as a member of the understorey layer. Further, a number of tree species, particularly among WTRF species, may develop a very bushy growth form up to a height of about 1.5 m such that they offer similar shelter opportunities for small fauna to those offered by genuine shrub species and hence share some ecological attributes with the genuine understorey species.

Some orchids and ferns occurred as both lithophytes and epiphytes in the sample areas. The actual substrate for these species was sometimes ambiguously recorded in the field so they were allocated a growth form according to the substrate on which they were most commonly encountered.

According to these rules, the numbers of species in each growth form group for each vegetation formation are shown in Table 4.16. From these data it is evident that the distribution pattern of plant growth forms in each vegetation group is fairly similar although a few interesting features can be highlighted. In the TZF, the large number of woody species in the understorey layer in relation to the number of tree species indicates the suitability of this forest habitat type to many taxa while the actual ratio of species of trees to species of understorey woody plants is about the same as WSF. There are marginally more climber species in the TZF than elsewhere, a superiority which might have been expected to be greater given the propensity of light-loving rainforest climbers and scramblers to occur commonly at the rainforest edge (Williams and Harden 1984).

The high numbers of epiphytes in the WSF and TZF compared to the WTRF at first glance might be regarded as a surprising result and, as indicated above, it is possible that the rainforest epiphyte count may be under-represented. The WTRF is, however, noted for the fewer numbers of epiphytes (Floyd 1990b) than the sub-tropical rainforest formation. The WTRF has a generally more uniform canopy (Floyd 1990b) such that within the canopy there is a significantly different light regime to that

Table 4.16    Count of species within each growth form across forest types

| Growth form | WSF | TZF | WTRF | Total |
|---|---|---|---|---|
| tree | 33 | 44 | 49 | 69 |
| canopy liane | 6 | 10 | 18 | 20 |
| palm tree | - | 2 | 2 | 2 |
| small-tree | 10 | 15 | 19 | 27 |
| u/s woody plant | 81 | 111 | 85 | 132 |
| u/s climber | 28 | 36 | 35 | 48 |
| ground fern | 8 | 8 | 7 | 9 |
| herb | 20 | 23 | 15 | 28 |
| grass | 2 | 2 | - | 2 |
| epiphyte | 11 | 10 | 9 | 15 |
| lithophyte | 1 | 1 | - | 2 |
| mistletoe | 2 | 2 | 1 | 3 |

of the uneven-canopied sub-tropical rainforest. Consequently, there are fewer habitat opportunities for the light-loving epiphytes in WTRF. The more uneven canopies in WSF and TZF provide ample light not only for epiphyte habitats and but also for the vegetation surveyor trying to count them.

The last significant point to make from Table 4.16 concerns the distribution of ground fern species. The understorey of WTRF typically has a well-developed fern component (e.g. Floyd 1989, Fig. 4d) and this component is comprised of a few very successful species. In WSF and TZF, where the ground light levels are higher, and competition from herb flora greater, ferns do not reach the same numerical dominance. There is one notable exception to that statement in the WSF. In that forest type *Sticherus lobatus* can occur in such numbers as to locally exclude all other ground species. In both WSF and TZF, however, the variety of understorey conditions provides habitats suitable to an increased number of fern species.

From the above comments about the data presented in Table 4.16, the following questions were signalled: how are the abundances of the individuals of each growth form group distributed across the vegetation gradient? and, what is the average abundance per species per unit area within a growth form group? The answer to the first of these questions is provided by Table 4.17 where the profile of the TZF is placed neatly between those of the WSF and WTRF for almost all growth form groups.

Table 4.17    Counts of component individuals by growth form across vegetation groups in a 0.1 ha sample.
The confidence limits are set to 95%. All values are rounded to the nearest whole number causing the result for the few mistletoes recorded to show as zero. WSF values significantly different from TZF and TZF values significantly different from WTRF are indicated by * (P < 0.05) or ** (P < 0.01). The very large confidence limits around grasses herbs and ground ferns reflects the large numbers in which these plants occur and the patchiness of those occurrences

| Growth form | WSF | | TZF | | WTRF |
| --- | --- | --- | --- | --- | --- |
| tree | 221 ± 69 | * | 151 ± 30 | | 184 ± 65 |
| canopy liane | 11 ± 10 | | 25 ± 28 | | 52 ± 39 |
| palm tree | - | * * | 9 ± 7 | * * | 30 ± 17 |
| small-tree | 9 ± 11 | | 15 ± 9 | * | 59 ± 33 |
| u/s woody plant | 798 ± 266 | * * | 1156 ± 330 | * * | 2621 ± 1168 |
| u/s climber | 606 ± 288 | | 757 ± 323 | * | 3620 ± 3565 |
| ground fern | 6041 ± 2174 | * * | 1609 ± 560 | | 1422 ± 772 |
| herb | 53749 ± 67940 | | 26658 ± 29696 | | 4091 ± 1710 |
| grass | 8382 ± 7222 | * | 2059 ± 1709 | * | - |
| epiphyte | 15 ± 19 | | 14 ± 8 | * * | 33 ± 18 |
| lithophyte | 5 ± 9 | | 1 ± 1 | | - |
| mistletoe | 0 ± 0 | | 0 ± 0 | | 0 ± 0 |

The average number of individuals per species in the understorey (woody plants and climbers) is much smaller in the TZF than in the rainforest. This result confirms the field impression of the TZF being a much less vegetatively cluttered community.

In comparison with the WSF, the greatly reduced numbers of herbs, grasses and ground ferns (in terms of abundances, not species) in the TZF results in a greater area of ground covered in tree litter which reinforces the same impression gained when entering the TZF from the WTRF, that is, at the understorey level, the TZF is a more open community of fewer plants. The very high error figures for the understorey layer flora, particularly the grasses, herbs and ground ferns, is due to the patchy nature of their occurrence. This patchiness is mainly in response to canopy gaps and the distribution of localised ground level disturbance. In summary, the understoreys of all three vegetation types studied are markedly heterogeneous, and as illustrated in the analysis of understorey floristics, several distinct assemblages of plants were identifiable in the understoreys.

Table 4.18    Tree stem packing density by size class for each vegetation formation 0.1 ha$^{-1}$.

|  | WSF | TZF | WTRF |
|---|---|---|---|
| Density of stems > 60 cm DBH | 6 | 7 | 5 |
| Density of stems 40-60 cm DBH | 5 | 4 | 7 |
| Density of stems 20-40 cm DBH | 17 | 19 | 18 |
| Density of stems 10-20 cm DBH | 30 | 29 | 44 |
| Density of stems < 10 cm DBH | 172 | 115 | 198 |

The notable exception to the general intermediate position of the TZF suggested by Table 4.17 is the tree growth form group. In this case the TZF is numerically markedly less endowed than the other formations. This is the structural feature of the transition zone. The TZF does not have the crown density of the canopy trees of the rainforest but the canopy is still sufficiently closed to limit the numbers of WSF mid-layer species from attaining the large abundances recorded in the WSF mid-layer. Table 4.18 provides a more detailed breakdown of the tree data. There the differences between the two main forest types and their boundary zone is indicated by the substantially reduced packing density of the TZF mid-layer.

Of associated interest was how populous, or how commonly encountered, were the species comprising any particular growth form group along the vegetation gradient. Table 4.19 provides this breakdown. As in Table 4.17, the high errors are due to variations in the dominant understorey flora from site to site. As demonstrated in floristics analysis, there was also significant within-site variation but that level of variation does not contribute to the confidence limits in either of Tables 4.17 or 4.19. The profiles displayed in Table 4.19 give an insight to the hybrid nature of the TZF. The average abundance/species ratio within the taller growth form groups in the TZF is similar to the WTRF while the same ratios for lower growth form groups have greater affinity to the WSF results.

4.2.2    Vegetation layers

Figures 4.24 a-f show plots of the sorted heights of tall plants recorded

Table 4.19    Average abundances per component species by growth form
across vegetation groups in a 0.1 ha sample.
The confidence limits are set to 95%. All values are rounded to
the nearest whole number causing the result for the few
mistletoes recorded to show as zero. WSF values significantly
different from TZF and TZF values significantly different from
WTRF are indicated by * (P < 0.05) or ** (P < 0.01). The
very large confidence limits around grasses herbs and ground
ferns reflects the large numbers in which these plants occur
and the patchiness of those occurrences

| Growth form | WSF | | TZF | | WTRF |
|---|---|---|---|---|---|
| tree | 17 ± 6 | * * | 8 ± 1 | | 7 ± 2 |
| canopy liane | 6 ± 4 | | 4 ± 2 | | 6 ± 4 |
| palm tree | - | * * | 9 ± 7 | * | 22 ± 16 |
| small-tree | 3 ± 2 | | 4 ± 1 | | 6 ± 2 |
| u/s woody plant | 22 ± 6 | | 22 ± 5 | * * | 49 ± 19 |
| u/s climber | 42 ± 16 | | 35 ± 13 | * | 180 ± 191 |
| ground fern | 1361 ± 686 | * * | 301 ± 150 | | 272 ± 125 |
| herb | 4374 ± 5652 | | 2044 ± 2018 | | 537 ± 249 |
| grass | 8362 ± 7236 | * | 1763 ± 1572 | * | - |
| epiphyte | 3 ± 3 | | 3 ± 2 | * | 6 ± 3 |
| lithophyte | 5 ± 9 | | 1 ± 1 | | - |
| mistletoe | 0 ± 0 | | 0 ± 0 | | 0 ± 0 |

from six WSF sample units of 0.1 ha. Even at that scale it is apparent
from those Figures that the canopy is very uneven in terms of both
height and regularity such that plant heights appear to represent a
continuum from canopy to forest floor. The reduction of the working
area by an order of magnitude to .01 ha to and concatenation of these
units enabled the pattern of any vertical stratification within each
forest type to became apparent.

In order to identify the presence of tree layers, it was necessary to
first identify the presence of regular discontinuities in the spectrum of
plant heights for each of the sample units. It was then necessary to
derive a formula to assist the determination of whether any particular
height discontinuity in a sample unit was significant or not. I
generalised that as the distribution of heights for each area is
lognormal, for a discontinuity to be significant then the further along
the height spectrum that it occurs the larger it must be. The formula
devised for discontinuity significance was that amongst the shortest
25% of trees the discontinuity must be at least 2 m, and a sliding scale
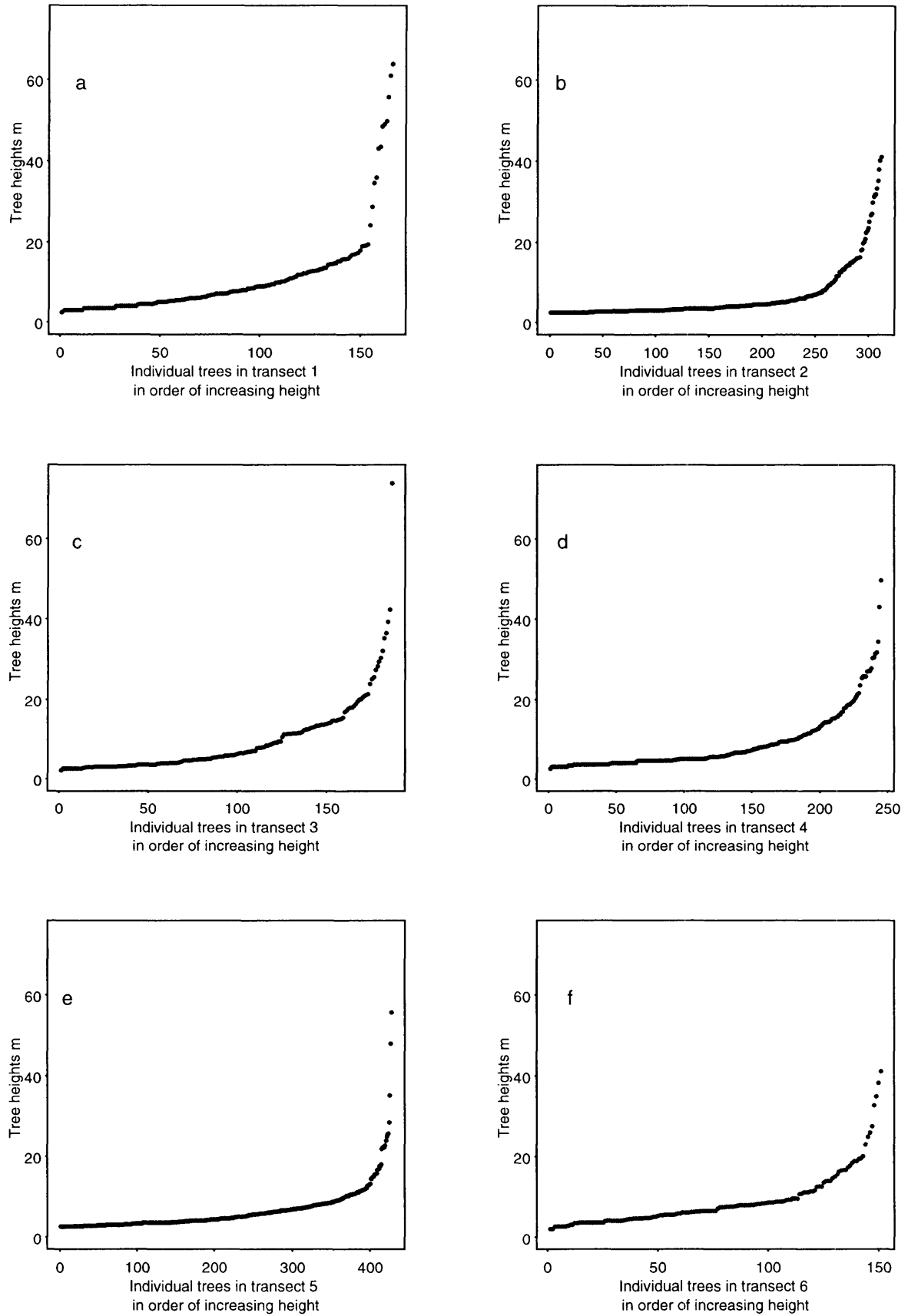
Figure 4.24   Range of tree heights for six WSF transect plots

of increasing size was required for a discontinuity to be recognised as separating layers within each succeeding 25%.

Height discontinuities and demarcation of layers are not always obvious, however, as the situation can be complicated by the presence of individuals in the process of growing from one layer to the next above. When there are a few plants in this transitory stage the layers can be regarded as being temporarily fused. Standing dead trees were ignored for the purposes of layer analysis as they were not considered as either being members of any particular layer or contributing in any significant way to layer formation.

The examination of the WSF height data using the .01 ha sample units revealed that the trees can be split into four layers. These I have termed upper and lower canopy layers and upper and lower mid-layers. The upper canopy layer is represented by the tallest trees in the forest and the lower canopy layer includes those (usually a different set of species) trees which will not reach the upper canopy but are capable of forming a canopy in the absence or death of the species that do. The upper mid-layer typically comprises individuals of the same species group as form the lower canopy layer. The lower mid-layer is a heterogeneous mix of understorey emergents, small tree species, saplings of potential canopy species as well as various lianes.

While elements of each of the four layers are present in over 40% of the samples, and while the lower mid-layer is always present, all combinations of the layer types occur in the data. The other two most frequent configurations (both at over 20%) are upper canopy with both mid-layer elements and lower canopy with both mid-layer elements. Figures 4.25-4.31 present these ranges of layer stratification for plants in the WSF transects, most of which were previously shown in Figures 4.24 a-f. In this set of Figures, each column of points represents the set of plant heights for the next contiguous 0.01 ha sample and the distinguishable layers are separated by the broken lines.

For all WSF sites, the understorey divides into two sub-layers. These are represented by a taller woody plant layer which includes seedlings and saplings of various tree species and a lower non-woody layer which

