

4.3 Litterfall survey

4.3.1 Litterfall within vegetation formations

The patterns of litterfall for each vegetation formation along the transects all showed similar trends but there are interesting and formation-specific differences in those patterns. The gross litterfall results for each floristic group are shown in Table 4.22. These figures confirm the early data of Webb *et al.* (1969) that the WTRF in this high rainfall region is substantially less productive, in terms of weight of litterfall, than the WSF. The most interesting result is that the total litterfall in the TZF falls almost exactly midway between the totals for WSF and WTRF. For almost all collections, there was an undistributed component of small plant parts and other matter. This component of the litter included inorganic and organic dust as well as plants parts not determinable without a magnifying glass. At times these residues were quite a significant component of the gross return for any particular trap. The contribution of these residues will not be analysed but from Table 4.22 they can be seen to have amounted to between 7-9% of the total litter for all formations. Of the other researchers mentioned, only Lowman (1988) reported on the contribution of residual matter. She found that in her WTRF sites the contribution was never greater than 5% which is markedly less than my result. A possible source of this difference may be attributable to differing concentrations of arboreal foragers (vertebrate and invertebrate) between the two sites. It was presumed that much of the very small leaf residue was due to arboreal invertebrate activity and much of the very small woody residue was due to the movement of vertebrates (birds and mammals) on tree branches.

The distribution of total litterfall for each vegetation is shown in Figure 4.55. This graph shows the distinct bimodal pattern of litterfall reported by several other workers including Hatch (1955), Hannon (1958), McColl (1966), Ashton (1975), Rogers and Westman (1977) and Birk (1979) in eucalypt forests, while Brasell *et al.* (1980) and Lowman (1988) found similar effects in rainforests. The first peak after the winter occurs in October and at which time the abscission rate is much more dramatic for mesophyllous species than for the sclerophyllous

Table 4.22 Total litter return ($t\ ha^{-1}\ yr^{-1}$) for the three vegetation formations. Values in brackets indicate the standard error.

	WSF		TZF		WTRF	
Leaf fall	5.22	(0.18)	4.55	(0.20)	4.33	(0.27)
Woody material	3.45	(0.51)	2.85	(0.31)	1.88	(0.66)
Reproductive parts	0.25	(0.05)	0.17	(0.02)	0.15	(0.02)
Residual comminuted material	0.76	(?)	0.77	(?)	0.61	(?)
Total litterfall	9.68	(0.65)	8.34	(0.40)	6.97	(0.87)

species. This is indicated in Fig. 4.55 by the abrupt rise in both WTRF and TZF litterfall while the WSF return, although also rising to a peak, is continuing a steady rise which began in August.

Attiwill *et al.* (1978) proposed that there was a causal relationship between litterfall and the cycle of temperature change. They noted that litterfall rates increased steadily as the temperature warmed but fell away quickly once the cooling cycle commenced. That hypothesis appears to be supported only by the pattern of WSF litterfall. Fig 4.55 shows a second litterfall peak occurs in January but this month appears to be of greater significance for sclerophyllous species than for the mesophyllous species. There is a third peak in July that was indicated by the litterfall in all vegetations. A midwinter peak in litterfall has not been reported by other investigators which suggests that the pattern obtained was probably a function of wind or storm. This conclusion is further supported by the graphs shown in Figs. 4.56 and 4.57. In these Figures, both leaf fall and woody litterfall are shown to have peaked for all communities in July. Such congruency indicates an allogenic event such as a windstorm.

Asynchrony in abscission phenology among dominant species has been attributed to the incidence of bimodality in litterfall. This has been reported by Rogers and Westman (1977) and Birk (1979) who worked with essentially two-species or two-genera forest canopies. In north Queensland, Spain (1984) found that litterfall in tropical rainforest is

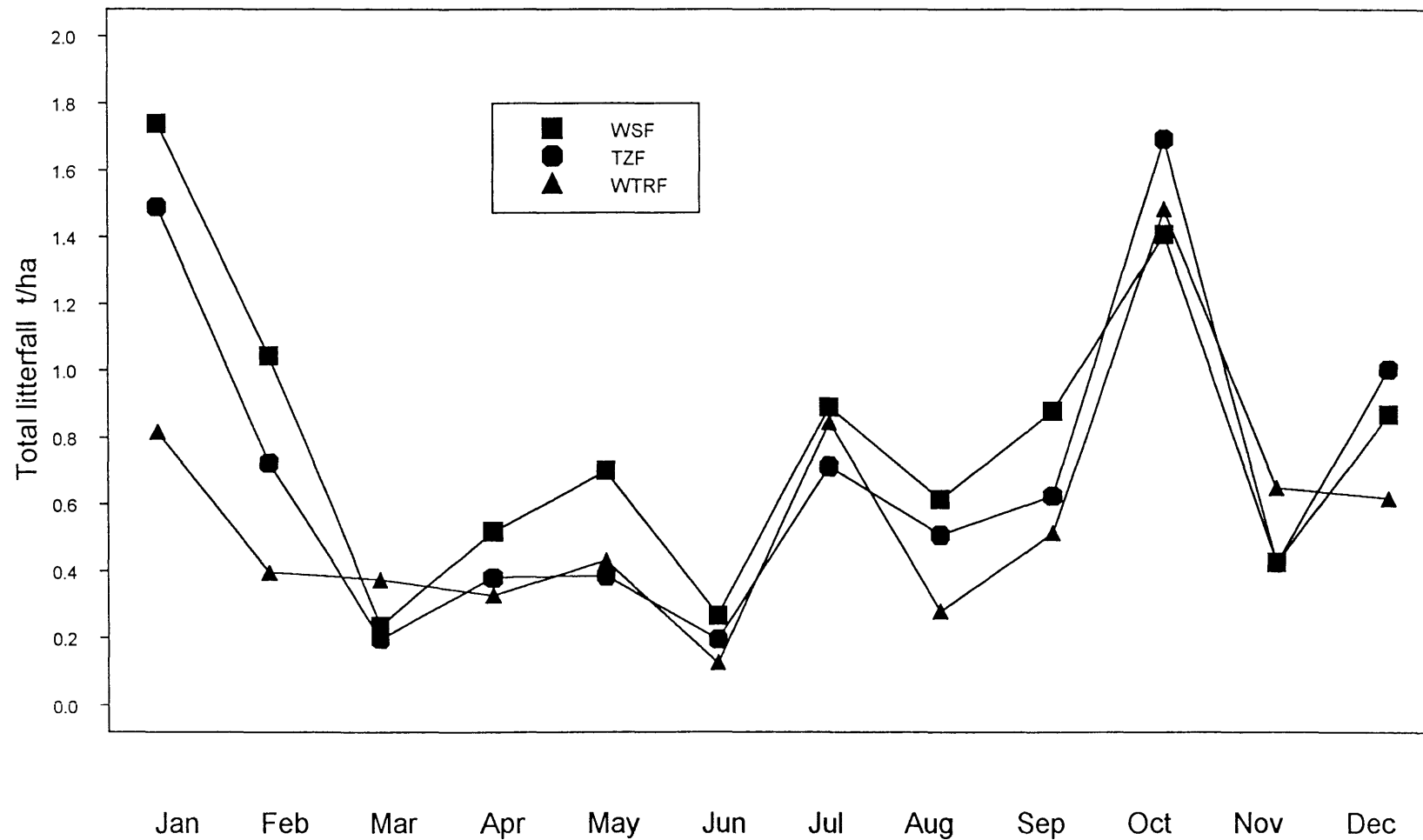


Figure 4.55 Comparison of total monthly litterfall pattern for the three vegetation formations.

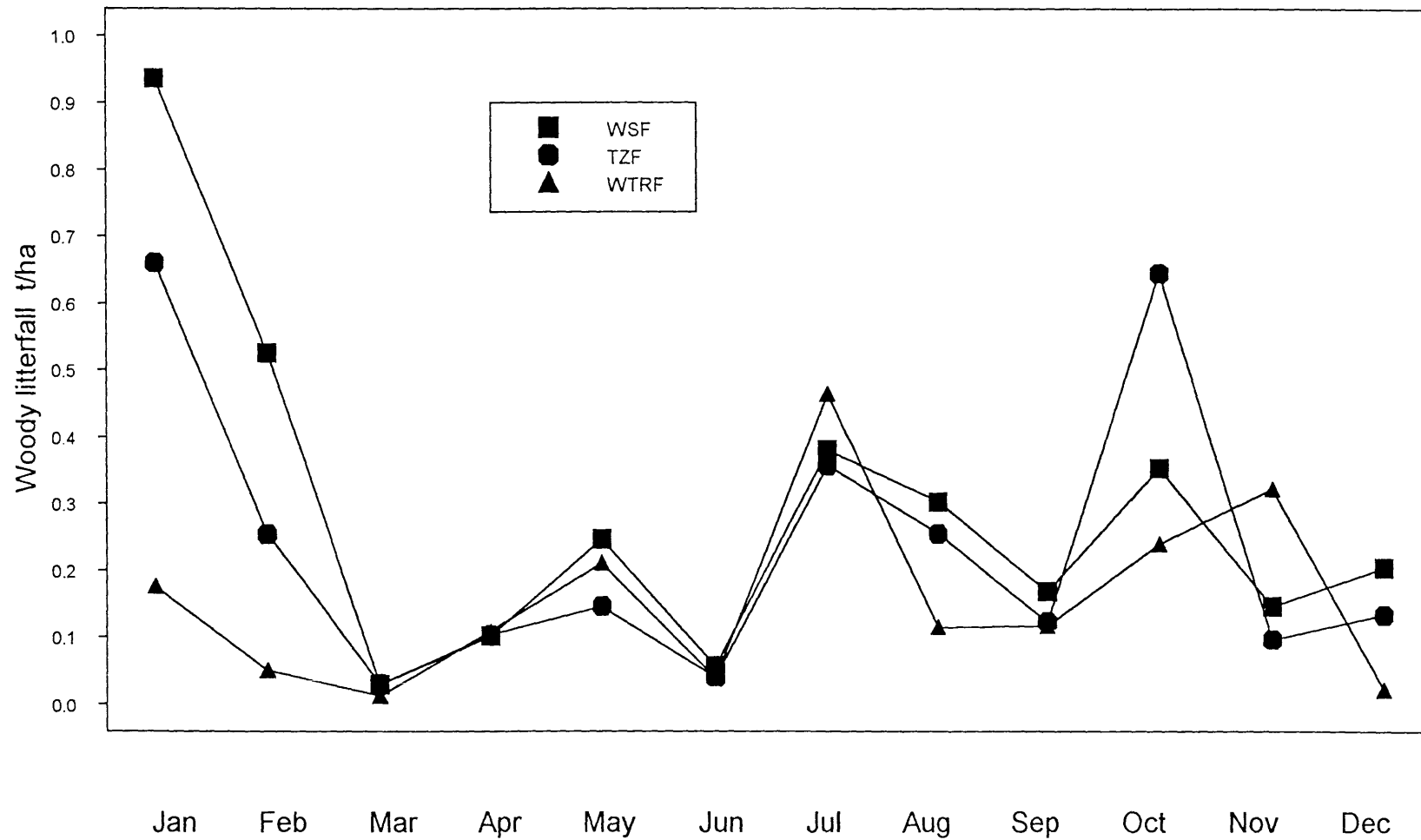


Figure 4.56 Comparison of monthly woody litterfall pattern for the three vegetation formations.

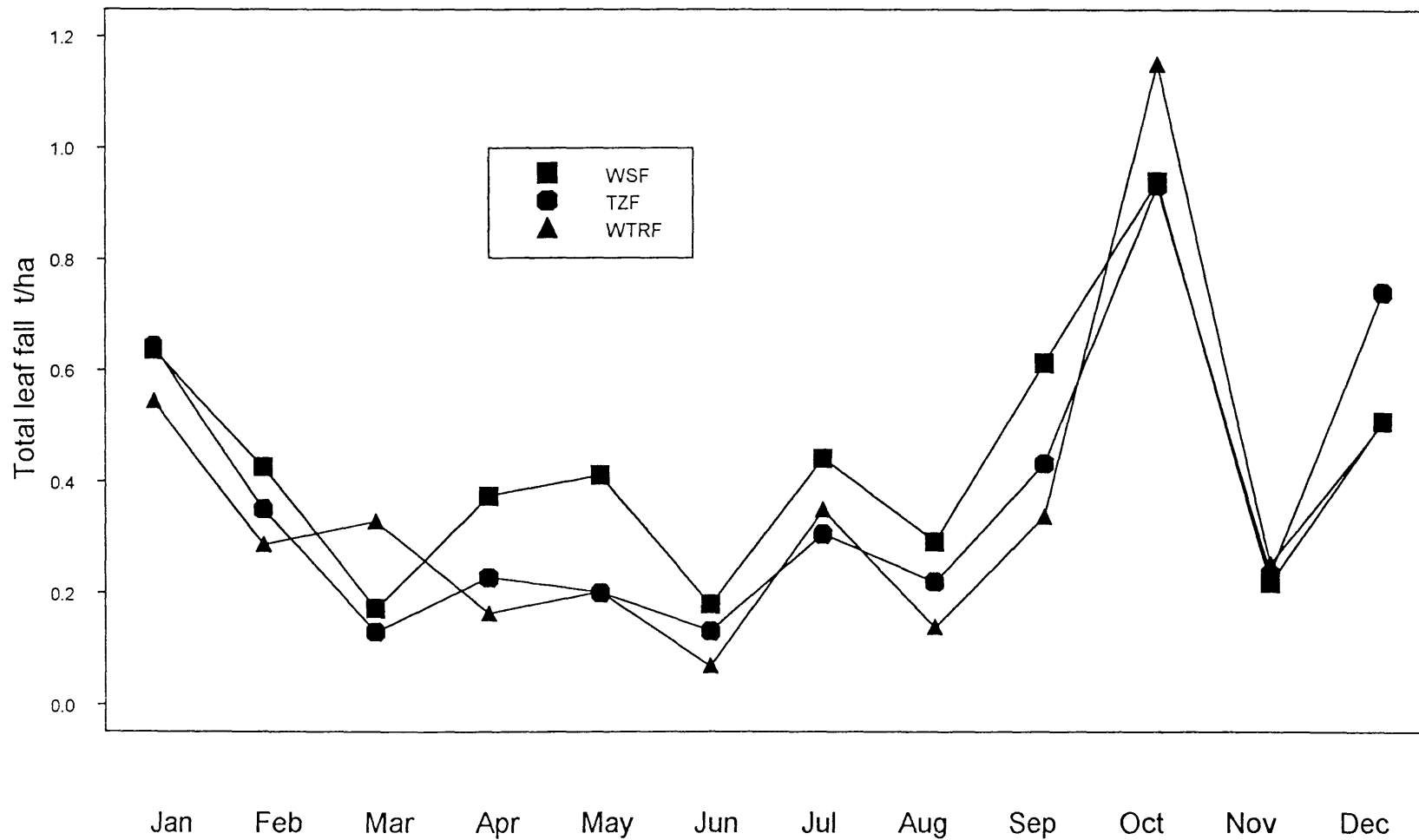


Figure 4.57 Comparison of total monthly leaf fall pattern for the three vegetation formations.

polymodal due to differing abscission times between species. The WSF in the study area is dominated by the single species *Eucalyptus pilularis* but the usual presence of a well-developed understorey may possibly represent an alternative "dominant" explaining the bimodality of litterfall in WSF. This point will be pursued in the next section when the abscission rates of the key species for each formation are examined.

Examination of Fig. 4.55 in terms of Figs. 4.56 and 4.57 shows that the majority of the large litterfalls for WSF and TZF which occurred in the January peak was made up of woody material (twigs, bark and branchlets). Ashton (1975), working in a 69-year-old forest, found wood and twig fall to be 21-27% of litter but variable, being greatly dependent on storms. He regarded this as a high figure and attributed it to the rapid ramification of shoots which is characteristic of the faster growing eucalypts (Jacobs 1955). The woody litter return of the old-growth forest in this study was 35% of the total litter. The reason for the disparity may be found in Jacobs (1955) where he says that over-mature trees (e.g. this study) should be expected to have a lower percentage of leaf fall than younger trees (e.g. Ashton 1975). The rainforest does not have a summer woodfall event. In a four-year survey, Lowman (1988) found that the litterfall in WTRF consisted of 30-33% wood. She did not experience any large branch or tree falls which suggests her results are a close guide to the fine wood litter production rate. The woody material return in the WTRF for this study area was satisfactorily close to that range, averaging about 27%.

The leaf fall component of the January peak was, in fact, very similar for all formations indicating that the abscission response of mesophyllous species at that time is more significant than was earlier suggested by Figure 4.55. Webb *et al.* (1969), however, working in WTRF on a mountain range southwest of the study area, did not detect a January peak in leaf fall, but they did find that the weight of the October leaf fall in WTRF exceeded that for WSF even though the overall leaf fall for WTRF was less than WSF. Figure 4.57 concurs with their results on this point. It should be noted here that a similarity of (dried) leaf fall weights in WSF and WTRF does not mean a similarity in numbers of leaves. The leaves of sclerophyllous species are much

heavier than those of the mesophyllous species. Given the range of leaf sizes of the main mesophyllous species (from about 30 mm for *Syzygium luehmannii* to about 130 mm for *Sloanea woollsii*), perhaps as many as 4 or 5 leaves are equivalent in weight to one typical eucalypt leaf.

Figure 4.58 shows the comparison of the weights of plant reproductive parts in the litter for each formation. The most common flowering period is the springtime and this is reflected in the volume of material, mostly flowers, reaching the traps in September. A peak in January reflects the first fruits from that setting but also includes a large number of immature fruit, especially *Eucalyptus*. The seed or fruit component of WSF included the main species (*Eucalyptus*, *Syncarpia*, *Acacia*, *Daviesia*, *Allocasuarina* and *Persoonia*) and no fruits from the adjacent TZF. In the TZF, the fruits of eleven species were found in the litter but again all of these species were already growing in the vicinity of the litter trap. The WTRF traps yielded the fruits of 13 species. Some of these were in very small quantities and three species were represented by just one fruit. This fruit sample, however, included two species (*Syncarpia glomulifera* and *Cryptocarya rigida*) which were not present in the immediate vicinity of the trap. The woody *Syncarpia* fruit is presumed to have been blown across from the TZF and the *C. rigida* fruit is presumed to have been dropped by a bird after having been carried into the trap area. The results indicate that the movement of propagules from one forest type to another, particularly from the rainforest toward the sclerophyll forest is not a common event.

