Water Relations, Phenology and Drought Adaptation of Understorey Trees in Tropical Lowland Rain Forest

A thesis submitted for the degree of Doctor of Philosophy at the University of Stirling

By
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I hereby declare that this thesis has been composed by myself except where otherwise stated the work contained herein is my own.

James Gibbons

"I shouldn't be surprised if it hailed a good deal tomorrow," Eeyore was saying. "Blizzards and what-not. Being fine today doesn't Mean Anything. It has no sig- what's that word? Well, it has none of that. It's just a small piece of weather."

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ABSTRACT

1. The ecology of common understorey species associated with ridges was compared with species found on lower-slopes and those species occurring ubiquitously in two 4-ha plots in lowland rain forest at Danum, Sabah, East Malaysia (4° 58' N, 117° 46' E) over 3 years.
2. During the study period one dry period occurred (psychrometer-measured ridge soil water potential, 20 cm depth -0.67 MPa), but other, more severe, dry periods have occurred since records began in 1985 (estimated ridge water potential -1.21 MPa, March 1992). Lower soil water potentials occurred on ridges which had up to 0.22 MPa lower water potentials than lower-slopes (estimated difference March 1992, 0.40 MPa).
3. At dry times, *Dimorphocalyx muricatus* (ridge species) had higher pre-dawn (-0.21 *v.* -0.57 MPa; all quoted differences are significant at $p<0.05$) and mid-day (-0.59 *v.* -1.77 MPa) leaf water potentials than *Mallotus wrayi* (ubiquitous). Leaf osmotic potentials of *D. muricatus* were higher (-1.11 *v.* -1.58 MPa), and both species osmotically adjusted between wet and dry times. *D. muricatus* trees were more deeply rooted (mean root depth, 97.4 cm) than *M. wrayi* trees (69.8 cm). *M. wrayi* seedlings on ridges had lower assimilation rates than on lower-slopes (1.9 *v.* 3.4 μmol CO_2 m^{-2} s^{-1}).
4. Leaf production of *Ardisia colorata* (ubiquitous), *Cleistanthus glaber* (ridge), *D. muricatus* and *M. wrayi* trees varied from year to year. *C. glaber*, *D. muricatus*, and *M. wrayi* all had peaks in leaf and flower production associated with sunnier drier spells, *A. colorata* did not. *A. colorata* leaves were longer lived (5.7 years, estimated from leaf turn-over) than *D. muricatus* (2.7 years) and *M. wrayi* (2.2 years). There were no size or site differences for leaf life-span or leaf production. More large trees flowered than small trees. More trees flowered on ridges than lower-slopes but more trees set fruit on lower-slopes.
5. *D. muricatus* seedlings grew equally well on ridges and lower-slopes under different water regimes. *M. wrayi* and *D. muricatus* cutting mortality was higher than *D. muricatus* seedling mortality for all treatments. *M. wrayi* cutting mortality was highest in lower-slope drought plots. Cutting mortality was higher in logged forest than primary forest.
6. *M. wrayi* seed germination rates (1 %) were much lower than *Baccaurea stipulata* (lower-slope) (65 %) and *D. muricatus* (53 %). Germination rates were higher on ridge than lower-slope sites. *D. muricatus* nursery germination rates (32 %) were lower than in the field. *B. stipulata* seed took longer to germinate (35 days) than *D. muricatus* (21 days).
7. Under nursery conditions *M. wrayi* wildings grown under 2.7 % daylight grew taller and increased leaf area, specific leaf area (SLA) and fine and coarse root weight than under 1.2 % daylight. Addition of phosphate had no effect on growth.
8. Un-watered *D. muricatus* seedlings took significantly longer to wilt (36 *v.* 16 days) and die (46 *v.* 29 days) than *B. stipulata* seedlings.
9. The results suggest that droughts may have an important effect on understorey ridge community species composition at Danum.

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CONTENTS

Chapter One. Introduction

Climatic variation

Until relatively recently the seasonal and geological stability of tropical rain forest (*sensu* Whitmore, 1984; forest where there is normally no seasonal water shortage) climate was emphasised (e.g. Ashton, 1969). This unchanging climate, it was thought, provided optimal conditions for plant growth (e.g. Richards, 1969). However, it is now clear that tropical rain forest climate variation occurs on the time scale of months (e.g. Brünig, 1969), years (e.g. Walsh, 1992), decades (e.g. Walsh, 1996), and greater time spans (e.g. Bush, 1994). Of key importance is that these variations, with the exception of glacial periods (see below), appear to be unpredictable and non-cyclic (Davis, 1986).

The most recent two million years, the Quaternary period, has been characterised by glacial/ inter-glacial periods on a 100,000 year cycle. During glacial periods there is a global reduction in atmospheric CO_2 levels (to about 170 ppm) and a reduction in rainfall (periodically about 20 %) in tropical regions (Bush, 1994). Pollen records indicate that changes in species distribution resulted from this increased aridity (e.g. Stuijts *et al.*, 1988). Glacial periods are of greater duration than inter-glacials so current species distributions may reflect climatic history rather than current conditions. Even before the Quaternary age there is evidence that strong fluctuations in rainfall have occurred.

Monthly, annual, and ten yearly variations in rainfall are less severe than that between glacial and inter-glacial periods. A large part of the variation is linked to the 'super-annual' El Niño Southern Oscillation (ENSO), a change in wind direction and ocean currents in the South Pacific that affects global weather patterns in an unpredictable way. The Southern Oscillation is the reversal of the normally positive sea level pressure deficit between Tahiti and Darwin. This reversal leads to the slackening of the South Pacific trade winds, and the normally cold current and sea upwelling off the South American coast is replaced by the warm El Niño current. The warm sea increases rainfall in the eastern and central Pacific region while the anomalous high pressure over the Indonesian region leads to a local reduction in rainfall. ENSO events vary greatly in duration, strength and geographical impact. Generally the event starts in March to May and lasts for a year. Specifically it can lead to a large reduction in rainfall in parts of South East Asia (Walsh, 1996), and elsewhere (Condit *et al.*, 1996). However, in north-eastern Borneo, super-annual droughts have also occurred independently of the ENSO (Walsh, 1996).

Tropical rain forest species diversity

Tropical rain forests are usually more diverse in plants than other terrestrial species communities. (Although tropical 'monodominant' forests, forests in which one species makes up >50 % of stems or basal area, do exist.) Knowledge of the forests has increased- for example 'the myth that tropical climates provide a stable environment for tropical forest organisms has long been buried' (Condit *et al.*, 1996) but no model exists 'which will predict and explain the number and relative abundance of tree species co-occurring...in defined stands of rain forest' (Newbery *et al.*, 1996). Whether such a model is possible is a matter of some debate.

At the centre of the debate is the rôle of chance and history in determining tree species composition. Hubbell & Foster (1986) considered forest on BCI, Panama, and concluded that within 'a dozen or so guilds' rain forest tree and shrub species are morphologically and phenologically similar. Within these groups of 'canopy species...pioneer species...edaphic and topographical specialists...shade tolerant shrubs and understorey trees...gap-edge specialists' 'adaptive convergence and generalisation occurs'. Species diversity is maintained, they argue, by biotic uncertainty and locally unpredictable disturbances, which outweigh pairwise and predictable biotic interactions. Unfortunately, Hubbell & Foster's inclusion of guilds is often ignored by authors, and their ideas misrepresented, e.g. '[all species compete] in the same fashion for resources' (Clark & Clark, 1992). In more recent work on BCI (Condit *et al.*, 1996) some species show higher rates of population change than that predicted by Hubbell & Foster. Other authors' explanations have favoured increased specialisation among species (Ashton, 1969; Richards, 1969). While these authors accept a rôle for chance, 'whether or not a single niche may be filled by one or several species [is] in part by historical accident' (Ashton, 1969), they conclude that predictable biotic interactions predominate. Part of this discrepancy in view is accounted for by a difference in emphasis. Ashton and Richards were more concerned with how diversity had arisen, Hubbell & Foster with the maintenance of diversity. However, there are real differences between the belief that tropical rain forests are in 'equilibrium' (stabilised by biotic interactions) or in 'non-equilibrium' (no or weak stabilisation by biotic interactions).

Influence of topography on species distribution

Tropical rain forest enumeration studies have found differences in species distribution associated with topography, both within plots (Austin & Grieg-Smith, 1968; Hubbell & Foster, 1983; Rogstad, 1990; Newbery *et al.*, 1996; Poulsen, 1996), and between plots (Lieberman *et al.*, 1985; Newbery, 1991; Ashton & Hall, 1992). Between plot studies are more difficult to interpret as there may be plot differences beyond topographic differences. However, the three Costa Rican plots (total area 12.4 ha) of Lieberman *et al.* (1985) did show a floristic gradient over an elevation change of 40 m, excluding permanently wet areas.

Changes in topography are associated with changes in soil physical structure, macro and micro nutrient availability, water availability, and aeration. Differences in species composition have been attributed to all these factors, but is difficult to determine which are important because they vary together in the field (Newbery, 1991). Nutrients may not be important: it has yet to be demonstrated that nutrients affect tree distributions within forest types (Proctor, 1995), and species composition varied with topography, independently of nutrients, at a forest at Danum, Malaysia (Newbery *et al.*, 1996).

Low lying areas, near water courses, are regularly flooded causing soil saturation. In Costa Rica, Lieberman *et al.* (1985) found that seasonally flooded sites were floristically distinct from sites on higher ground. They postulated that some species are intolerant of water-logged soils and are thereby excluded. Similarly, Ho *et al.* (1987) suggest that the differences in species composition between two plots in Malaysia were the result of a previous catastrophic flooding event in one of the plots. Elsewhere in Malaysia, Rogstad (1990) provided experimental evidence that a species excluded from regularly inundated areas is intolerant of water-logged soils.

On higher ground and ridge tops lower soil water potentials occur than in valleys and on lower slopes. In a 50 ha plot in Panama, Becker *et al.* (1988) found that slopes were wetter than plateau areas. The small stature species associated with these slopes have undergone a population decline following a 30 year reduction in rainfall (Condit *et al.*, 1996). Of the 11 understorey tree and shrubs species associated with slopes, 10 species have declined in numbers between 1981 and 1990. Larger stature slope specialists were less affected, with 9 out of 19 species declining in numbers. For the whole tree and shrub population ($n \geq 20$, dbh ≥ 10 cm), 61 out of 149 species have declined in numbers. It is not clear whether the decline is a long term trend or solely the result of a severe drought in 1983. Becker *et al.* (1988) demonstrated differences in drought resistance between two understorey species, *Trichilia tuberculata* and *Psychotria horizontalis*. However, both are classed by Condit *et al.* (1996) as generalists. Poulsen (1996), in Brunei, concluded that the best explanation for low herb populations on a hill top was the measured reduction in soil water content from valley to hill top.

Any topographic variation of soil water will interact with the shorter-duration climatic variations described above. An unusually wet year may result in flooding and soil anaerobis on low lying, normally free draining soils. Conversely an unusually dry spell may result in soil water potentials on ridges low enough to limit plant growth and cause plant death

(Condit *et al.*, 1996). In the former case, species tolerant of flooded soils will be selected on lower slopes; in the latter case, drought tolerant species will be selected on ridges. The frequency, regularity and strength of the extreme event will determine how far the ridge and valley plant communities diverge. Frequently, regularly, and strong, and the communities will be quite different and the differences will be stabilised; infrequently, irregularly and strong and the communities will remain similar and be destabilised.