Tree heights m

60

50

40

30

20

10

upper canopy

lower canopy

upper mid-layer

lower mid-layer

0   10   20   30   40   50   60   70   80   90   100
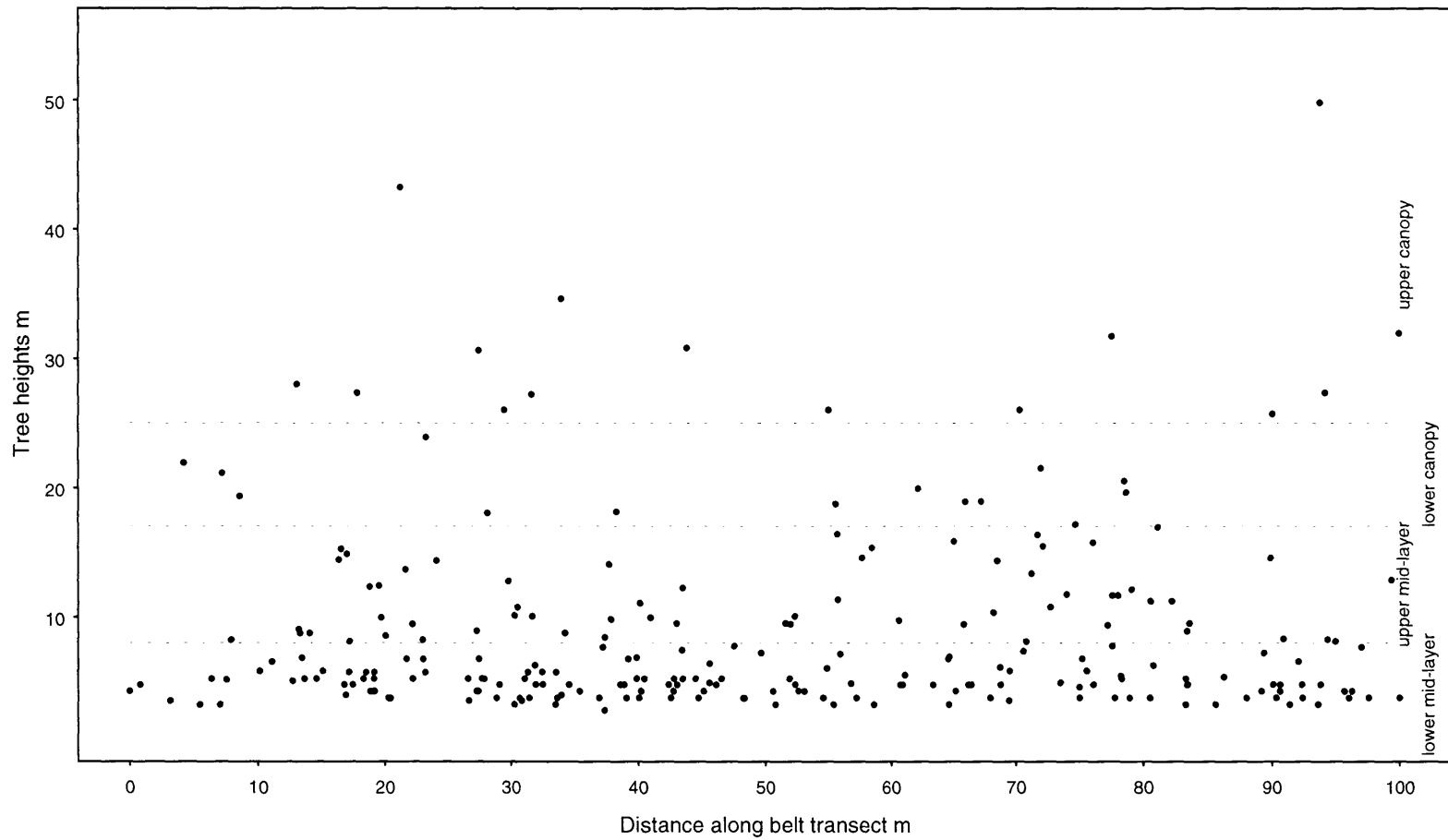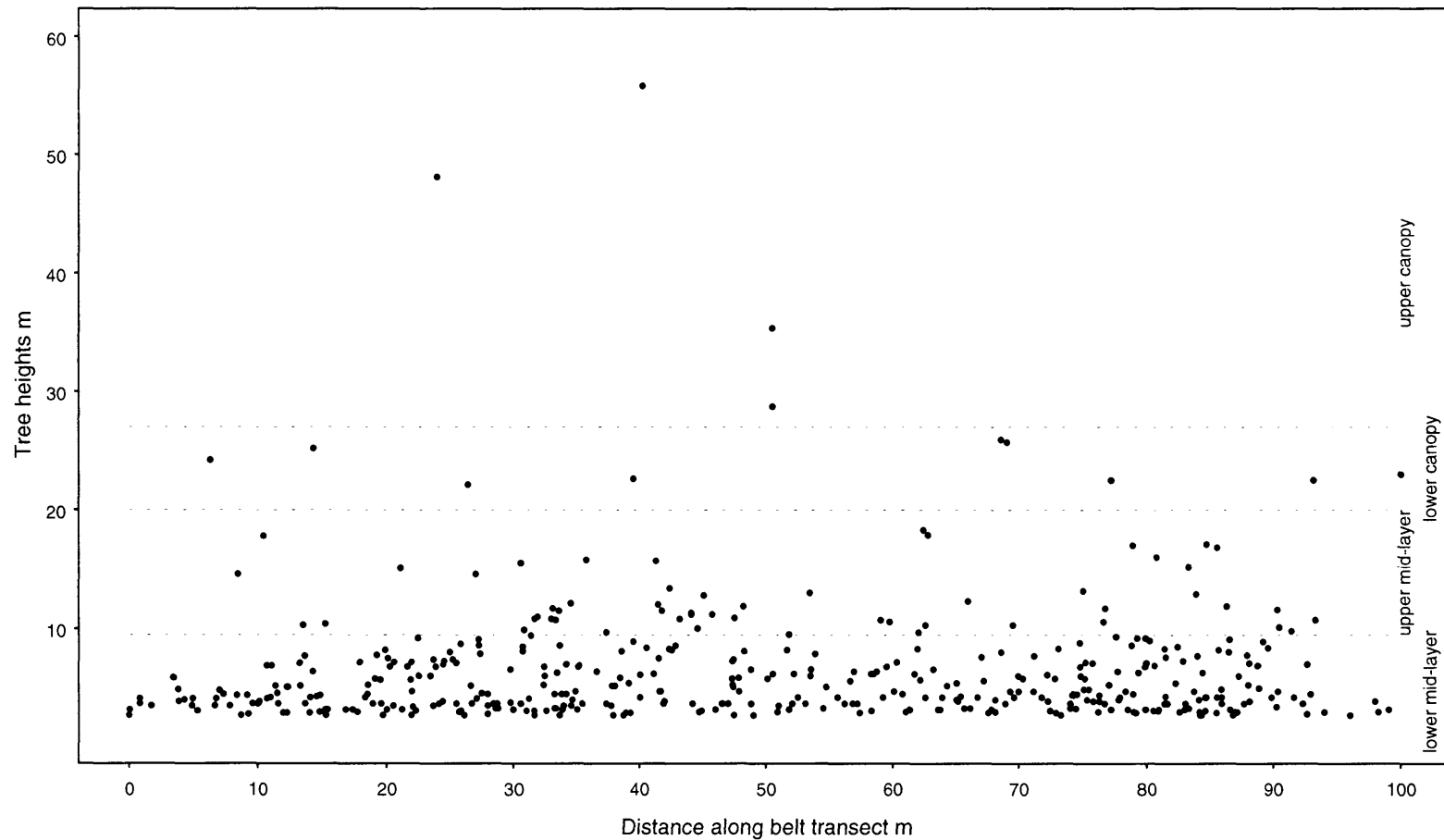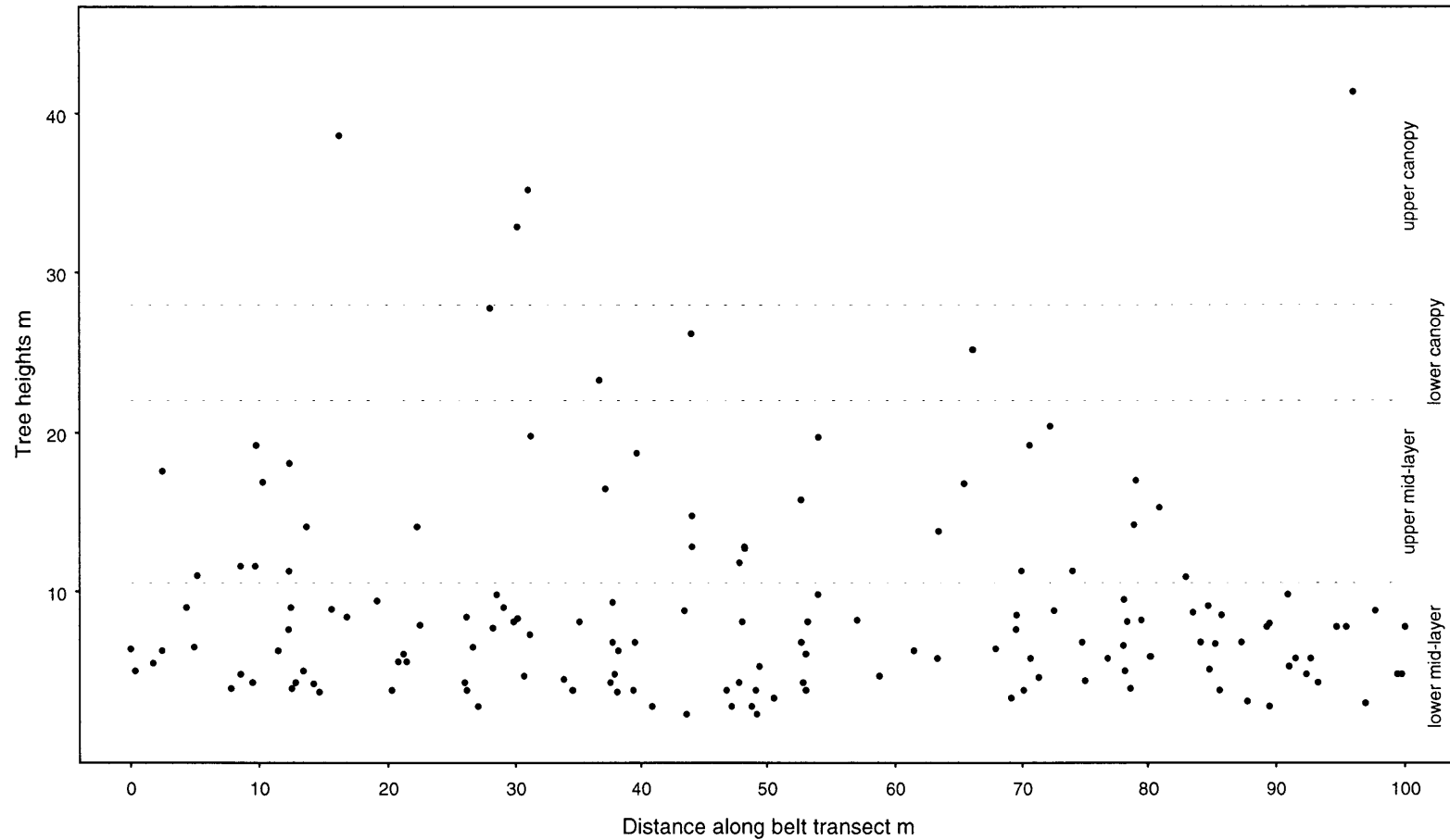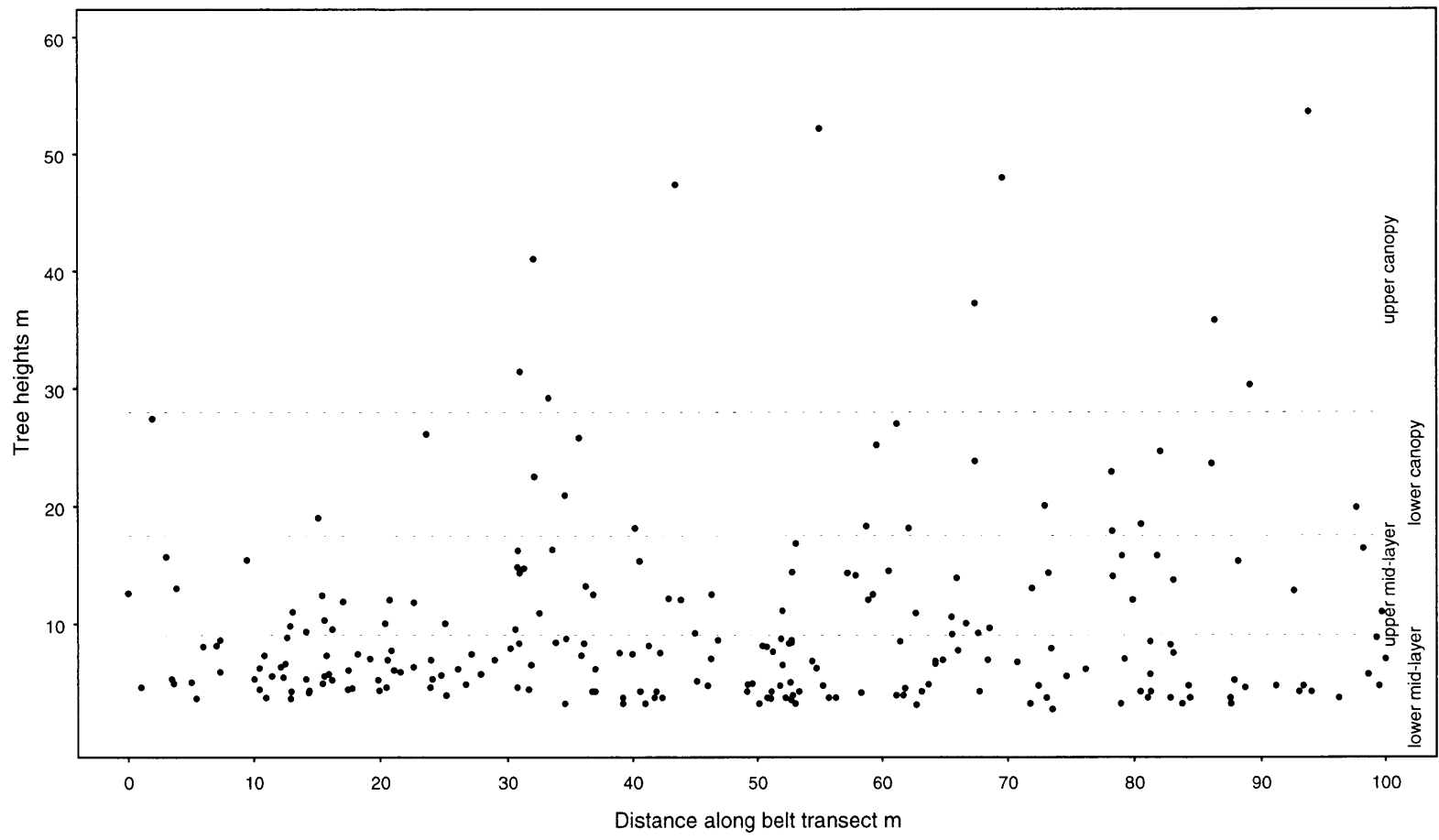
Distance along belt transect m
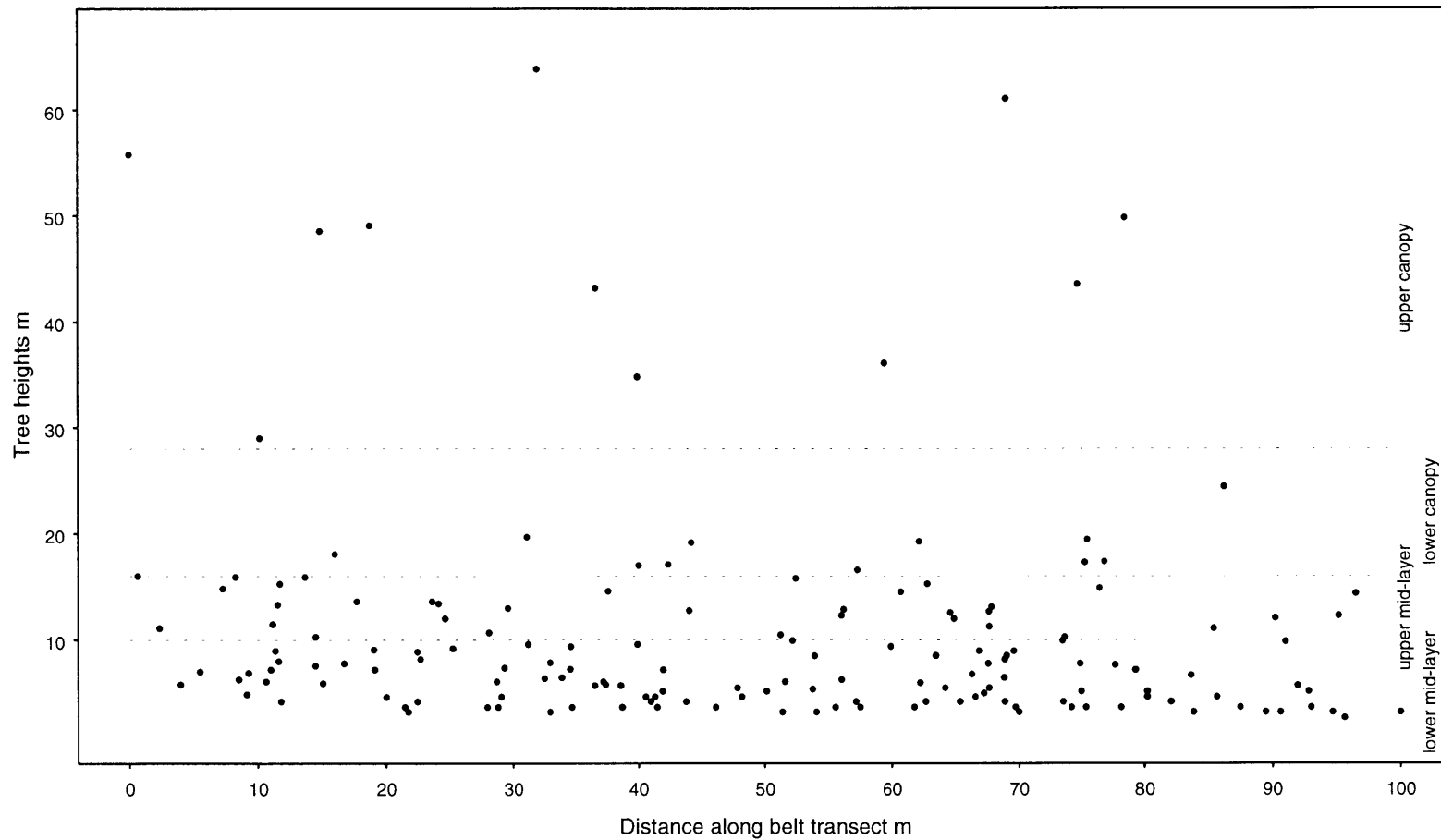
Figure 4.25   Vertical stratification of WSF on transect 1.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names of
the layer zones appear on the right hand edge of the plot.
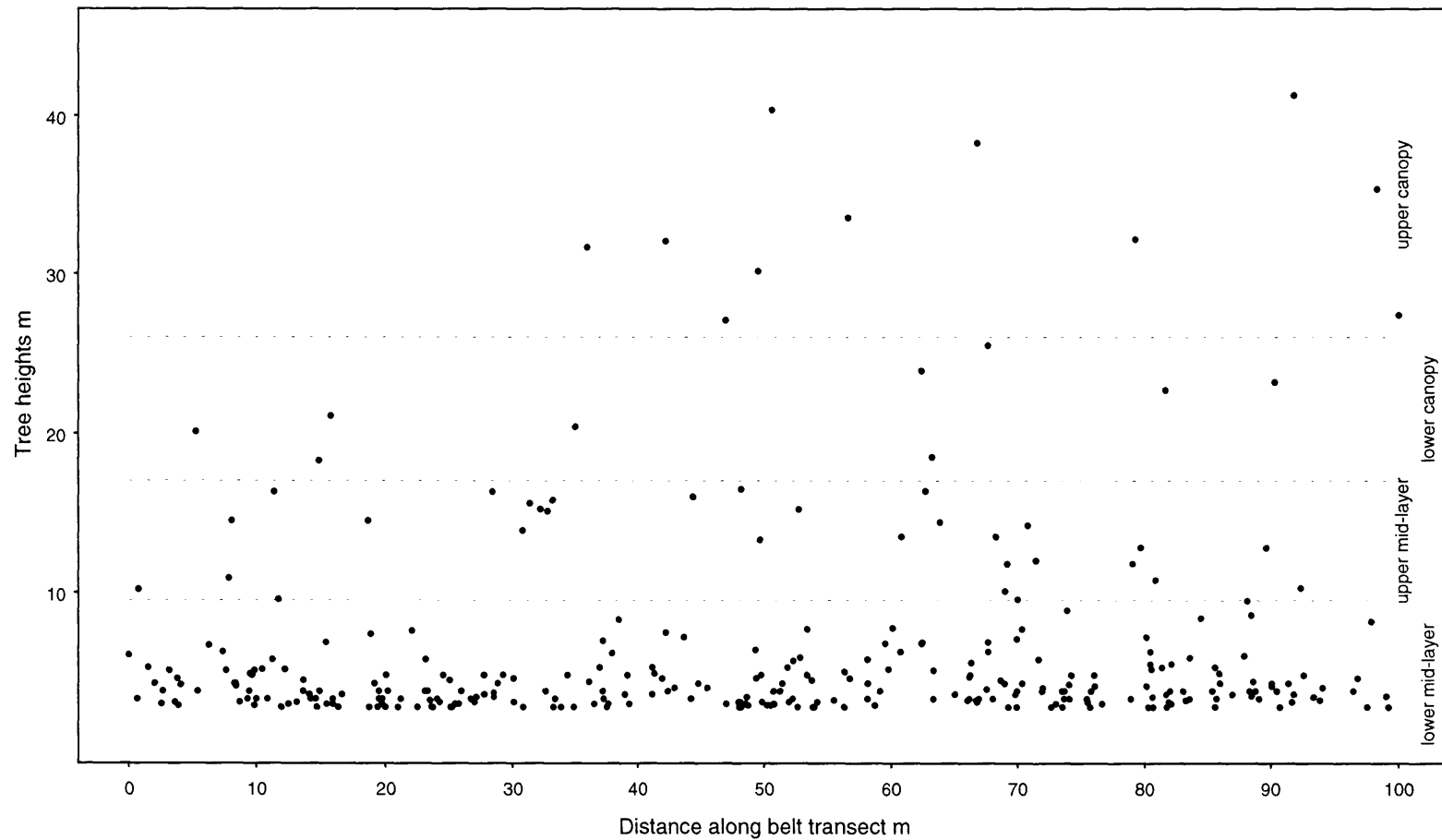
Figure 4.26   Vertical stratification of WSF on transect 2.   Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names of
the layer zones appear on the right hand edge of the plot.
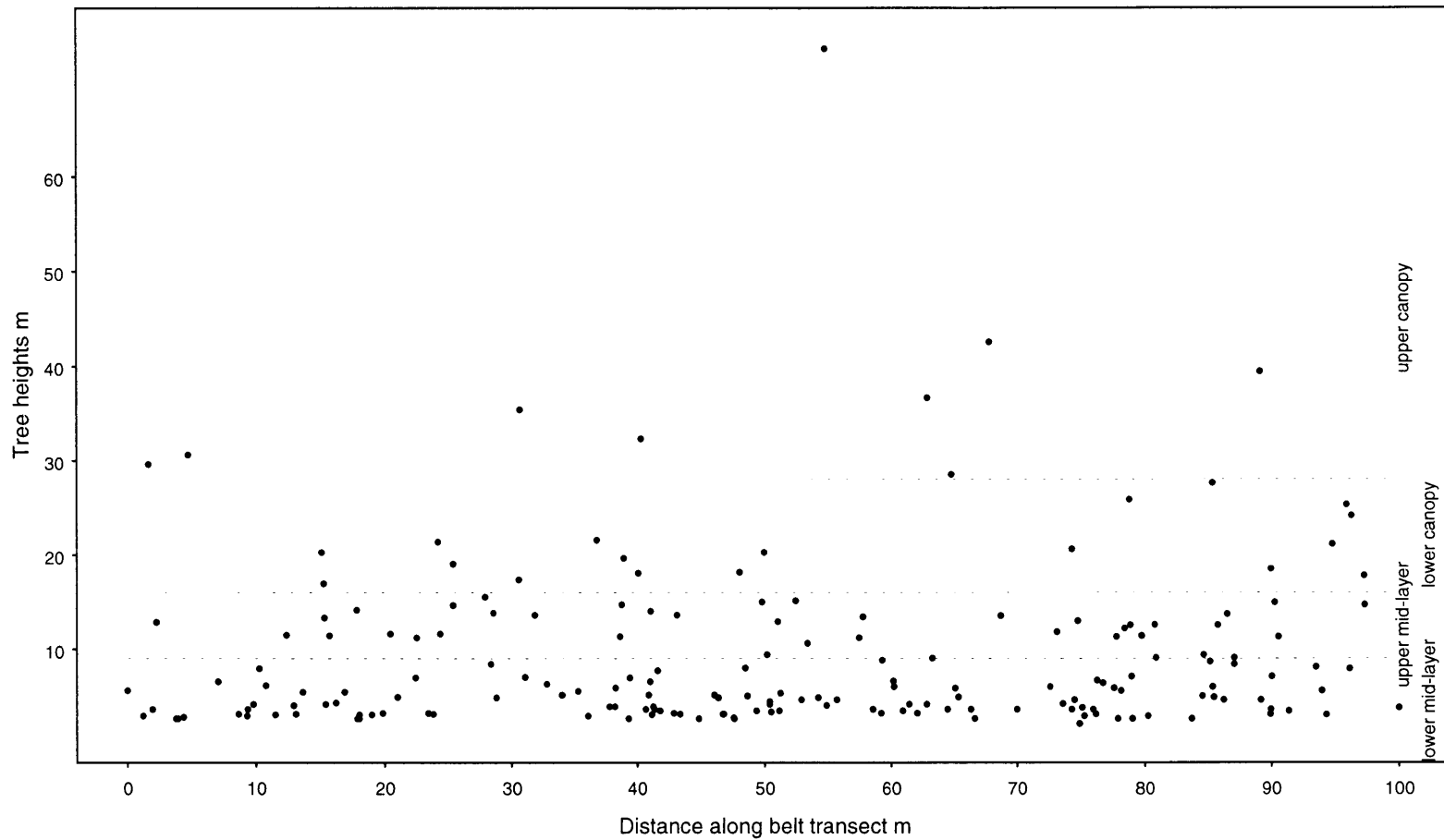
Figure 4.27   Vertical stratification of WSF on transect 3.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