A comparison of the weights of WSF fruits and WTRF fruits is dependent on the density of trap placement. The tall, spreading crowns of *Eucalyptus* trees enable the fruit to be widely distributed across the site, whereas the bulk of the fruit of the only rainforest tree with a woody fruit production volume comparable to *Eucalyptus*, *Archontophoenix cunninghamiana*, falls directly to the base of its stem. A further difficulty lies in the fruiting irregularity or uncertainty of many of the trees of the mature rainforest (Floyd 1990a). This irregularity clearly influenced the seed and fruit component of the litter, particularly in the WTRF. Lowman (1988) recorded between 0.7

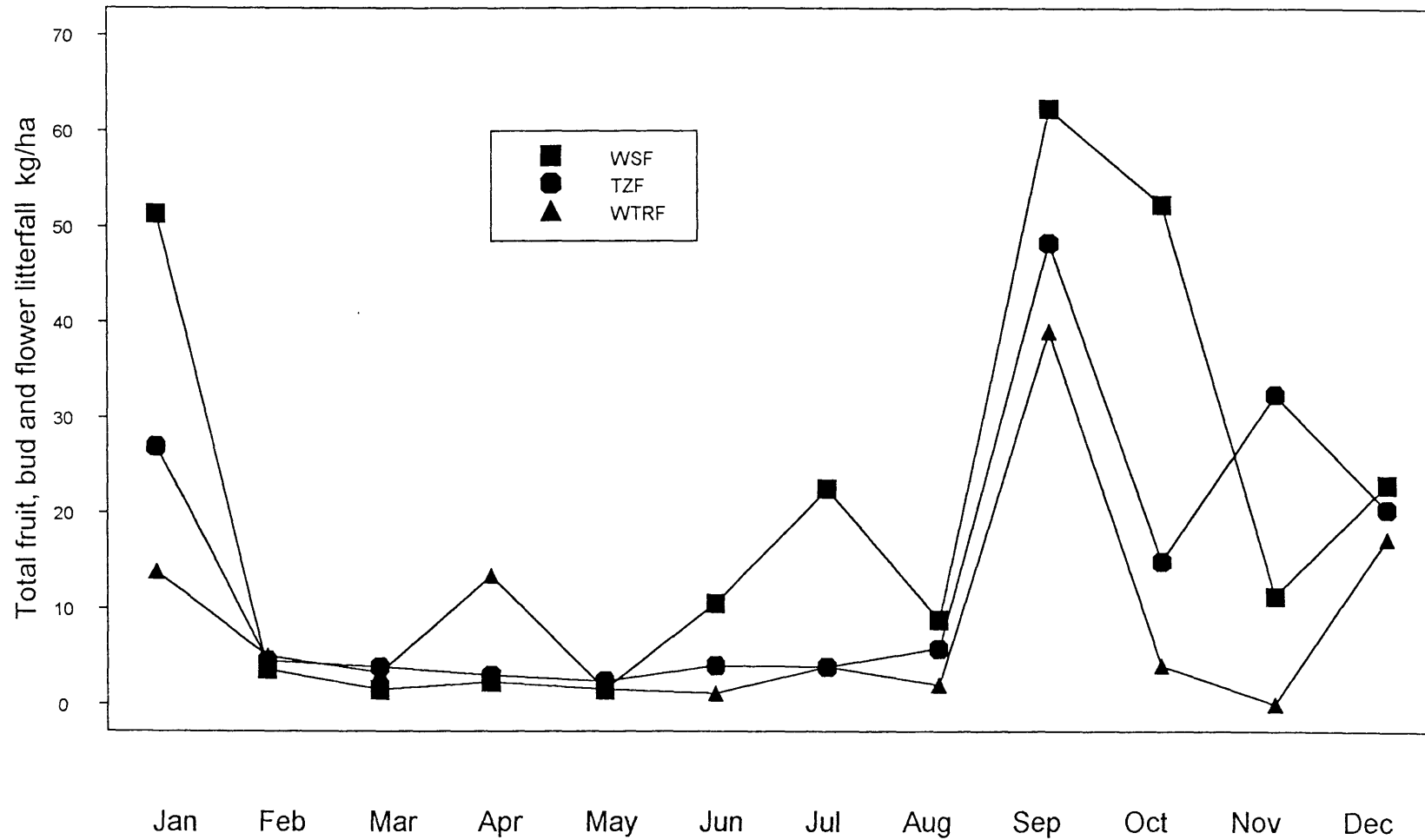


Figure 4.58 Comparison of total monthly reproductive parts litterfall pattern for the three vegetation formations.

and 1.3 t ha⁻¹ fruit fall in WTRF which greatly exceeded my results of less than 0.2 t ha⁻¹.

4.3.2 Distribution of litter by species

4.3.2.1 Wet sclerophyll forest

The bulk of the litterfall that was attributable to particular species was the leaf fall. The leaf fall in WSF was dominated by the two canopy species *Eucalyptus pilularis* and *Syncarpia glomulifera* and the mid-layer species *Allocasuarina torulosa*. Table 4.23 shows that the remaining species contributed just 22% of the leaf fall. This domination parallels the physical domination of these three species which amounted to 91% of the basal area of live trees within the plots containing the traps. The canopy species together contributed 56% of the leaf fall. These proportions of the leaf fall were fairly consistent throughout the year. The only aberrations to this pattern (in February and May) were due to instances of the fronds of *Cyathea australis* falling into the litter traps.

Ashton (1975) found that the understorey contributed 25% of the litter in a mature (69 year old) *E. regnans* forest. In this forest the understorey contributed just 8.5% of the total leaf litter and, as its woody litter was minimal, the understorey comprised even less of the total litterfall. This difference may reflect the difference of our definitions of understorey. If all plants below the eucalypt canopy are regarded as understorey, then it is apparent that as WSF approaches old-growth status, the sub-canopy litter comprises an increasing proportion of the total litter.

The Figures 4.59-4.63 show the main leaf fall results for WSF. Fig. 4.59 reproduces the WSF component of Fig. 4.57 and shows the 95% confidence limits for the data. Considering the sample size, the range of the confidence limits is very good. Fig. 4.60 shows the contribution of each main structural layer to the gross leaf fall. Birk (1979) had found that the leaf fall of understorey species in her study area was out of phase with the overstorey. Some asynchronous results show up in the autumn and the canopy species do not maintain the same rate of

Table 4.23 Monthly percentage by dry weight of total leaf litter return in WSF for each species for which at least some leaves were recorded in a litter trap in any month. Values may not sum to 100 due to rounding.

* = month of maximum percentage return.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
<u>Canopy species</u>													
<i>Eucalyptus</i> spp	45	36	65	55	42	57	59	61	53	39	40	49	48
<i>Syncarpia glomulifera</i>	13	9	9	7	5	11	4	6	5	9	8	10	8
<u>Mid-layer species</u>													
<i>Allocasuarina torulosa</i>	22	14	10	13	16	21	26	17	29	31	27	22	22
<i>Caldcluvia paniculosa</i>	-	-	-	-	-	-	-	-	-	*	-	-	-
<i>Callicoma serratifolia</i>	1	2	2	1	1	-	1	1	1	9	5	1	3
<i>Cryptocarya rigida</i>	1	-	2	1	-	2	1	2	2	3	3	1	2
<i>Daviesia /Acacia orites</i>	6	7	4	3	4	3	3	5	4	3	5	8	5
<i>Duboisia myoporoides</i>	-	-	-	-	-	-	*	-	-	-	-	-	-
<i>Elaeocarpus reticulatus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-
<i>Persoonia media</i>	-	1	-	-	1	-	-	-	-	-	-	1	-
<i>Phebalium squamosum</i>	-	-	-	-	-	1	1	-	-	-	2	-	-
<i>Schizomeria ovata</i>	-	-	-	1	-	-	1	1	1	-	1	-	-
<u>Understorey species</u>													
<i>Acrotriche aggregata</i>	-	*	-	-	-	-	-	-	-	-	-	-	-
Pteridophytes	8	22	-	15	29	-	2	-	-	-	-	-	6
<u>Vines and mistletoes</u>													
<i>Cissus hypoglauca</i>	1	-	-	-	-	-	-	-	1	-	-	1	-
Mistletoes	1	-	-	-	-	-	-	-	-	2	5	1	1
<i>Smilax australis</i>	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Smilax glyciophylla</i>	-	1	1	-	-	1	-	-	-	-	1	-	-
<u>Miscellaneous leaves</u>													
	3	9	6	4	3	5	3	8	3	3	4	4	4

increase of leaf fall before and after September as the subsidiary layers do. For most of the year the peaks in the understorey leaf fall are in phase with the other structural layers. As mentioned above, several researchers (e.g. Lowman 1988) have found an asynchronous leaf fall pattern between co-dominant species. A comparison of the leaf fall pattern of the three main species of Figs. 4.61-4.63 does not indicate that the bimodality shown in the WSF leaf fall return (Fig. 4.59) is attributable to individual species.

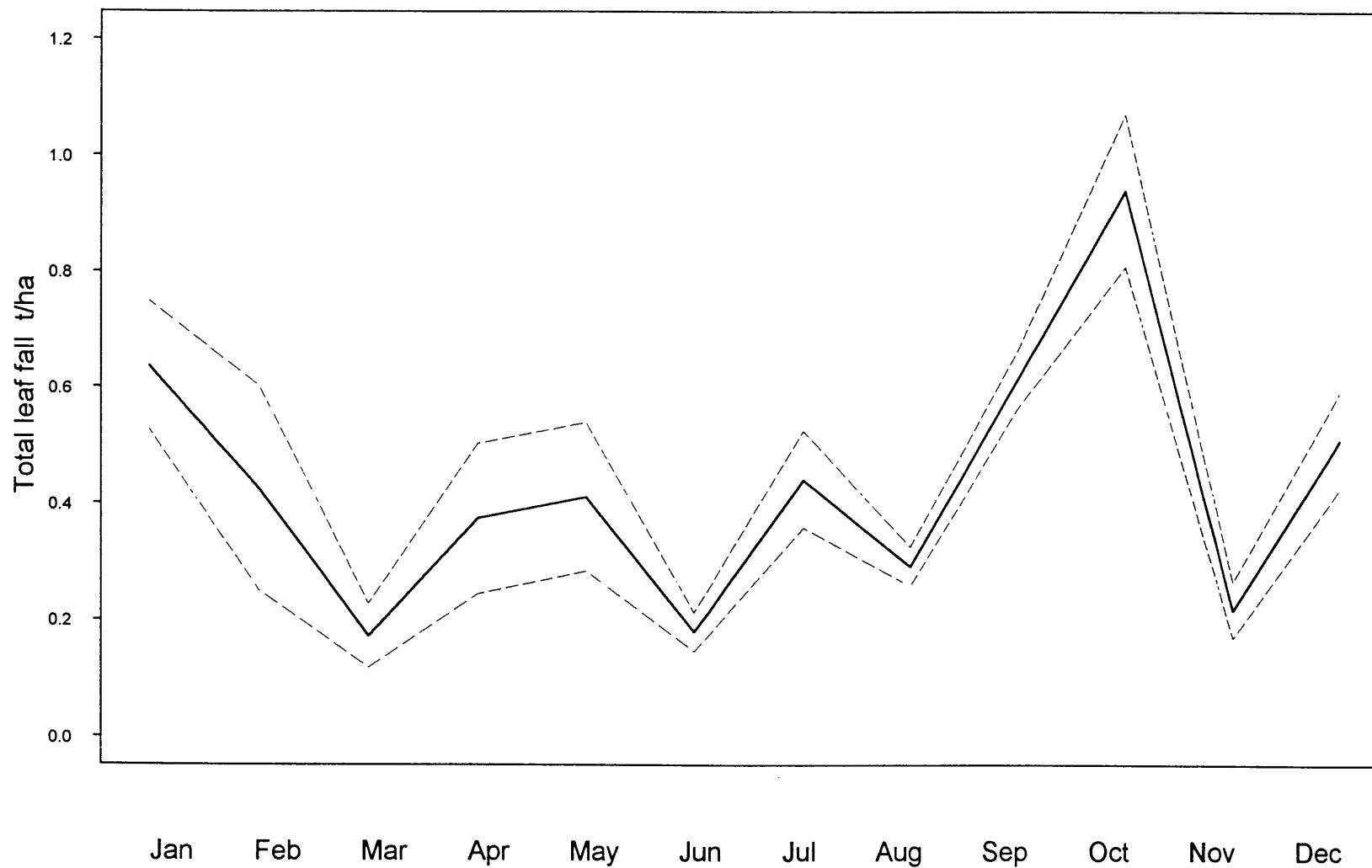


Figure 4.59 Total monthly leaf fall pattern for WSF with 95% confidence limits.

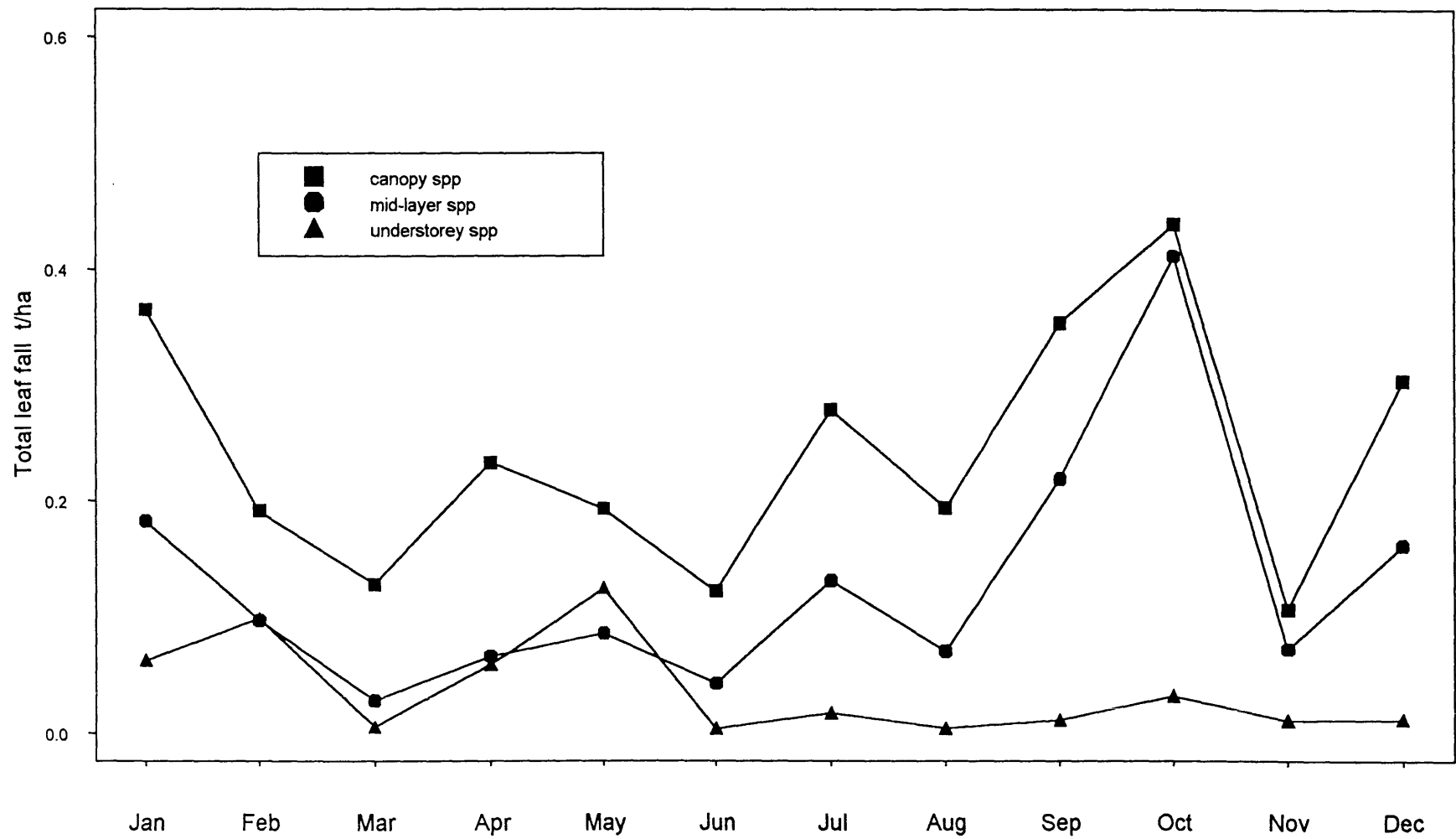


Figure 4.60 Comparison of total monthly leaf fall pattern for canopy, mid-layer and understorey species in WSF.

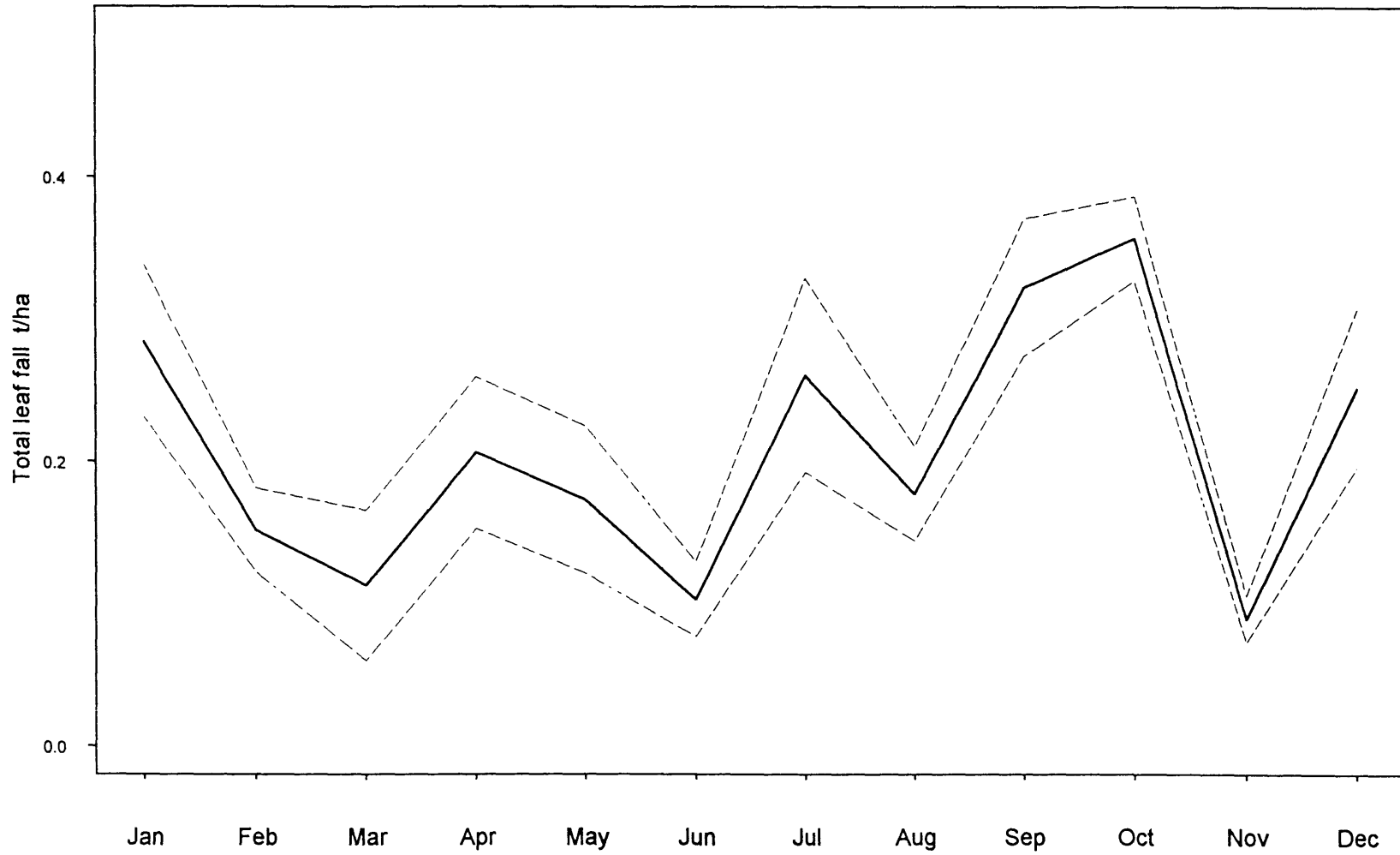


Figure 4.61 Total monthly leaf fall pattern of *Eucalyptus pilularis* in WSF with 95% confidence limits.