During glacials, and other long term reductions in rainfall, rain forest areas shrank and immigration of dry forest (*sensu* Whitmore, 1988; forest that is leafless during the dry season) species occurred (Bush, 1994). Especially at the rain forest margins, but also elsewhere, the drier climate would have reinforced any ridge valley differences, possibly isolating communities. Mixing with dry forest species could also have occurred. It is possible, given sufficient extreme drought events, that these dry forest species could persist on ridge sites during wetter inter-glacial periods. If, as Hubbell & Foster (1986) suggest, populations of rain forest trees take a long time to become extinct, any populations of ridge species could be relics from the last or previous glacial periods.

Forest at Danum, Sabah, north-east Borneo

Compared with other forests in the region, two replicate 4 ha plots at Danum are relatively species poor and the basal area abundance is low (Newbery *et al.*, 1992). Compared with the mean of nine rain forest sites in Borneo and West Malaysia, Danum has 84 % of the density, 74 % of the basal area and 60 % of the species richness for trees ≥30 cm gbh. Newbery *et al.* suggest that this relative paucity, coupled with a low frequency of gaps and a high density of lianas, is indicative of a previous moderate disturbance. Analysis of spatial distribution of understorey species showed a vegetation change from lower slope to ridge, independent of soil nutrients (Newbery *et al.*, 1996). A group of species that were found almost exclusively on ridges was identified. A second group of species were found throughout the plots, while a third group were possibly associated with lower slopes and valleys. There were too few trees of many species (51 % of species had <5 trees per plot) for conclusions to be drawn about their distribution. No association with soil chemistry was found. Newbery *et al.* (1996) hypothesised that the observed patterns in the understorey are due to differential responses to low water supply, the ridges tending to dryness more than the lower slopes and that ridge species show greater drought adaptation than ubiquitous or lower-slope species. It was further postulated that any physiological adaptations ridge species have to dry conditions constrain their survival on lower slopes. Any extreme dry period would reinforce ridge/ lower slope differences, as discussed above. So any differential effect on mortality or growth on the understorey species would be greatest at these times. Walsh (1996) examined rainfall data from several stations in northern Borneo, and concluded that severe droughts have previously occurred in eastern Sabah. Newbery *et al.* suggest that the paucity of species and large trees is evidence that the forest at Danum is recovering from the effect of one of these droughts.

Ecology of understorey tree species

Owing to taxonomic uncertainty and commercial unimportance, understorey tree species have received little attention in South East Asian studies. In contrast, relative growth rates, light requirements, and phenology of trees in the Dipterocarpaceae, the dominant timber group, have received much study. In the region, with the exception of the plots at Danum (see above) and at Pasoh, peninsular Malaysia (Manokaran & Kochummen, 1987), no enumeration studies have completely identified the smaller trees (<10 cm dbh) in a large (>5 ha) area of lowland dipterocarp rain forest (Newbery *et al.*, 1992). Hence, little is known about understorey tree ecology, and their rôle in forest structure and functioning. Their rôle may not be unimportant. Understorey species must compete directly with immature canopy trees for light, and with all canopy trees for water, nutrients and pollinators.

Study objectives

The primary objective of this study was to test the hypothesis of Newbery *et al.* (1996) outlined above.

Specifically:

- Are areas where ridge species occur drier than elsewhere; do any differences become greater at drier times?
- Do severe droughts occur at Danum?
- Do ridge species have greater drought adaptation than other species? What are the adaptations?
- Why do ridge species not grow on lower-slope sites? Do ridge species' drought adaptations constrain the survival of ridge species on lower slopes?

The secondary objectives were to find out more about the general ecology of understorey species.

Specifically:

- Are there patterns of understorey leaf and flower production?
- How does understorey ecology compare with that of canopy species?
- How well do understorey species grow in logged forest?

Chapter 2 characterises the study environment. In chapter 3 the Danum climate record is examined for evidence of previous droughts, and ridge and lower slope soil water potentials are reported. In chapter 4 the field plant water relations of a ridge and ubiquitous species are compared. Chapter 5 reports the phenology and leaf life-span of two ridge species and two lower-slope species, and the leaf structure of the 20 most common species. Chapter 6 investigates the growth and mortality of a ridge species and ubiquitous species under different soil water conditions in the field. Chapter 7 compares seed establishment for a ridge, ubiquitous and lower-slope species. Chapter 8 reports the results of two nursery experiments that investigate the interactive effect of light, water regime and, phosphate addition on wilding growth, and compares time to death for a ridge and a lower-slope species with no water addition.

Chapter Two. Study sites and their environment

Fieldwork was carried out at the Danum Valley Field Centre, Sabah (DVFC; 4° 58' N, 117° 46' E; Figure 2-1), over four periods, 4 December, 1994 to 26 October 1995, 15 January to 12 December, 1996, 9 April to 30 June, 1997, and 7 November to 8 December, 1997. DVFC lies on the Segama river, immediately to the east of the Danum Valley Conservation Area (DVCA), a 43,800 ha block of primary forest within the 973,000 ha Yayasan Sabah concession area. The DVCA is 'Class I' forest meaning it is legally protected from commercial exploitation, and it has never been logged. Most of the remaining concession area is 'Class II' forest, and has been or is in the process of being logged. Other parts of the concession are currently excised from the area to be logged, and are either small Virgin Jungle Reserves (Class VII forest) or have no formal protection. For example, approximately 4,000 ha of forest around the stream, the Palum Tambun, from which DVFC draws water is excised. Logging takes place in 2,000 to 5,000 ha annual areas or 'coupes'. The history of logging of the concession area is documented, and hence the position of previous coupe boundaries can be determined. Forest 500 m from the field centre was logged in 1988.

STUDY SITES

Primary forest sites

Most work took place in the primary forest. Initial work took place in two 4 ha permanent plots (commonly referred to as the 'Stirling Plots', hereafter referred to as the large permanent plots or LPPs) 400 m and 700 m east and 200 m above the Segama river (Figure 2-2). The plots measure 100 m east-west and 400 m south-north. An initial enumeration of the plots was made in 1985 - 1987 for all trees ≥ 10 cm gbh (girth at breast height). Each individual has been tagged, its co-ordinates recorded, and identified, in most cases to species level. For a more complete description see Newbery *et al.* (1992). A second enumeration was made by Stirling University and Sabah Forestry Department concurrently with this study.

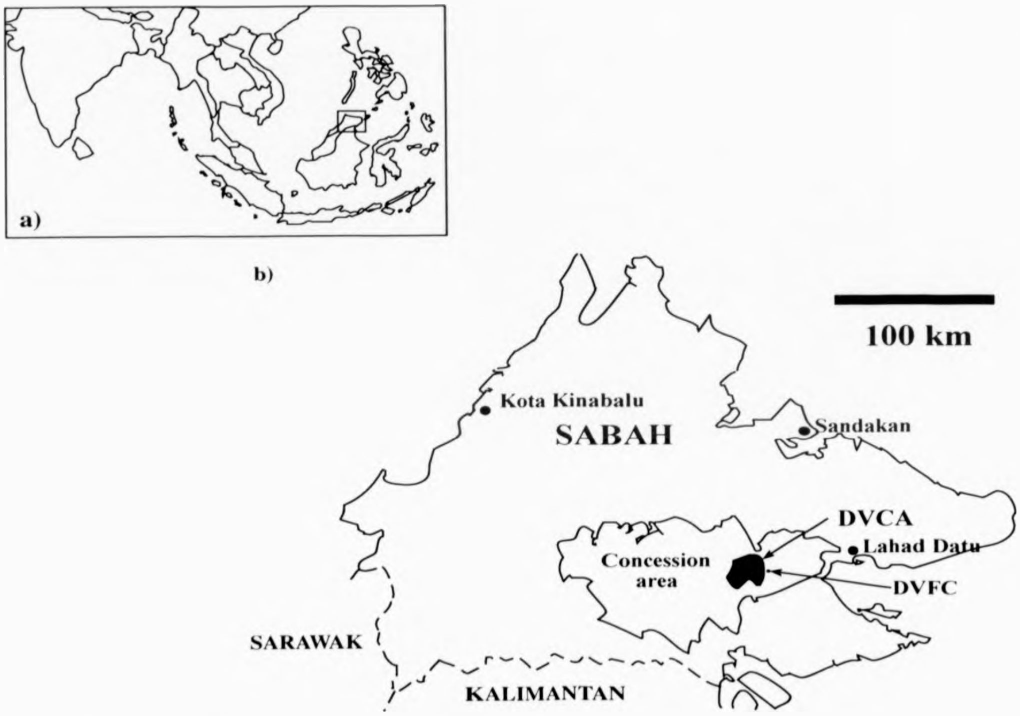

Figure 2-1. a) The location of Sabah in SE Asia; b) The location of Danum Valley Conservation Area (DVCA) and Danum Valley Field Centre (DVFC).

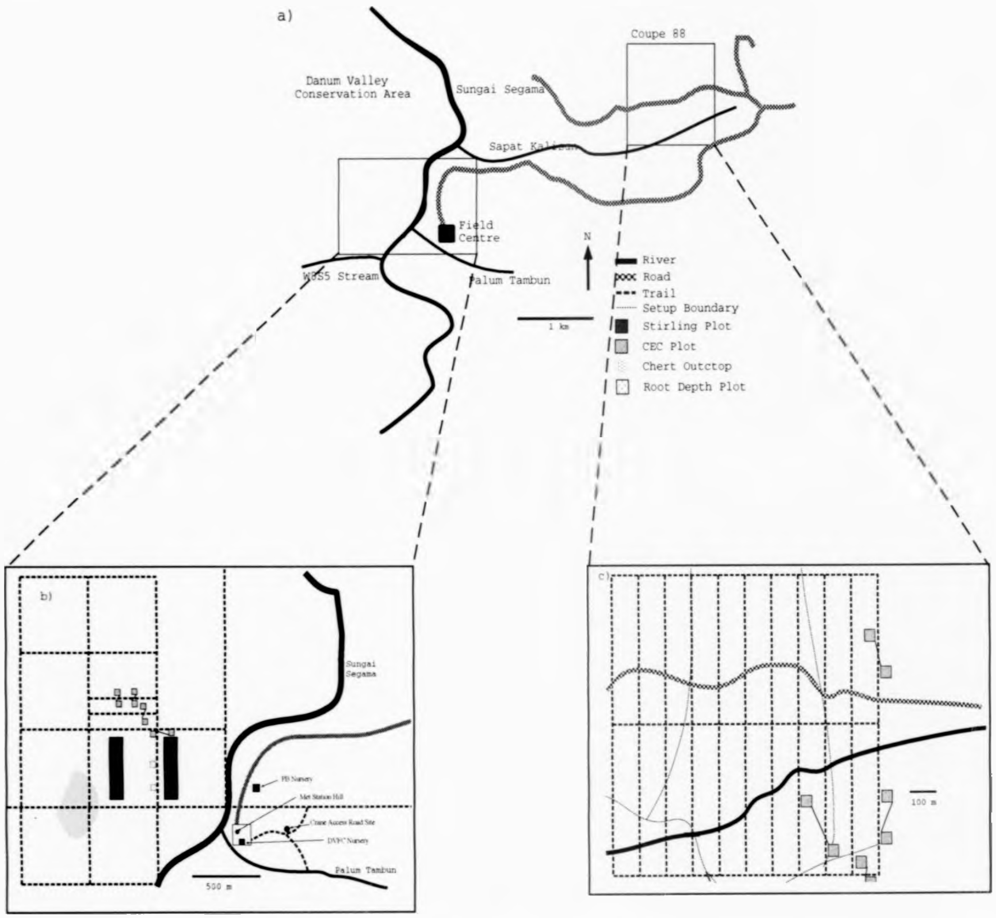

Figure 2-2. Map showing a) relative location of b) primary and c) logged forest sites.