Figure 4.28   Vertical stratification of WSF on transect 4.  Each point represents an

individual tree and the plot presents the deciplot data as a 10 m wide belt transect.

The dotted lines show the location of apparent height discontinuities and the names

of the layer zones appear on the right hand edge of the plot.

Figure 4.29 Vertical stratification of WSF on transect 5. Each point represents an individual tree and the plot presents the deciplot data as a 10 m wide belt transect. The dotted lines show the location of apparent height discontinuities and the names of the layer zones appear on the right hand edge of the plot.

Figure 4.30   Vertical stratification of WSF on transect 6.  Each point represents an individual tree and the plot presents the deciplot data as a 10 m wide belt transect. The dotted lines show the location of apparent height discontinuities and the names of the layer zones appear on the right hand edge of the plot.
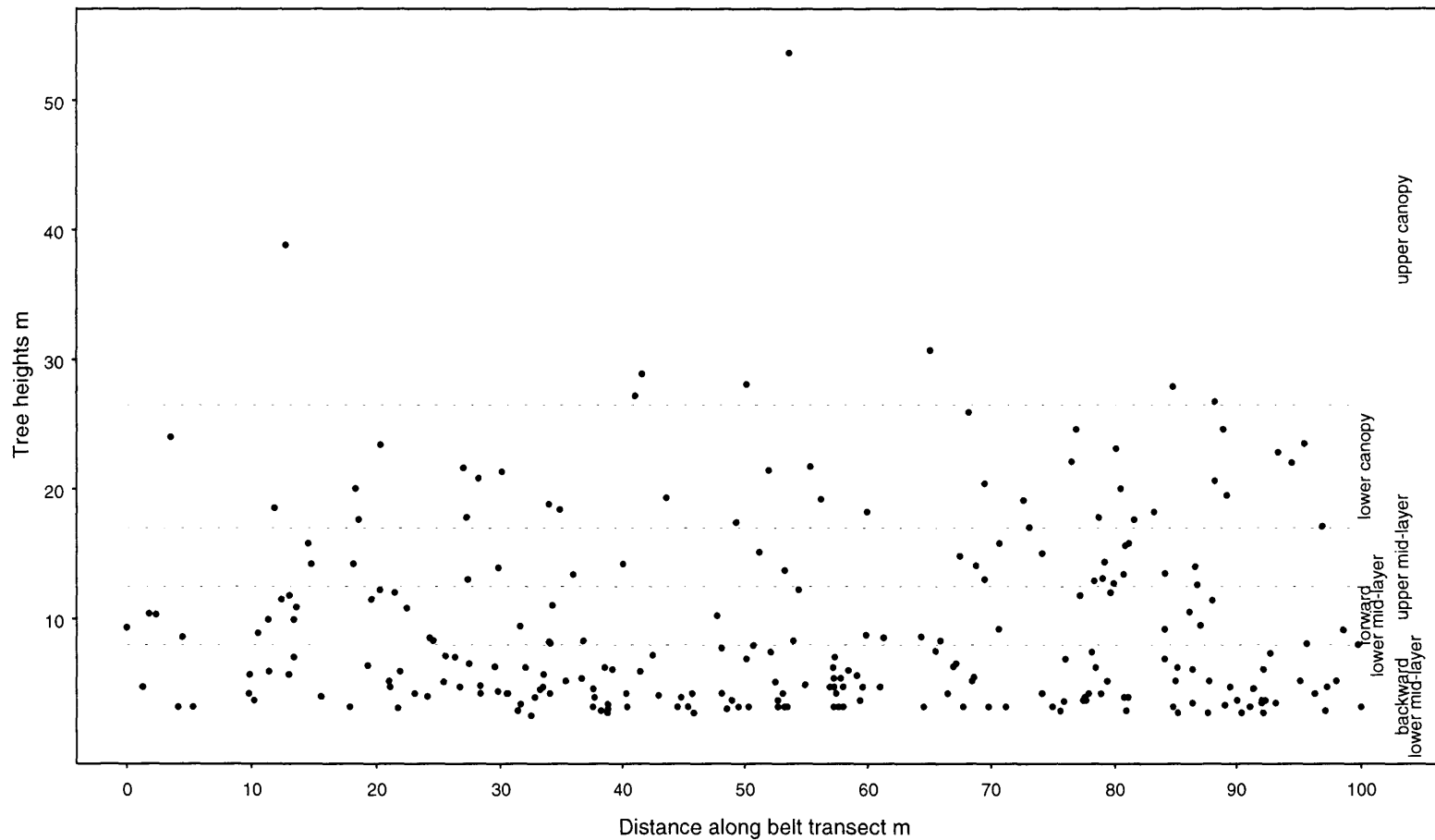
Figure 4.31   Vertical stratification of WSF on transect 7.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

is comprised predominantly of sedges or ferns and occasionally grasses and other perennial herbs. Therefore, the net breakdown of the vertical stratification of the WSF results in an identification of three layer zones each being potentially divisible into two sub-layers.

Layer identification in both the TZF and WTRF was pursued in the same fashion as undertaken for WSF. For the TZF, a preliminary examination of the range of plant heights in the TZF plots confirmed the same tree height continuum that was noted in WSF and illustrated in Figures 4.24 a-f. By reducing the sample size to 0.01 ha and plotting the spectrum of heights for each contiguous sample in a concatenated two-dimensional fashion, the layers and sub-layers present in the TZF could be identified. All the layers noted in the WSF were variously present in the TZF with the additional factor of rainforest influencing the characteristics of the lower mid-layer. This influence resulted in the lower mid-layer being frequently further composed of two layer elements. These I have called the forward (taller) and backward (lower) lower mid-layers. All the TZF tree stratifications are illustrated in Figures 4.32-4.38 where the interpretation is the same as for the WSF transects.

The understorey of the TZF is comprised of a fairly constant sub-layer of woody flora and a herbal sub-layer which is comprised of species which have a somewhat clumped distribution in the TZF (see Table 4.17) such that this sub-layer is alternatively only present as either a very minor element of the understorey or else as very much the dominant understorey sub-layer.

Layer patterns in the WTRF also became evident when the plot data were separated into 0.01 ha sample units and these were concatenated into a two-dimensional representation of the forest type. By this method the vertical stratification of this formation was shown to be markedly more complicated than either of the other two vegetation types. For simplification the presence and abundance of lianes were not taken into account. The height groups in the WTRF data indicated that the upper mid-layer of the WSF and TZF was often able to be divided into two sub-layers which I have called the forward (taller) and backward (lower) upper mid-layers. This resulted in the mid-layer of