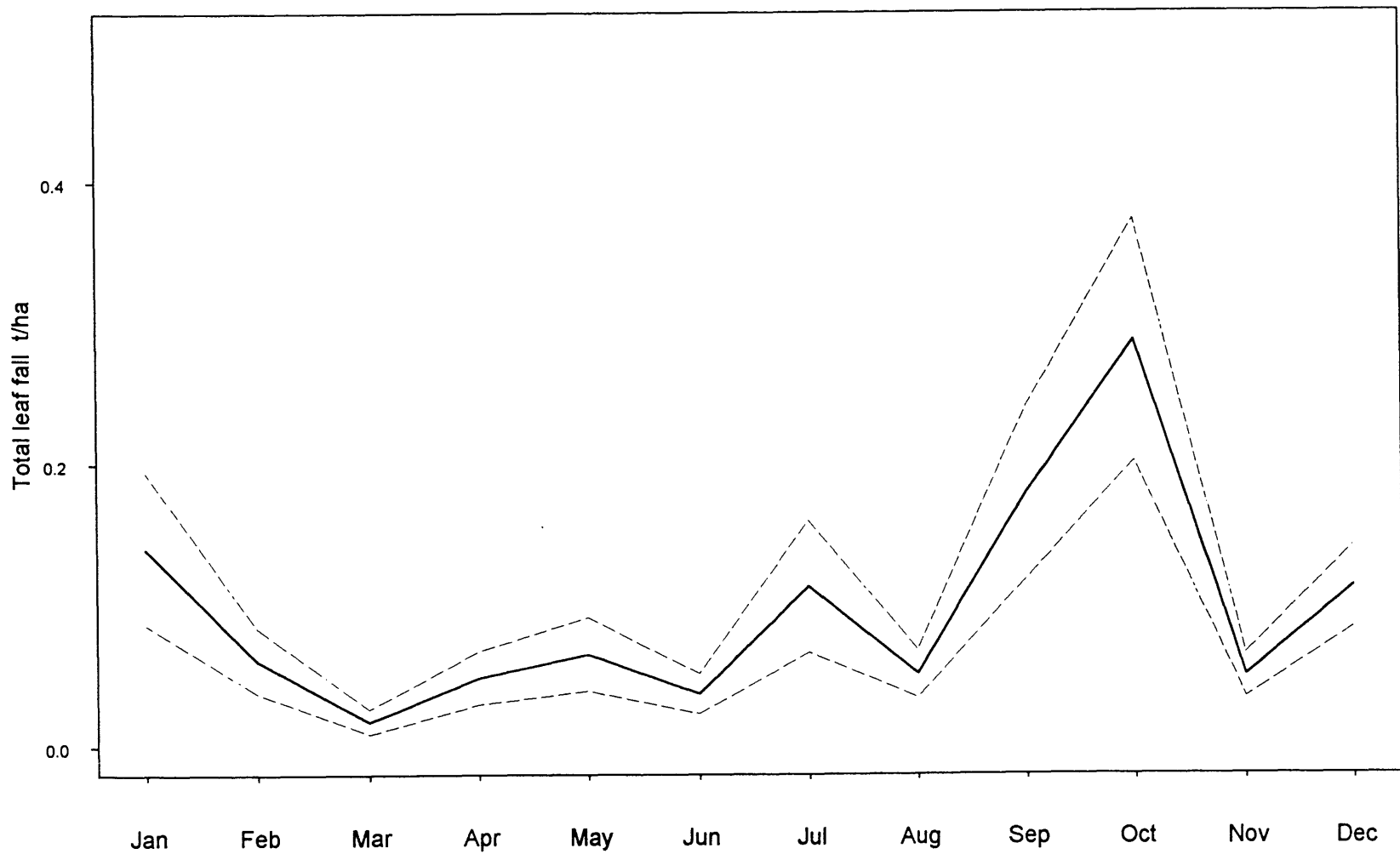


Figure 4.62 Total monthly leaf fall pattern of *Allocasuarina torulosa* in WSF with 95% confidence limits.

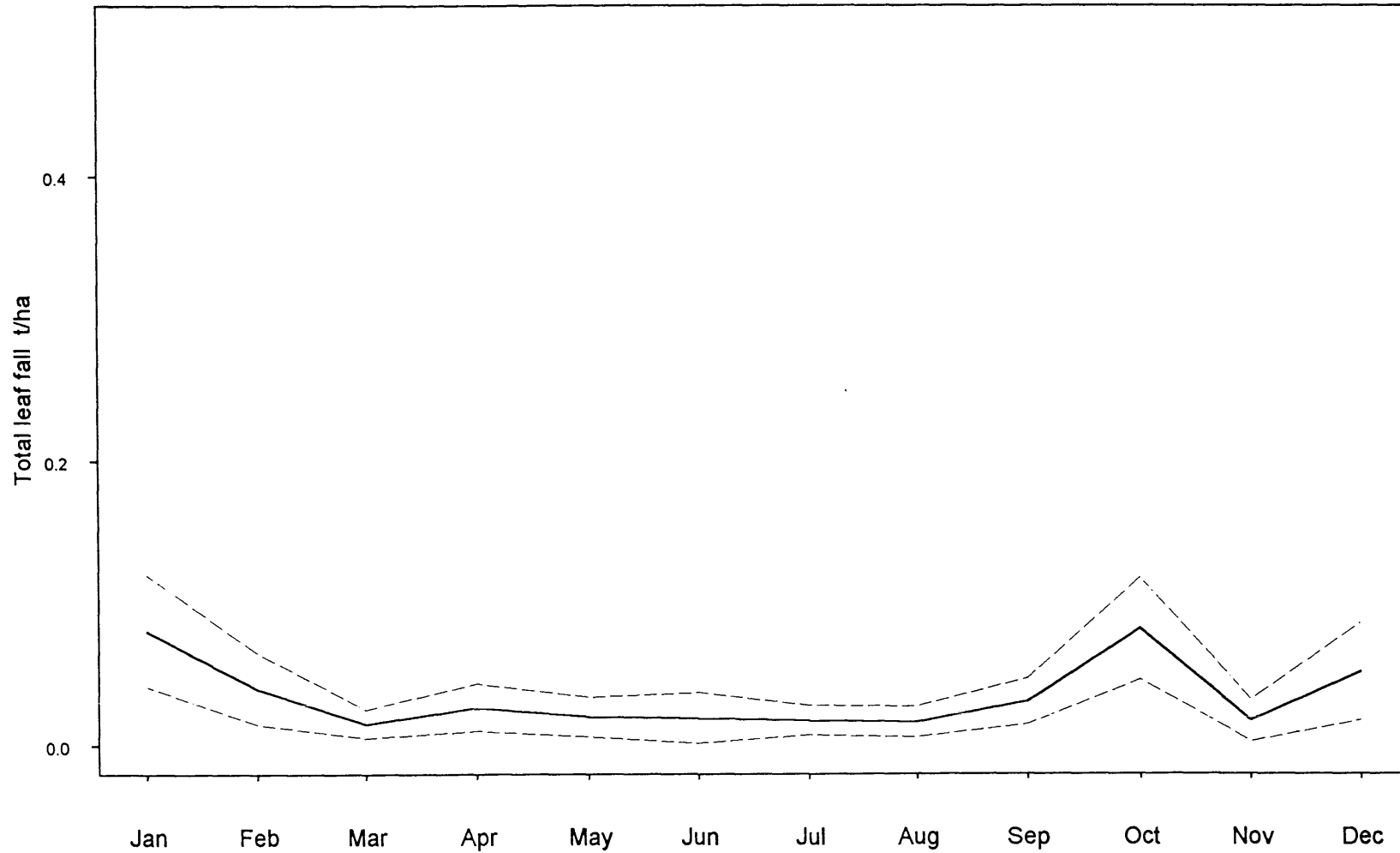


Figure 4.63 Total monthly leaf fall pattern of *Syncarpia glomulifera* in WSF with 95% confidence limits.

4.3.2.2 Transition zone forest

As with the WSF, the leaf fall was used to indicate the relative contribution of each species to the litter fall. The percentage of the total leaf fall for each species recorded is shown in Table 4.24. The leaf fall pattern is slightly more difficult to interpret than that for the WSF because, unlike the WSF, the mid-layer normally included some individuals of those species which formed the canopy. Therefore, the indication from Table 4.24 that 80% of the leaf fall emanated from the canopy is an overestimation. However, the increased depth and density of the TZF canopy suggests that the canopy leaf fall is definitely greater than the 56% of the WSF.

The total leaf fall was dominated again by *E. pilularis* and *S. glomulifera*, and, together with *Callicoma serratifolia*, they contributed about 70% of the leaf fall while representing 84% of the basal area of live trees in the plots containing the litter traps. The breakdown of leaf fall for the TZF is shown in Figures 4.64-4.69. Fig. 4.64 reproduces the TZF component of Fig. 4.57 with the addition of the 95% confidence ranges for the data. These confidence spreads are noticeably wider than those for the WSF due to a definite asynchrony of leaf fall which is apparent in Figs. 4.66-4.69. Fig. 4.65 shows the extent to which the species which comprise the canopy layer in TZF dominate the leaf fall. The understorey return is so small that little comment can be made with respect to Birk's (1979) finding that the understorey peak leaf fall precedes that of the overstorey. If anything, the opposite is the case with ferns (mainly treeferns) contributing to a peak in January well after the normal October peak for trees. As with the WSF, the mid-layer shows some slight asynchrony with the canopy in late summer but essentially its leaf fall pattern aligns with that of the canopy. Among the dominant species, there is better evidence of asynchrony than in the WSF. *C. serratifolia* has a pronounced peak in October (Fig. 4.66) while *A. orites* peaks in December-January (Fig. 4.67). *E. pilularis* and *S. glomulifera* are both bimodal with the former having its main leaf fall during the spring (Fig. 4.68) and the latter has its main leaf fall in December-January (Fig. 4.69).

Table 4.24 Monthly percentage by dry weight of total leaf litter return in TZF for each species for which at least some leaves were recorded in a litter trap in any month. Values may not sum to 100 due to rounding.
* = month of maximum percentage return.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
<u>Canopy species</u>													
<i>Acacia orites</i>	8	12	9	8	6	4	4	4	5	4	10	8	7
<i>Allocasuarina torulosa</i>	3	3	2	2	4	3	4	2	5	4	2	1	3
<i>Callicoma serratifolia</i>	12	11	14	17	21	22	21	17	14	28	23	14	18
<i>Eucalyptus</i> spp	28	33	44	34	36	36	44	45	42	21	17	22	30
<i>Schizomeria ovata</i>	-	-	-	-	1	2	1	-	2	2	3	1	1
<i>Syncarpia glomulifera</i>	31	18	14	19	14	14	12	16	21	19	19	27	21
<u>Mid-layer species</u>													
<i>Archontophoenix cunning.</i>	-	14	-	-	-	-	-	1	-	6	-	17	5
<i>Caldcluvia paniculosa</i>	1	-	-	1	2	3	3	2	5	3	1	1	2
<i>Ceratopetalum apetalum</i>	1	1	6	5	4	2	2	1	1	5	7	2	3
<i>Cinnamomum oliveri</i>	-	-	1	-	-	-	1	-	-	-	-	-	-
<i>Cryptocarya rigida</i>	-	-	-	-	-	-	-	-	-	*	-	-	-
<i>Duboisia myoporoides</i>	-	-	-	1	1	1	-	-	-	-	1	-	-
<i>Geissois benthamiana</i>	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Litsea australis</i>	-	*	-	-	-	-	-	-	-	-	-	-	-
<u>Understorey species</u>													
Pteridophytes	8	-	-	-	-	-	-	-	-	-	-	-	1
<u>Vines and mistletoes</u>													
<i>Cissus hypoglauca</i>	1	1	-	1	2	4	3	3	2	3	6	2	2
Mistletoes	-	*	-	-	-	-	-	-	-	-	-	-	-
<u>Miscellaneous leaves</u>													
	6	7	9	11	10	9	5	8	4	4	9	4	6

4.3.2.3 Warm temperate rainforest

The percentage distribution of leaf fall in the WTRF is shown in Table 4.25. The striking feature of this Table is the jump in the number of species recorded compared with the TZF. Typically, the canopy is much more diverse and, unlike the TZF, it does not represent an overestimation of the contribution that the canopy made to the leaf fall because the non-canopy individuals of these species tended not to be present in the mid-layers, but mainly in the understorey as seedlings. The most productive species was *Ceratopetalum apetalum* with 28% of the total leaf litter while the canopy as a whole contributed 70%. *Acacia orites* is shown as contributing 16% of the total leaf litter but

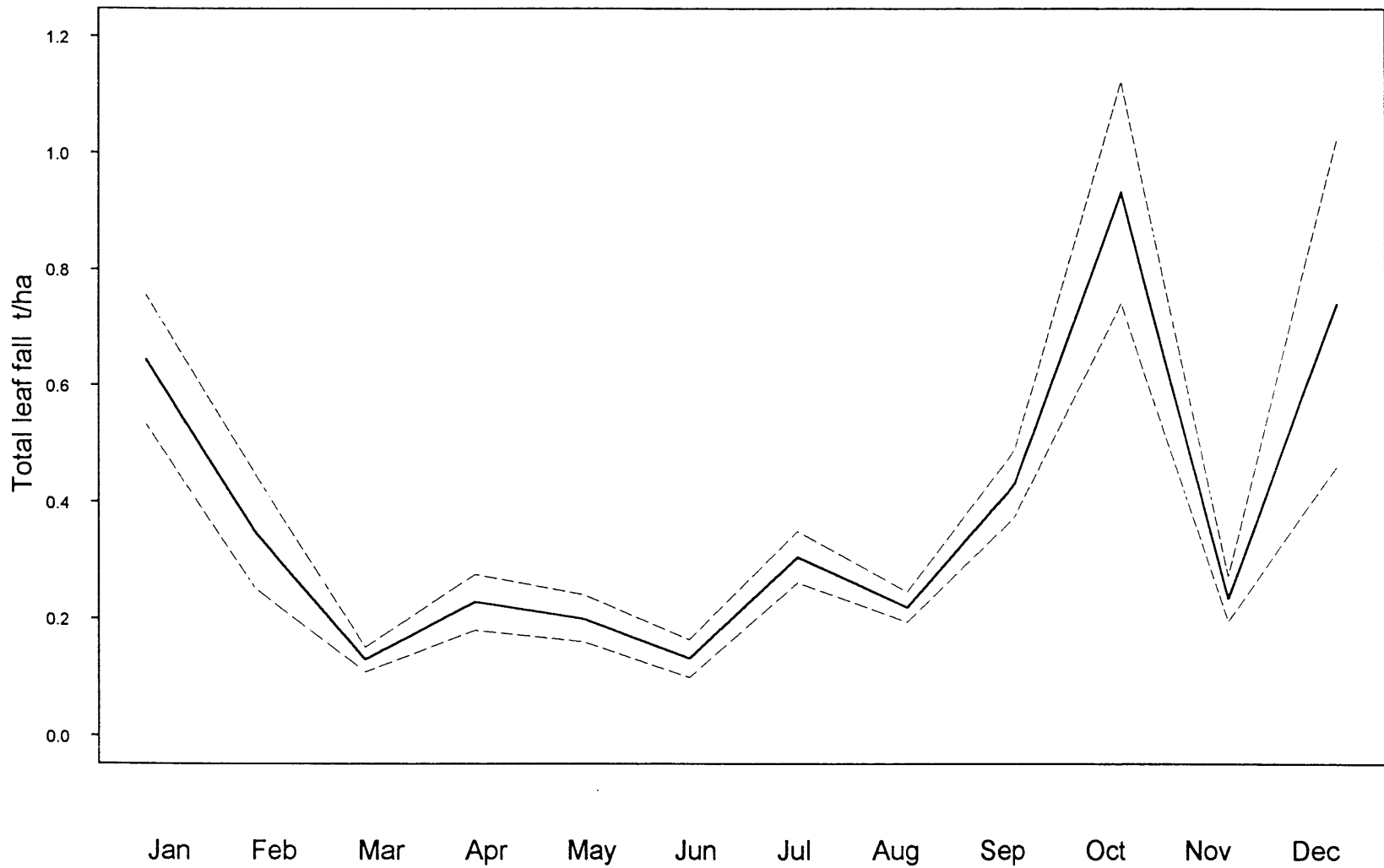


Figure 4.64 Total monthly leaf fall pattern for TZF with 95% confidence limits.

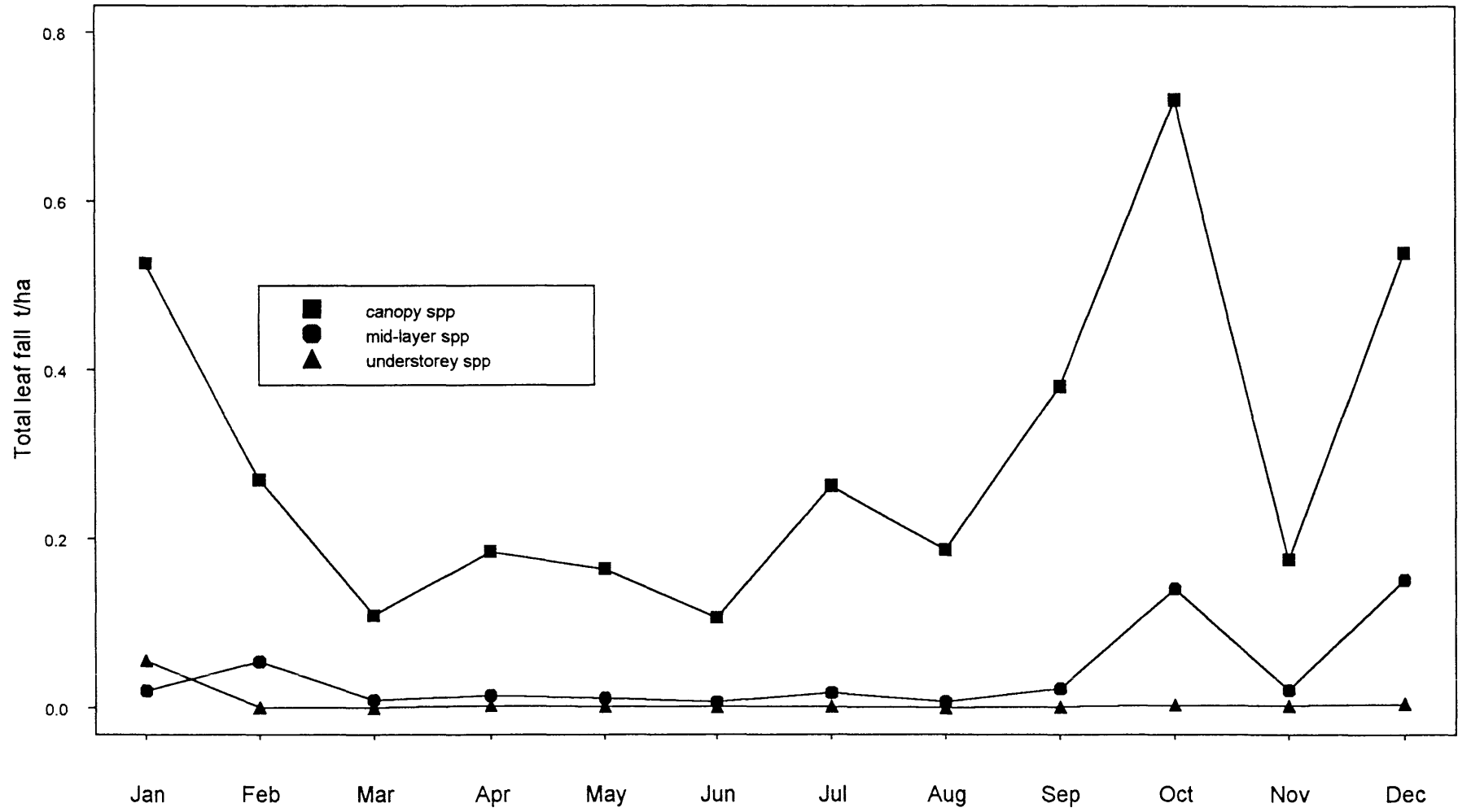


Figure 4.65 Comparison of total monthly leaf fall pattern for canopy, mid-layer and understorey species in TZF

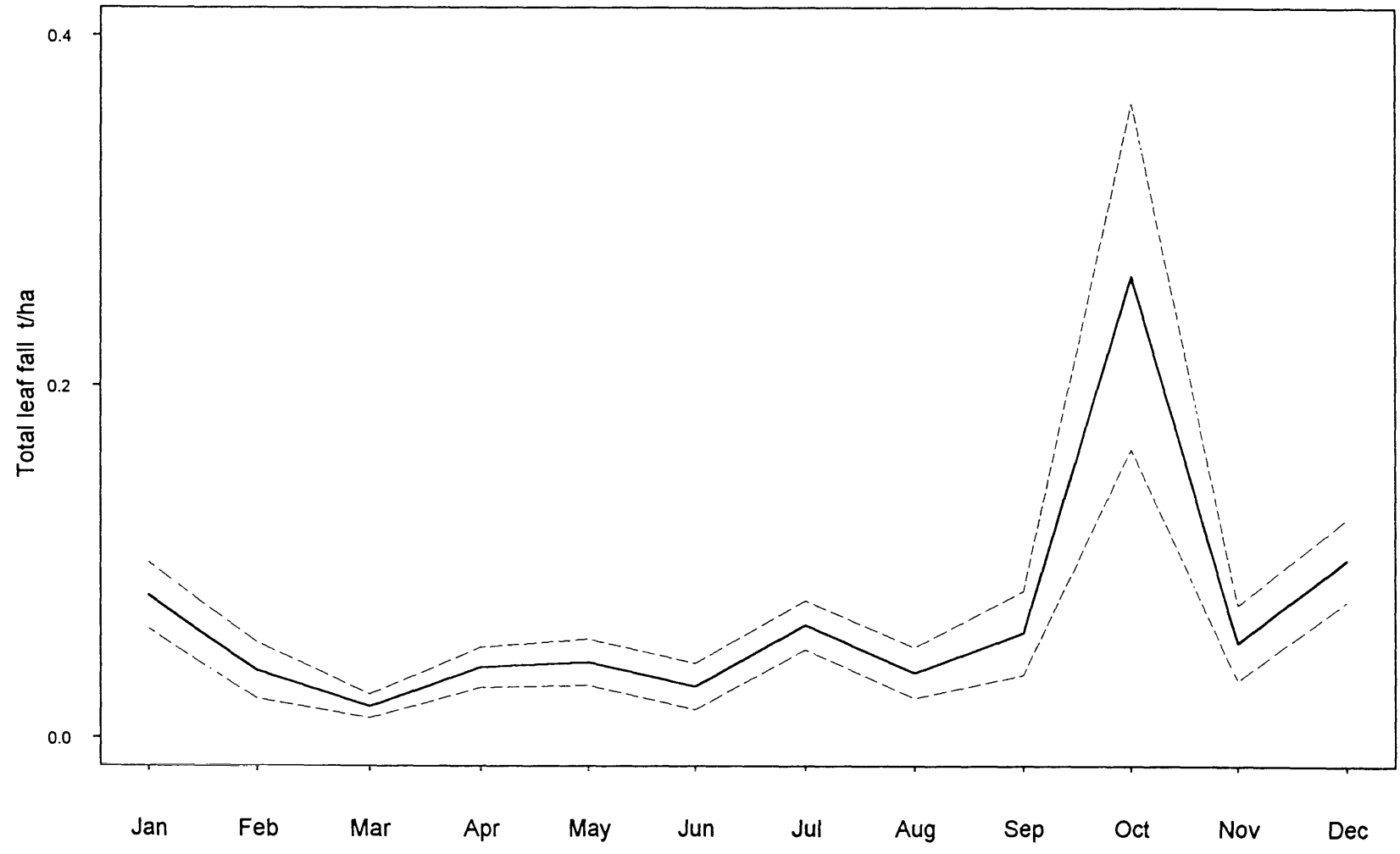


Figure 4.66 Total monthly leaf fall pattern of *Callicoma serratifolia* in TZF with 95% confidence limits.