Later work was also carried out in 0.16 ha plots set up concurrently with this work under a related project (commonly referred to as the 'CEC plots', hereafter referred to as the small primary plots or SPPs; Petol, unpublished report). Ten 40 m x 40 m paired plots, five on ridge sites, five on lower-slope sites, were set up of which eight (four ridge, four valley) were used. The discounted pair was the one least suitable. For example, in the primary forest the discounted pair had a large pig wallow in the ridge plot. The plots lie in a roughly 25 ha area immediately to the north of the LPPs (Figure 2-2).

Logged forest site

Logged forest work was carried out in a forest site logged in 1988, 'Coupe 88', about 5 km east from the field centre (Figure 2-2). The forest had been logged using tractor yarding under standard Sabah practices (Yayasan Sabah, unpublished data). All healthy trees of commercial species greater than 60 cm dbh were harvested. These trees are selected in a pre-logging survey, or 'cruise'. While only 8 to 15 trees are harvested per hectare the logging techniques result in damage of up to 40 % of remaining trees (Pinard *et al.*, 1996).

Under the same project as above a further ten 40 m x 40 m plots were established (R. Schnäckel, T.W. Scheider, D.M. Newbery & R. Ong, unpublished report), again in five ridge/ lower slope pairs. As in the primary forest four of these pairs were used (hereafter referred to as logged small plots or SLPs). The plots lie in several 'setups', each area cruised separately (the smallest sub-division of the coupe area from which detailed extraction data are available; Table 2-1, Yayasan Sabah, unpublished data). Data are not available from one setup which is immediately adjacent to the road and, therefore, may have been a log landing site.

Table 2-1. 1988 timber extraction from Coupe 88 setups.

Setup	752	718	741	unknown[1]
Number of SLPs within setup	1	2	5	2
Area (ha)	24	41	22	-
Timber volume extracted (m^3 ha^{-1})	79.3	84.3	53	-

[1] Data are not available for setup unknown

Nursery experiments

Nursery experiments, seed germination, cutting propagation and seedling storage were carried out at one of two nurseries both at DVFC. The InFaPro (an enrichment planting project) research, or Padang Baru nursery (PB nursery), and the DVFC nursery (Figure 2-2).

GEOLOGY, TOPOGRAPHY AND SOILS

No detailed description of the geology of the study area exists. From a general description by Leong (1974) the area contains three main formations, namely, crystalline basement, chert-spillite and kuamut. This mosaic of formations results in an actively eroding and very uneven terrain. The altitude of DVCA ranges from 200 m at DVFC to 1,200 m at the highest point, Gunung Danum. Most of the area is below 760 m, and hence is lowland forest, but is still strongly undulating. While the complex geology has lead to the formation of very heterogeneous soils, virtually all of the study areas lie on one soil type, Bang, an association of orthic acrisols and dystric cambisols, derived from mudstone, sandstone and other rocks (Wright, 1975). Work was also carried out on an outcrop of chert, approximately 1 km west of the field centre (Figure 2-2b).

VEGETATION

The dominant vegetation formation of the lowland part of DVCA is Tropical Lowland Evergreen Rain Forest (Whitmore, 1984). The primary forest sites are of the *Parashorea malaanonan* subtype of Fox (1972). Within the LPPs there are 511 species of trees within 164 genera and 59 families (Newbery *et al.*, 1992). The rough 30 to 50 m canopy is dominated by trees in the Dipterocarpaceae, while the understorey is dominated by the Euphorbiaceae. Emergents occur at heights of up to 60 m.

Logging results in a change of forest structure. Very heavily disturbed sites have little true canopy and are characterised by extensive growth of climbing bamboo (*Dinochloa spp.*), which suppresses further regeneration. Less heavily disturbed sites have a low canopy (roughly 20 m) containing a mixture of pioneer species such as *Macaranga spp.*, *Neolamarkia cadamba*, *Neonauclea spp*, and *Octomeles sumatrana*. Primary forest species regenerate under these pioneer species. There also exist remnant patches of primary forest. While the extent of logging damage is the most important factor in determining the resulting regeneration, other factors such as the composition of the seed bank are important (Howlett, pers. comm.).

CLIMATE

Climate data have been collected since 4 July, 1995. A standard rain gauge, bright sunlight recorder and wet and dry bulb thermometers, placed within a Stevenson screen, are located on a small mound, 200 m above sea level, in a 70 % gap (Figure 2-2) at DVFC.

Rainfall

The mean annual rainfall from 1986 to 1996 was 2777 mm. Rainfall varied strongly from year to year (Figure 2-3), ranging from 2378 mm in 1987 to 3277 mm in 1995. While 1987 was the driest year in terms of annual rainfall, 1992 had more months with rainfall less than 100 mm. In this period the mean monthly rainfall was 231 mm. The driest month, both in terms of average rainfall and the most number of months with less than 100 mm rainfall was April (Figure 2-4). The second driest month was August. The wetter periods correspond to the two monsoons (the Northeast, November to March and Southeast, June to July) which affect the area (Walsh, 1996).

It should be noted that there is a strong annual variation in monthly rainfall and with the current data it is impossible to predict which months will be drier or wetter than average. This is demonstrated by the monthly totals for the study period (Figure 2-5), where, for example, the normally dry April was one of the wetter months in 1996.

Temperature and sunshine

Mean monthly temperatures, 1986 to 1996, fluctuated less than mean rainfall (Figure 2-6), minimum temperatures hardly varied at all, while maximum temperatures were lowest at the wettest time of year (December to February). Sunshine data are currently only available from 1 October, 1991 until 6 April, 1996. The sunniest months (April, May, August) are the same as the driest months, but, sunshine fluctuates more than temperature.

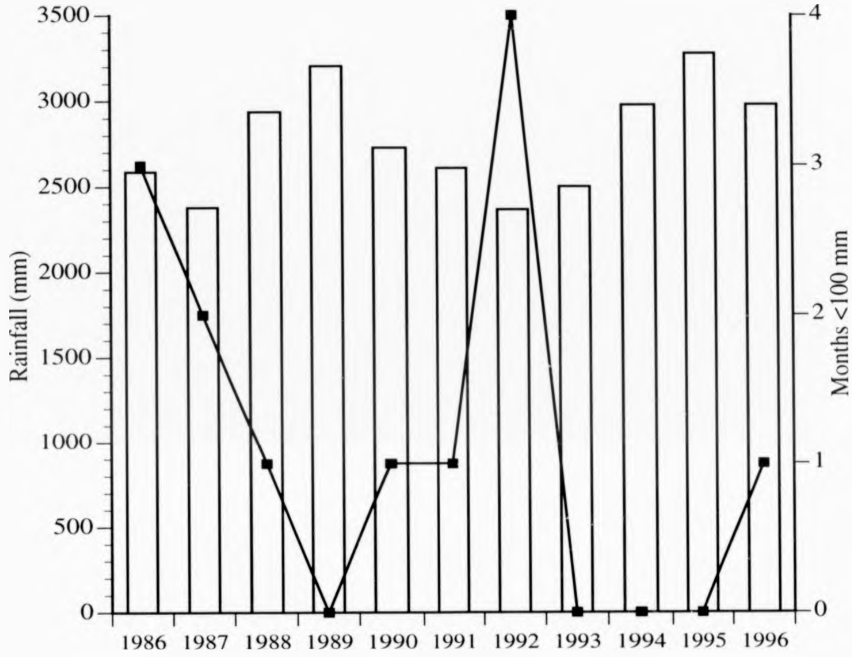

Figure 2-3. Annual rainfall at DVFC, 1986-1996 (bars) and number of months with less than 100 mm rainfall (line).

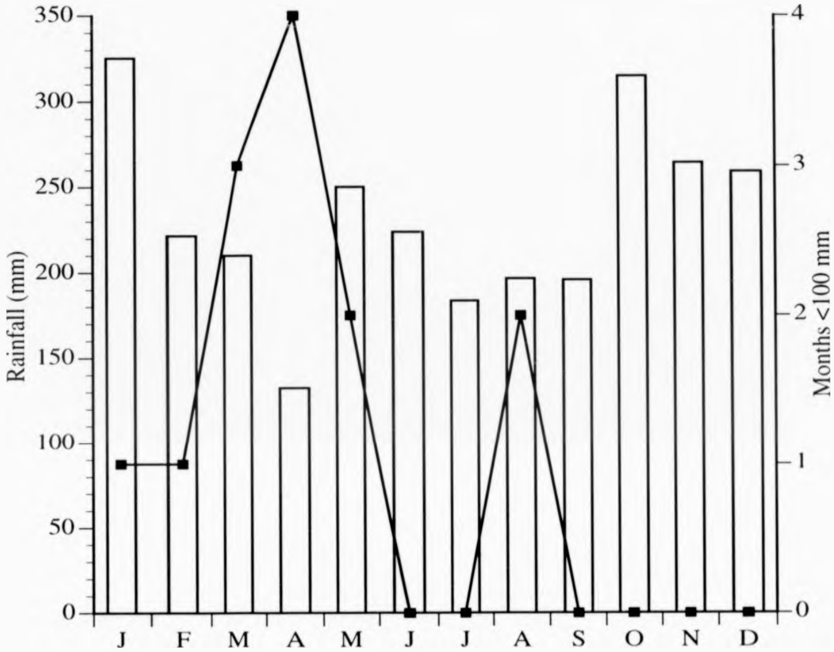

Figure 2-4. Mean monthly rainfall at DVFC, 1986-1996 (bars) and number of months with less than 100 mm rainfall (line).

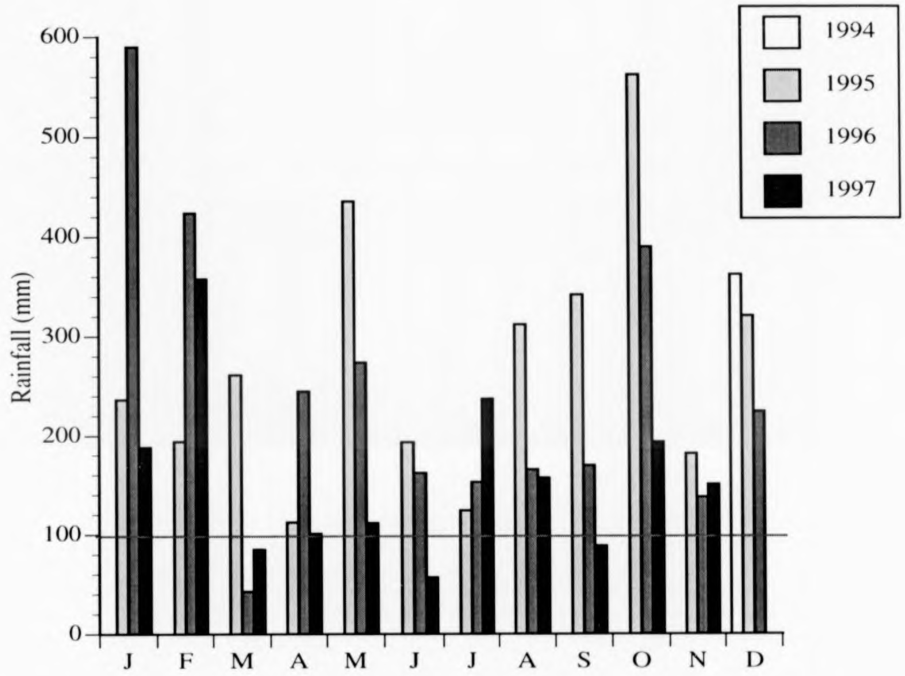

Figure 2-5. Monthly total rainfall during study period (December, 1994 to November, 1997). Reference line is at 100 mm.