Figure 4.32   Vertical stratification of TZF on transect 1.   Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
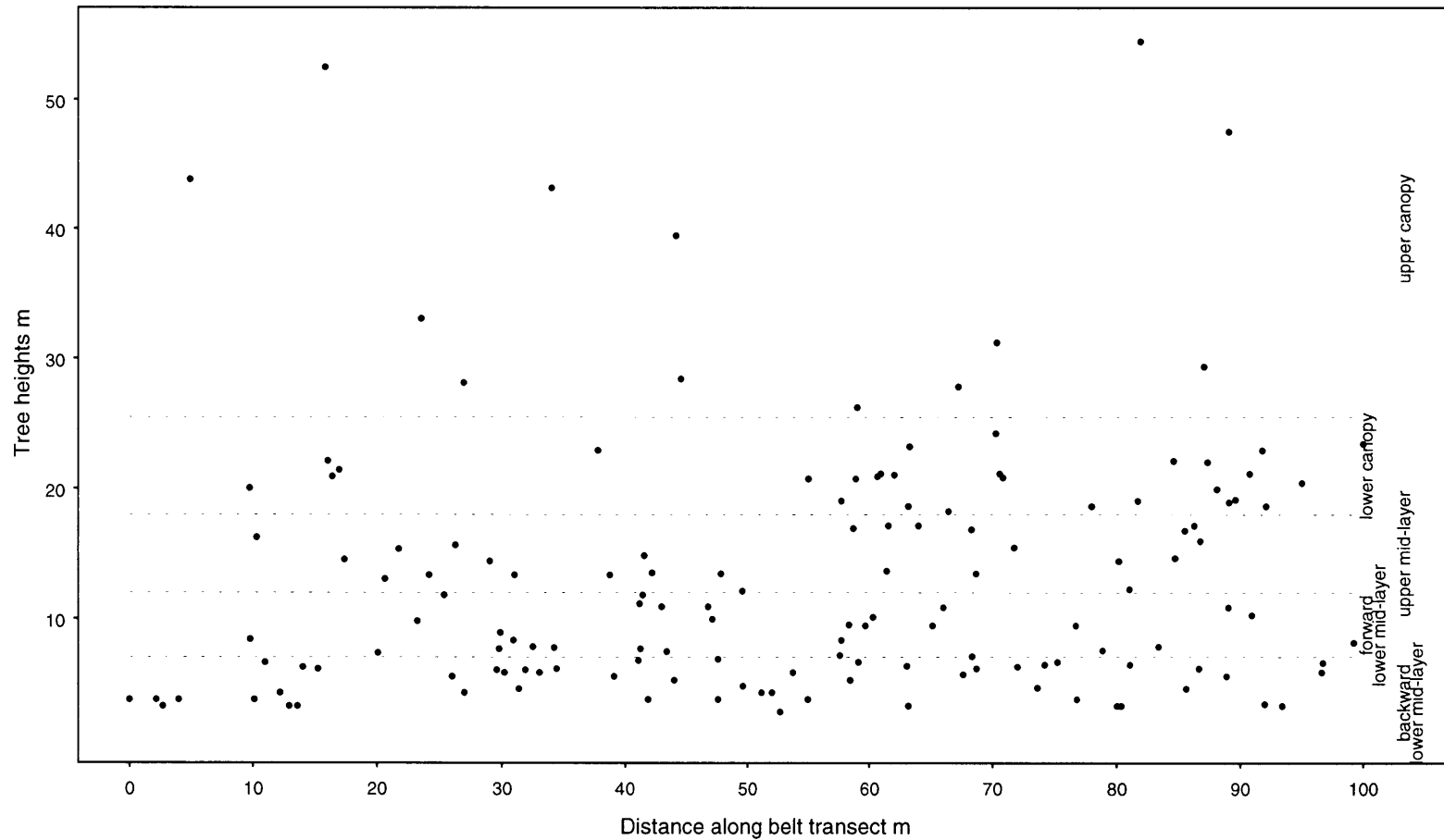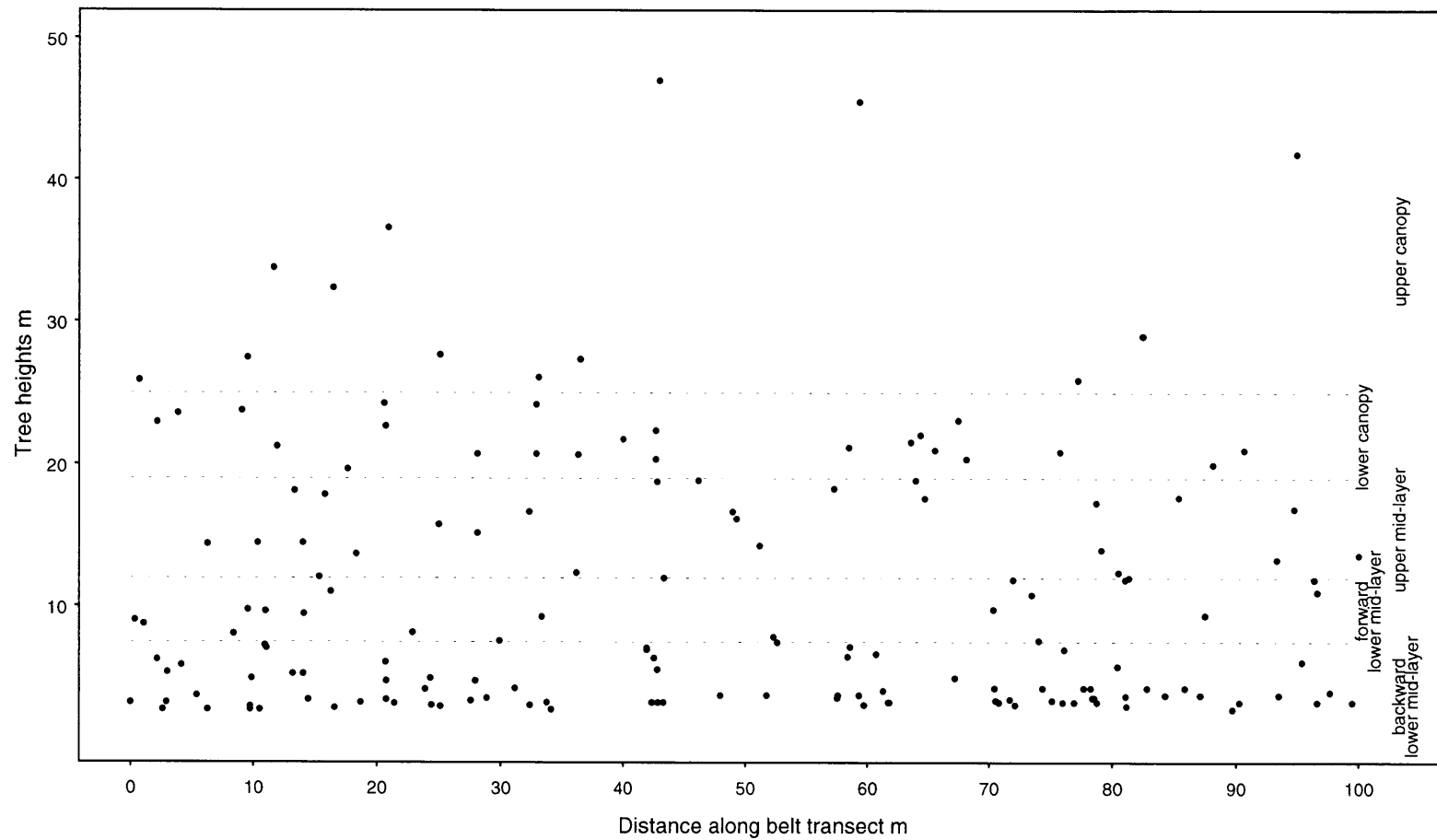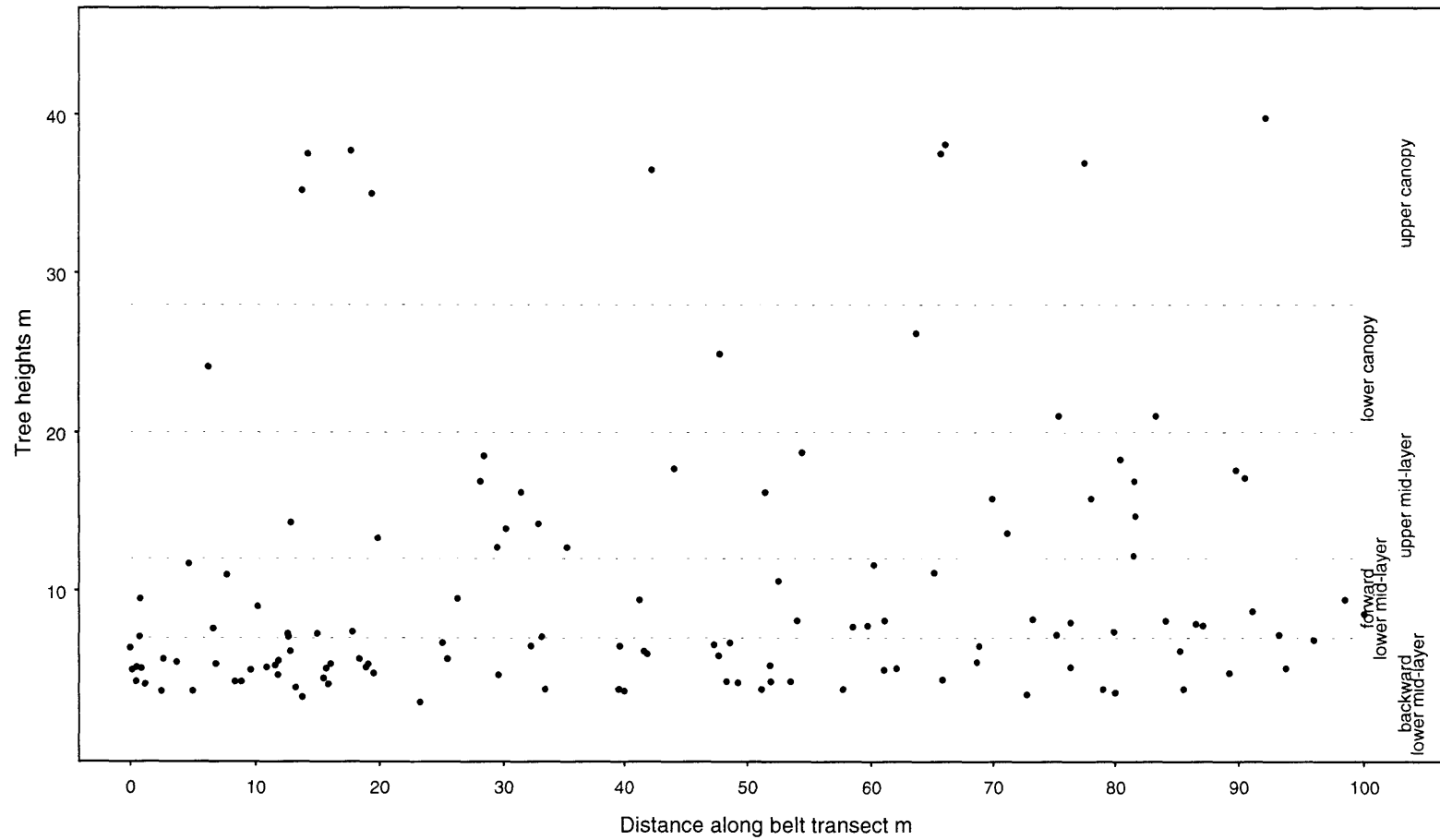of the layer zones appear on the right hand edge of the plot.
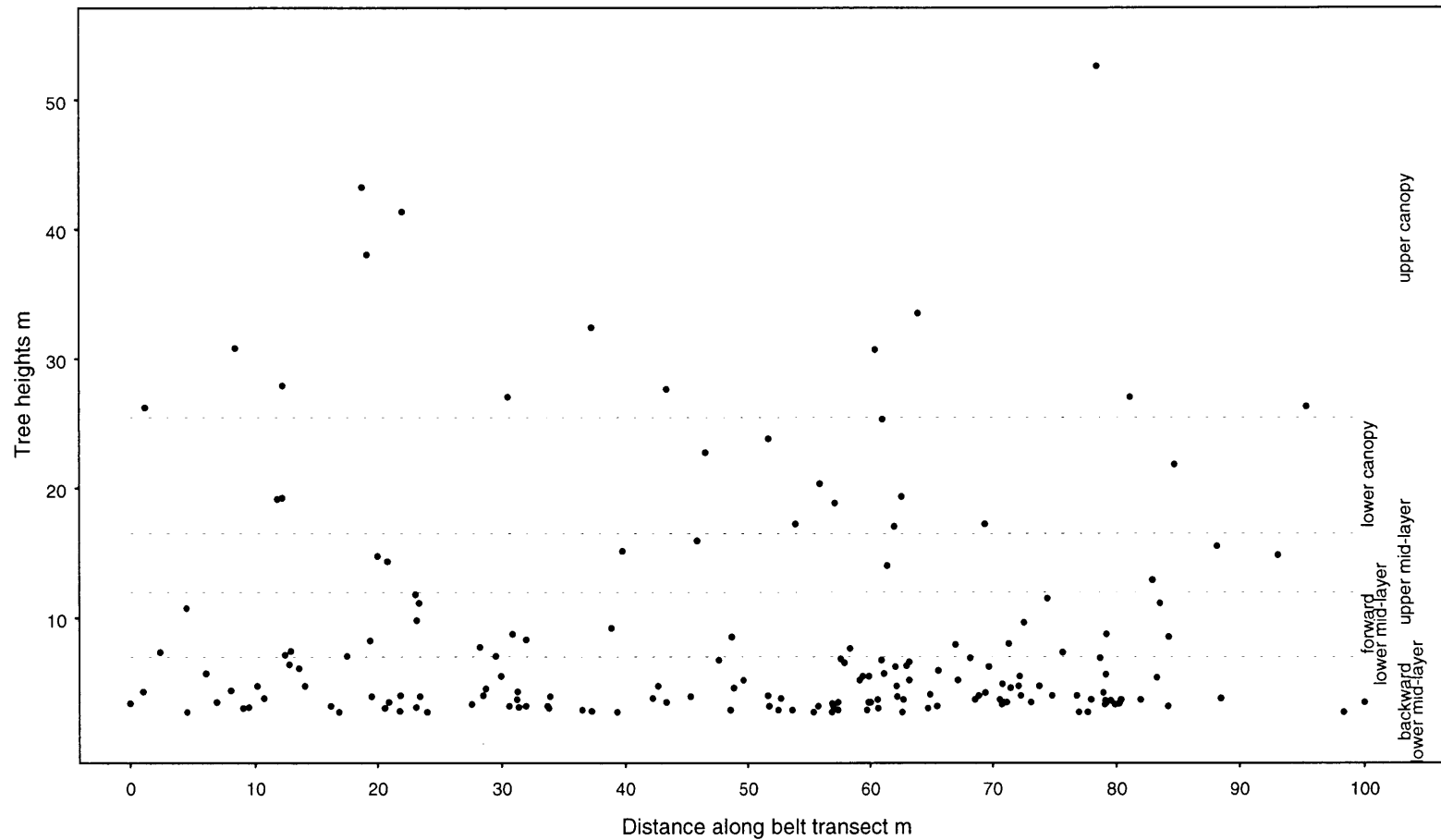
Figure 4.33   Vertical stratification of TZF on transect 2.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
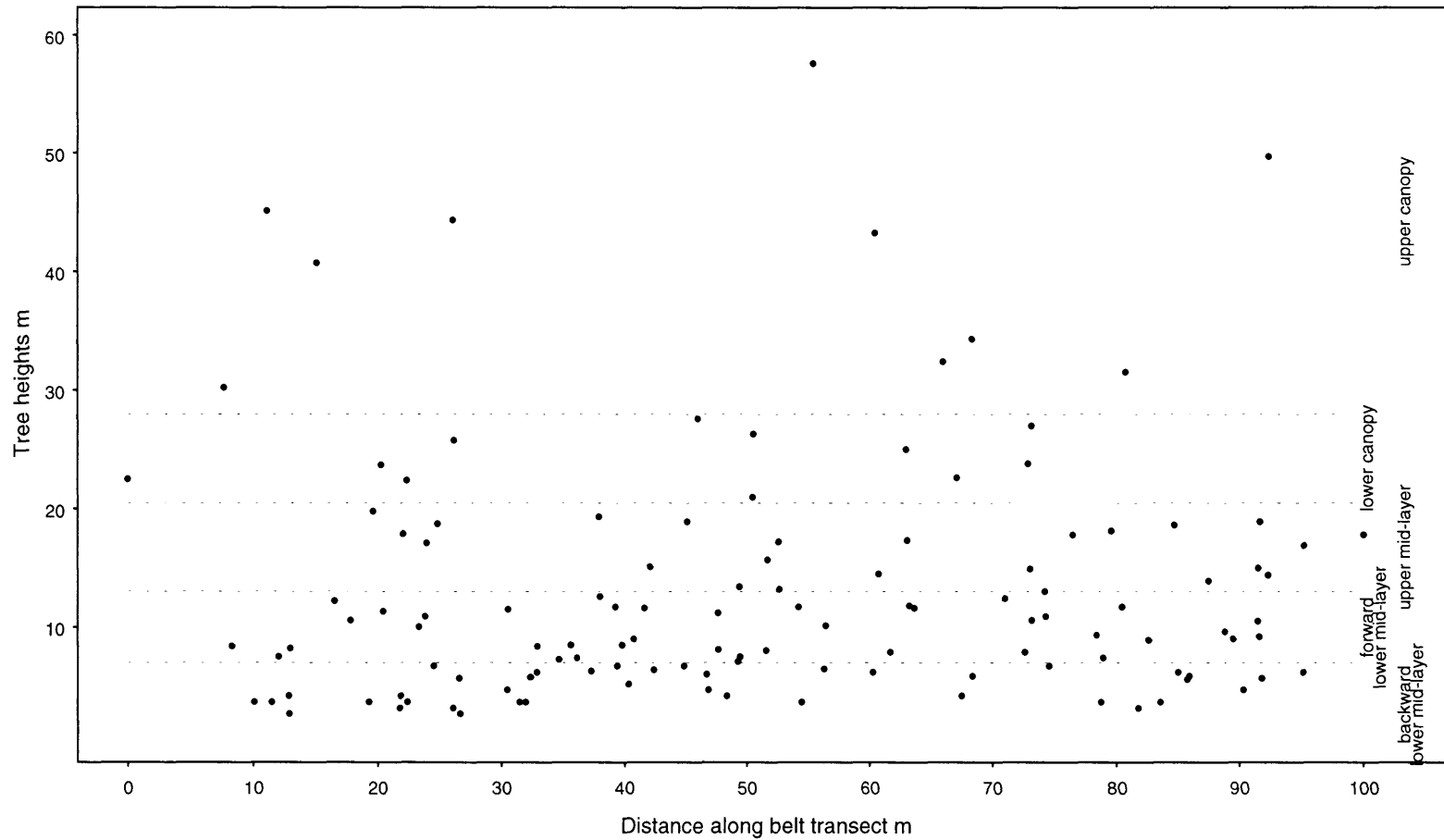of the layer zones appear on the right hand edge of the plot.
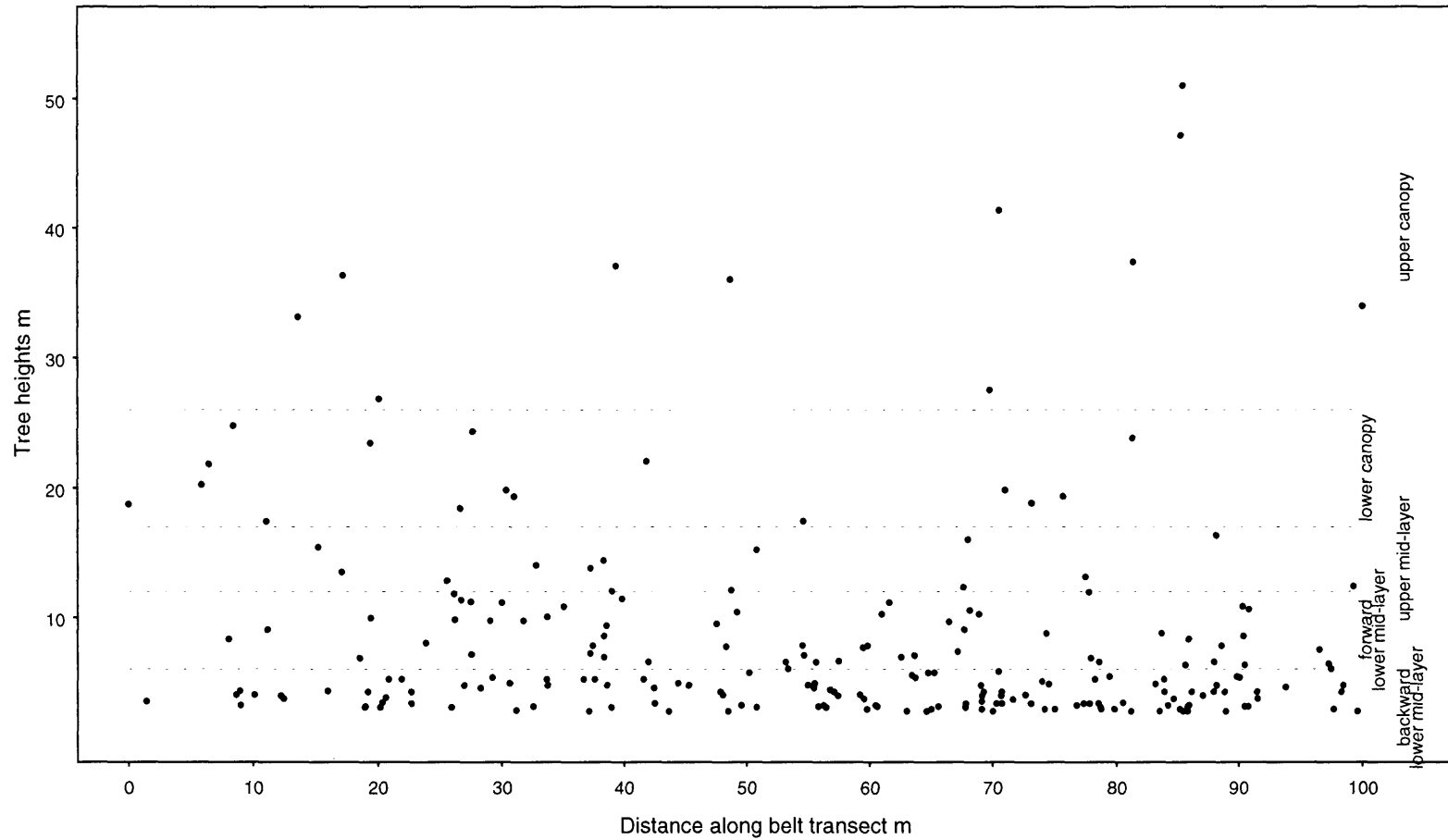
Figure 4.34   Vertical stratification of TZF on transect 3.  Each point represents an

individual tree and the plot presents the deciplot data as a 10 m wide belt transect.

The dotted lines show the location of apparent height discontinuities and the names

of the layer zones appear on the right hand edge of the plot.

Figure 4.35  Vertical stratification of TZF on transect 4.  Each point represents an individual tree and the plot presents the deciplot data as a 10 m wide belt transect. The dotted lines show the location of apparent height discontinuities and the names of the layer zones appear on the right hand edge of the plot.

Figure 4.36   Vertical stratification of TZF on transect 5.  Each point represents an individual tree and the plot presents the deciplot data as a 10 m wide belt transect. The dotted lines show the location of apparent height discontinuities and the names of the layer zones appear on the right hand edge of the plot.

Figure 4.37   Vertical stratification of TZF on transect 6.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

Figure 4.38   Vertical stratification of TZF on transect 7.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

the WTRF being comprised of four separate sub-layers. With six recognisable layers in the distribution of tree heights in the WTRF, with addition of understorey sub-layers the range of possible layer combinations was extensive but occasionally only as few as three layers were present.

Numerous examples of individual plants between layers tended to confuse the layer arrangement but when the particular species were identified, it was usually possible to show that they were in a state of progress from one sub-layer to the next. When this appreciation of transitory individuals was established, the structure reappeared. The patterns of tree layer organisation in the WTRF are shown in Figures 4.39-4.44 in which the particular transitory individuals have been retained. The understorey of the WTRF is much less variable than the TZF with both the woody plants component and the non-woody component of ferns and herbs occupying fairly consistent proportions of the understorey structure. The main contribution to variability in the rainforest understorey layer flora came from the patchy distribution of climbers and scramblers (see confidence limits in Table 4.17) centred on forest canopy gaps.