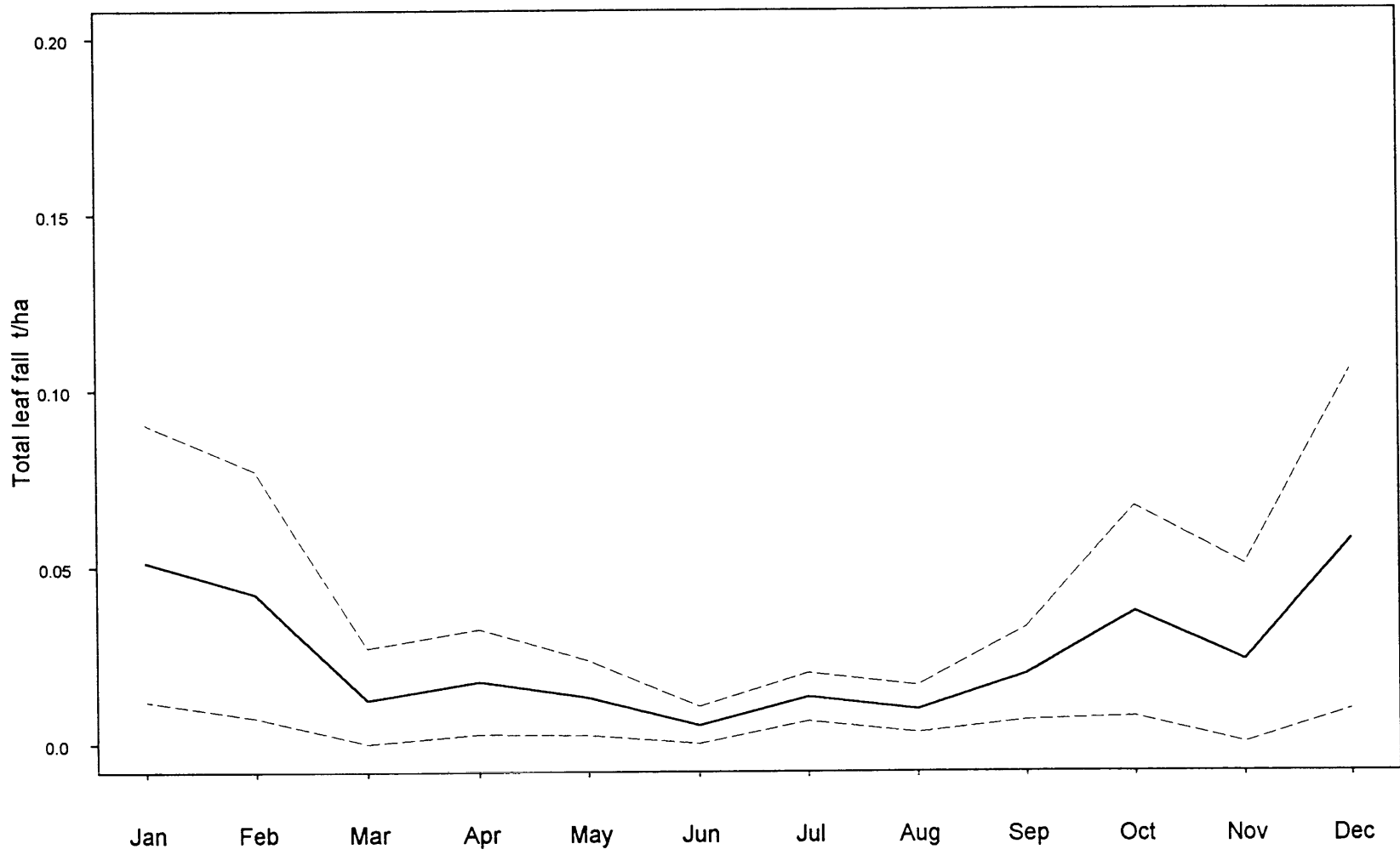


Figure 4.67 Total monthly leaf fall pattern of *Acacia orites* in TZF with 95% confidence limits.

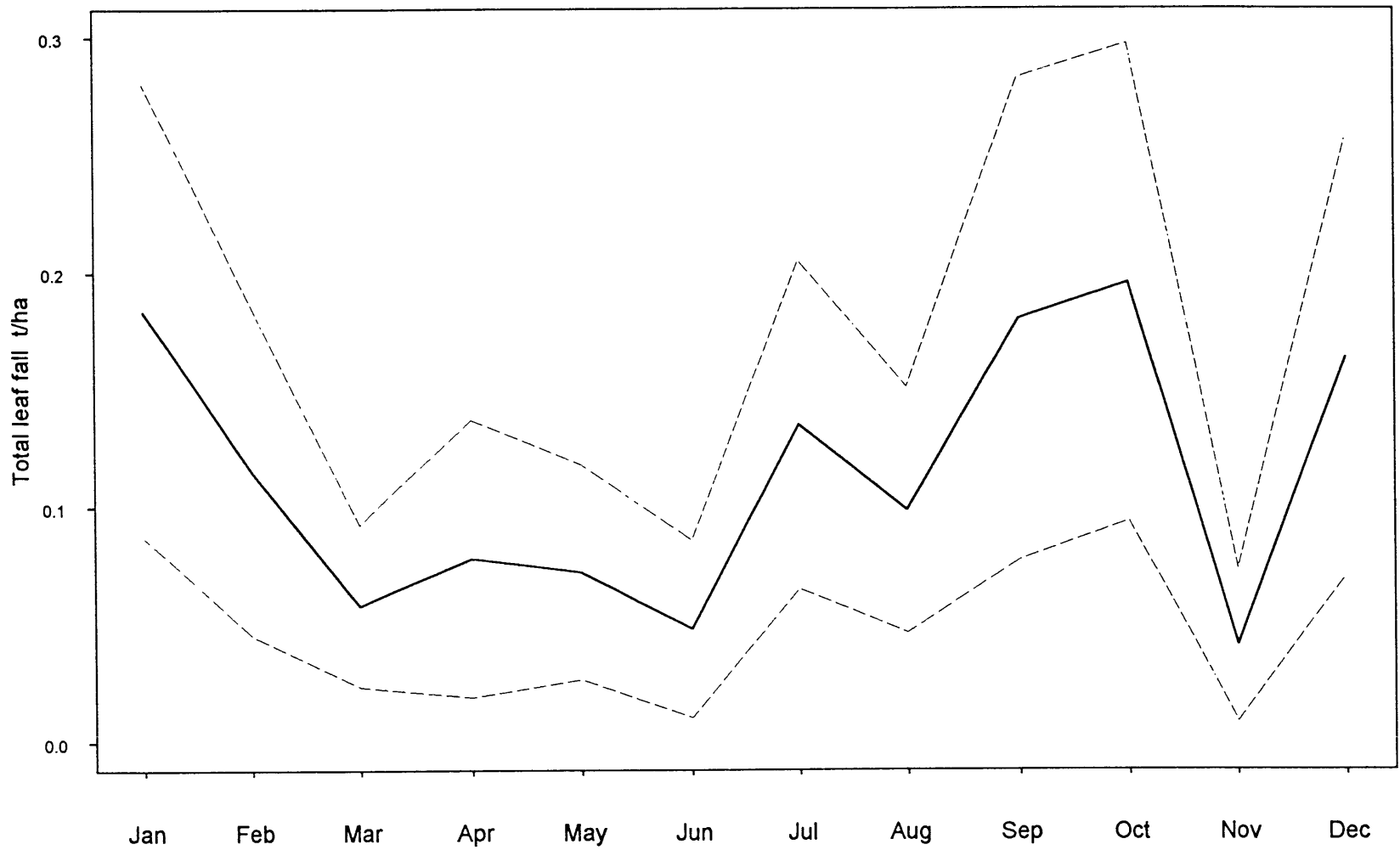


Figure 4.68 Total monthly leaf fall pattern of *Eucalyptus pilularis* in TZF with 95% confidence limits.

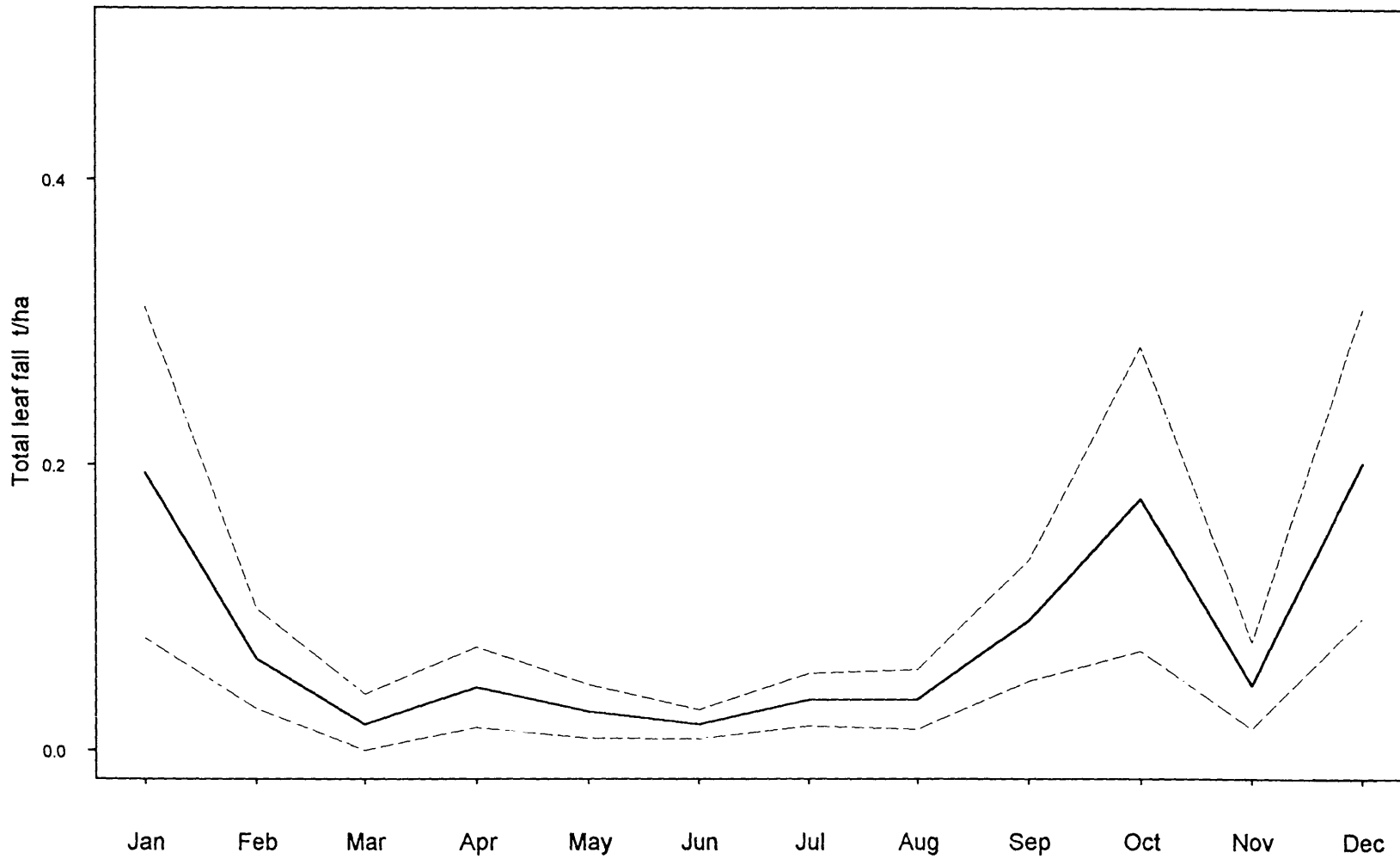


Figure 4.69 Total monthly leaf fall pattern of *Syncarpia glomulifera* in TZF with 95% confidence limits.

Table 4.25 Monthly percentage by weight of total leaf litter return in WTRF for each species for which at least some leaves were recorded in a litter trap in any month. Values may not sum to 100 due to rounding. * = month of maximum percentage return.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
<u>Canopy species</u>													
<i>Acacia orites</i>	31	43	7	17	12	22	9	18	9	4	13	25	16
<i>Acronychia suberosa</i>	1	1	-	-	-	-	-	1	-	-	1	2	1
<i>Caldcluvia paniculosa</i>	2	3	-	3	3	9	5	9	9	7	8	5	5
<i>Ceratopetalum apetalum</i>	9	11	6	25	19	22	8	11	29	58	36	22	28
<i>Cinnamomum oliveri</i>	2	4	1	4	1	2	2	7	1	2	-	4	2
<i>Cryptocarya glaucescens</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diospyros pentamera</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Endiandra discolor</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eucalyptus</i> spp	5	6	2	3	1	2	43	10	6	2	-	3	7
<i>Geissois benthamiana</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Litsea reticulata</i>	1	1	-	-	-	-	-	-	-	-	-	3	-
<i>Orites excelsa</i>	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Schizomeria ovata</i>	8	8	4	10	8	2	2	7	8	7	15	10	7
<i>Sloanea australis</i>	-	-	-	1	1	-	-	-	-	1	1	-	-
<i>Sloanea woollsii</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Syncarpia glomulifera</i>	4	2	-	1	1	-	-	4	11	4	3	7	4
<u>Mid-layer species</u>													
<i>Allocasuarina torulosa</i>	-	-	-	-	-	-	-	-	-	*	-	-	-
<i>Archontophoenix cunningg.)</i>	-	-	71	1	23	1	1	-	-	-	-	-	7
<i>Linospadix monostachya)</i>													
<i>Callicoma serratifolia</i>	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Helicia ferruginea</i>	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Litsea australis</i>	*	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhodamnia rubescens</i>	-	-	-	-	-	-	-	-	-	-	-	-	*
<i>Sarcopteryx stipata</i>	2	2	-	-	-	-	-	-	-	1	-	2	1
<i>Syzygium luehmannii</i>	-	1	-	1	2	1	-	-	-	1	-	-	1
<i>Wilkiea huegeliana</i>	-	2	-	-	-	3	-	2	1	-	-	1	-
<u>Understorey species</u>													
<i>Archirhodomyrtus beckl.</i>	-	-	-	1	-	3	-	-	-	-	-	1	-
<i>Cryptocarya meissneriana</i>	1	2	1	6	5	4	-	-	-	-	1	-	1
Pteridophytes	16	-	1	9	-	-	13	-	-	-	1	-	4
<i>Randia benthamiana</i>	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Triunia youngiana</i>	-	-	-	-	-	-	-	-	-	-	-	1	-
<u>Vines and mistletoes</u>													
<i>Cissus hypoglauca</i>	2	1	-	1	1	2	1	3	6	3	1	3	2
Mistletoes	1	1	-	2	-	-	-	-	1	-	1	2	1
<i>Parsonsia straminea</i>	-	-	-	-	-	-	-	-	-	1	1	-	-
<i>Rubus</i> sp. A	1	1	-	-	-	2	1	-	1	1	1	1	1
<u>Miscellaneous leaves</u>													
	10	11	6	15	22	25	14	27	18	7	15	6	11

as this return was virtually restricted to half the traps, there is a high error associated with this assertion.

The other contributions by *E. pilularis* and *S. glomulifera* are very interesting because they illustrate the role of wind in the distribution of litter from outside the rainforest. Some of the *Eucalyptus* data are due to a veteran individual of *E. microcorys* growing near a rainforest litter trap. All of the 43% for July is the result of a branch fall from this tree. *C. apetalum* (44%) and *Schizomeria ovata* (21%) make up 65% of the basal area of WTRF trees but return only 35% of the leaf fall, a finding which departs from the relationship between basal area and leaf fall of the dominant species revealed by the WSF and TZF results. The very high contribution attributed to "miscellaneous leaves" reflects the high number of species which make a trivial contribution to the leaf fall and also the high incidence of leaf fragments. Lowman (1984) suggested that these fragments indicate the high level of herbivory occurring in the rainforest.

Fig. 4.70 shows the 95% confidence limits of the WTRF leaf data shown earlier in Fig. 4.57. The greater variability of the leaf fall in this forest compared with the TZF and WSF is revealed by the spread of the confidence limits. The pattern of leaf fall from each of the main structural layers is shown in Fig. 4.71. The occasional fall of a frond from the palm *A. cunninghamiana* (e.g. March) can be seen to have a dramatic effect on the shape of the mid-layer response. The return for this species includes the small amount of leaf litter for the understorey palm, *Linospadix monostachya*. As with the other forest types on the transect there appears to be no evidence to support Birk's (1979) findings that understorey litter abscission precedes that of the overstorey.