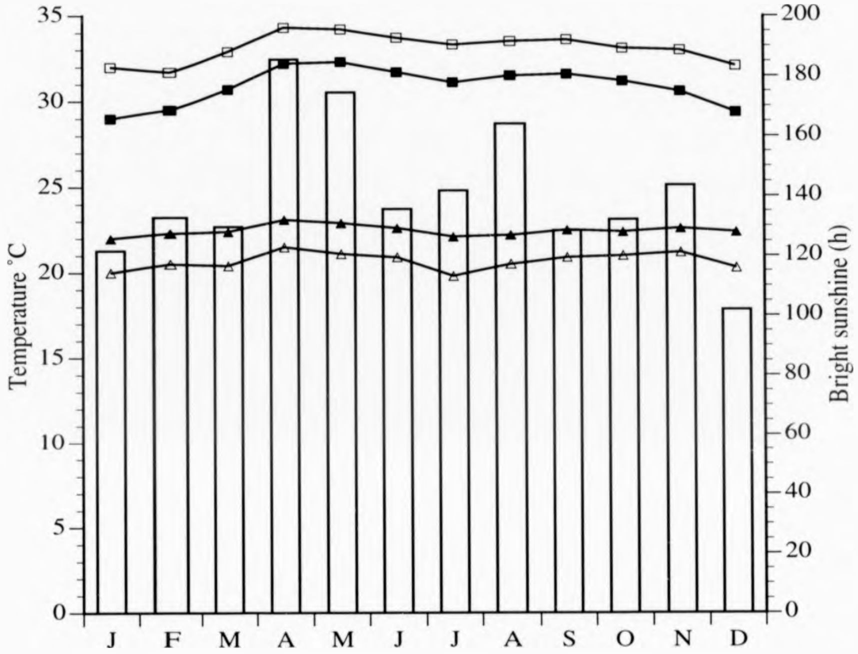

Figure 2-6. Mean monthly temperature at DVFC, 1986-1996; Left hand axis, absolute monthly maximum (—□—); monthly maximum (—■—); monthly minimum (—▲—); absolute monthly minimum (—△—). Mean monthly sunshine hours 1992-1995 (bars).

MATERIALS AND METHODS

Set up and enumeration of primary forest plots

The size of the LPPs limits any work on the patterns of species distribution to the common understorey species (Newbery *et al.*, 1996). There are too few individuals of canopy and rare species for meaningful results to be calculated and, therefore, only common understorey species were considered in this study. These small stature species had the added advantage of being easily accessible without climbing.

Selection of species

Within the LPPs there are 511 species, many of which are represented by few or single individuals (Newbery *et al.*, 1992). From this species list it was necessary to select a few understorey species on which to work. Several criteria were applied to produce a 'short-list' of utilisable species from which six species were selected, 3 'clustered' or 'ridge' (species associated with ridges) and 3 'non-clustered' or 'ubiquitous' (species found throughout the plots). Species which had problems of identification were rejected, for example, *Polyalthia cauliflora* has several closely related species present in the plots. Other restrictions considered were petiole length and leaf size. The pressure chamber, used in later work, could only be used with leaves up to about 100 mm long and with long petioles. The species list used is shown in Table 2-2.

Table 2-2. The selected study species.

Species	Family	Clustered
Ardisia colorata [1] Roxb.	Myristicaceae	-
Cleistanthus glaber Airy Shaw	Euphorbiaceae	+
Dimorphocalyx muricatus [2] (Hk. f.) Airy Shaw	Euphorbiaceae	+
Fordia splendidissima (Miq.) Buijsen	Leguminoseae	-
Lophopetalum beccarianum Pierre	Celastraceae	+
Mallotus wrayi [3] King ex Hk. f.	Euphorbiaceae	-

Common names [1] surosop, [2] obah puteh, [3] mallotus sagar-sagar

The study species

Little information was available about the study species and no complete tree flora exists for Sabah. Airy Shaw (1975) includes all Bornean Euphorbiaceae but is little more than a key to herbarium specimens and contains no complete species descriptions. Whitmore (1972) has more information but only covers those species that also occur on the Malay peninsula. From these sources, the selected species can grow up to about 20 m tall except for *Lophopetalum beccarianum* which can be up to 40 m tall, and all are primary forest species. The trees in the LPPs are generally much smaller than these upper height limits (pers. obs.). Burgess (1966) has some information about the timber properties of some of the species (Table 2-3). Although timber hardness can be an indicator of tree growth rates (slow growing trees have hard timber) the relationship is not perfect. The remuneration of the LPPs will provide extensive information about relative tree growth rates.

Table 2-3. Timber properties of the study taxa. Information from Burgess (1966).

Taxa	Hardness	Density (g cm^{-3} at 15 % moisture)[1]	Growth rings
Ardisia colorata	-	-	-
Cleistanthus spp.	moderately hard	0.59-0.86	none
Dimorphocalyx spp.	hard	0.99	yes
Fordia splendidissima	-	-	-
Lophopetalum beccarianum	-	-	-
Mallotus spp.	soft to moderately hard	0.61-0.87	sometimes

[1] Converted from lb./ cu ft

Collection location of herbarium specimens.

To find out more information about the distribution of the study species, the collection notes of all the specimens in the Forest Research Centre Herbarium, Sandakan (SAN) were examined. Frequently there was no description of the collection site. Where a description was present it was noted whether the site was 'hill', 'ridge', 'hill side/ slope' or 'stream side/ valley'. Also noted was whether the forest had been logged.

Selection of subplot locations

A subplot size of 10 m x 20 m (10 m E-W, 20 m N-S) was selected so as to provide a large enough area to include enough individuals to provide adequate replication. Using the data set from the 1985-87 enumeration and a program written in FORTRAN 77, by D.M. Newbery, the number of the selected species within each possible subplot was determined. The sample step interval chosen was 5 m in both directions (the origin of the first subplot was 0 m E, 0 m N the second 5, 0 and so on), so for each plot there were 1368 possible subplots (0-380 m on the north/ south axis by 0-90 m on the east/ west axis, in 5 m steps). The output from the program was put into a database and those subplots containing the target species at or above the required density extracted (Table 2-4). To avoid bias in the subplots selected, presence or absence of the clustered species was used to determine 'ridge' versus 'lower slope' sites rather than the contour maps available for the plots (Newbery *et al.*, 1996). Any off-ridge clusters were thereby not excluded. From this reduced list of subplots, for each LPP, six ridge and six lower-slope subplots were selected, at random, making 24 subplots in total. Overlapping subplots were rejected, as were contiguous plots, where alternatives existed. Unfortunately, because of the relatively small area where clustered species occurred, it was sometimes necessary to accept contiguous ridge subplots. Using these criteria only five possible ridge subplots were present in LPP 1. For the final subplot the criteria were slackened such that subplots with one *Lophopetalum beccarianum* were accepted. Figure 2-7 shows the location of the subplots. The maximum elevation difference between subplots was roughly 37 m.

Table 2-4. The required number of individuals > 10 cm gbh to be present in each study subplot.

Species	'Ridge' Site	'Lower slope' site
Ardisia colorata	-	> 1
Cleistanthus glaber	> 1	0
Dimorphocalyx muricatus	> 7	0
Fordia splendidissima	-	> 1
Lophopetalum beccarianum	> 1[1]	0
Mallotus wrayi	-	> 7

[1] 0 accepted in one subplot in LPP 1

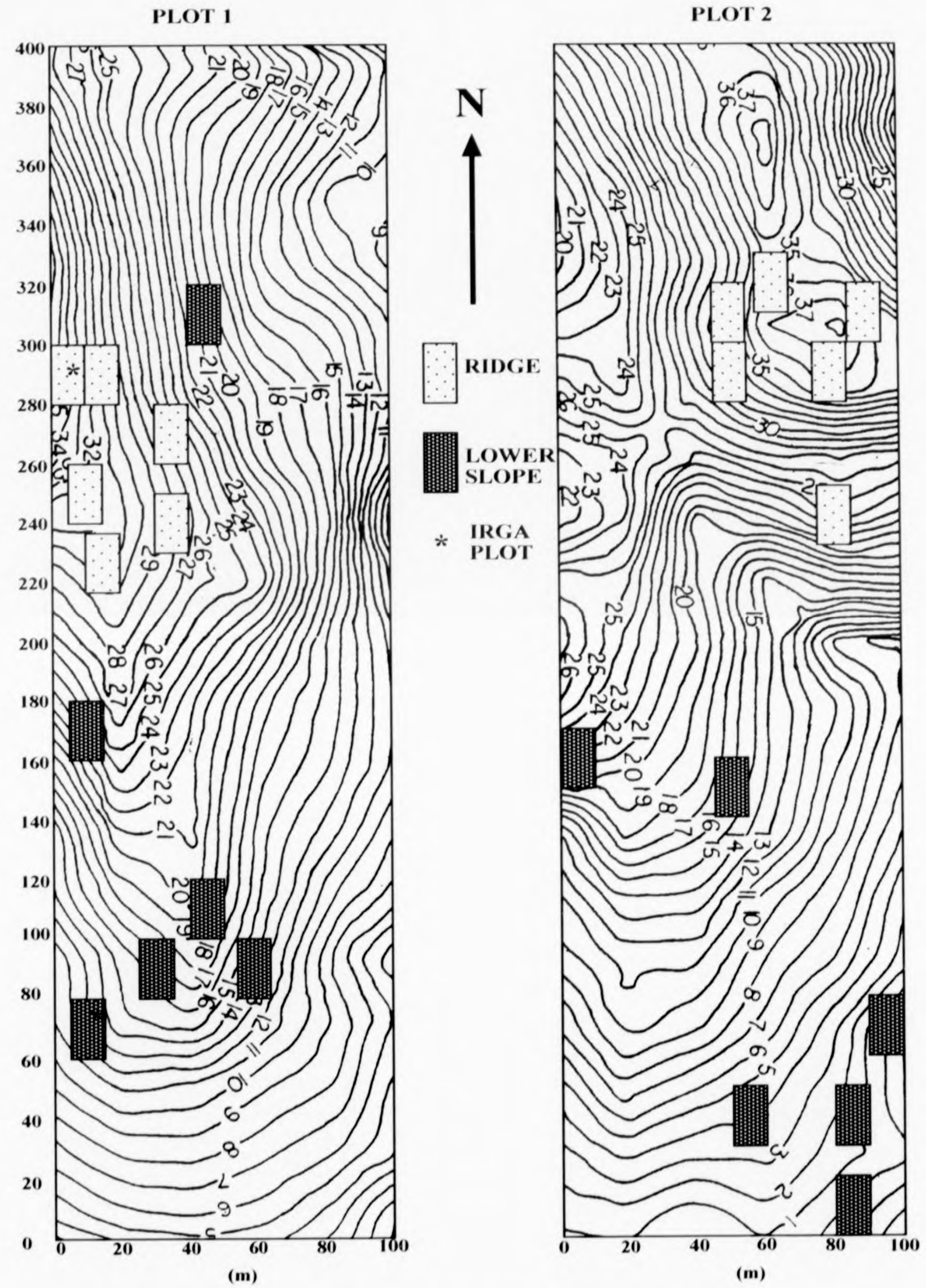

Figure 2-7. Contour maps and location of subplots within LPPs.