## 4.2.3    Crown density and light levels

In order to calculate the crown packing arrangement for each sample area, the program CROWNDENS (Appendix II) was written to provide a numerical representation of the vertical variation of crown density at each sample area and also to calculate an index of shading based on the species comprising the tree layers. CROWNDENS worked from the top of the highest tree crown for the sample unit to the bottom of the lowest tree crown in steps of 1 m. At each level it calculates the three dimensional space occupied by the crown of each plant that was measured as occurring in that sample unit. All crowns were assumed to be elliptical with the axes of the ellipse being the measured variables of crown width and crown depth. Some trees were recorded with large, spreading crowns such that the projections of their crowns were not contained in the sample unit. As it was unknown where each crown was situated with respect to the sample area boundaries, the assumption
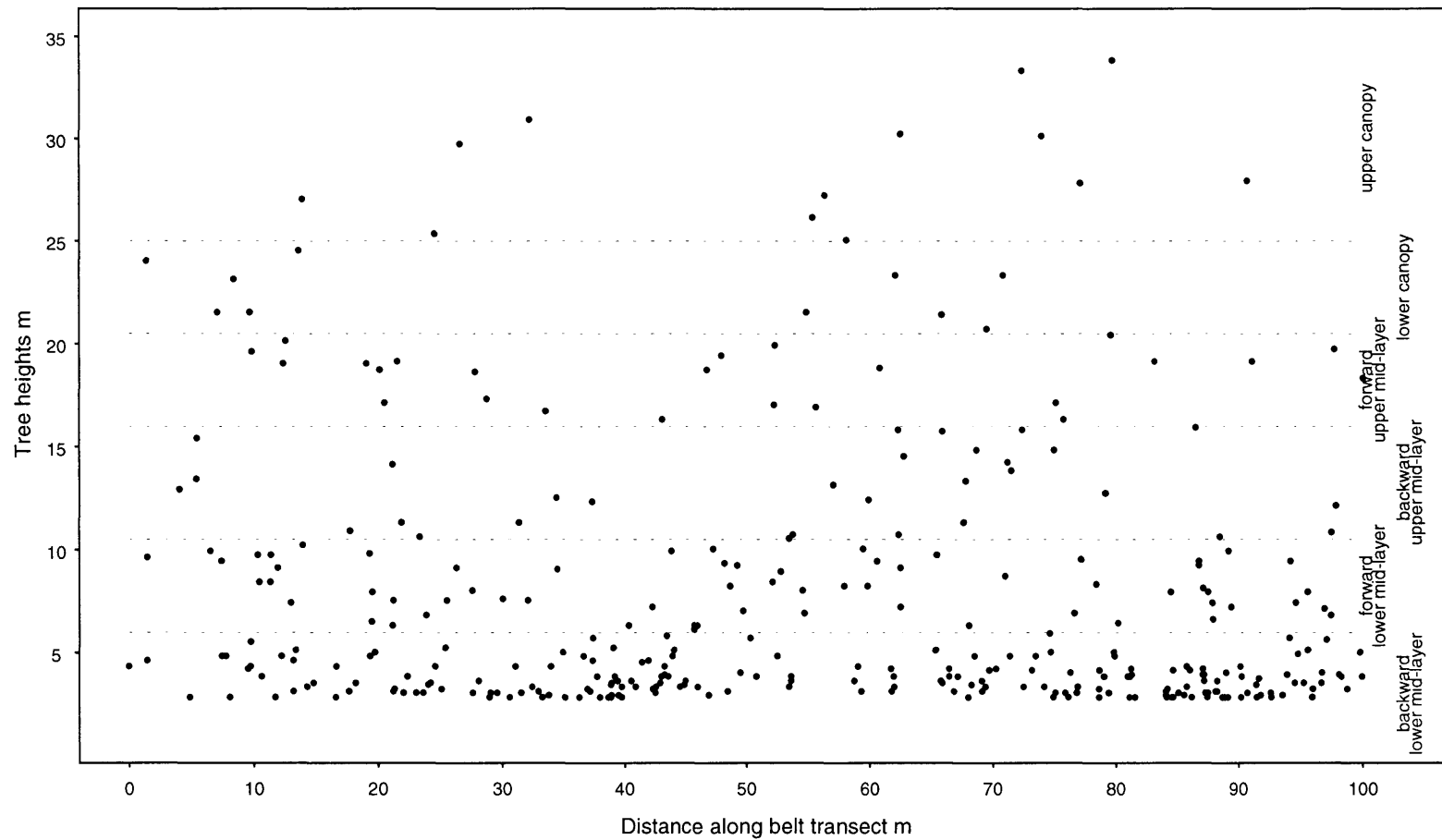
Figure 4.39   Vertical stratification of WTRF on transect 1.   Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
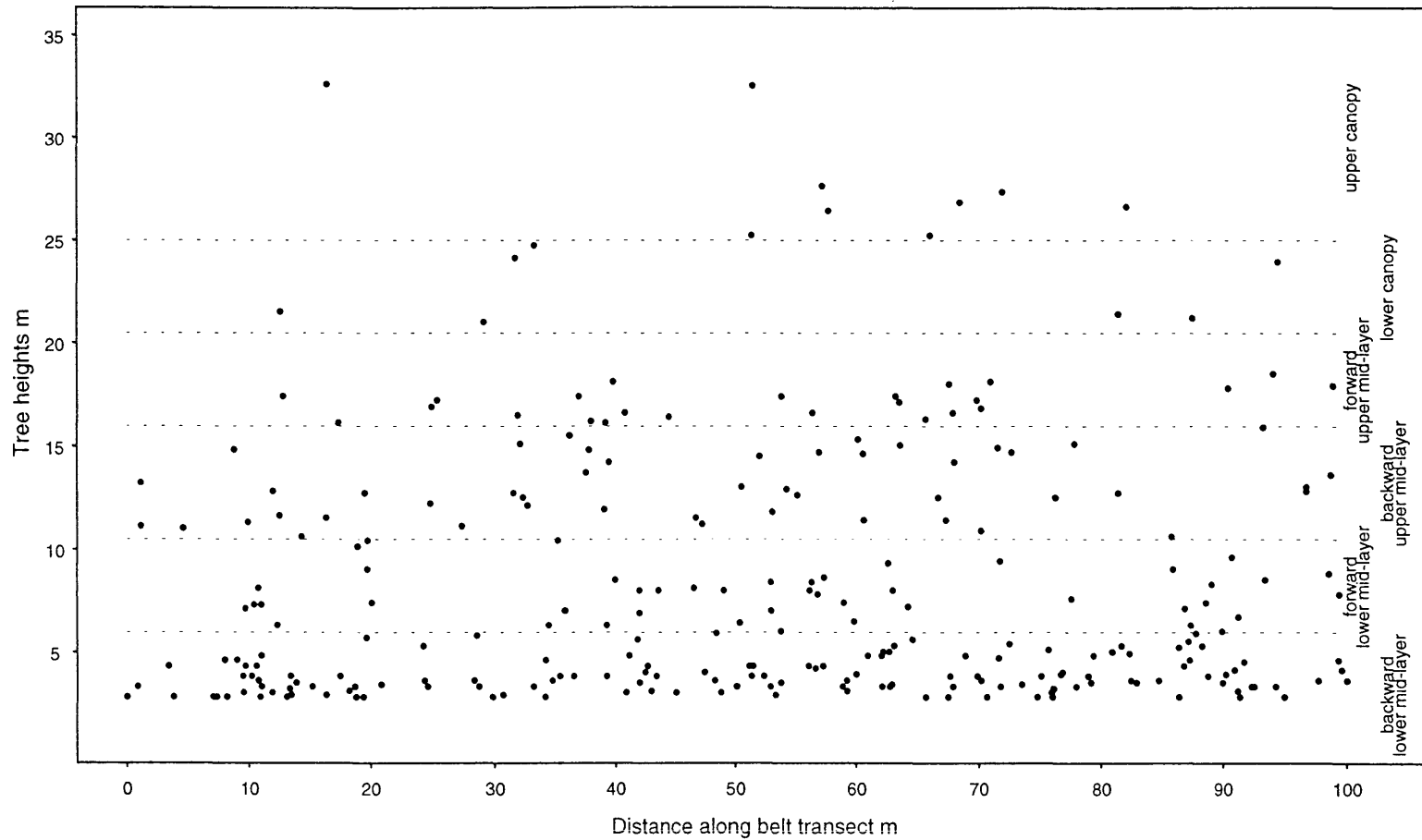of the layer zones appear on the right hand edge of the plot.

Tree heights m

35

30

25

20

15

10

5

upper canopy

lower canopy

forward
upper mid-layer

backward
upper mid-layer

forward
lower mid-layer

backward
lower mid-layer

0   10   20   30   40   50   60   70   80   90   100

Distance along belt transect m

Figure 4.40   Vertical stratification of WTRF on transect 2.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
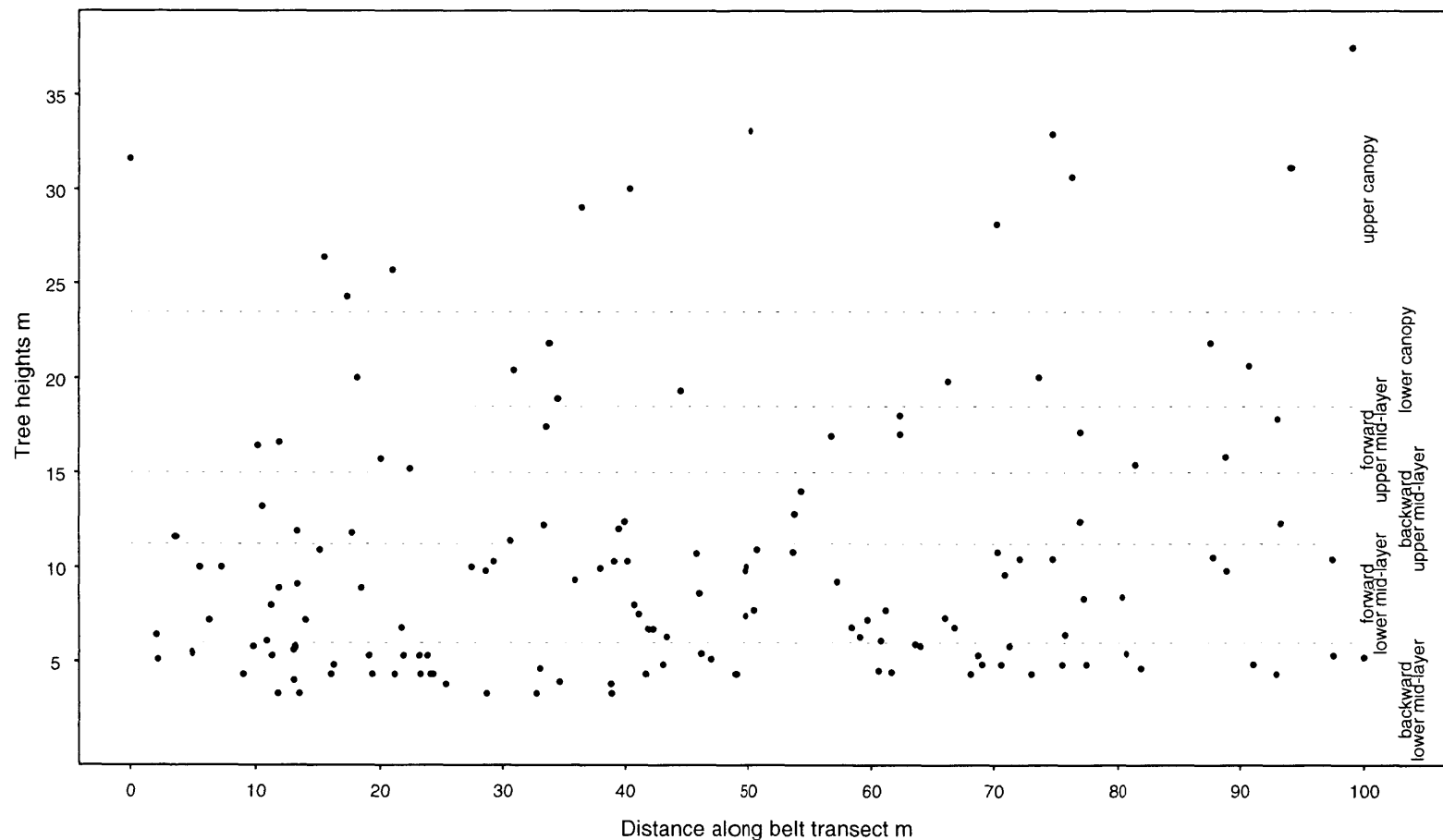of the layer zones appear on the right hand edge of the plot.
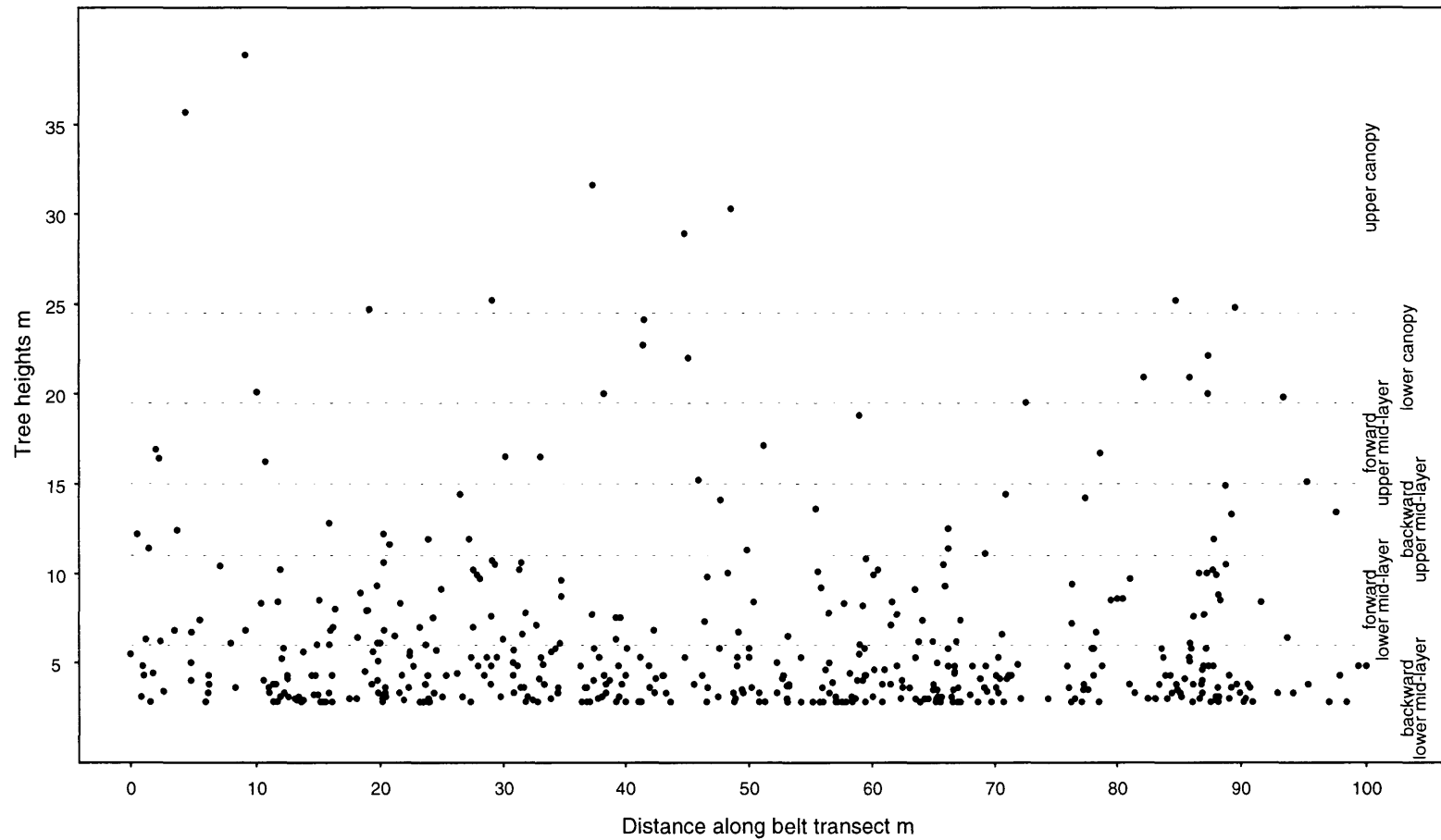
Figure 4.41 Vertical stratification of WTRF on transect 3. Each point represents an individual tree and the plot presents the deciplot data as a 10 m wide belt transect. The dotted lines show the location of apparent height discontinuities and the names of the layer zones appear on the right hand edge of the plot.
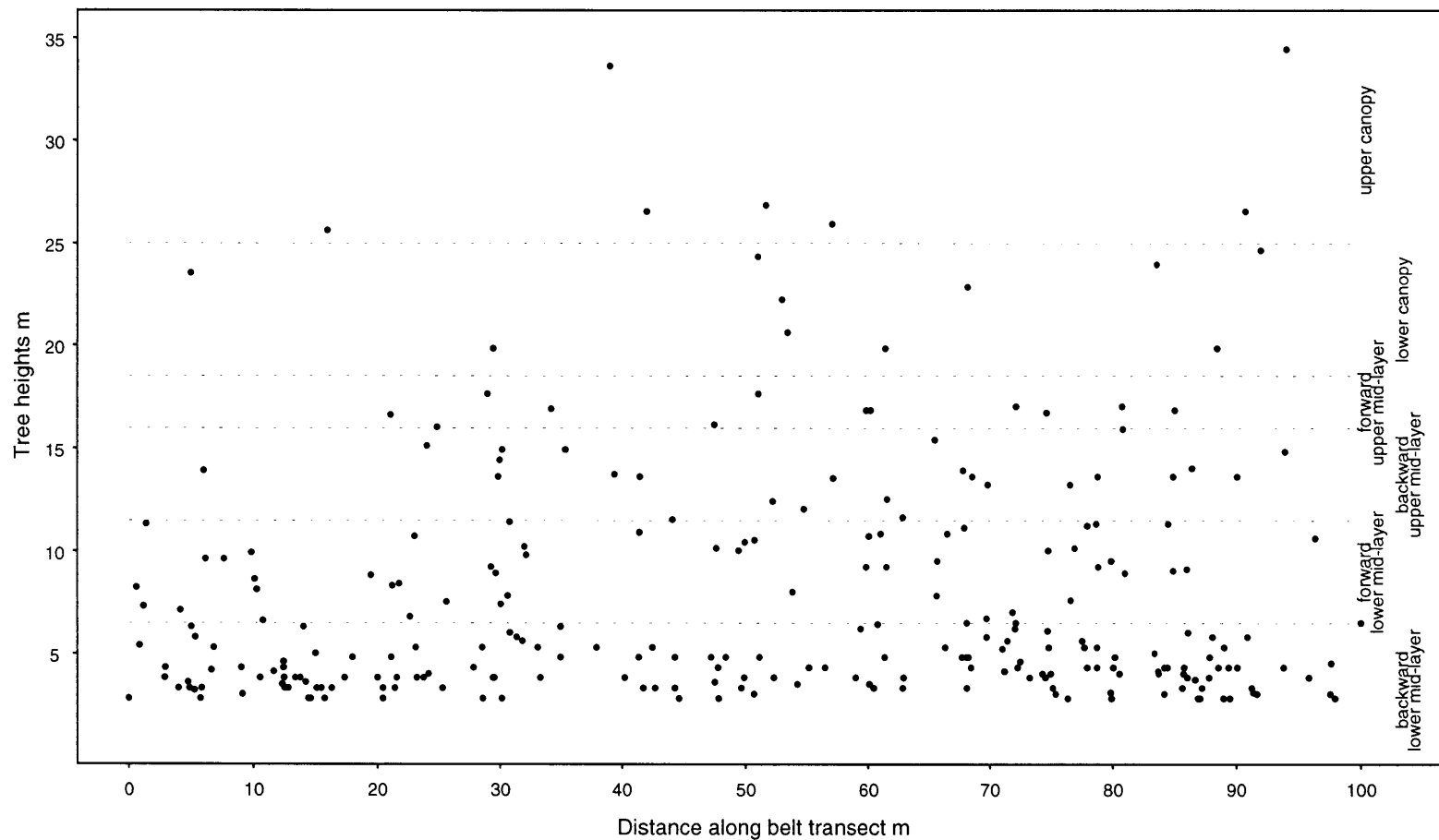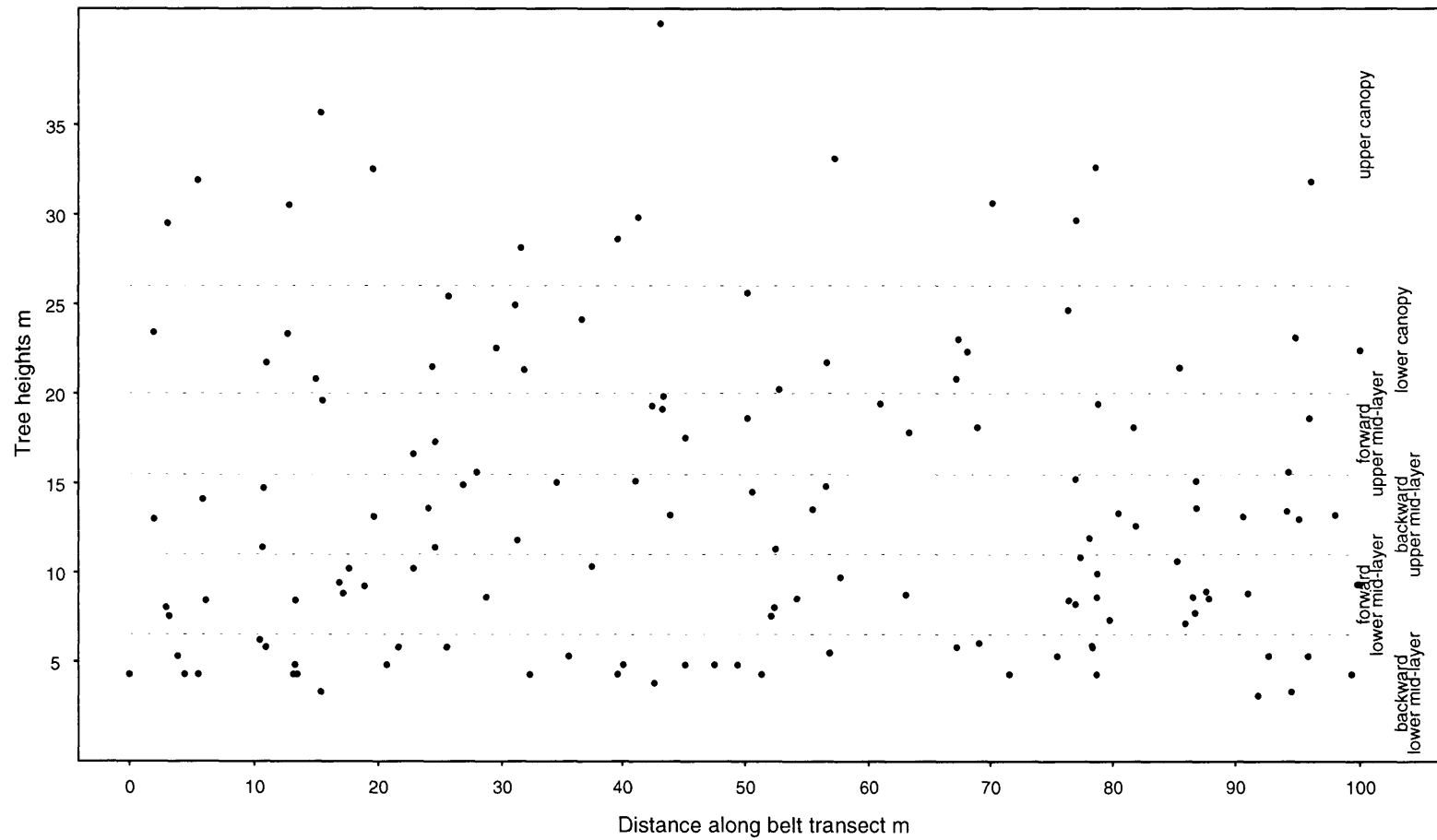
Figure 4.42  Vertical stratification of WTRF on transect 4.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

Tree heights m

35

30

25

20

15

10

5

0   10   20   30   40   50   60   70   80   90   100

Distance along belt transect m

upper canopy

lower canopy

forward
upper mid-layer

backward
upper mid-layer

forward
lower mid-layer

backward
lower mid-layer

Figure 4.43   Vertical stratification of WTRF on transect 6.  Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

Figure 4.44   Vertical stratification of WTRF on transect 7.   Each point represents an
individual tree and the plot presents the deciplot data as a 10 m wide belt transect.
The dotted lines show the location of apparent height discontinuities and the names
of the layer zones appear on the right hand edge of the plot.

was made that when the cross-sectional area of a crown, measured at the point of maximum crown width, exceeded the area of the sample unit, then that excess was attributed as falling outside the sample area and not relevant to the calculation of the shading index. When sample areas were contiguous, the excess was allocated proportionately to the adjacent sample unit. The shading contribution of each crown was derived from the net space occupied by the crown, after accommodation of intersecting crowns, multiplied by a crown density factor which ranged from 1 to 5 and which was previously allocated to each species on the basis of the field assessment of typical crown density. On the basis of field observations, the only species to exhibit significant variation in crown density was *Allocasuarina torulosa* and the crown density factor for this species was set at what was regarded as an average value. The crown density was treated as constant for each species regardless of the forest type in which the species was recorded.