Among the canopy species, there are interesting suggestions of asynchrony. *C. apetalum* maintains a prominent background level of leaf fall throughout the year but in October (Fig. 4.72), the leaf fall easily exceeds its total for the rest of the year. This is a pattern displayed by *C. serratifolia* in the TZF and also by *S. ovata* in the WTRF (Fig. 4.73). Most of the minor canopy species in the WTRF achieve their maximum leaf falls in January although the competitive advantage for this is not

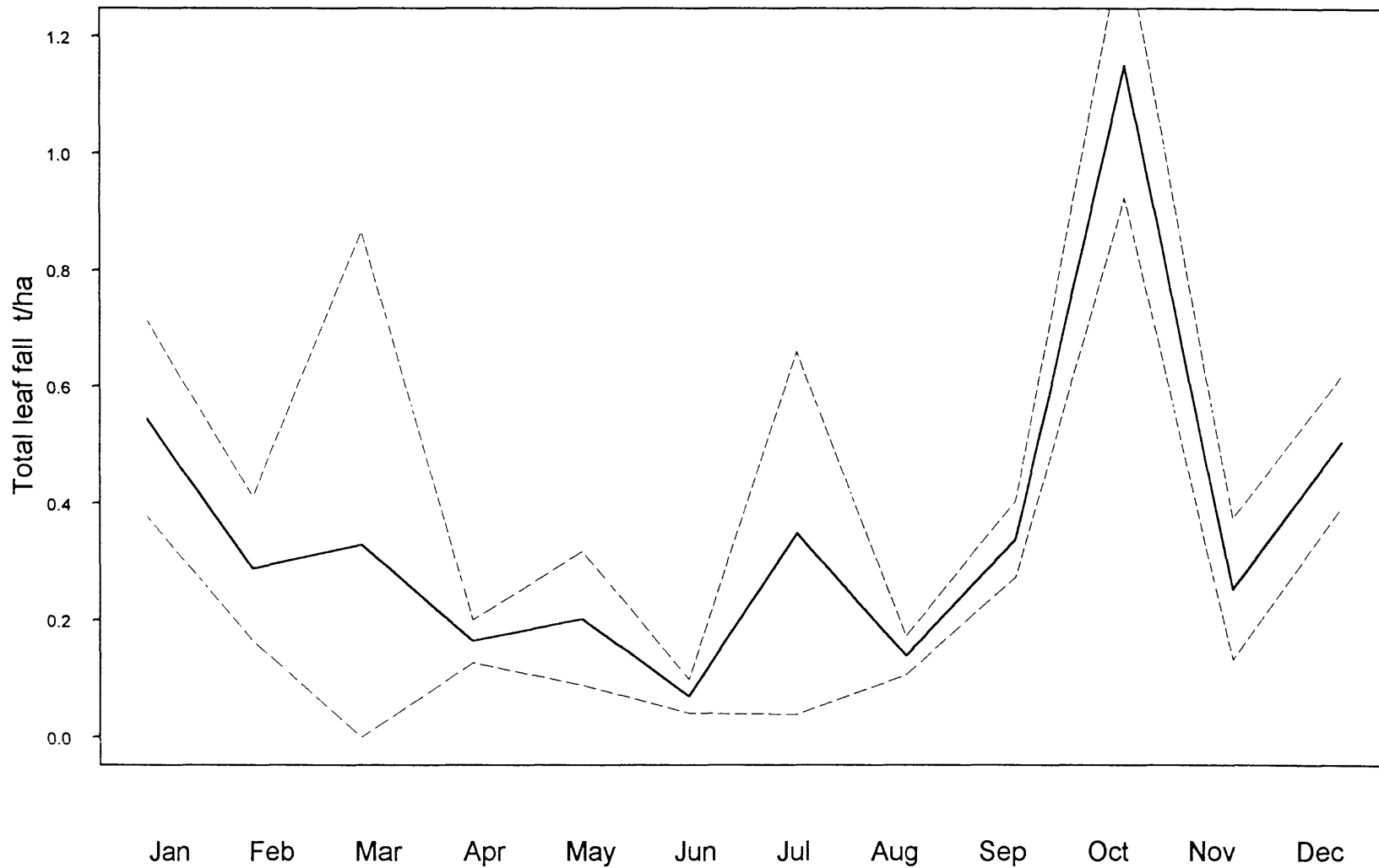


Figure 4.70 Total monthly leaf fall pattern for WTRF with 95% confidence limits.

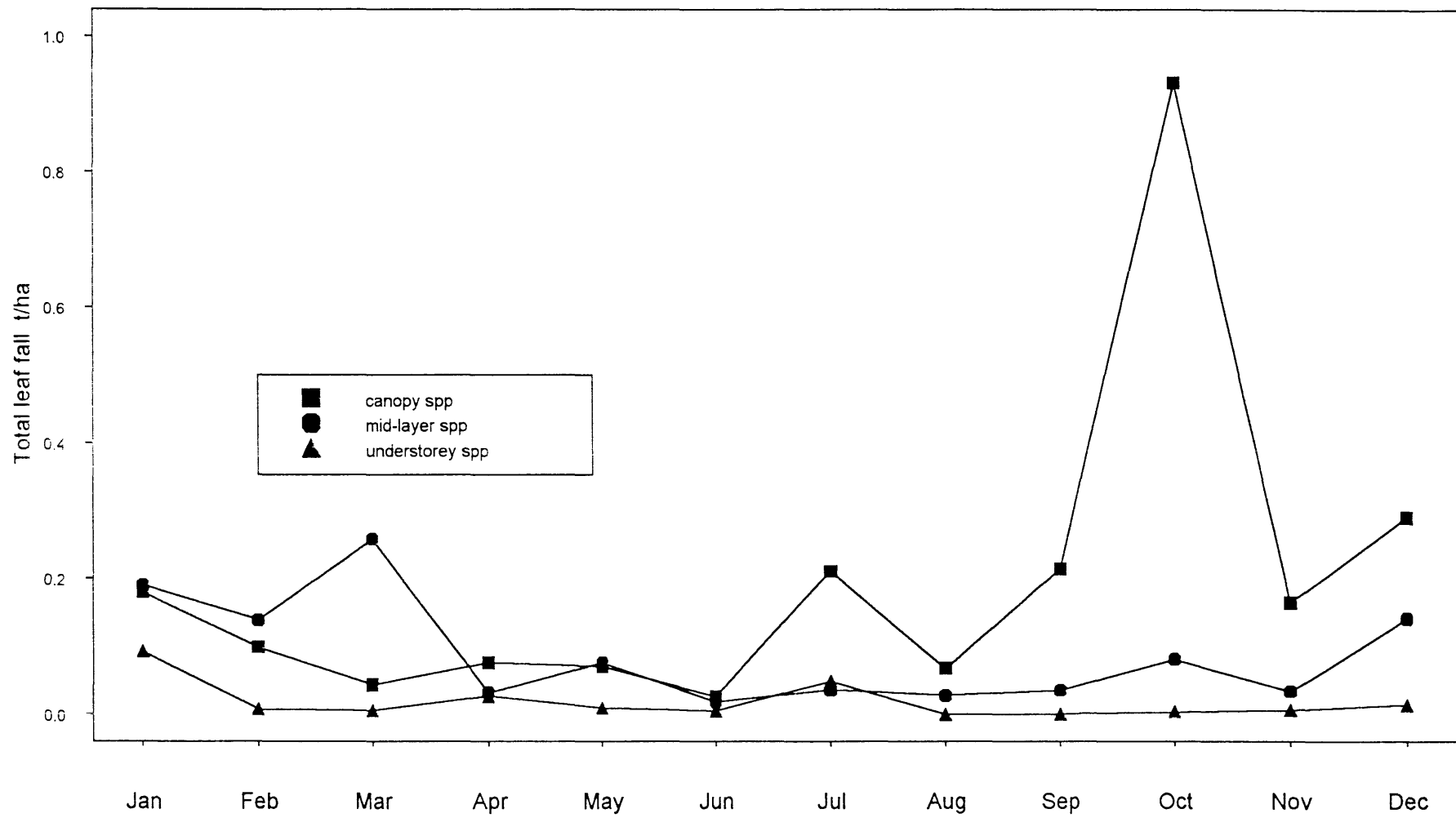


Figure 4.71 Comparison of total monthly leaf fall pattern for canopy, mid-layer and understorey species in WTRF.

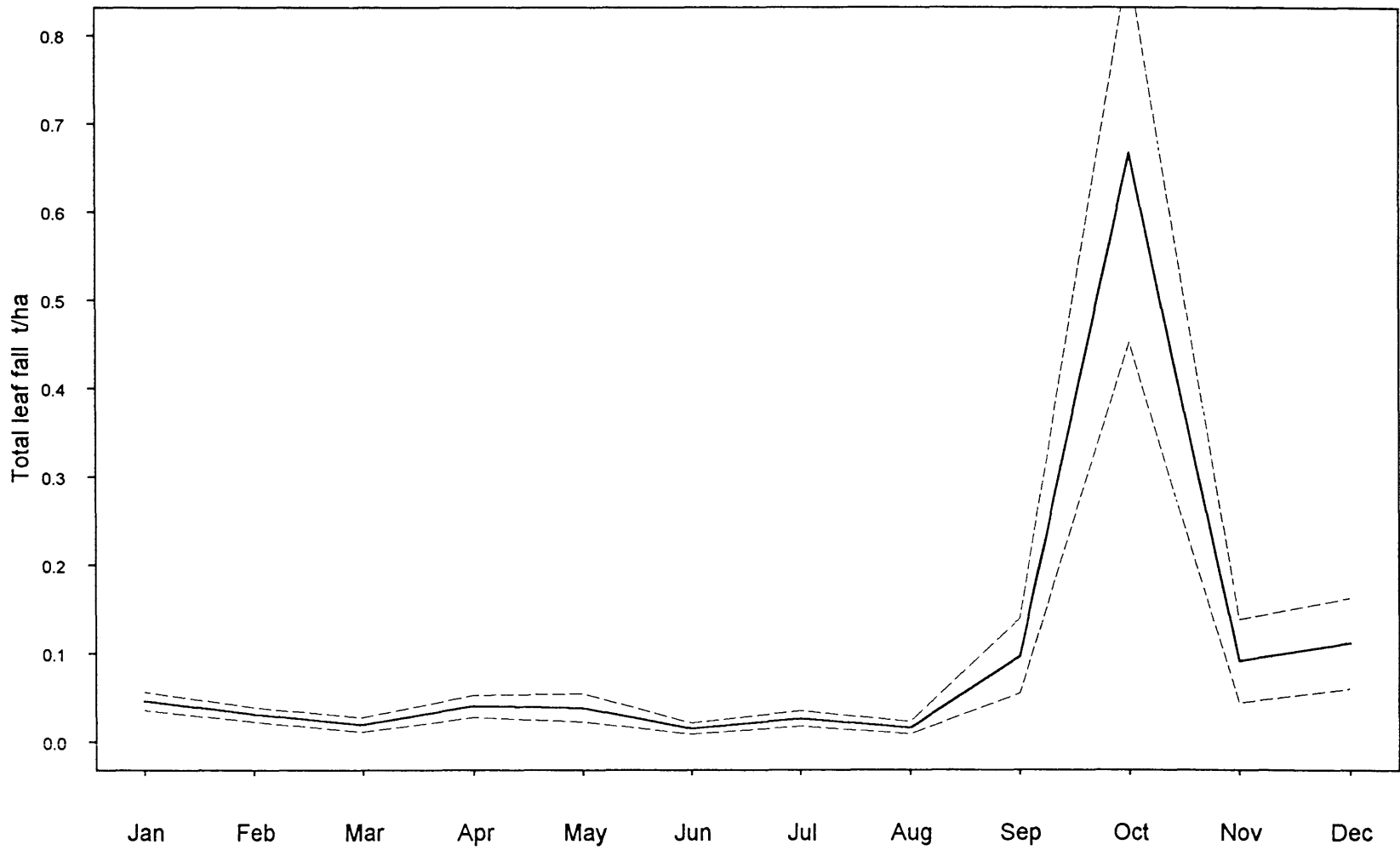


Figure 4.72 Total monthly leaf fall pattern of *Ceratopetalum apetalum* in WTRF with 95% confidence limits.

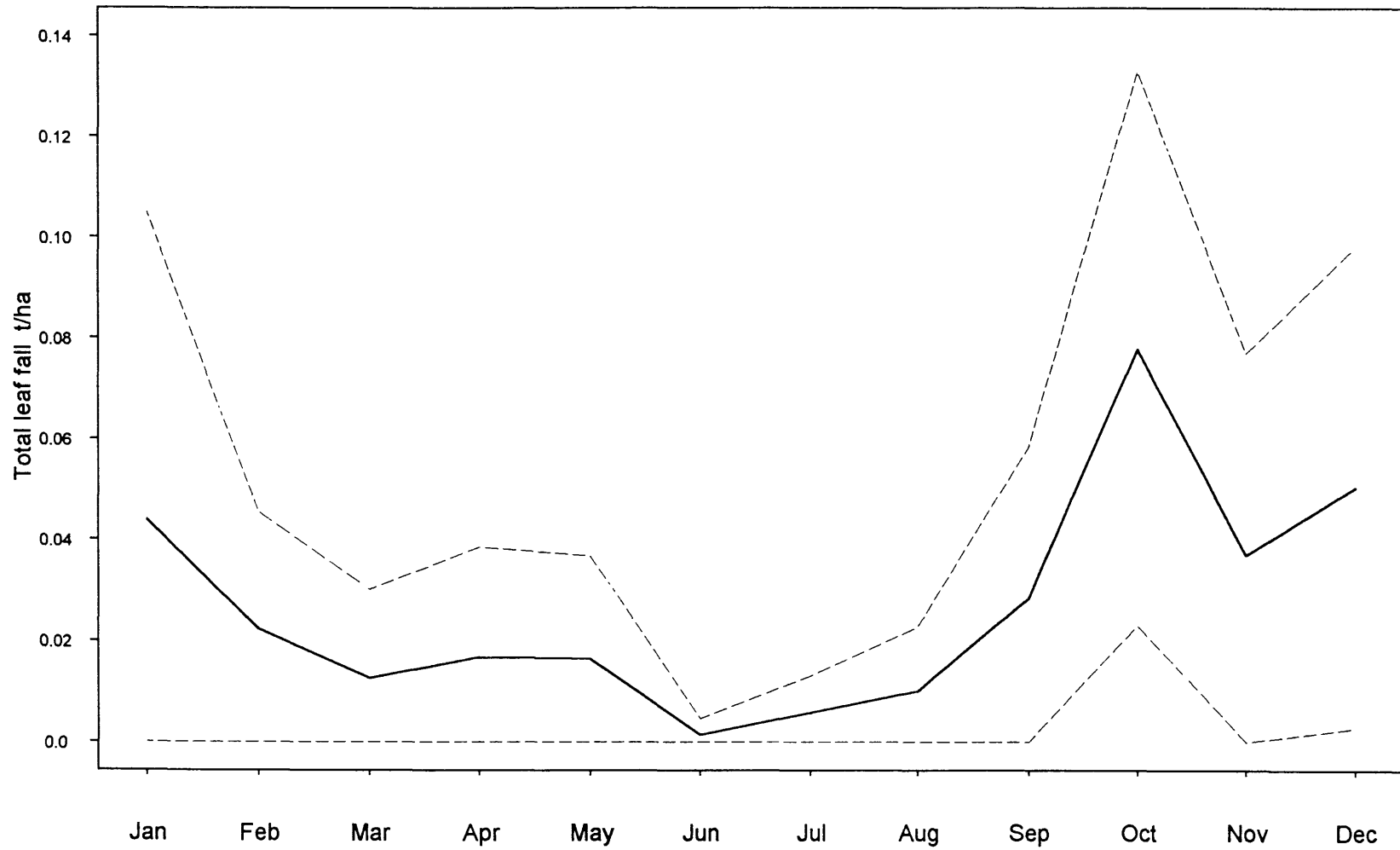


Figure 4.73 Total monthly leaf fall pattern of *Schizomeria ovata* in WTRF with 95% confidence limits.

clear. *C. apetalum* is a known aluminium accumulator (Webb 1954) and the leaf fall results for the other species may be related to strategies evolved to deal with the sudden return of the aluminium rich leaves to the standing litter.

Hegarty (1991) found that in subtropical rainforest, lianes contributed 24% of the annual leaf fall. The reduced numbers of lianes in WTRF, which is one of keys to the structural definition of the formation, is indicated by the liane component not exceeding 5% of the annual figure.

4.3.3 Wind and litterfall

A number of researchers have reported the relevance of high wind events to the measurement of litterfall levels. Brasell *et al.* (1980) reported that litterfall noticeably increased during short periods of high wind speed but found no correlation with the weekly wind run. Hopkins and Graham (1989) found that winds greatly influence litterfall and easily produce false peaks or cycles in data. McColl (1966) showed how winter winds inflated leaf fall with the subsequent effect of depressing the summer leaf fall and Ashton (1975) suggested that wind and snow storms accounted for a 30-40% variation in litterfall.

As indicated above, the litterfall data for July appear to suggest the consequences of a wind event. An examination of the wind data for July, however, shows that, on the basis of average wind speed throughout the month and incidence of high wind events, that month was the second calmest of the year. The differences in the wind pattern for July as shown in Table 4.29 are that the average windspeed before 9am was the highest for the whole year. It may be that the early morning winds on leaves and branchlets still cold from the winter's night were able to effect abscission. Further, a low standard error for the July data (5 knots for 6 a.m.) indicated that although there were no unusually strong winds or storms for the month, a moderate wind was sustained throughout the month. It could be that not only do strong winds or storm events cause an increase in abscission but that a sustained wind run can have similar effects.

Notwithstanding that wind-based explanation for the peak in the July litterfall, the relationship between the general wind pattern and litterfall results is inconsistent. November and March were two of the windiest months yet were among the months with the lowest litterfall while June, which had the lowest wind speeds, also had the lowest litterfall. The litterfall peaked in January and October, months in which other researchers had recorded litterfall maxima, yet while the wind in October was greater than the annual average, the January wind was less (see Tables 4.29 and 4.30).

4.4 Microclimate survey

4.4.1 Temperature

The month by month results of temperature survey along the vegetation gradient are shown in Table 4.26. These results expose some interesting trends and relationships which are reviewed in conjunction with references to the graphical portrayal of these relationships contained in Figures 4.74 to 4.86. The overall temperature profile from within the forests of the study area can be discerned from the Whole Year section of Table 4.26. Annual average temperature exceeded 20°C, the lowest maximum recorded was 11.5°C and the mean daily temperature range was about 12°C. The lowest temperature recorded was 4.5°C which indicates that there was no frosting inside the forest at any time during the entire duration of the microclimate monitoring program.

From Fig. 4.74, mean monthly temperatures all show the obvious dip during the winter months but the seasonal decline of temperature is significantly more gradual than the subsequent rise although the variability is much greater during the spring. This trend is due to the latent heat properties of the essential plant processes of evapotranspiration and photosynthesis which moderate the cooling trend and accentuate the warming trend. The shape of the graphs in Fig. 4.74 derive from and are intermediate to the shapes in Figs. 4.75 and 4.76. Maximum temperatures at all points along the transect show little variability for each month in summer and autumn but more

Table 4.26. Summary of weekly data recorded by maximum-minimum thermometers from June 1990 to February 1992 and averaged by month.

January	Wet sclerophyll		Transition		Warm temp. rf.	
	0.0m	1.5m	0.0m	1.5m	0.0m	1.5m
mean max.	31.5	31.58	29.5	29.7	28.17	29.17
mean min.	17.5	16.83	17.33	17	17.25	17.3
(max+min)/2	24.5	24.11	23.44	23.35	22.71	23.24
highest max.	32.25	32.75	29.75	30.5	29.5	29.5
lowest min.	16	15.5	16	15.5	16	15.75
lowest max.	30.25	30.5	29	28.85	26.75	28.5
highest min.	18.5	18	18.5	18	18.25	18.4
February						
mean max.	30.69	28.44	27.5	27.76	27.44	29.69
mean min.	17.81	17.44	17.75	17.25	17.73	17.56
(max+min)/2	24.25	22.94	22.63	22.51	22.59	23.63
highest max.	32.75	30.5	29.5	30.5	31	31
lowest min.	16.5	15.5	16	15.5	16.5	16.25
lowest max.	28.5	25	25	24.25	22.75	28.5
highest min.	20	19.5	20	19.5	19.5	19.5
March						
mean max.	28	25.35	24.15	23.75	23	24.55
mean min.	15.9	15.2	15.6	15.45	15.65	15.5
(max+min)/2	21.95	20.28	19.88	19.6	19.33	20.03
highest max.	30	28	26	25	25	28.75
lowest min.	14.75	14.5	14.5	14.75	14.25	14.5
lowest max.	25.25	23.75	23	22.75	21.25	22.75
highest min.	16.5	15.75	16.25	16	16.5	16.25
April						
mean max.	26.38	23.63	22	21.25	20.56	21.13
mean min.	14.25	18.54	17.97	17.47	17.35	17.54
(max+min)/2	20.32	21.09	19.99	19.36	18.96	19.34
highest max.	28.5	25.5	24	23.5	22.5	23
lowest min.	12.25	11.5	12.25	12	12.5	12.25
lowest max.	24	22.75	20.5	19.5	19	20
highest min.	15.5	14.5	15	14.75	15.5	15
May						
mean max.	20.38	19.25	18.88	18.31	17.56	17.88
mean min.	12.88	11.81	12.44	12.13	12.88	12.13
(max+min)/2	16.63	15.53	15.66	15.22	15.22	15.01
highest max.	24.25	22	21	20.25	19	19.75
lowest min.	11	10.25	10.75	10.5	11.5	10.5
lowest max.	17	16.5	16.5	16	15.75	16.25
highest min.	15	13.75	14.5	14	14.5	14

Table 2.1 (cont.)