Enumeration of subplots

During the enumeration each subplot was divided into eight 5 m x 5 m squares with string. Each square was then enumerated in turn, starting at the south-west and finishing at the north-west square. The subplots were thus divided to make the enumeration more manageable, reducing the likelihood of missing individuals. Within each square all individuals of the target species ≥1 cm basal diameter were tagged and measured and individuals <1 cm basal diameter were tallied. Both basal diameter and dbh (at 1.3 m) were measured, using dial callipers, with a resolution of 0.1 mm. The individuals were then labelled with coloured oval aluminium tags secured with slip-knotted nylon fishing line. It was very important that the species were identified accurately, so any doubtful individuals were excluded. No knowledgeable taxonomist was on hand to confirm identifications. However, the identifications from the 1985-87 enumeration were available so the identity of any tree above 10 cm gbh could be confirmed. These data were used for error checking, identities were assigned in the field and checked from a master list on return. Some of the larger trees were impossible to identify quickly in the field, frequently the leaves were out of sight, or too high to be identified reliably. In these cases the tag number was noted and checked from the master list. Three of the species, *Ardisia colorata, Dimorphocalyx muricatus* and *Mallotus wrayi* were very distinctive and presented no identification difficulties. *Cleistanthus glaber* and *Lophopetalum beccarianum* were more problematic but were reliably identified. Unfortunately *Fordia splendidissima* could not be identified with sufficiently reliability, often being confused with other trees and climbers with compound leaves, therefore it was excluded from the study. At this point it was also necessary to exclude *Lophopetalum beccarianum* as it became relatively tall at small diameter classes. Leaves were out of reach making it difficult to use this species for the later work.

Subplot environment

Subplot temperature and humidity were measured using a whirling hygrometer. A trial study confirmed that the decline in humidity was roughly linear between 09:00 and 11:00. Therefore, time could be used as a covariable in an ANOVA analysis. For each LPP six ridge/ lower slope pairs were selected at random. Starting at 09:00, whirling hygrometer readings (wet bulb and dry bulb temperatures) were taken in each subplot pair, above the centre of the subplot. Because of the time constraint it was only possible to take readings in one LPP per day, readings were taken on sequential days when the weather was similar. While inadequate to fully characterise the subplot environment these measurements were taken to see if large differences existed between sites. At later stages in the project, subplot light, soil water potential, soil temperature and soil particle size were all measured.

RESULTS AND DISCUSSION

Collection location of herbarium specimens

Generally, more herbarium specimens of the clustered species had been collected from hill and ridge sites, while more specimens of the non-clustered species had been collected from hill side/ slope and stream/ valley sites (Table 2-5). The hill side/ slope category was ambiguous and may have included both upper and lower ridge sites, therefore, the partitioning between sites may be stronger than is apparent from the data. It is unfortunate that so many specimens had incomplete field notes. Compared with the other species, logged forest specimens of *D. muricatus* were over represented. The difference in total numbers in the herbarium is probably more attributable to a collection bias towards large trees rather than the relative rarity of the species.

Table 2-5. The collection site of specimens of the study species in the Forest Research Centre, Sandakan herbarium (SAN).

Species	N	Hill	Ridge	Hill-side/ slope	Stream/ Valley	Unknown	Logged forest
Ardisia colorata	36	3	3	10	4	15	2
Cleistanthus glaber	6	2	1	2	1	0	0
Dimorphocalyx muricatus	22	5	1	1	1	7	7
Fordia splendidissima	0	-	-	-	-	-	-
Lophopetalum beccarianum	92	7	15	19	1	41	9
Mallotus wrayi	22	2	2	2	1	13	2

Size distribution of the study species

Out of 1870 individuals of the study species enumerated in the study plots there were 304 *A. colorata*, 95 *C. glaber*, 420 *D. muricatus*, 201 *F. splendidissima*, 69 *L. beccarianum* and 781 *M. wrayi* individuals. These numbers roughly reflect their abundance in the LPPs (Newbery *et al.*, 1996). There were fewer individuals of the ubiquitous species in the ridge subplots than in the lower-slope subplots (Figure 2-8). For *A. colorata* there are fewer individuals in all size-classes but for *M. wrayi* fewer in smaller size-classes, but similar numbers of large trees. No individuals of the ridge species were found in the lower-slope plots (Figure 2-9).

Regressing dbh on basal diameter reveals a strong relationship, dbh =-2.6 + 0.709xBasal Diameter (r^2=0.82, p<0.001). However, frequently many of the larger trees of all the study species were scarred at the base, indicating that they had snapped and resprouted. These trees had a far larger basal diameter to dbh ratio than the above equation would suggest. Basal diameter size class data are, therefore, presented as is probably a better indicator of tree age than dbh. Further, using basal diameter subdivides the class where individuals were less than 1.3 m in height. The scarring suggests that damage by falling debris regularly occurs, and that the trees may regenerate in gaps from their bases.

For all the species except *L. beccarianum* there were most individuals in the smallest size-class (Figure 2-8, Figure 2-9). There were fewer of the ubiquitous species in ridge sites than lower-slope sites. However, the biggest individuals of *A. colorata* and *M. wrayi* were on ridge sites. Of the ubiquitous species *M. wrayi* had a 'reverse J' type decline in numbers as basal diameter increased on both rise and lower-slope sites. *A. colorata* had a similar, although more uneven, decline on ridge sites, but the decline on lower-slope sites was more progressive. The rough decline in *F. splendidissima* numbers on both sites is probably a result of the inclusion of spurious individuals. All the ridge species had a very uneven decline in numbers. The few small trees of *L. beccarianum* and the second peak for *D. muricatus* suggests that, for the ridge species, establishment events may be very infrequent. In the LPPs the overall frequency distribution for all trees ≥10 cm gbh (Newbery *et al.*, 1992) is most similar to that of *M. wrayi*

Temperature and humidity

Time was significant as a covariable (temperature, $F_{1,31}$=167.20, p<0.001; humidity, F=22.45, p<0.001). The covariate adjusted means of temperature and humidity were significantly different between ridge and lower-slope sites (temperature F=22.45, p<0.001; humidity, F=15.01, p<0.01), with ridge sites being drier and less humid. However, the difference in temperature means is small. The significant differences between plot means are probably attributable to the surveys being carried out on different days, rather than any underlying difference. The lower humidity on ridge sites may result in higher stomatal conductance rates. These measurements are inadequate to characterise subplot temperature and humidity and it would be desirable to log temperature and humidity over several weeks at different times of year.

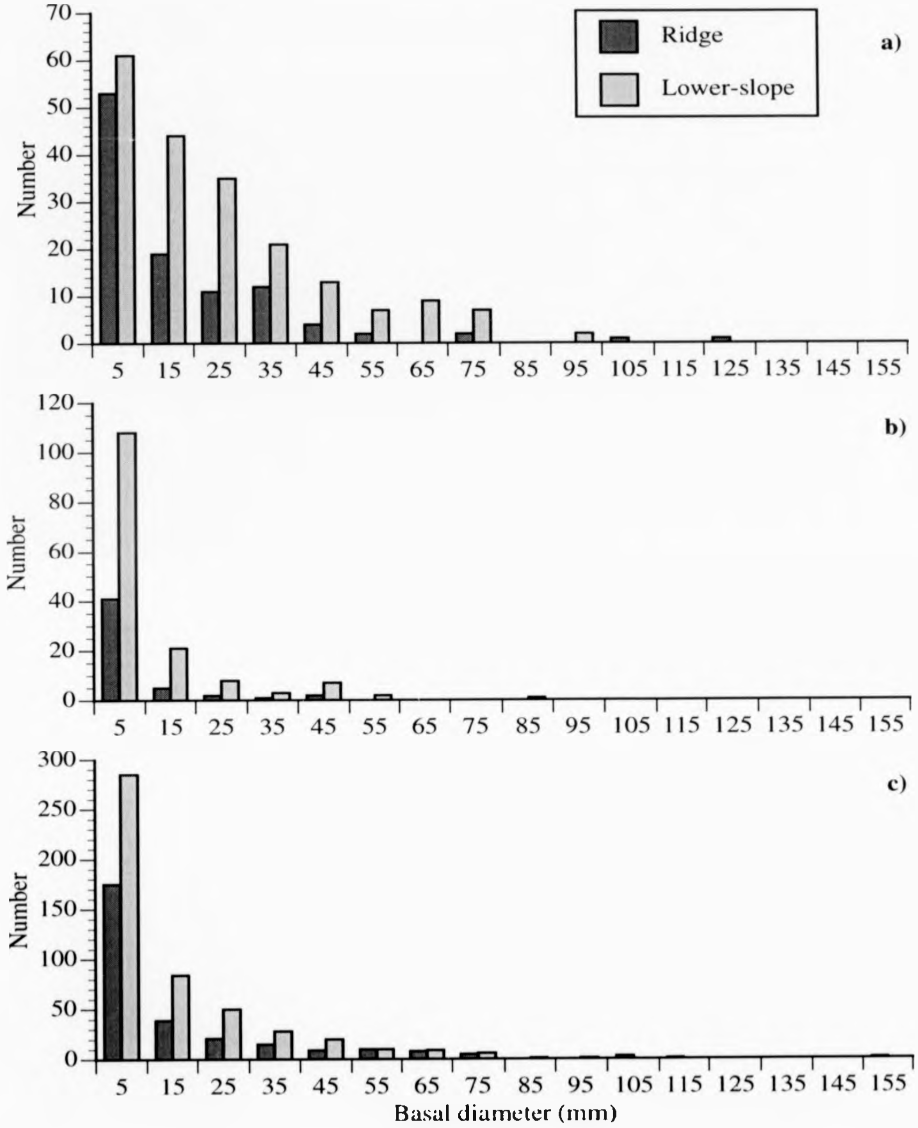

Figure 2-8. Size-class distribution of the non-clustered study species on ridge and lower-slope sites. a) *Ardisia colorata*; b) *Fordia splendidissima*; c) *Mallotus wrayi*. Note different y-axis scales.