The treatment of lianes also required some careful consideration. The liane crowns were not measured in the field but the extent of their crowns in the WTRF was noted as being much less than in sub-tropical rainforest. It was also noted that the crowns of lianes in the rainforest were more profuse than those in the tall open wet sclerophyll forest. Consequently, liane crown contribution to shading of the forest floor was evaluated on the basis of the habitat in which it was found in conjunction with its crown density factor.

An index of shading was calculated by CROWNDENS for each sample unit. The index is expressed as an unlimited scalar value without units. This index was to be used to investigate the correlation between the amount of shading due to the tree layers with such attributes as the number of vegetation layers, the species complement of the understorey, the amount of exposed ground or, alternatively, the abundance of understorey plants and, finally, the area occupied by fallen trees which may represent gaps in the canopy. The index can be taken further and used as an attribute for vegetation structure pattern analysis and for the modelling of vegetation structure. The shading index for all 0.01 ha sample units is plotted against each of the above variables in Figures 4.45 a-d.
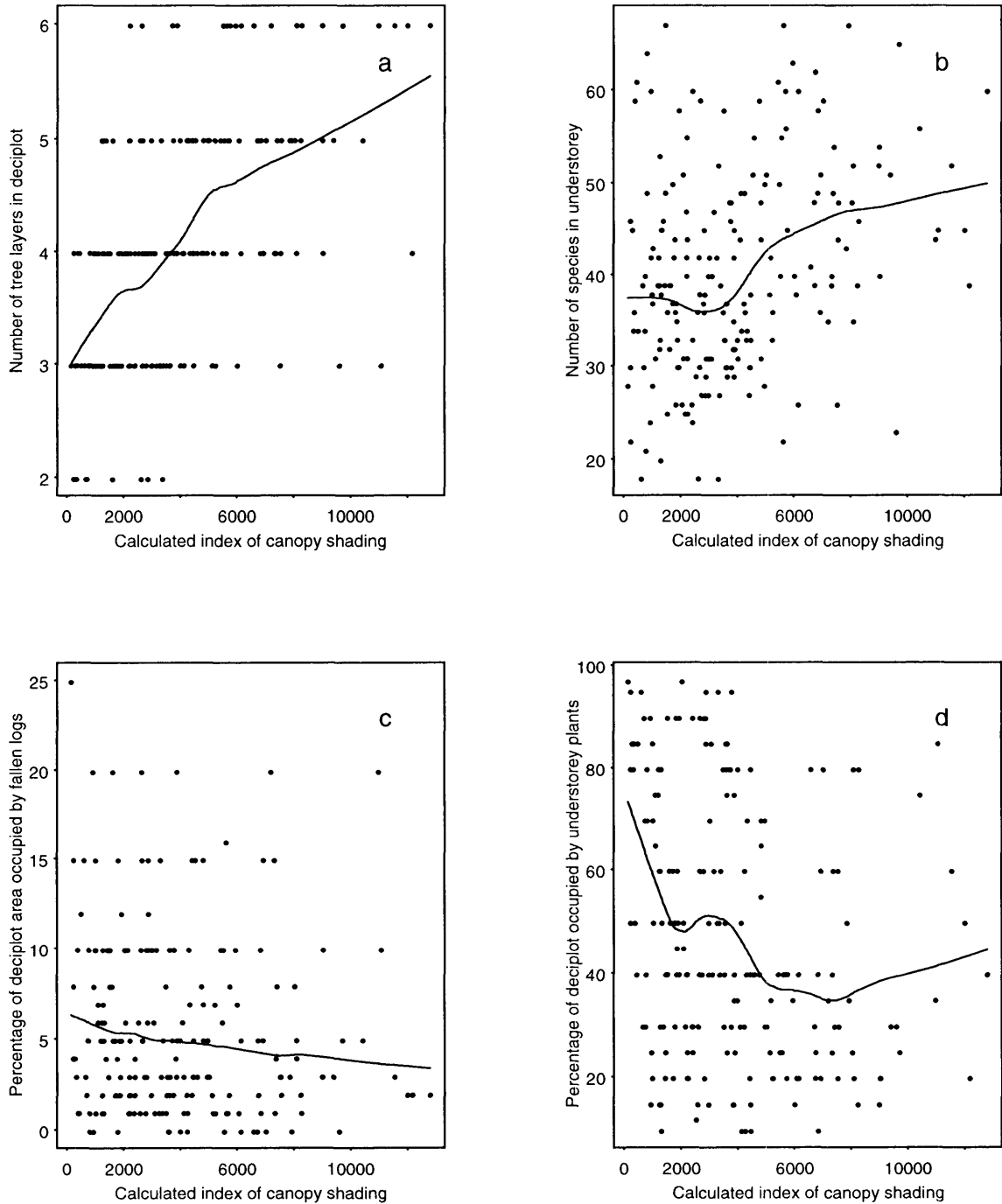
Figure 4.45   Relationship of increasing extent of canopy shading with selected
variables.  Solid lines on plots are smoothed representations of the
relationships.  They are fitted regression functions which were calculated
using a local regression model with a smoothing parameter of 0.5.

The positive association between crown shading and the number of layers (plot a) confirmed the trend in the crown shading index and the increase in understorey species with shading (plot b) indicates the negative impact shading has on, particularly, the spread of otherwise locally dominant sedges and some species of ferns. The decrease in shading with the amount of ground occupied by fallen logs (plot c) suggests that the crown density in these forests takes a long time to re-establish after a treefall. Shading has a different relationship with the abundance of understorey individuals (plot d). As shading increases with greater complexity of canopy and development of forest layers, the number of understorey plants initially increases. This is presumed to be due to the extra shelter provided. However, plant numbers fall away as layer development continues past a critical point which may be due to reduced light but may also be due to increased competition from the tree strata for other resources.

## 4.2.4    Basal areas of trees

In north Queensland, Bell *et al.* (1987), Ash (1988) and Unwin (1989) all reported the exaggerated biomass of the sclerophyllous species growing in the rainforest ecotone. This may be due to the protection from fire afforded to those species when at a young age near the rainforest margin as well as a likely change in nutrient relations in the vicinity of the rainforest providing improved growth conditions. It was of interest whether a similar increase in the biomass of sclerophyllous species could be identified for the TZF in the study area. The field data obtained for vegetation structure analysis enabled such an investigation to be made.

For this test, the species selected needed to be canopy species which occurred prominently inside and outside the TZF. Three sclerophyllous species, *E. pilularis*, *S. glomulifera* and *A. torulosa*, had good representation in the TZF. The tallest 20 trees from each forest type for each species were selected and a comparison was made of their mean height and dbh in each forest type. The results are presented in Table 4.20. These results do not indicate a height difference for WSF species growing in the TZF except for *S. glomulifera* which, when free from the domination of *E. pilularis*, does achieve significantly

Table 4.20    Results of tree dimension variation analysis between forest
types for three sclerophyllous tree species (n=20). In north
Queensland it has been reported that certain WSF species
achieve greater physical size when growing in the transition
zone than in the sclerophyll forest. Values are mean height
(m) and mean dbh (cm) with standard deviations in brackets.
Significance levels are indicated by ns (not significant, p <
0.05) and ** (significant,  p < 0.01).

| Species | Height in WSF | Height in TZF | Signif |
|---|---|---|---|
| E. pilularis | 49.9  (8.9) | 44.6  (7.4) | ns |
| S. glomulifera | 27.3  (7.0) | 36.5  (7.0) | * * |
| A. torulosa | 26.6  (2.3) | 26.1  (5.2) | ns |
| | DBH in WSF | DBH in TZF | |
| E. pilularis | 103.3  (30.8) | 134.2  (35.8) | * * |
| S. glomulifera | 55.5  (24.2) | 84.5  (27.9) | * * |
| A. torulosa | 45.3  (15.4) | 40.7  (21.8) | ns |

greater heights in the TZF. The dimensions for A. torulosa appear
unrelated to the forest type of occurrence.

A correlation with the reports from north Queensland is, however,
revealed by the differences in dbh. Both E. pilularis and S. glomulifera
have attained significantly greater bole diameters, and hence woody
biomass, in the TZF. Florence (1964) has described the high moisture
requirements of Blackbutt and given the higher soil moisture levels
likely to be found near the rainforest patches, which all straddle
drainage lines, these results suggest the areas occupied by rainforest
may be closer to optimum habitat for this species than the large tracts
of land it occupies beyond the rainforest stands. The suitability of
elevated soil moisture to Blackbutt notwithstanding, the similarity of
these findings to those of north Queensland, involving an unrelated
Eucalyptus species, suggest that there may be further benefits, in
terms of life prospects, available to sclerophyllous trees fortunate
enough to have been able to germinate near rainforest.

As alluded to above, basal area could be used as a character in a
physiognomic classification of trees as the extent to which trees
develop biomass is a genetic characteristic albeit the expression of
which is sometimes influenced by habitat. By the same process, it may
be possible to classify vegetation along a gradient using tree basal area

characteristics. The following section provides results that bear on the usefulness of basal area data in the determination of a transition zone structural profile as distinct from similar profiles for WSF and WTRF.

Table 4.21 provides a profile of the basal areas which occur in each of the tree forest types. These results were obtained by extrapolating the results for each 0.1 ha transect plot to the hectare scale and then calculating the mean and standard deviation of the transect data. The profiles show that small trees ( < 20 cm DBH) are most prolific in the WTRF, medium trees (30-50 cm DBH) are most prolific in the WSF and large trees ( > 60 cm DBH) occupy the most area in the TZF. Although these data indicate the  basal area is significantly different among size classes between forest types, the structural profile, or model, of the TZF incorporates several other factors.

I am interested in the relationship between basal area and tree layer heights, crown density pattern and understorey structural features. Understorey structural features of relevance include the relative abundances for all growth form groups, and the extent to which the woody plants divide between the two understorey sub-groups of tree seedlings and permanent understorey layer woody plants. Large basal areas in conjunction with a paucity of tree seedlings may infer the presence of allelopathy (Florence and Crocker 1962).

The plots of these structural attributes against basal area data are able to show how these relationships change between the WSF and the TZF and between the TZF and the WTRF. Figure 4.46 a-c shows the relationship between tree heights and basal area from the plot data in each vegetation formation. Taking into account the y-axis scale, it can be seen that the slope of the best fit to these data is steepest for the TZF which indicates that the trees in the TZF are taller in relation to their basal area than for the WSF where the very tall trees occur and also for the WTRF where very large basal areas are absent.

Figure 4.47 a-c shows the relationship between basal area and crown sizes for each formation. Despite the differences in actual tree numbers in each plot,  the trends are very similar. The explanation for this lies in the compensating changes in the two components of tree

Table 4.21    Average basal areas by size class for each vegetation formation ha⁻¹. All values are $m^2$ and the standard deviation is in brackets. WSF values significantly different from TZF and TZF values significantly different from WTRF are indicated by * (P < 0.05) or ** (P < 0.01).

|  | WSF | TZF | WTRF |
|---|---|---|---|
| Basal area of stems > 60 cm DBH | 49.56 (10.30) | 63.76 (17.64) ** | 24.67 (8.78) |
| Basal area of stems 50-60 cm DBH | 3.86 (3.23) | 3.10 (1.89) | 10.16 (5.59) |
| Basal area of stems 40-50 cm DBH | 5.27 (3.28) | 4.75 (2.65) | 4.36 (1.50) |
| Basal area of stems 30-40 cm DBH | 5.97 (1.53) | 4.71 (3.51) | 4.24 (2.95) |
| Basal area of stems 20-30 cm DBH | 4.61 (2.20) | 6.15 (2.75) | 5.47 (2.26) |
| Basal area of stems 10-20 cm DBH | 4.55 (1.25) * | 5.05 (0.65) ** | 8.42 (2.47) |
| Basal area of stems < 10 cm DBH | 3.48 (1.65) | 2.51 (0.70) | 4.01 (1.73) |

architecture that were measured (crown width and crown depth) along the vegetation gradient. In WSF, the tendency is for canopy crowns to be wide and comparatively shallow with respect to overall plant height. Some mid-layer species develop more rounded crowns. At the other extreme in the WTRF, there are many more crowns per unit area with the consequence that they tend to be much less wide than the WSF but of greater depth. This applies especially to the mid-layer trees but also to many canopy trees. The TZF tends to be intermediate with respect to these attributes.

The extent to which large trees suppress the increase of biomass of adjacent individuals is revealed by Figure 4.48 a-c which plots the results of tree stem count against total sample unit basal area. Although there is a slightly positive relationship between net basal area for each sample unit and the number of stems in both WSF and WTRF, essentially the net biomass attained (in terms of basal area of trees) is not correlated with the number of stems for any of the forest types.