June	Wet sclerophyll		Transition		Warm temp. rf.	
	0.0m	1.5m	0.0m	1.5m	0.0m	1.5m
mean max.	18.7	18.25	17.6	17.25	16.65	17.28
mean min.	11.05	10.05	10.5	10.45	10.93	10.5
(max+min)/2	14.88	14.15	14.05	13.85	13.79	13.89
highest max.	20.25	19.5	18.75	18.25	18	18.5
lowest min.	8.5	7	8	8	8.5	8.25
lowest max.	17.5	17	16.25	16	15.25	15.67
highest min.	12.75	11.5	12	12	12.75	12
July						
mean max.	18	17.95	16.75	16.35	15.45	16.1
mean min.	7.45	6.45	7.2	7.08	7.8	7.21
(max+min)/2	12.73	12.2	11.98	11.72	11.63	11.66
highest max.	21	21.25	19	19	17.5	18.5
lowest min.	5.5	5	6	5.75	6.5	5.75
lowest max.	16	16.25	15.5	14.75	14.5	15
highest min.	9.5	9.25	9.25	9.4	9.5	9.5
August						
mean max.	20	18.94	17.81	17.75	15.97	17.33
mean min.	7.33	6.39	7.03	6.89	7.87	7.28
(max+min)/2	13.67	12.67	12.42	12.32	11.92	12.31
highest max.	23.25	22	21.25	21.5	19	20.5
lowest min.	5.5	4.5	5	5	6	5.25
lowest max.	14.5	15	13	14	11.5	12.5
highest min.	9.75	9	9.25	9.25	9.5	9.5
September						
mean max.	25.81	24.28	23	22.61	20.72	21.75
mean min.	9.81	8.92	9.39	9.17	9.81	9.44
(max+min)/2	17.81	16.6	16.2	15.89	15.27	15.6
highest max.	32	28.5	27.75	27	25.25	26.25
lowest min.	8.5	7.5	8	7.5	8.5	7.5
lowest max.	23	20.75	19	18.5	16.5	17.5
highest min.	12	10.5	11.5	11	11.75	11.25
October						
mean max.	30.64	28.25	26.71	26.43	24.54	26.71
mean min.	11.61	10.96	11.39	11.29	11.96	11.46
(max+min)/2	21.13	19.61	19.05	18.86	18.25	19.09
highest max.	33	30	29.5	28.75	28.25	30.25
lowest min.	9.75	9	9.5	9.25	10	9.5
lowest max.	29.25	26	25.25	25.25	22.5	25.5
highest min.	13	12.5	12.75	13	13.25	13.25

Table 2.1 (cont.)

November	Wet sclerophyll		Transition		Warm temp. rf.	
	0.0m	1.5m	0.0m	1.5m	0.0m	1.5m
mean max.	32.04	30.89	29.43	29.29	28.46	29.39
mean min.	12.68	12.21	12.57	12.21	12.61	12.25
(max+min)/2	22.36	21.55	21	20.75	20.54	20.82
highest max.	35	35	31.5	31.75	30.75	32.25
lowest min.	10.5	10.25	10.5	10	10.25	10.25
lowest max.	28	25.5	25.25	25.5	22.25	23.75
highest min.	14.25	13.5	13.75	13.5	13.75	13.5
December						
mean max.	34.56	33.56	31.19	31.38	31.81	31
mean min.	16.88	16.19	16.63	16.34	16.5	16.5
(max+min)/2	25.72	24.88	23.91	23.86	24.16	23.75
highest max.	36	37	32.75	33.5	34.5	33.5
lowest min.	16	15	15.75	15.35	16.25	15.5
lowest max.	32.5	31	29.5	29.75	30	29
highest min.	18	17.25	17.75	17.5	17	17.75
Whole Year Average						
mean max.	26.02	24.62	23.33	23.09	21.98	23.04
mean min.	12.06	11.28	11.77	11.55	12.12	11.74
(max+min)/2	19.04	17.95	17.55	17.32	17.05	17.39
highest max.	36	37	32.75	33.5	34.5	33.5
lowest min.	5.5	4.5	5	5	6	5.25
lowest max.	14.5	15	13	14	11.5	12.5
highest min.	20	19.5	20	19.5	19.5	19.5

variability from winter to spring. The mean maximum temperatures are similar for the period May to August at all points whereas they are much less similar for the four warmest months. The pattern of mean minimum temperatures is exactly the opposite. The minimum temperatures for December to March are within about three degrees while the four coolest months show mean minima more widely separated. The pattern of slow descent to lowest values and rapid rise after winter, as described for the overall mean temperatures, is apparent for both maxima and minima at most observation points. It is in fact the detail of the mean maximum seasonal temperature decline which reveals the first differences in microclimate and vegetation. In the WSF and TZF, the shape of temperature decline is linear to slightly

Figure 4.74 Mean monthly temperatures at three gradient points and at two different heights. Dotted lines indicate the 95% confidence interval

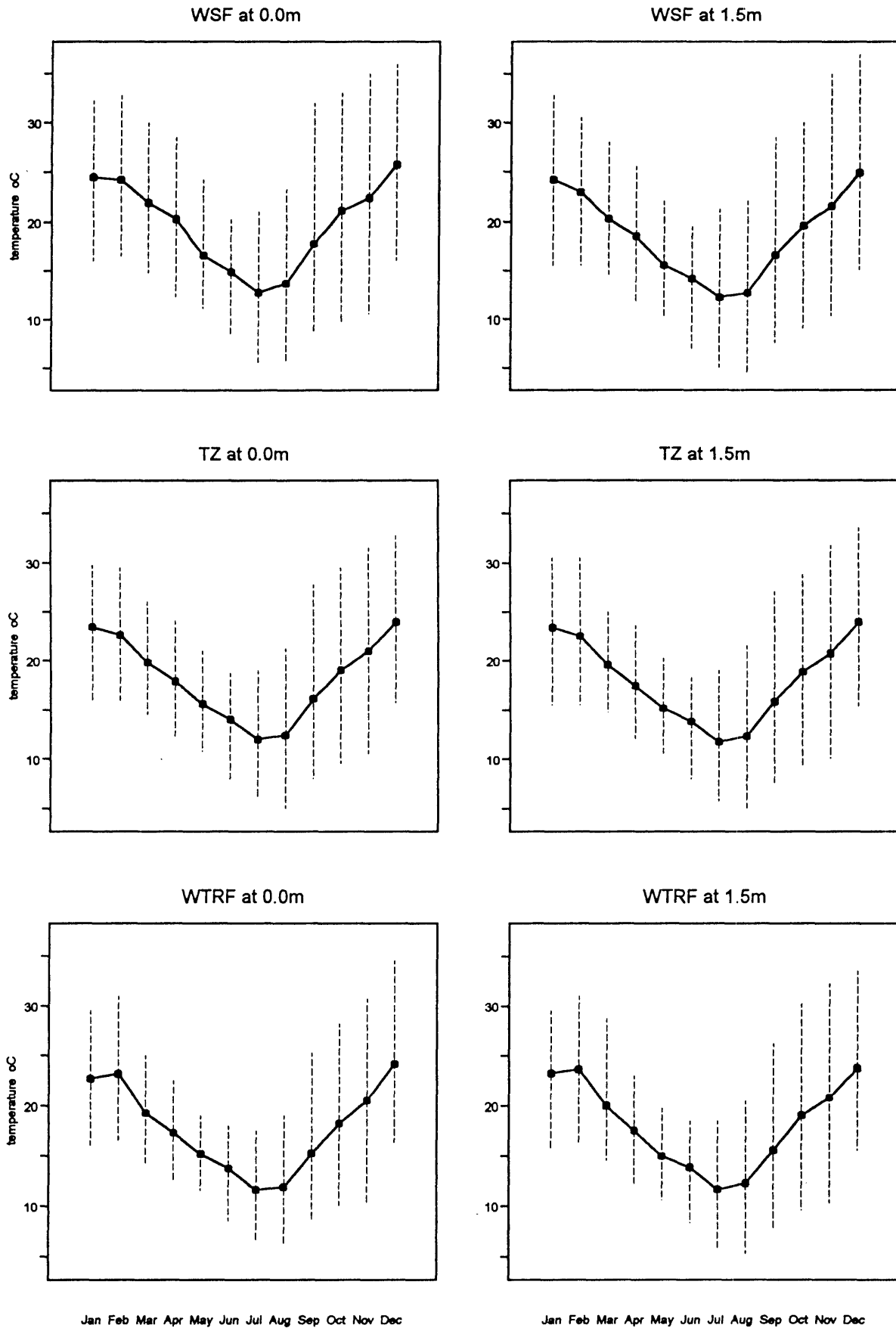


Figure 4.75 Mean monthly maximum temperatures at three gradient points and at two different heights. Dotted lines indicate the 95% confidence interval

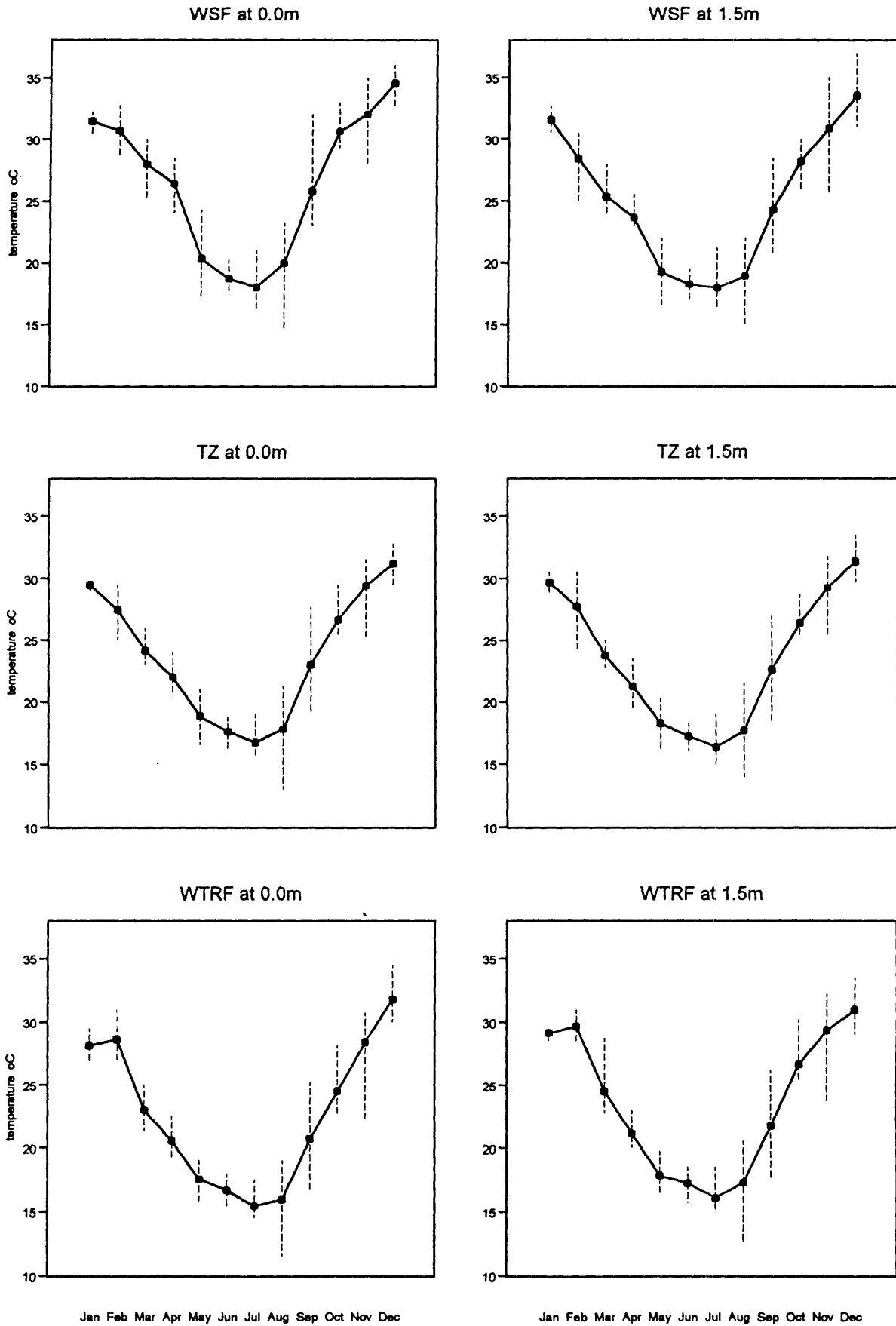


Figure 4.76 Mean monthly minimum temperatures at three gradient points and at two different heights. Dotted lines indicate the 95% confidence interval

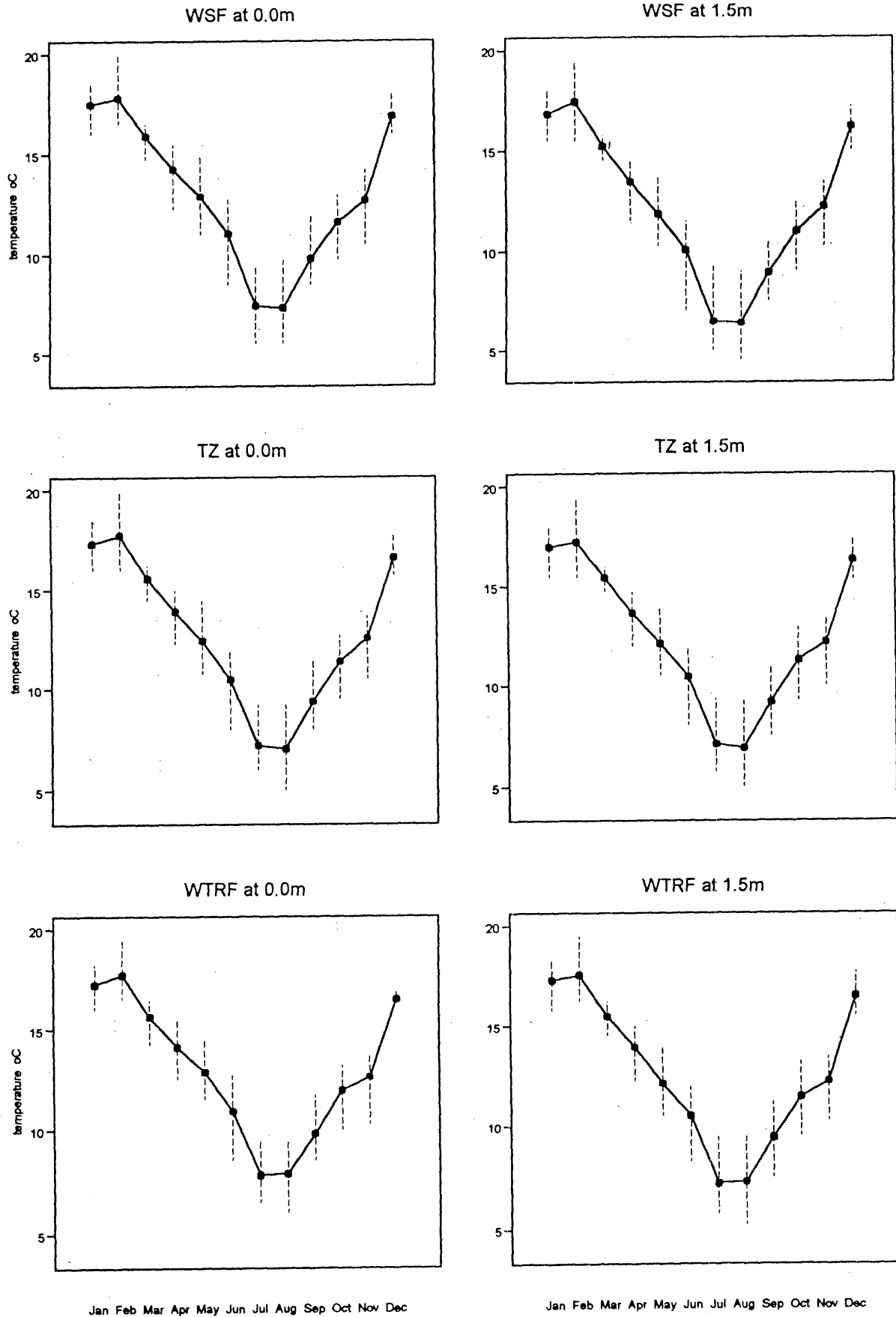


Figure 4.77 Mean monthly temperature ranges at three gradient points and at two different heights. Dotted lines indicate the 95% confidence interval

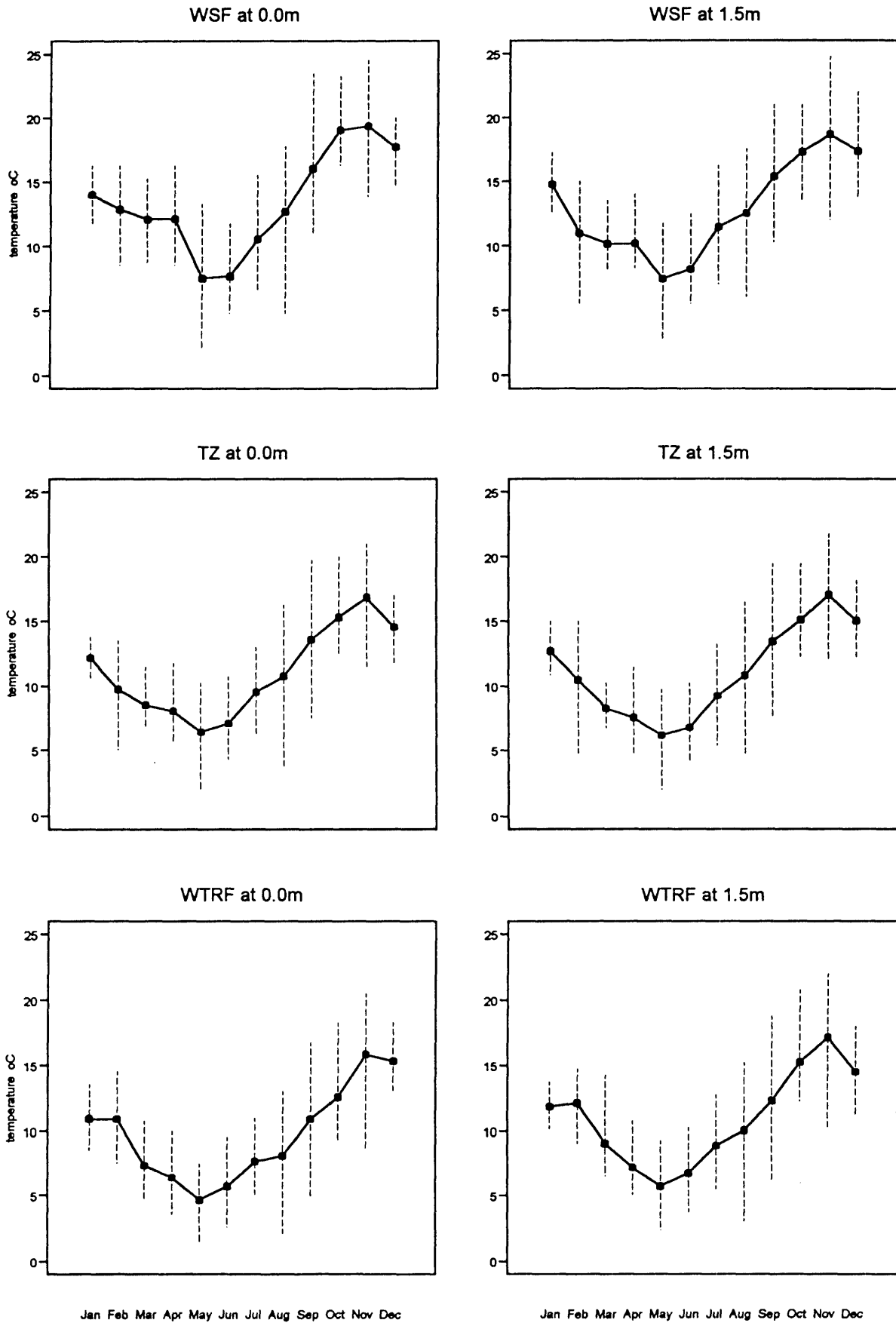


Figure 4.78 Highest monthly maximum temperatures at three gradient points and at two different heights.