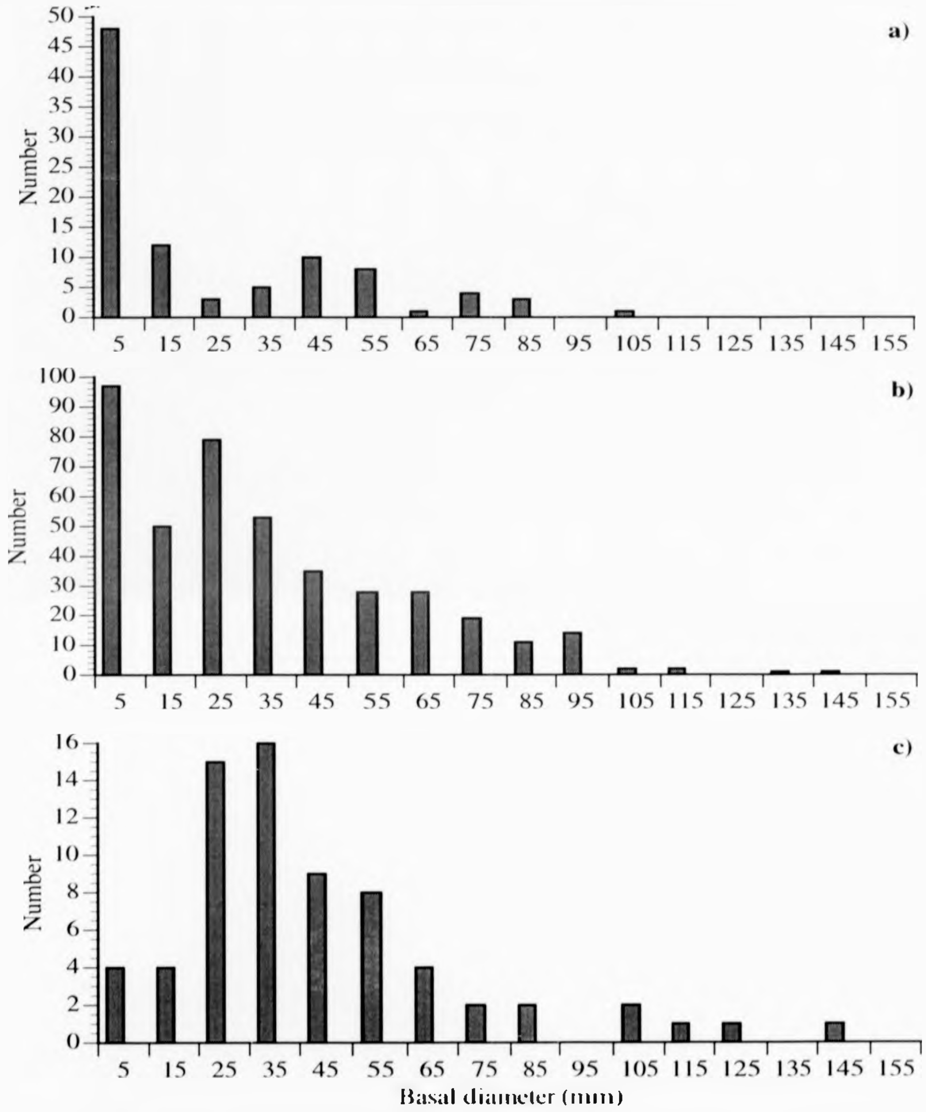

Figure 2-9. Size-class distribution of the clustered study species. a) *Cleistanthus glaber*; b) *Dimorphocalyx muricatus*; c) *Lophopetalum beccarianum*. Note different y-axis scales.

Chapter Three. Occurrence of drought and topographic variation in soil water availability

INTRODUCTION

Dry periods and droughts in the climatic record

In the tropics the generally accepted definition of a dry period is a month or a period of 30 days during which rainfall is less than 100 mm (e.g. Brünig, 1969; Walsh, 1992). A monthly rainfall of 100 mm is roughly equal to the monthly potential transpiration from tropical forest, and hence the point at which a soil water deficit would start to develop (Walsh, 1992). The point at which the deficit becomes large enough to cause plant stress depends on soil water capacitance and rooting depth (Baillie, 1976).

Studies comparing the occurrence of dry periods between different sites in the region have used a variety of measures and indices. Daily water balance is often taken as the definitive measurement to which other estimators are compared (e.g. Baillie, 1976; Nieuwolt, 1982; McCaskill and Kariada, 1992). Calculation of daily water balance requires access to daily rainfall totals, and measures or estimates of daily transpiration, runoff and leaching, and soil water capacity (Baillie, 1976). For many sites estimates or measures of these variables are not available. Where only daily rainfall totals are available, 30-day totals, which avoid the arbitrary monthly boundary which may split a dry period between months, can be calculated (Brünig, 1969). Periods of rain-free days are another indicator of a dry period and Nieuwolt (1982, 1989) proposed a method of calculating the proportion of time within each month that was spent within dry periods of 7 days or more (D7) and 10 days or more (D10). Rainfall of less than 1 mm was not considered sufficient to break a dry spell. Often, the only data available for a station are monthly totals, which are summarised as monthly means. McCaskill & Kariada (1992) compared daily water balance, mean monthly rainfall mean monthly raindays, D7 and D10 indices, from 16 stations in Australia and Indonesia, as predictors of water stress. They concluded that all indices were good predictors when compared with daily water balance, but the goodness of fit depended on the estimated soil water capacitance. Walsh (1992) proposed the 'Perhumidity Index' or PI to classify tropical forest types by monthly rainfall totals. Using the following scores 'drought' (<50 mm rainfall) months are scored as -2, 'dry' (<100 mm) as -1, 'wet' (<200 mm) as 1 and 'superwet' (>200 mm) as 2. A dry or drought month following a wet or superwet month is scored -1.5 or -0.5, respectively. Therefore, any year could be scored from -24 to 24. PI is calculated from mean monthly totals, while PI_i is calculated from monthly totals. A PI from 5 to 9.5 is 'Wet Seasonal' forest, 10 - 19.5 'Wet' and > 20 'Superwet'. An extension of this index is cumulative rainfall deficit (CRD) which is the sum of the values by which rainfall totals fall below 100 mm in consecutive dry months (Walsh, 1996). Walsh, apparently arbitrarily, considered that a drought with a CRD >300 mm is sufficient to cause canopy tree deaths.

Measurement of soil water

While rainfall data give a useful indication of the occurrence and relative magnitude of dry periods, prediction of soil moisture status from climate data is a poor substitute for actual measurements (Webster & Beckett, 1969).

Soil water can be measured as soil water content (volumetric or gravimetric) or soil water potential. Soil water potential is made up of two components, the matric potential (the affinity of soil water for the soil matrix) and the osmotic potential of the soil solution (Mullins, 1991). In non-saline soils osmotic potentials are small relative to matric potentials, and water potential is often taken as equal to matric potential. For this study water potential was of more interest than water content, because, water moves from the soil to plants to the atmosphere down a water potential gradient (Elfving *et al.*, 1972).

Several different methods for measuring soil water potential are widely used. The simplest methods are indirect where water content is measured, either by sampling soil or by measuring electrical resistance, and converting to water potential (e.g. Green, 1992). As the relationship between water content and water potential is non-linear, especially at low water potentials, and varies from soil to soil, a multi-point calibration must be carried out for each soil being investigated. Indirect methods are less accurate than direct methods such as soil tensiometers which measure matric potential and soil psychrometers which measure water potential (Mullins, 1991). This study used soil psychrometers which are less accurate than tensiometers (resolution of 0.25 kPa and 50 kPa, respectively) but have a greater range (0.085 MPa and 7 MPa, respectively; Mullins, 1991).

MATERIALS AND METHODS

Analysis of climate data

Rainfall data were collected as described in Chapter 2. Daily rainfall totals were examined and the climate indices described above were calculated for each available year.

Measurement of soil water potential

Soil water potential was measured with soil psychrometers (P55T, Wescor Inc, USA). Each psychrometer was calibrated in four different KCl solutions (0.05, 0.3, 0.5 and 0.8 molal, in deionized water) at 25 °C. No water bath was available to maintain a constant temperature through the calibration process. Instead a polystyrene insulated chamber was constructed which proved successful in reducing temperature fluctuations and keeping temperatures at around 25 °C. The psychrometers were equilibrated in 1 l of solution, in batches of 12, for a period >10 h. Readings were taken using a dewpoint microvoltmeter (P33T, Wescor Inc, USA) in both dewpoint and psychrometer modes (Anonymous, 1979). Water potentials for the KCl solutions were obtained from Campbell & Gardner (1971). Linear regression, forcing the line through zero, was then performed for each probe to give a calibration value, for each mode, used to convert readings to water potentials ($r^2 \geq 0.970$ for all probes). The psychrometers were then cleaned in deionised water.

During a trial study it was discovered that the rubber boot sealing the ceramic cup to the psychrometer and protecting the temperature thermocouple was very palatable to soil invertebrates, possibly subterranean ants. Therefore, to reduce invertebrate damage, each psychrometer was wrapped in aluminium foil and cloth tape, leaving the ceramic cup exposed, and sprayed with a persistent insecticide before installation.

On 24 and 25 March, 1995 one soil psychrometer was installed, at a random location (>1 m from the subplot edge), at 20 cm depth, in each subplot within the LPPs. A depth of 20 cm was chosen because the majority of root endings are at or above this depth (Green, 1992) and the depth allowed comparison with other studies (e.g. Becker *et al.*, 1988). Water potentials were not measured at other depths because it was thought more important to sample at as many different locations as possible. At a later stage in the study soil water contents were measured at depths from 20 cm to 100 cm. For each subplot soil temperature and soil water potential was then recorded at weekly intervals, in dewpoint mode, until 6 June, 1997. Weekly intervals were selected so short term changes in soil water potential would be detected but any hysteresis effect avoided. If probe failure occurred, the probe was dug up, and if possible repaired with epoxy resin or heat shrink, and then reinstalled.

Soil water potential and temperature data were analysed using a modified repeated measures analysis of variance (RM ANOVA) procedure. For these data repeated measures analysis is appropriate, as the same units were measured on several occasions and the time-site interaction is of interest (Mead, 1988). Time can be regarded as a split unit factor in a split plot analysis, providing an important assumption is satisfied (Underwood, 1997). The assumption, of complete sphericity (also called circularity), is only satisfied if the variance of all pairwise differences between repeated measures is constant. The assumption rarely holds (Huynh & Mandeville, 1979). Violation of the assumption results in an increased likelihood of Type I (false positive) error. Two methods have been proposed for overcoming this difficulty. Instead of a split plot analysis a MANOVA can be carried out, but this method is not appropriate, when, as in this case, the number of time intervals sampled exceed the number of replicates (Vasey & Thayer, 1987). Alternatively, epsilon, a measure of the sphericity of the data can be estimated (Geisser & Greenhouse, 1958; Huynh & Feldt, 1970) and this estimator is used to correct the degrees of freedom for time and time interactions. Unfortunately, currently available statistical software carries out RM ANOVAs on data sets containing missing values in an inefficient manner. For example, for the soil water potential data, any subplot containing missing values will be completely excluded from the analysis. To overcome these problems, the data were analysed as a split plot experiment using Genstat 5 (release 3.1, NAG, UK) which also uses an iterative procedure to estimate missing values. These estimated missing values were manually inserted into the data set and, this now complete data was used to calculate estimates of epsilon with SuperANOVA (release 1.1, Abacus Concepts, USA). The Genstat calculated p values for time and time interactions were then adjusted using the epsilon estimates.

Soil depth

A limited investigation of soil depth was carried out using two techniques. One soil pit was dug to 1 m depth at a ridge and lower-slope site. The depth of the pit was then extended using a 1.5 m tall Dutch auger until bedrock was reached. As no destructive sampling is permitted in the LPPs the pits were dug immediately adjacent but out side the plots (Figure 2-7). In addition cuttings alongside the 'crane access road' (Figure 2-2) were examined and the depth of bedrock, where visible noted.