Figure 4.49 a-c shows the relationship between net basal area for each sample unit and crown density pattern (shading index) for all formations. This Figure shows the strong connection between basal area and canopy development especially for the WTRF. Canopy senescence, the gradual decline of crown size and density which is a
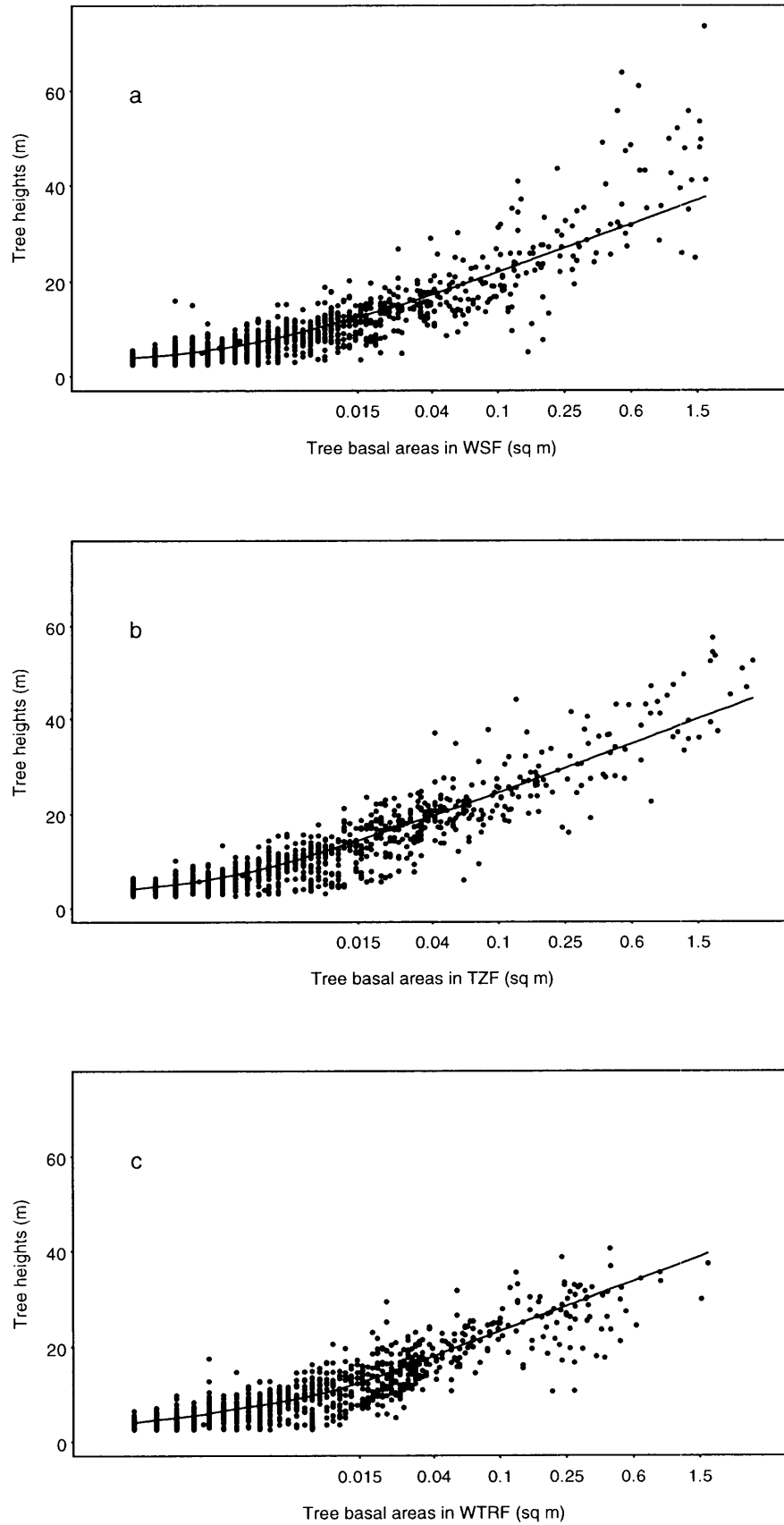
Figure 4.46   Relationship between basal areas of trees and tree heights
for each forest type.  Only trees with DBH > 25 mm are shown.
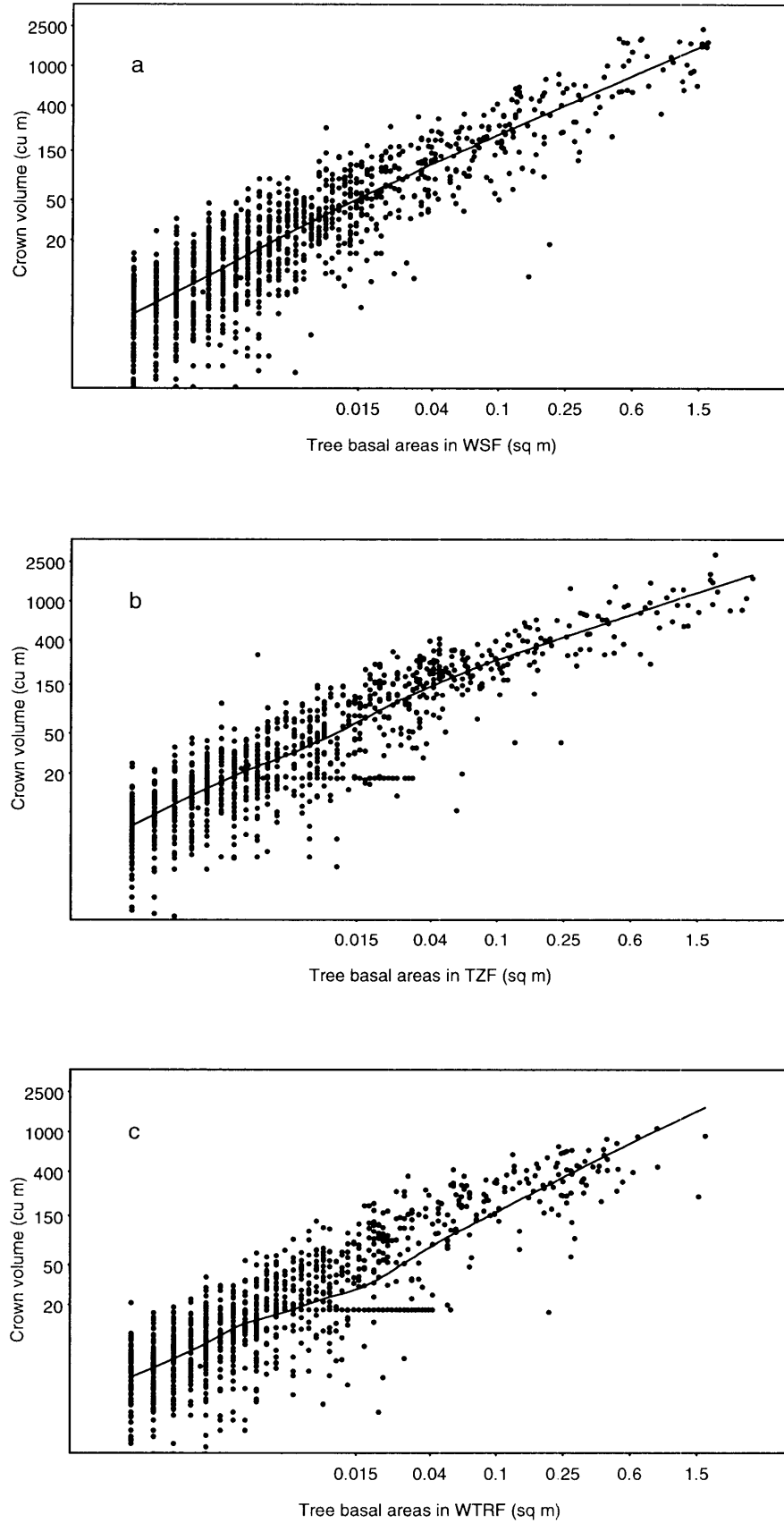Solid lines on plots are smoothed representations of the
relationships.

Figure 4.47   Relationship between tree basal areas and crown size for
each forest type.  Only trees with DBH > 25 mm are shown.
Solid lines on plots are smoothed representations of the
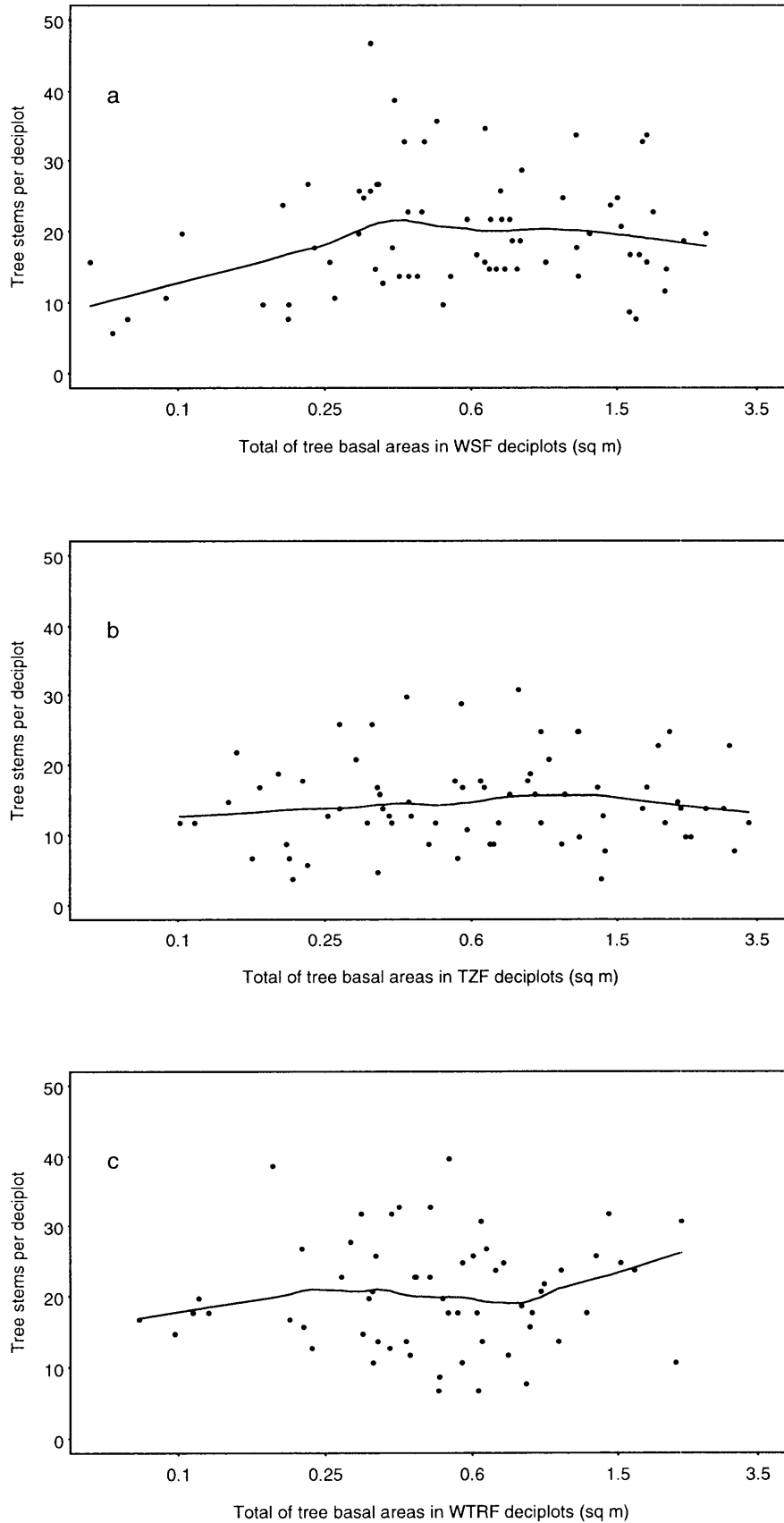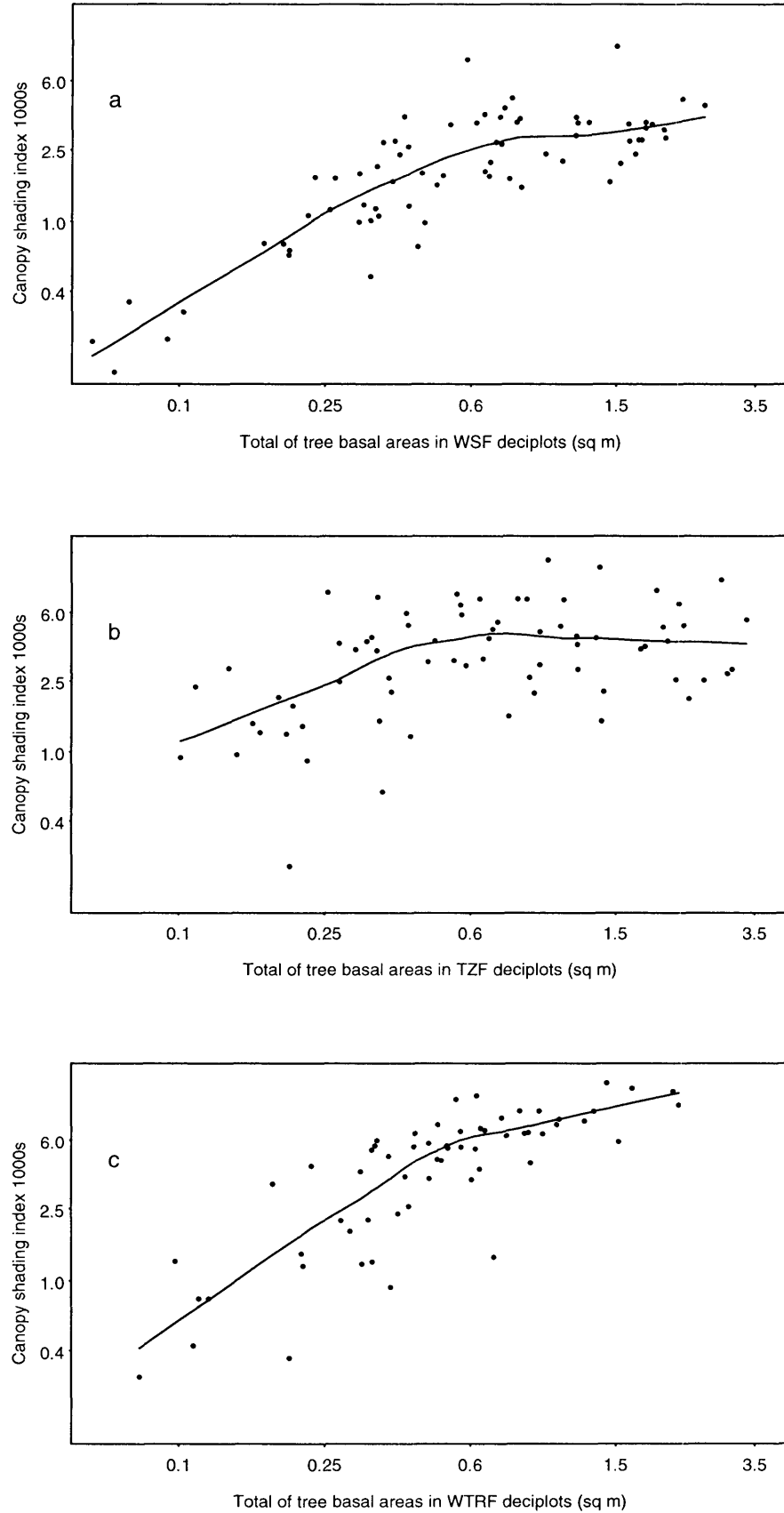relationships.

Figure 4.48 Relationship between the net basal areas of trees in the deciplot and the number of tree stems recorded for each forest type. Only trees with DBH > 25 mm have been included. Solid lines on plots are smoothed representations of the relationships.

Figure 4.49   Relationship between the net basal areas of trees in the deciplot and the shading index for each forest type.  Only trees with DBH > 25 mm have been included.  Solid lines on plots are smoothed representations of the relationships.

feature of tall, aged *Eucalyptus* species, contributes to the flattening of the curve for WSF. The curve for the TZF is not intermediate between the other two curves. In this forest type, for medium to large net basal areas, the shading index does not increase with net basal area. This is due to the presence of the prominent densely-crowned rainforest elements typically compensating when large-crowned Turpentine or Blackbutt are few or absent.

The series of plots relating net basal areas to the understorey structure begins with Figure 4.50 a-c which shows the relationship between basal area and number of species in the understorey for all formations. The increase in net basal area of trees appears unrelated to the number of understorey species supported by the sample units in all formations. The mechanisms of competition enable those understorey species disadvantaged to be replaced by other understorey species as the net basal area of trees increases.

Figure 4.51 a-c shows the relationship between basal area and abundances of understorey plants by using the area of exposed ground as a surrogate for those abundances across all formations. Again in this example, the understorey flora of the TZF show the least sensitivity to increase in net tree basal area. The trends for the other two forest types show a distinct decline in abundances of understorey plants with increasing basal areas to a threshold of 40% exposed ground (*i.e.* down to a threshold of 60% understorey occupation) for WSF and 60% exposed ground (40% understorey occupation) for WTRF after which further increases in basal area have no effect. The trends exhibited by Figure 4.51 reinforce those displayed by Figure 4.50.

The incidence of adult suppression of juvenile trees (Jacobs 1955; Florence and Crocker 1962; Incoll 1979) is tested by the plots of Figure 4.52 a-c. These show the relationship between basal area and abundance of tree species present as seedlings in the sample unit for each formation. This suppression is apparent in the WSF where the abundance of tree species at the seedling stage declines as net basal area increases. We already know from Figure 4.49a that the shading index has begun to flatten at high net basal areas yet there is no influx of seedlings from species which prefer reduced light regimes.
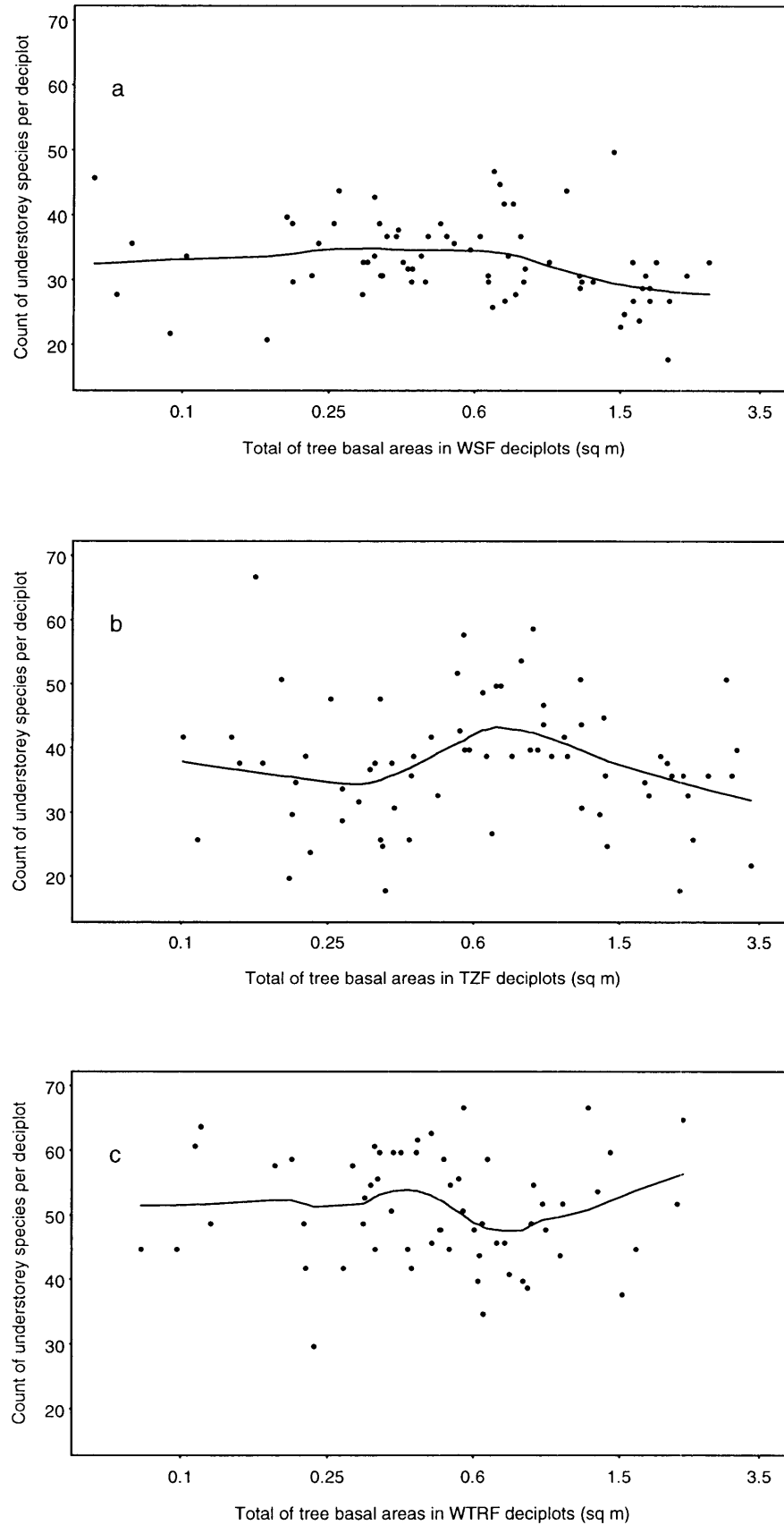
Figure 4.50   Relationship between the net basal areas of trees in the
deciplot and the number of understorey species recorded for each
forest type.  Only trees with DBH > 25 mm have been included.
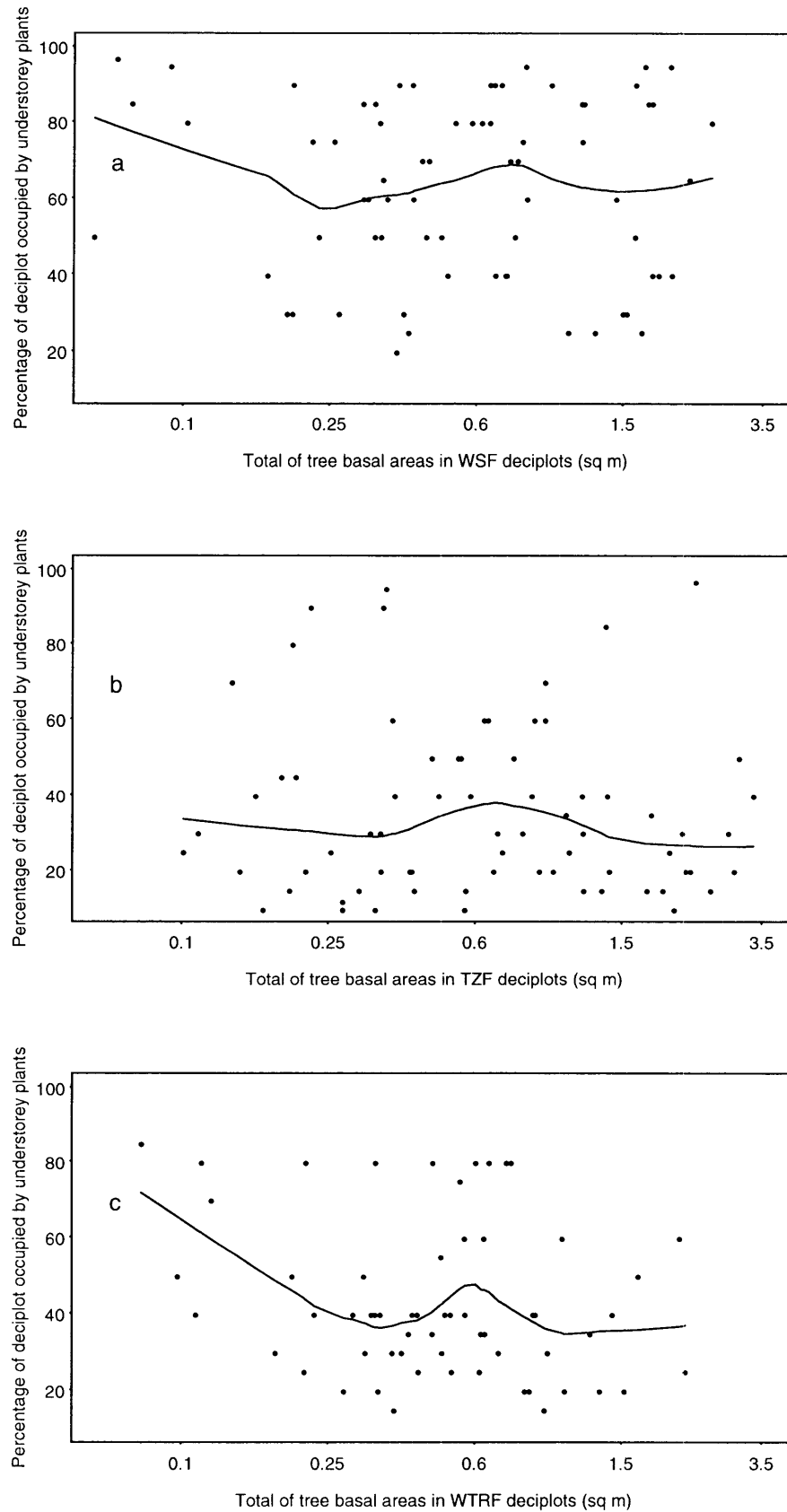Solid lines on plots are smoothed representations of the relationships.