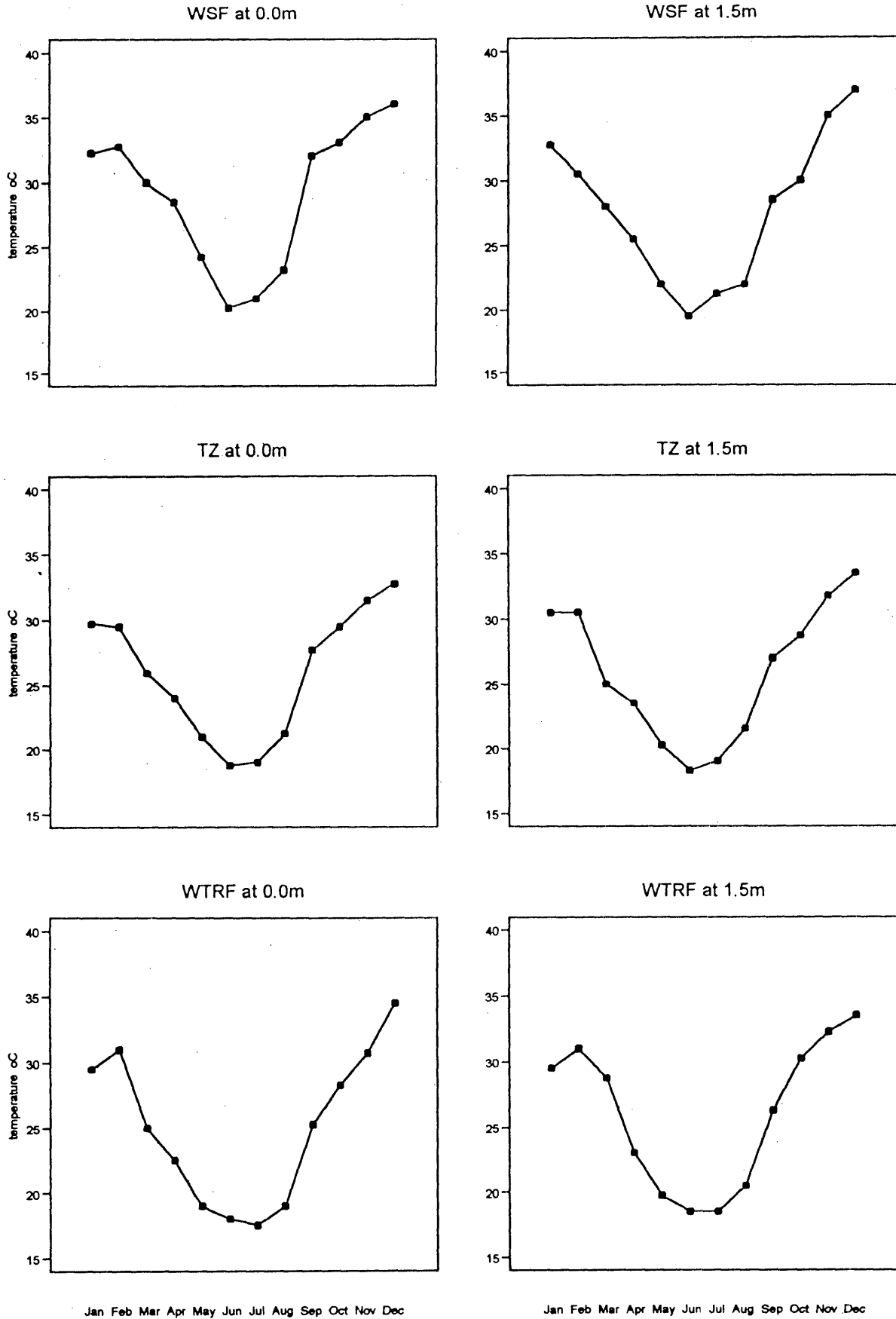


Figure 4.79 Lowest monthly maximum temperatures at three gradient points and at two different heights.

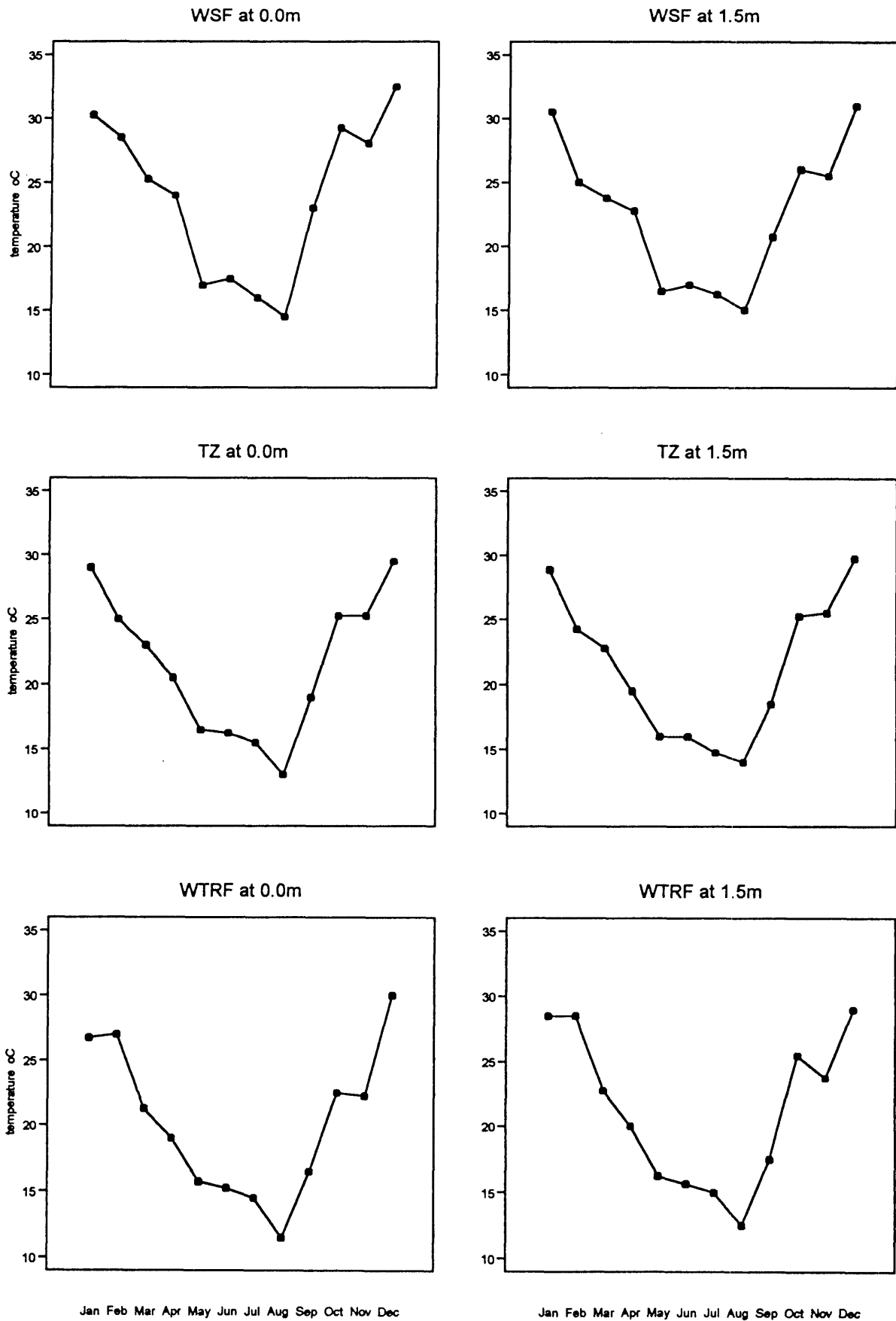


Figure 4.80 Highest monthly minimum temperatures at three gradient points and at two different heights.

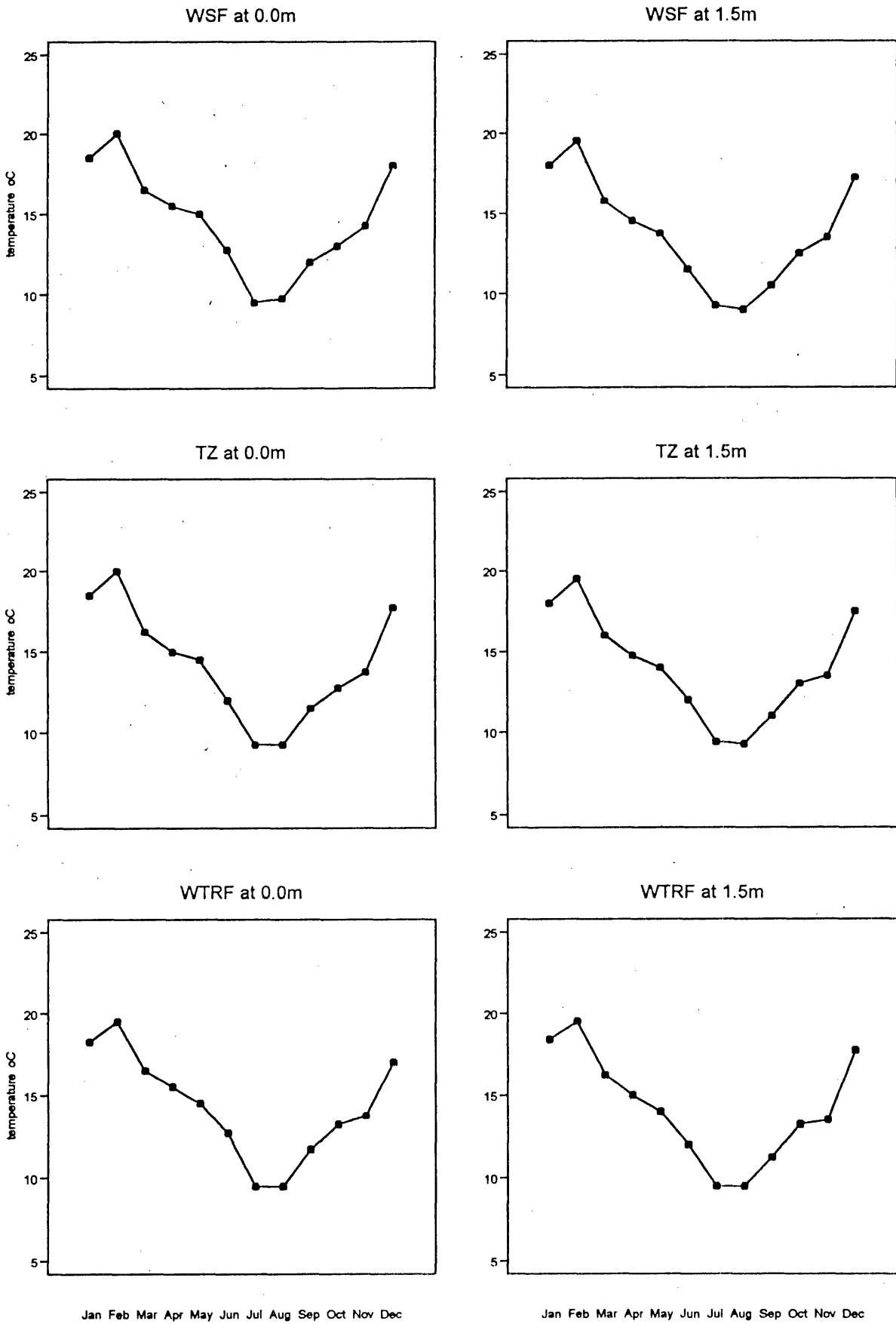
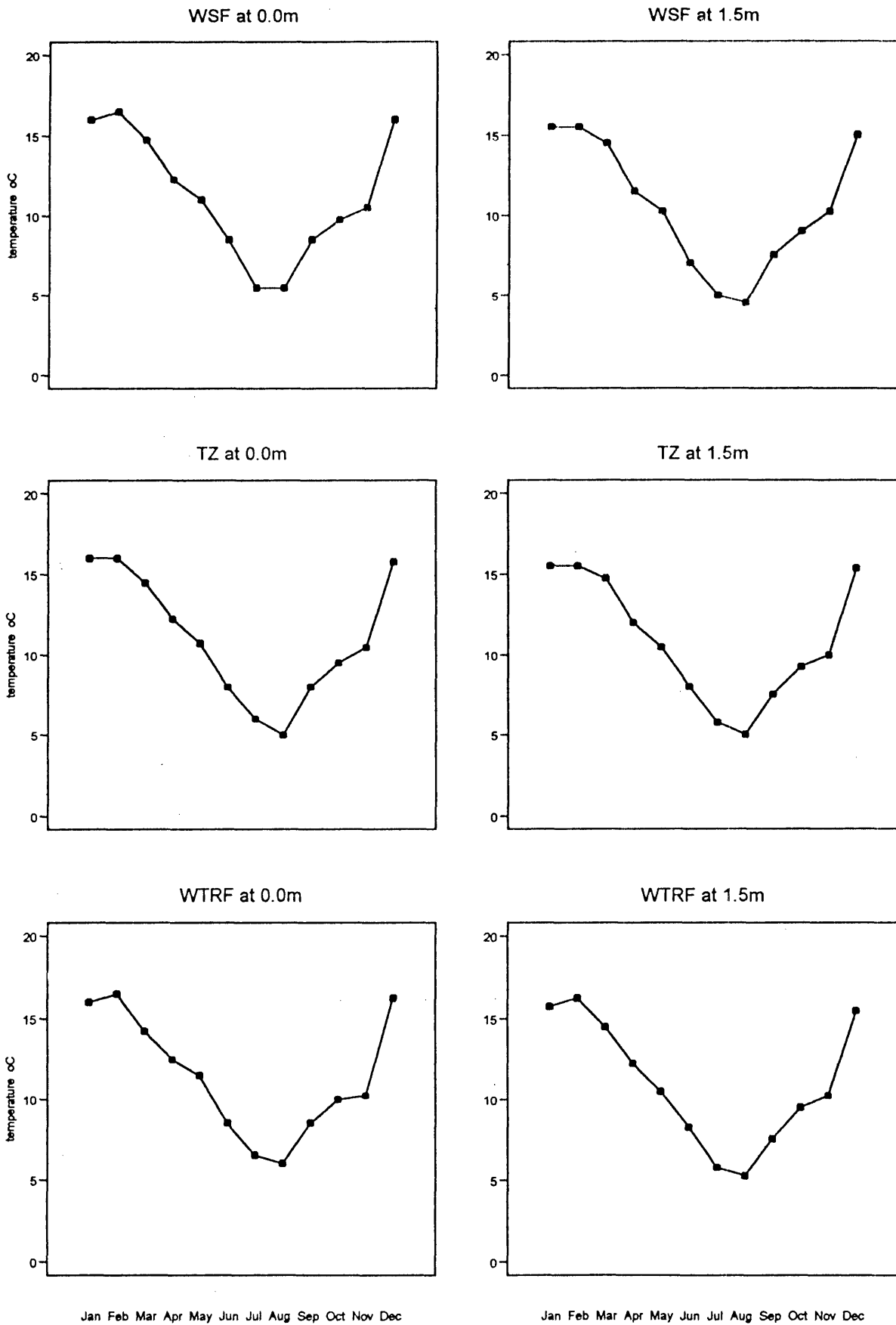


Figure 4.81 Lowest monthly minimum temperatures at three gradient points and at two different heights.



convex whereas in WTRF the fall is distinctly concave. A rise in the mean minimum temperature at all points for February was only reflected in the mean maximum readings for WTRF and it is unclear why this is the case.

The range of variation of minima (11 °C, Fig. 4.75) is less than the range of maxima (18 °C, Fig. 4.75) which indicates that the monthly temperature range contains another dimension of temperature variability.

Fig. 4.77 shows the pattern of larger temperature ranges in late spring and early summer (October to December) than for other seasons but it also shows a record of greater variability of temperature range during the spring months.

Fig. 4.78 shows the annual pattern of the highest monthly maximum temperatures. The interesting result to note here is the comparable winter patterns for the different vegetation. The dense growth of the rainforest in conjunction with the low solar angle restricts direct radiation and serves to keep temperatures low while the open WSF allows highest maximum temperatures to increase after a nadir in June.

The plots in Fig. 4.79 all indicate coolest maxima for August. This result is a consequence of the data collection procedure. That is, temperatures were read weekly and during the first year a very cold day occurred on the 30th July which was recorded for the week ending 3rd August. The plots would have been more in line with my experiences had these data been included in with the July data. The readings for that week also served to inflate the variability for August as shown by Fig. 4.75.

The patterns of highest and lowest minima as shown by Figs. 4.80 and 4.81 indicate an unexpected congruency for all points along the transect. The notion that the closed forest serves to moderate temperatures applies only to the upper end of the temperature spectrum. All these minima occurred during the night but it is worth returning briefly to Fig. 4.79 to see that the coldest maximum temperatures were recorded at the two stations in closed forest.

Figure 4.82 Monthly temperature variation at three gradient points all at 0.0 m. Note different scale for minimum temperature data

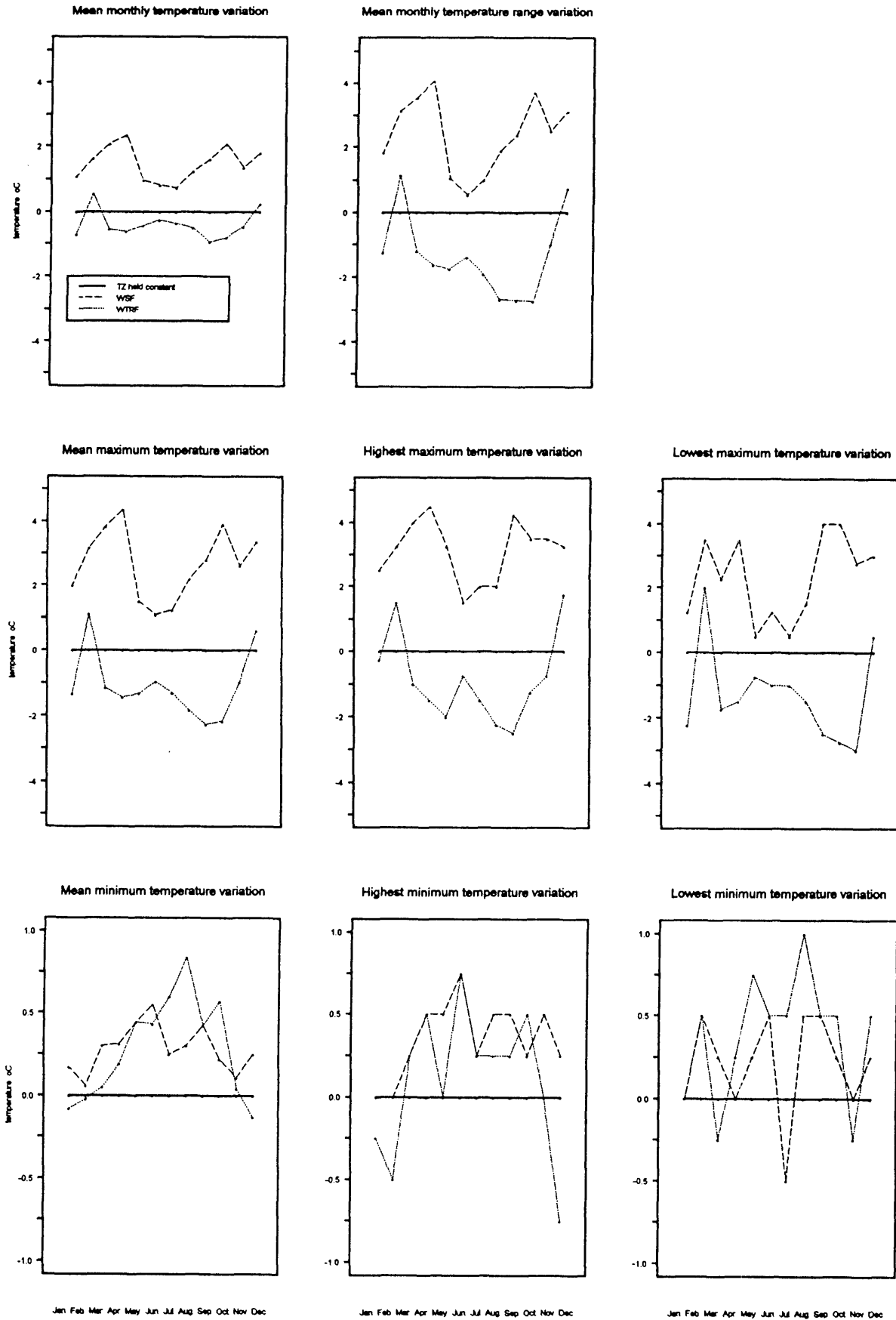
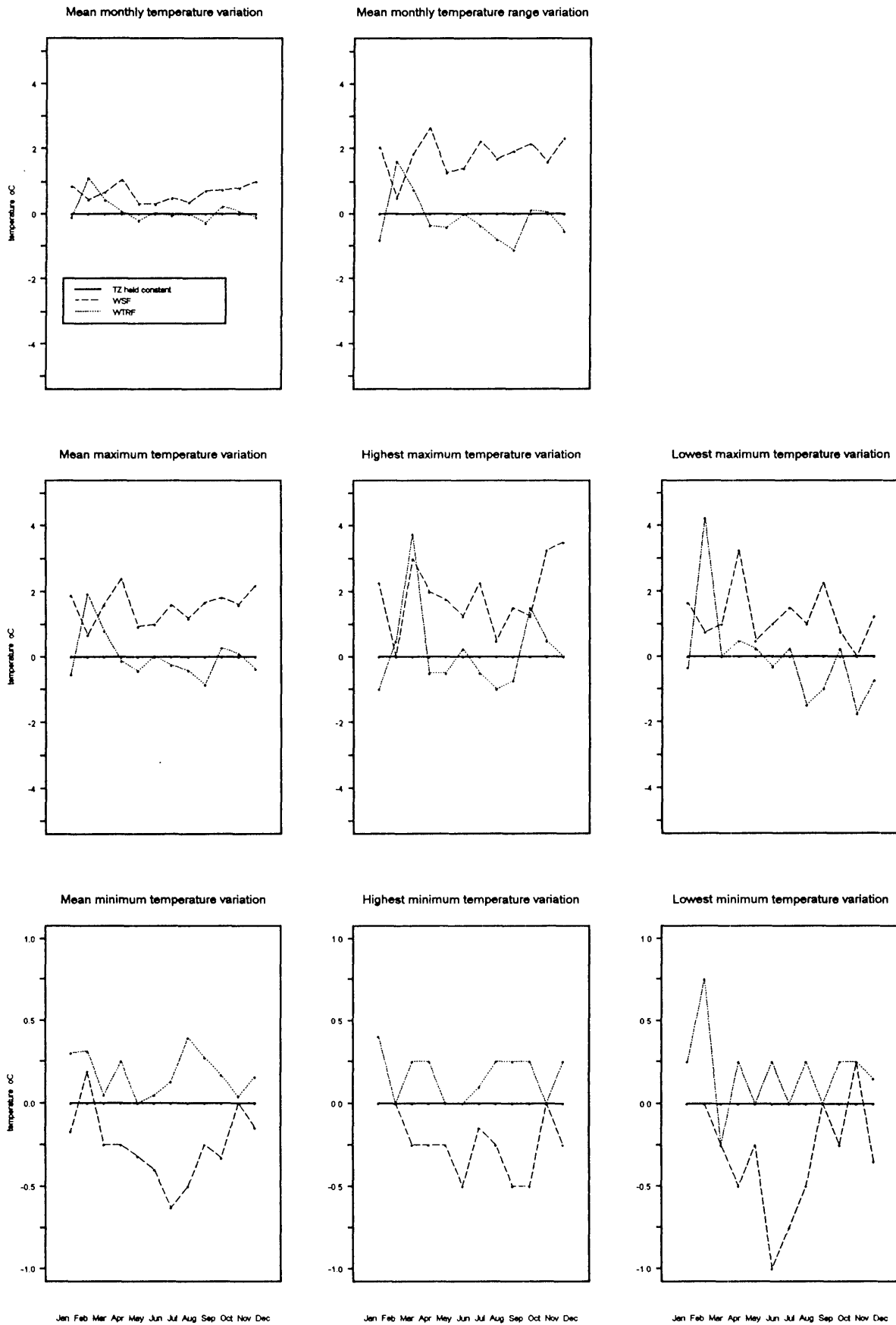