Relating rainfall data to soil water potential

Rainfall data were related to soil water potential on an empirical rather than theoretical basis. It was assumed that soil water potential was an exponential function of a weighted 40-day rainfall total (W40), an estimate of soil water content. Soil matric potential is commonly assumed to be a power function of water content, although the fit is poor near soil saturation (Clapp & Hornberger, 1978). However, a power function of W40 fitted the psychrometer data very poorly so an exponential function fitted was used instead which fitted well.

W40 is a crude estimate of soil water content, it largely ignores run-off (although W40 values >100 mm were set to 100 mm), and implicitly assumes that stored rainfall declines exponentially with time. Support for this assumption is provided by the relationship between current moisture fraction and the initial moisture fraction which can be described by a negative exponential function, driven by potential evaporation and time (Hobbs *et al.*, 1984). W40 is a better estimate of water content than a simple running total which assumes no decline in stored rainfall until the figure drops out of the total. Forty day weighted totals were selected over 30-day totals as they improved the spread of values at low rainfall totals. W40 was calculated as Equation (3-1) where n is number of days before present day and r_n is the rainfall on day n. N starts at one rather than zero because water potentials were recorded in the morning, before that days rain had been measured. Weighted 40-day totals were fitted to measured values of ridge and lower slope water potentials with an exponential formula (Equation (3-2)) using Genstat 5. Parallel curves were fitted as there is no evidence that there is a difference in soil texture between sites (Newbery *et al*, 1996).

$$\sum_{n=1}^{40} \frac{r_n}{n} \qquad \textbf{(3-1)}$$

$$WP = A + B \times R^{W40} \qquad \textbf{(3-2)}$$

RESULTS

Analysis of climate data

Daily and monthly rainfall totals for 1986 to 1997 were used to calculate climate indices. The DVFC climate record is summarised in Chapter 2, and monthly climate indices are shown in Table 3-1. Dry periods occurred in seven out of the eleven years and only in 1986 did two dry periods occur. The PI for 1986-1996 is 20, higher than then mean PI_1, 16.2. The driest year, by some margin, is 1992. The 1992 dry period caused general wilting of understorey trees and some bare crowns in canopy trees (K. Bidin, pers. comm.). Therefore, a CRD of 123.4 mm is great enough to reduce soil water to a level where plant water stress occurs. Although the climate record only covers a short period of time it appears that dry and wet years are grouped.

Running totals for 1986-1996 (Table 3-2; Figure 3-1) show that 30-day totals fell below 100 mm for some time in most years in the record, including three where the monthly data suggested that no dry period occurred. The only year where no dry period occurred was 1989, although in 1994 the 30-day totals were below 100 mm for one day only. While several dry periods occurred in most years, the majority of recorded dry days are within the longest dry period. Ninety-day totals never fell below 100 mm, an indication of severe drought (Beaman *et al.*, 1985), but were below 300 mm in 1987, 1992 and 1997. The running totals confirm that 1992, with the longest dry period and the lowest 30-day total, was the driest year on record. Of the study years, 1995 was wetter than the long term average, and while in terms of annual rainfall so was 1996, the 1996 PI_1 value was lower than average.

Periods of dry days as measured by the D7 and D10 indices (Figure 3-2) coincide with periods of low rainfall. A period greater than two months with seven or ten day dry periods are rare. While the D-Indices reliably predict the occurrence of dry periods, they are poor indicator of the magnitude, the highest D-Indices occur in 1986 and 1987, not 1992.

Table 3-1. Rainfall indices calculated from monthly data. PI_i is the perhumidity index, calculated as Walsh (1992). A dry period is a month or consecutive months with <100 mm rainfall. CRD (cumulative rainfall deficit), calculated as Walsh (1996) is the total deficit below 100 mm for each month in the longest dry period.

				Longest period <100 mm	
Year	Total (mm)	PI_i	Number of dry periods	Months	CRD (mm)
1986	2586.6	12	2	2	57.1
1987	2378.2	14.5	1	2	76.2
1988	2937.5	18.5	1	1	28.7
1989	3204.7	22	0	0	0
1990	2729.0	14.5	1	1	62.6
1991	2608.7	15.5	1	1	75.6
1992	2366.8	9.5	1	4	123.4
1993	2500.6	18	0	0	0
1994	2976.6	19	0	0	0
1995	3277.0	19	0	0	0
1996	2978.5	15.5	1	1	57.1
MEAN	2776.7	16.2	0.7	1.1	43.7

Table 3-2. Rainfall indices calculated from 30- and 90-day rainfall running totals

	30-day Periods < 100 mm				90-day
Year	Number	Longest (days)	Total (days)	Lowest total (mm)	Lowest total (mm)
1985 [1]	1	1	1	97.0	634.3
1986	4	37	67	30.5	277.1
1987	1	63	63	33.5	194.6
1988	2	17	18	66.5	356.9
1989	0	0	0	113.9	590.7
1990	5	28	50	37.4	327.4
1991	5	41	55	24.4	337.6
1992	3	93	106	8.6	156.7
1993	3	10	14	84.9	359.7
1994	1	1	1	98.0	465.0
1995	4	5	12	82.0	548.3
1996	3	12	20	42.2	348.6
1997 [2]	2	26	43	45.7	226.5
MEAN [3]	2.8	27.9	36.9	56.9	360.2

[1] August to December;

[2] January to June;

[3] Excluding 1985 and 1987

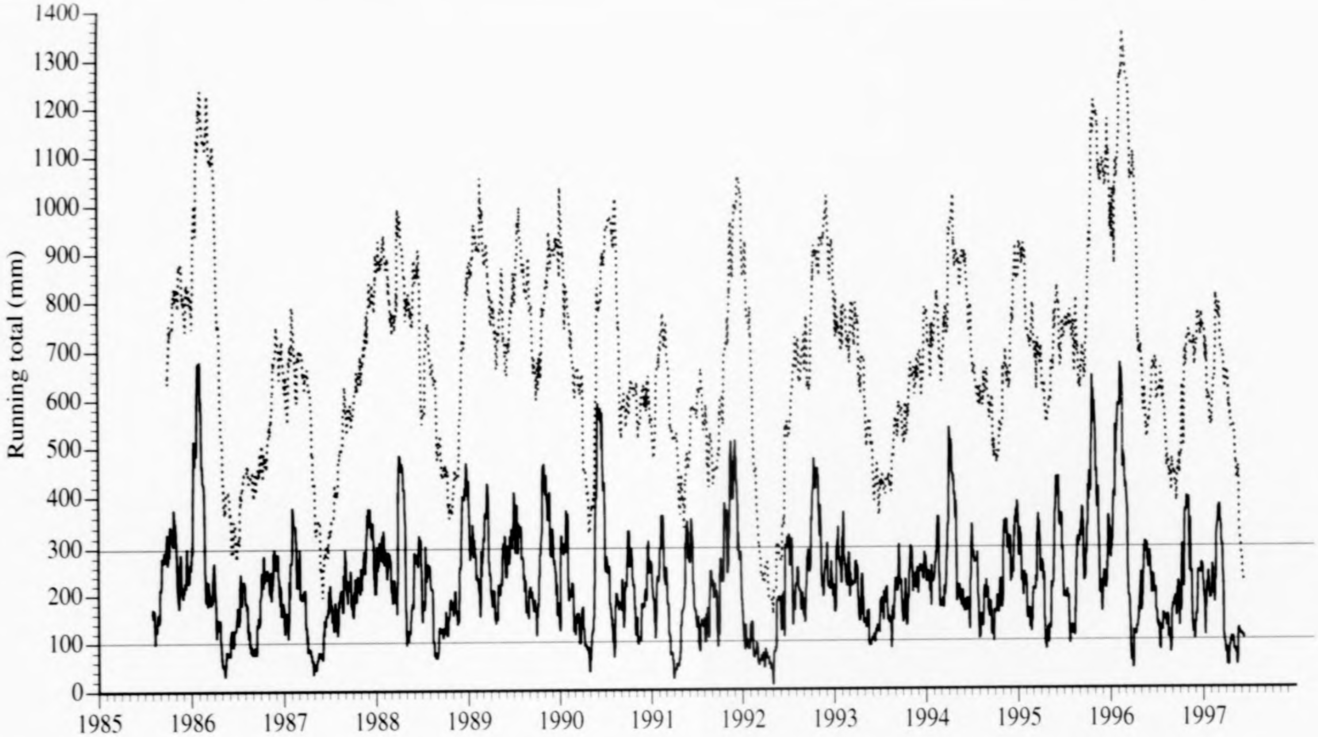

Figure 3-1. 30- (—) and 90- (---) day running rainfall totals for 1986-1997. Reference lines are at 100 and 300 mm.

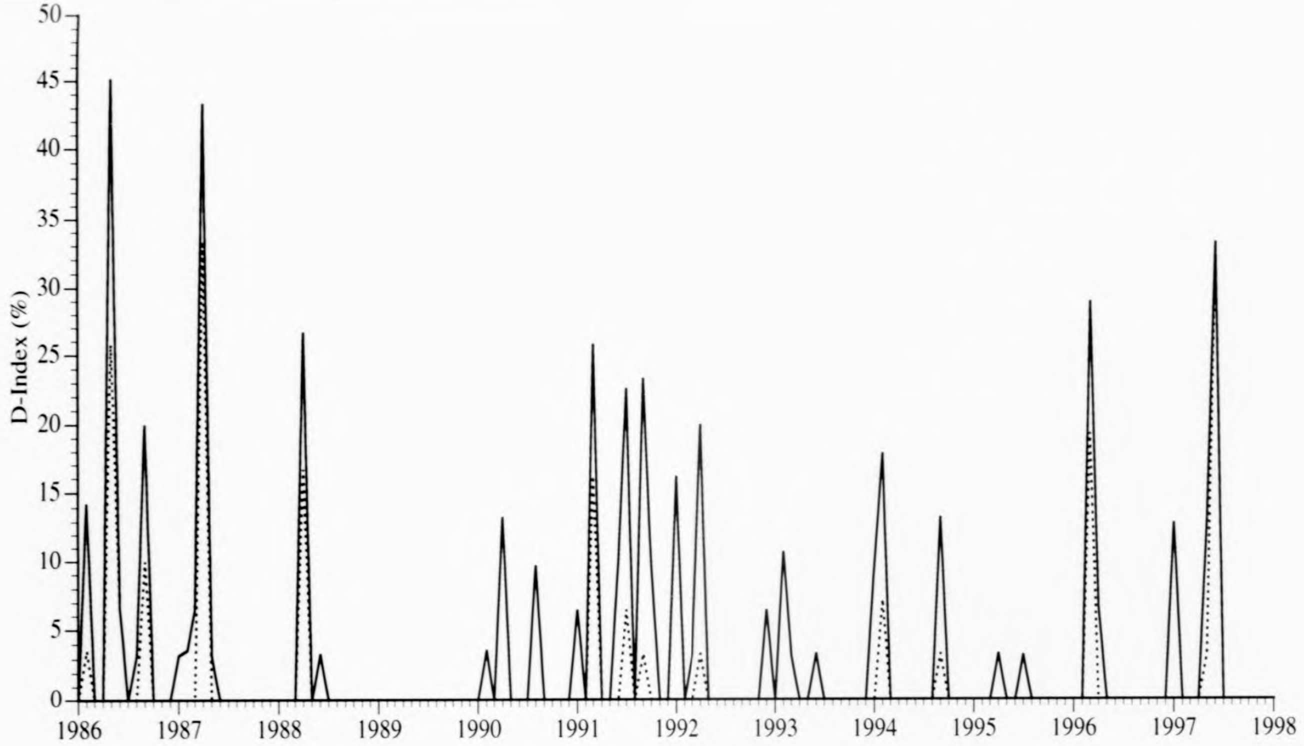

Figure 3-2. D7 (—) and D10 (---) indices, 1986-1996. Calculated as Nieuwolt (1989)

Soil water potential

Soil water potentials were measured, weekly, with psychrometers, at ridge and lower-slope sites over a 26 month period. Trends in soil water potentials (Figure 3-3) are similar to the rainfall data, the lowest water potentials were recorded in the driest year, 1997, and high water potentials were recorded in the wettest year, 1995. Lowest water potentials occur at the same times as lowest running totals (April-May and August). However, the difference between years, especially between 1996 and 1997, is much greater than would predicted from the running rainfall totals alone.