Figure 4.51   Relationship between the net basal areas of trees in the
      deciplot and the abundance of understorey plants recorded for each
      forest type.  Only trees with DBH > 25 mm have been included.
      The net abundance of understorey plants is based not on a count
      but on the percentage of exposed ground in the deciplot.  Solid
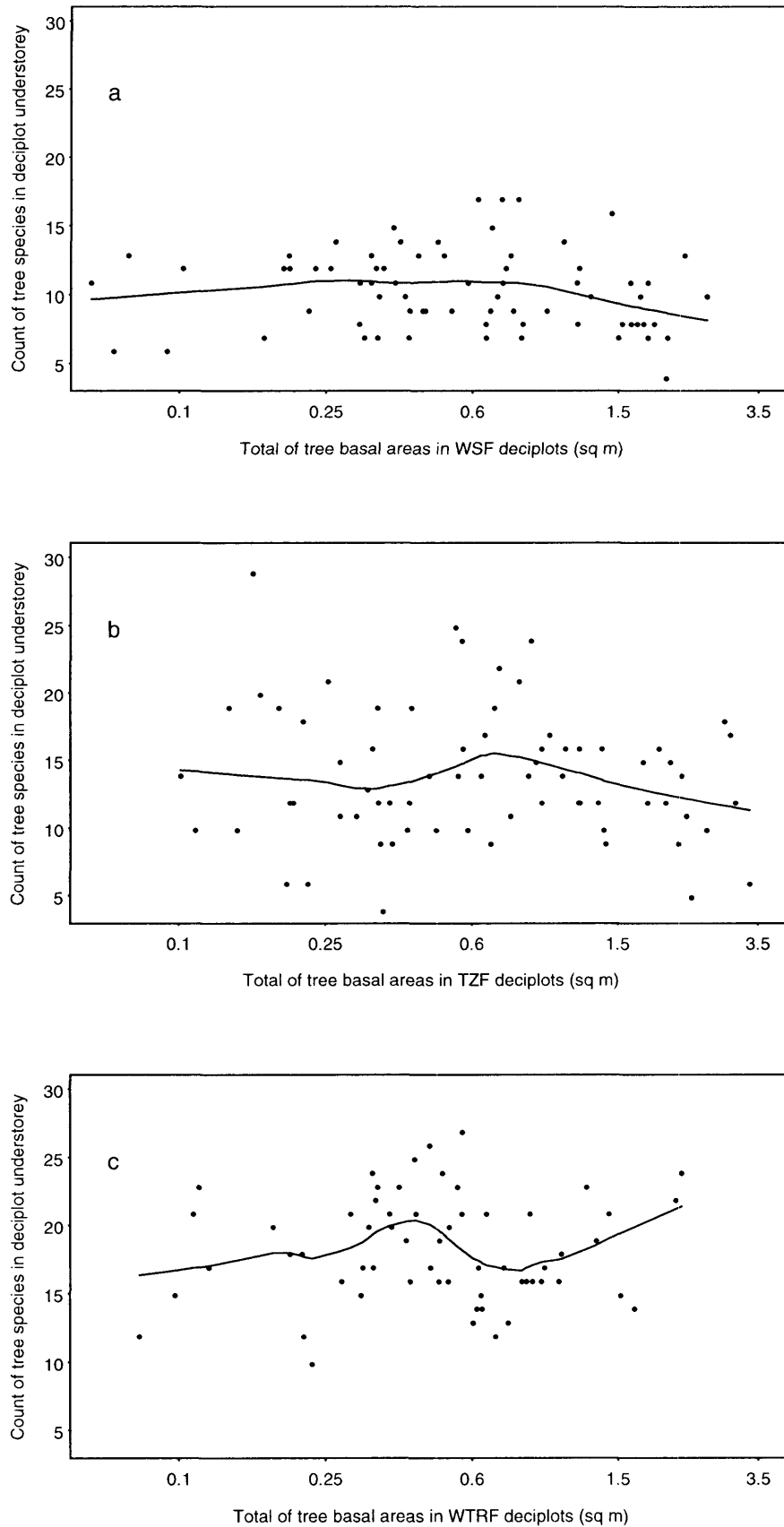      lines on plots are smoothed representations of the relationships.

Figure 4.52    Relationship between the net basal areas of trees in the deciplot and the number of tree species in the understorey recorded for each forest type. Only trees with DBH > 25 mm have been included. Solid lines on plots are smoothed representations of the relationships.
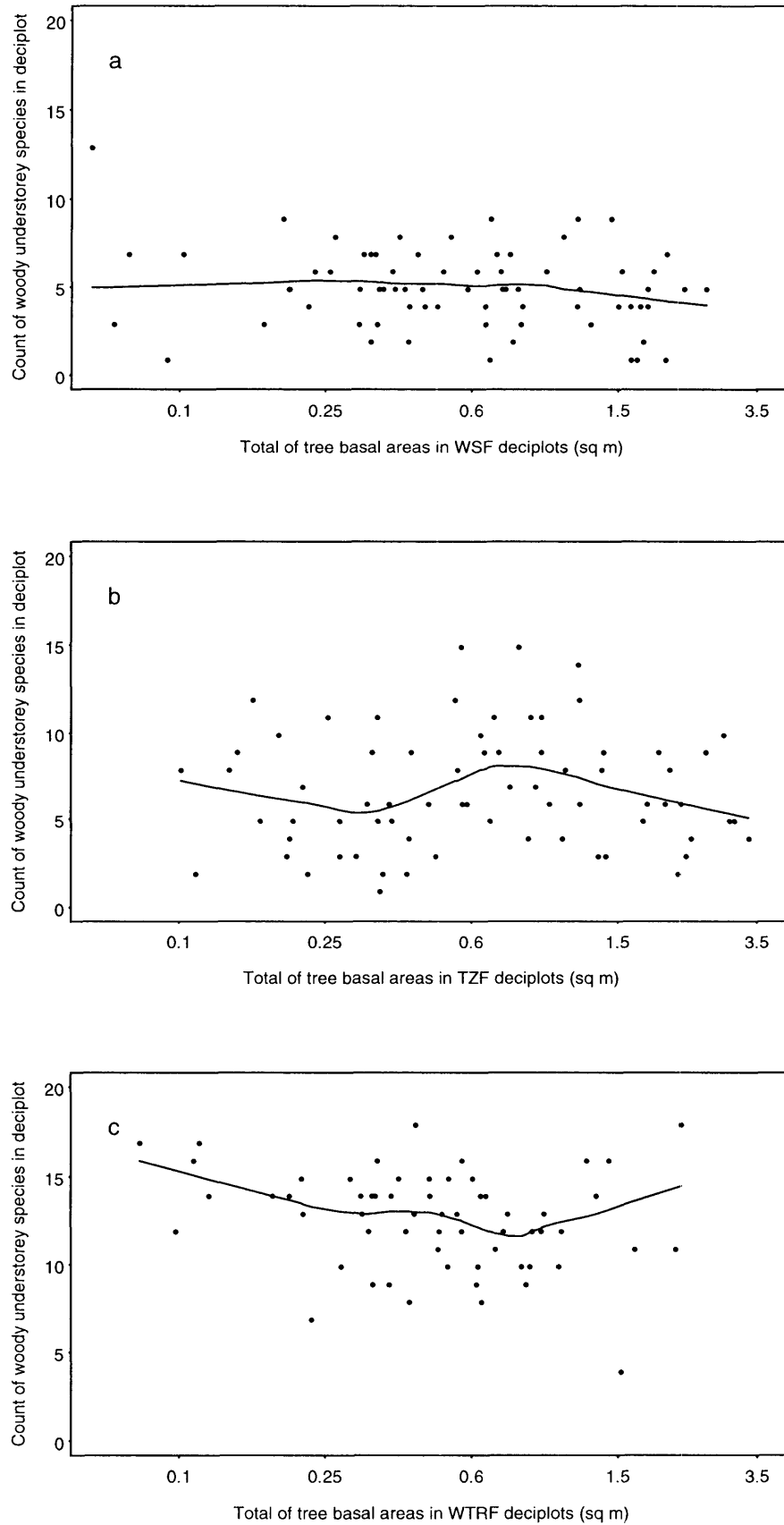
Figure 4.53   Relationship between the net basal areas of trees in the
deciplot and the number of woody permanent understorey species
recorded for each forest type.  Only trees with DBH > 25 mm have
been included.  Solid lines on plots are smoothed representations
of the relationships.

Suppression of tree seedlings is shown in plots b and c to become increasingly less apparent as the vegetation changes to warm temperate rainforest. In the rainforest the increase in net basal area in the sample units tends to emanate not so much from larger trees but from an increase in canopy trees. Where there is an increase in canopy trees it is comprised of an increase in species which is subsequently reflected in an increase in tree species richness of the understorey.

Figure 4.53 a-c shows the relationship between basal area and richness of permanent woody understorey species in the sample unit for each formation. These plots indicate that the species richness of "genuine" understorey woody plants is not related to the dominance of tree biomass in any of the forest types.

## 4.2.5    Classification of structural types

The components used in this thesis to identify a structural type have now been described. They include:

- the number of layers in the vertical profile of the vegetation;
- the actual heights of the layers;
- the number of plants per unit area within each layer;
- the diversity of growth forms present;
- the dominant growth form(s) of the understorey;
- two components of crown architecture;
- crown packing density within the tree layers, and, hence, the amount of shading of the forest floor;
- the presence of site inhibitors of structural diversity (typically exposed rocks); and
- the measurable amount of site disturbance.

Using these variables it is possible to classify all the sample units of the study area and locate the distribution of these classes on the vegetation gradient from WSF to WTRF. The data matrix is compiled on the basis of the presence or absence of each of the structural features mentioned. Where continuous variables are concerned, for example the heights of tree layers, the data are split into range classes and the matrix contains a present or absent indicator for each class for each

layer for each sample area. The underlying assumption of this procedure is that all the structural attributes have equal importance. The unsatisfactory consequences of this assumption are illustrated below.

The vegetation structure of the sample areas was classified using the same software and procedures as described in Chapter 3 for the classification of the floristics. The amount of site disturbance was an index derived from the presence of fire scars, the presence of dead trees, the incidence of trees leaning away from the vertical (this variable was treated as a surrogate for soil surface disruption due to the uprooting of fallen logs; actual damage done to tree trunk by falling trees or large limbs; and the change in growth direction of the tree in response to canopy disturbance); the incidence of trees with poorly developed crowns (this variable unfortunately includes those trees in decline due to age and inability to compete for essential resources) and the area of ground covered of fallen logs per sample unit.

The classification is shown by Figure 4.54. It is based on a flexible UPGMA technique which is a space-conserving strategy in that it preserves the ecological relationships in sample space as clustering proceeds. The cluster analysis reveals definite patterns in the structural variations along the vegetation gradient. These patterns are discernable notwithstanding the high levels of similarity between the sample units with many being less than 10% dissimilar.

Rainforest is clearly significantly different from the other two forest types as more than half of them separate out at the 4-group level and at the 7-group level four of the groups are essentially rainforest groups. The main structural features which separate rainforest are the complexity of the mid-layer arrangements, the overall consistency of the height of layers and low levels of disturbance evidence. Of the other groups at the 7-group level (beyond which some groups become difficult to reconcile with field impressions) are

• the large group 1 which contains 50% WSF sites and includes sites with upper and lower canopy layers, a medium understorey and a medium disturbance rating;
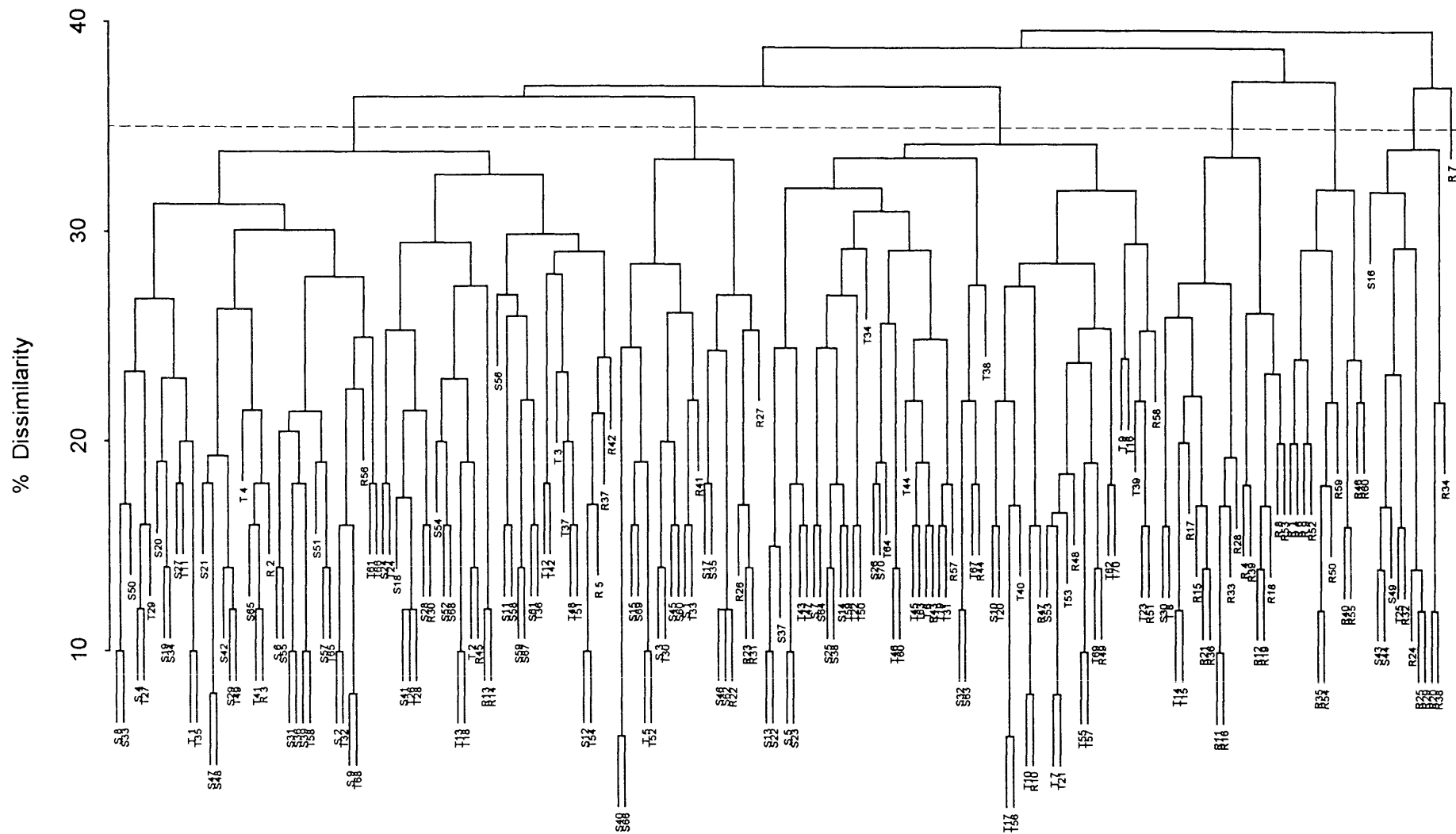
Figure 4.54    Classification of deciplots using structural attributes

Broken line is the 7-group level cutoff described in the text.

The clustering used a UPGMA algorithm after application of the Bray-Curtis association measure.

Deciplot codes are: S1-S70 (WSF), T1-T70 (TZF), R1-R60 (WTRF)

• group 2 which contains over 50% WSF sites which are those having upper canopy only, lower mid-layer and a well-developed understorey with a relatively high disturbance rating; and

• group 3 which is about 60% TZF sites which have upper and lower canopy layers, an upper mid-layer with a well-developed understorey and low disturbance rating.

Johnston and Lacey (1984) have pointed out that the problem with the plethora of classification systems that have been proposed in Australia stems from the fact that they use different combinations of floristic and/or structural attributes to define the classes. When applied to the same data the class boundaries identified by these systems rarely coincide. A comparison of the classifications based on floristics (Figs. 4.18-4.20) and that based on perceived structural attributes (Fig. 4.54) illustrates the reasons why. Floristic classifications, regardless of whether they are based on quantitative or qualitative data, treat all the variables (species) as having equal chances of observation (occurrence) and therefore of equal value. Physiognomic or structural characteristics, on the other hand, are not equal. They are recognised by both the importance of their contribution to the visual perception of structure (e.g. diversity of growth forms present) and also by their association with another attribute (e.g. hierarchical relationship between identified layer, plants per layer and layer height). Hence, a comparison of the floristics-based clusters and the structure-based cluster have several places of disagreement. Whereas the floristic classifications showed tight within-transect fidelity, the structural classification has tended to scatter the sample units indicating that, at the sample unit scale, structure and its co-variate, disturbance are highly heterogeneous. This scattering is much more pronounced with the TZF and WTRF. The structural classification of WSF sample units (shown as "S" sites in Fig. 4.54) groups them broadly similarly to the arrangement of transects indicated by Fig. 4.18. This suggests that the derivation of a floristic-structural classification for the WSF formation should have a much higher reliability than one derived for either of the other two types.