Figure 4.83 Monthly temperature variation at three gradient points all at 1.5 m. Note different scale for minimum temperature data.



Direct comparisons of temperature variation between vegetation types are portrayed in Figs. 4.82 and 4.83. In both these figures, all variations are expressed in terms of variation from the pattern recorded for the transition zone forest. The results for ground-level temperatures (Fig. 4.82) show, for means and maxima, a general but not consistent gradation from a cooler rainforest to a warmer open forest. The differences are least during the colder months and most, not during the warmest months but during the intermediate seasons of spring and autumn. The transition zone forest is slightly the coldest place on the ground-level transect during summer and the respective minima, although all very similar, show that the transition zone forest is also the coolest place on the ground-level transect during winter. The relationships of the observation points at 1.5 m along the transect (Fig. 4.83) are less clear. At 1.5 m, the range of temperatures for WSF encompasses the temperature range in the TZF at both extremities. The WTRF experiences warmer minima than the TZF but the maxima for these two vegetation types do not follow the same patterns as the variation in WTRF maxima regularly exceeds and falls short of that for the TZF.

Figs. 4.84 to 4.86 show the same relationships as Figs. 4.82 and 4.83 but in a vertical dimension within vegetation type as opposed to a horizontal dimension across vegetation types. For each of these plots the data for 1.5 m are plotted in terms of their variation from the 0.0 m data. Geiger (1965 p.321) suggests that air on the ground will be warmer than that at 1.5 m in winter but cooler than at 1.5 m in summer. Notwithstanding that Geiger's data were collected in the Northern Hemisphere, and, of course, depending on which temperature statistic is considered, the data obtained during this project which are summarised in Table 4.27, indicated that these rules almost certainly do not apply in the forests of northern New South Wales. At only one site, the WTRF, based on mean monthly temperature, did the seasonal relationship between the ground temperatures and those at 1.5 m concur with the Geiger model. In the other two zones, based on the same statistic, the temperature was warmer on the ground than at 1.5 m in the summer and in the winter. Depending on the statistic used, different interpretations are possible or difficult, for example, the behaviour of seasonal lowest maxima appears to be quite complex. These data

Figure 4.84 Monthly temperature variation at two heights in WSF.

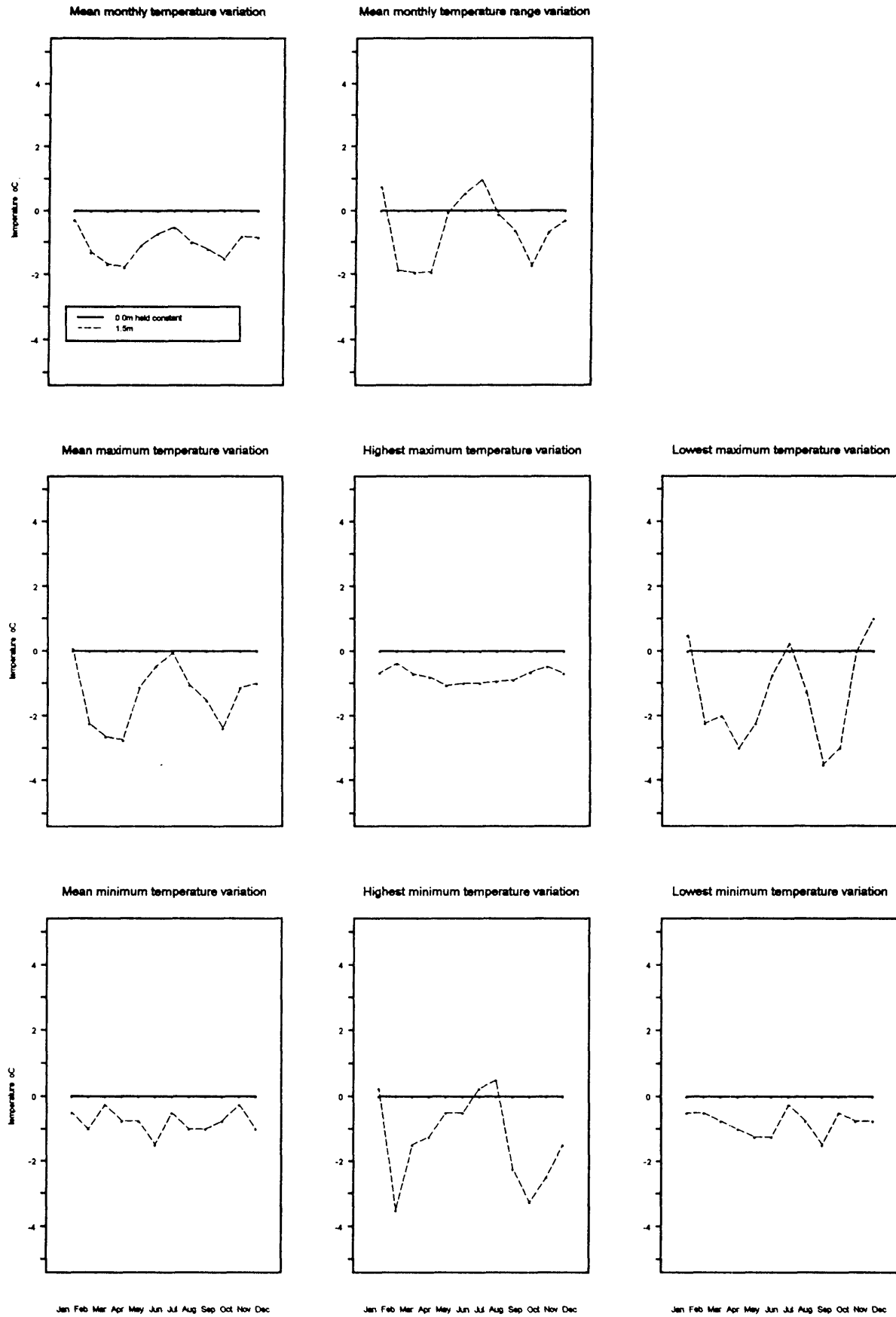


Figure 4.85 Monthly temperature variation at two heights in TZF.

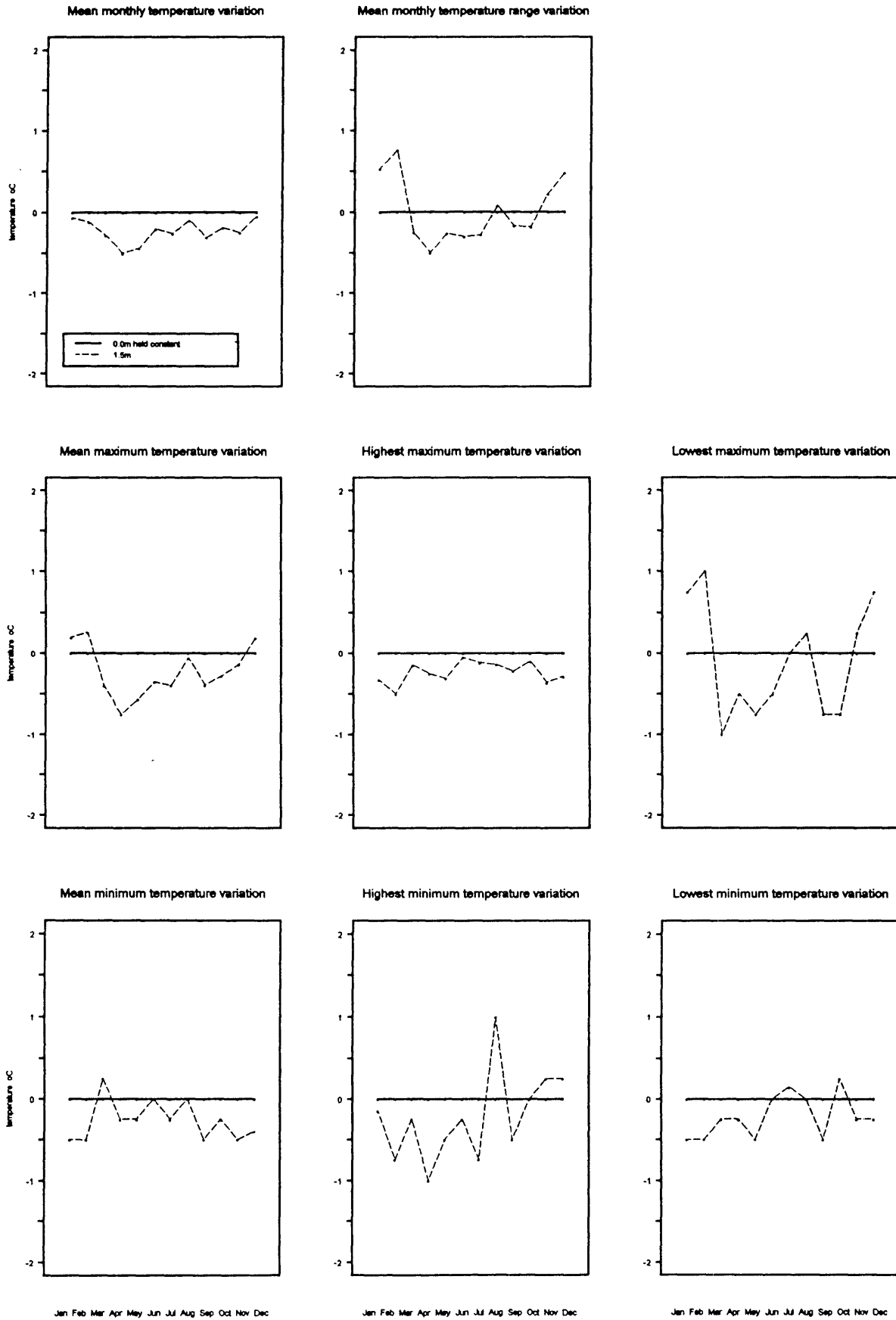


Figure 4.86 Monthly temperature variation at two heights in WTRF.

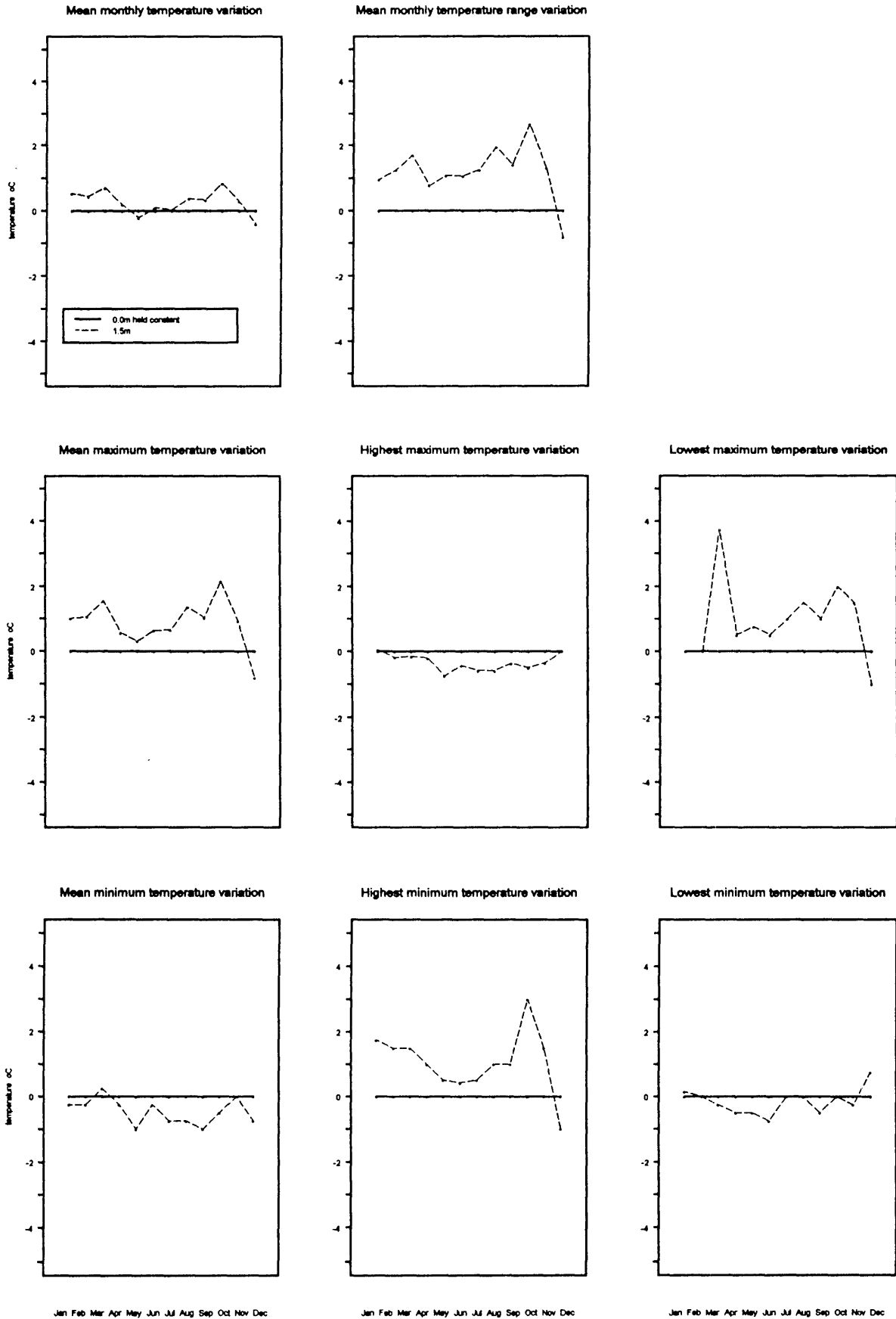


Table 4.27

The height position of seasonally warmer temperature for all observation points along the WSF-TZF-WTRF gradient. The two heights sampled were 0.0 m and 1.5 m. The question marks indicate that the data are inconclusive and the height value shown is assumed.

	WSF		TZF		WTRF	
	summer	winter	summer	winter	summer	winter
mean monthly	0.0m	0.0m	0.0m	0.0m	1.5m	0.0m
mean max.	0.0m	0.0m	1.5m	0.0m	1.5m	1.5m
highest max.	0.0m	0.0m	0.0m	0.0m	0.0m	0.0m
lowest max.	1.5m	1.5m?	1.5m	0.0m	0.0m	1.5m
mean min.	0.0m	0.0m	0.0m	0.0m	0.0m	0.0m
highest min.	0.0m	1.5m	0.0m?	0.0m	0.0m	0.0m
lowest min.	0.0m	0.0m	0.0m	1.5m	1.5m	0.0m

overall indicate that the temperature gradient from WTRF to WSF is not a gradual transition but one that has special characteristics in the region of changeover between vegetation types.

Analysis of the hygrothermograms was facilitated by first digitising the curve in each hygrothermogram. The digitising process is not guaranteed error free, but few errors were noted during the subsequent analysis.

A computer program THGTRANPOSE (Appendix II) was written to calculate the area under each graph using the scale of units allocated by the digitiser. The area thus obtained was a surrogate for the average temperature at that site for the recording period. The area was calculated by first transposing the digitised data through 90° such that the base of the hygrothermogram became the y-axis and the left hand side became the x-axis on the negative side. It was then possible to calculate the area under the line which was parallel to the curved pattern of the hygrothermogram and which connected a digitised point to the y-axis. From this figure, the area under a parallel curve involving the previous digitised point, calculated in the same way, was subtracted, giving the area under the curve attributable to the current digitised reading. The sum of all these small areal increments became the area under the digitised curve. The mathematical techniques used to obtain these values are documented in the description of

THGTRANPOSE and these include an integration subroutine obtained from Ellis (1990). The areas were summed and from these sums it was possible to derive an average weekly temperature for each hygrothermogram.

From this result, one year's data from each of the three recording sites is presented in Fig 4.87. The graph shows that at 75 mm above the ground the average temperature is highest in the transition zone with the other two zones being more or less similar. Assuming that the equipment was properly calibrated in the laboratory and even allowing for the intrinsic operating error of this equipment (MacHattie 1958), the transition zone result is notable. The contributing factor to this result is likely to be related to the greatly reduced herbaceous layer compared to the WSF, leading to an increase in ground level airflow producing a lower level of transpired water vapour close to the ground, in conjunction with the different canopy structure compared to the rainforest.

As has been noted by all researchers of local temperature variation inside or outside forests, air temperatures peak at a time somewhat later than the solar peak. Specifically, this lag is extended by the total heatable surface areas of the plants present. The hygrothermograms indicate that this lag time ranges from about 1 to 2.5 hours inside the forest (Fig. 4.88). That the lag is greatest in the WTRF (Fig. 4.88) is consistent with that zone having the greatest number of leaves in its tree crowns which reflect or absorb the rising temperature more effectively than is the case in the other two vegetation zones. The lag is somewhat shorter in the TZF where there are fewer plant surfaces and least in the open-canopy WSF.

The hygrothermograms displayed in Fig. 4.88 also show the source of the results portrayed in Fig. 4.87. The shape of the temperature line for TZF has affinities with both of the adjacent vegetation zones but does not achieve either their maxima or minima for the period. This suggests that the mix of vegetation from the WSF and WTRF in the TZF serve to ameliorate temperature effects better than the dense canopy of the WTRF might have been expected to do.