Water easily available to plants is often considered to be between -5 kPa (field capacity) and -200 kPa (Hall *et al.*, 1977). Total available plant water is frequently taken to be between field capacity and permanent wilting point (-1.5 MPa; Marshall and Holmes, 1979). Soil water potentials never fell below, or even approached permanent wilting point and were only below the easily available level during the driest periods in 1996 and 1997. However, Elfving *et al.* (1972) suggest that soil water potential starts to become limiting to water absorption below -30 kPa and measured soil water potentials were frequently below this level.

Apart from one point in 1997 mean ridge site water potentials are consistently below those for lower-slope sites (Figure 3-3). This difference between ridge and lower-slope sites became greater during dry periods. During the driest period in 1997 ridge and lower-slope site water potentials were similar. However, this is probably an artificial result owing to probe failure, as during the 1997 field season only two lower slope, and four ridge psychrometers remained. It is possible that the psychrometers installed at wetter locations were more prone failure. For this reason the 1997 data were excluded from further analysis. The 1997 data are still presented because of the uniquely severe dry period. During 1996 dry periods ridge water potentials fell below the easily available water level while lower slope water potentials remained above this level. The variability of the data suggest that wet micro-sites may exist in ridge subplots and dry micro-sites in lower-slope subplots.

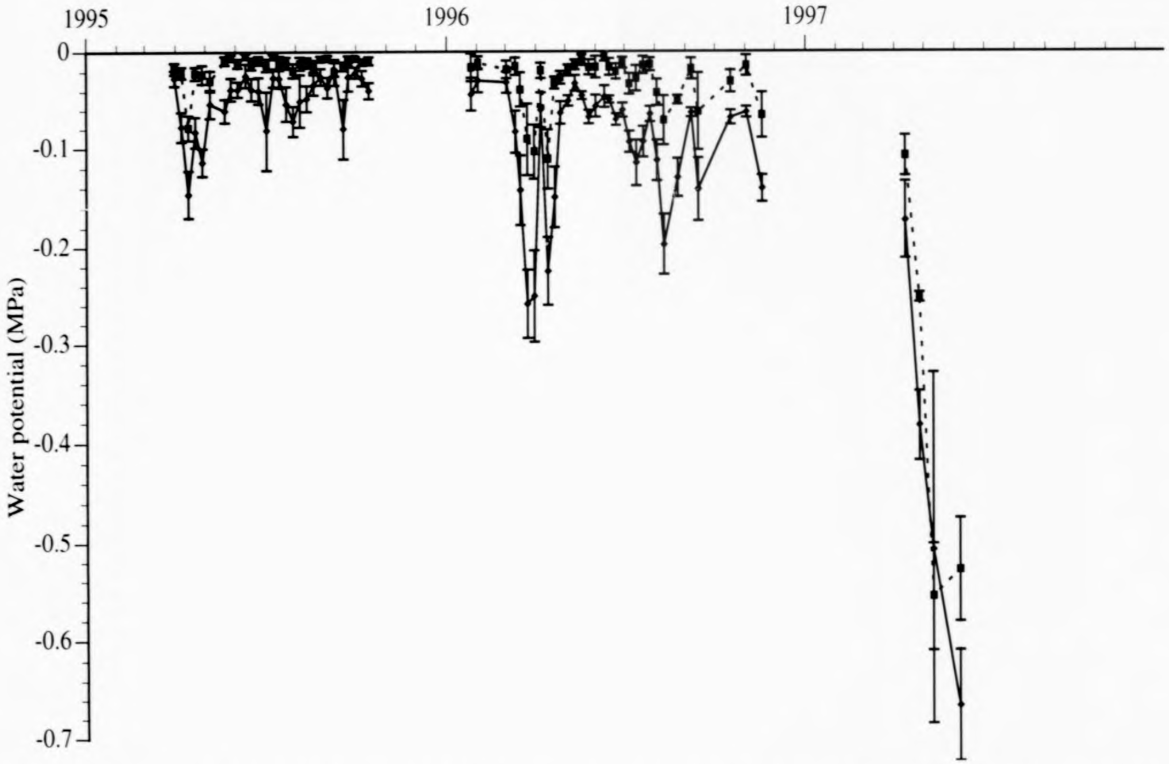

Figure 3-3. Soil water potentials at 20 cm depth for ridge (—◆—) and lower-slope sites (---■---), 1995-1997. Error bars are standard error of the mean.

Variances were not significantly heterogeneous (Cochran's C, $p>0.05$). The RM ANOVA for soil water potential is shown in Table 3-3. Interpretation of the results is straightforward because there is little difference between the calculated and adjusted p values. Site, time and the site.time interaction are all significant, confirming the trends apparent from the graphical analysis.

Table 3-3. Repeated measures ANOVA for soil water potential

Source of variation	df (missing)	SS	F	p	$p_{\varepsilon a}$[1]	$p_{\varepsilon b}$[2]
plot stratum	1	0.03	0.78			
plot.subplot stratum						
site	1	0.73	16.20	**<0.001**		
residual	20 (1)	0.90				
plot.subplot.units stratum						
date	59	2.18	24.53	**<0.001**	**<0.001**	**<0.001**
site.date	59	0.44	4.90	**<0.001**	**0.002**	**<0.001**
residual	853 (445)	1.28				
total	993 (446)	4.26				

Epsilon correction as estimated by [1] Geisser & Greenhouse, 1958 (0.078); [2] Huynh & Feldt, 1970 (0.112).

Soil temperature

Soil temperatures were recorded at the same times and at the same sites as soil water potential. Soil temperature was stable over the study period, the total range measured was 2.5 °C and most readings were between 24 °C and 25 °C (Figure 3-4). The lowest temperatures recorded were during the wettest part of the study, January and February, 1996. There was no significant difference between ridge and lower-slope sites (Table 3-4), temperatures were significantly different at different times but there was no significant interaction between time and site.

Table 3-4. Repeated measures ANOVA for soil temperature

Source of variation	df (missing)	SS	F	p	$p_{\varepsilon a}$	$p_{\varepsilon b}$
plot stratum	1	10.40				
plot.subplot stratum						
site	1	3.13	1.24	0.271		
residual	20 (1)	48.78				
plot.subplot.units stratum						
date	59	190.11	31.25	**<0.001**	**<0.001**	**<0.001**
site.date	59	7.23	1.21	0.142	-	-
residual	853 (445)	86.57				
total	993 (446)	255.80				

Relating rainfall data to soil water potential

Soil water potentials during the whole climate record were estimated from a weighted rainfall total (W40) and measured soil water potentials. Figure 3-5 illustrates the difference between running totals and weighted totals. The pattern of change is similar, but W40 peaks are of shorter duration than running total peaks. In the case of running totals a storm event will have the same influence over the whole period, while for weighted totals the influence of the storm declines over time.

Weighted 40-day totals were fitted to measured values of ridge and lower slope water potentials with an exponential formula (Equation (3-2)). Although the 1997 data are questionable (see above) they were included to increase the range of soil water potentials measured. The formula explained 58.4 % of the variance ($F_{4,1013}$=357.89, p<0.001), calculated estimates are shown in Table 3-5, fitted curves in Figure 3-7. Few data exist at low W40 levels so the fit here must be considered approximate.

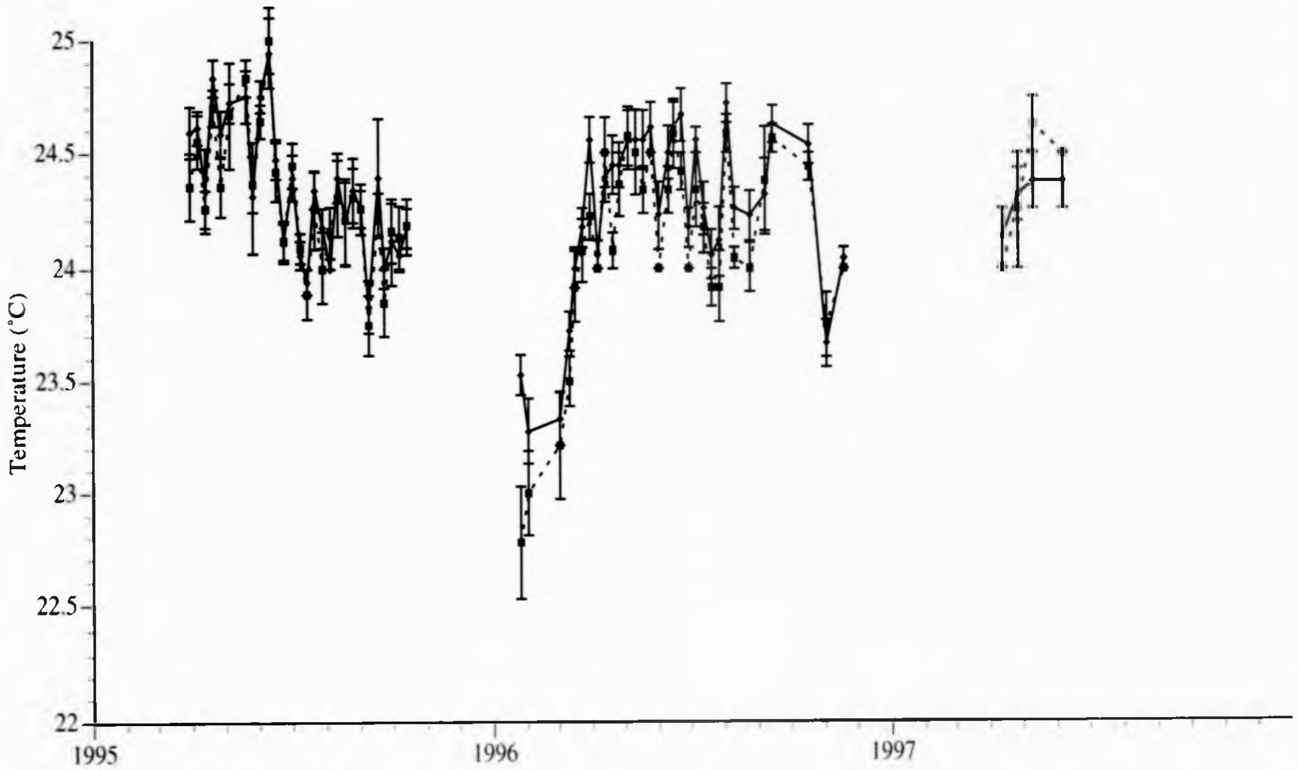

Figure 3-4. Soil temperature at 20 cm depth on ridge (—◆—) and lower slope (---■---) sites, 1995-1997. Error bars are standard errors of the mean.

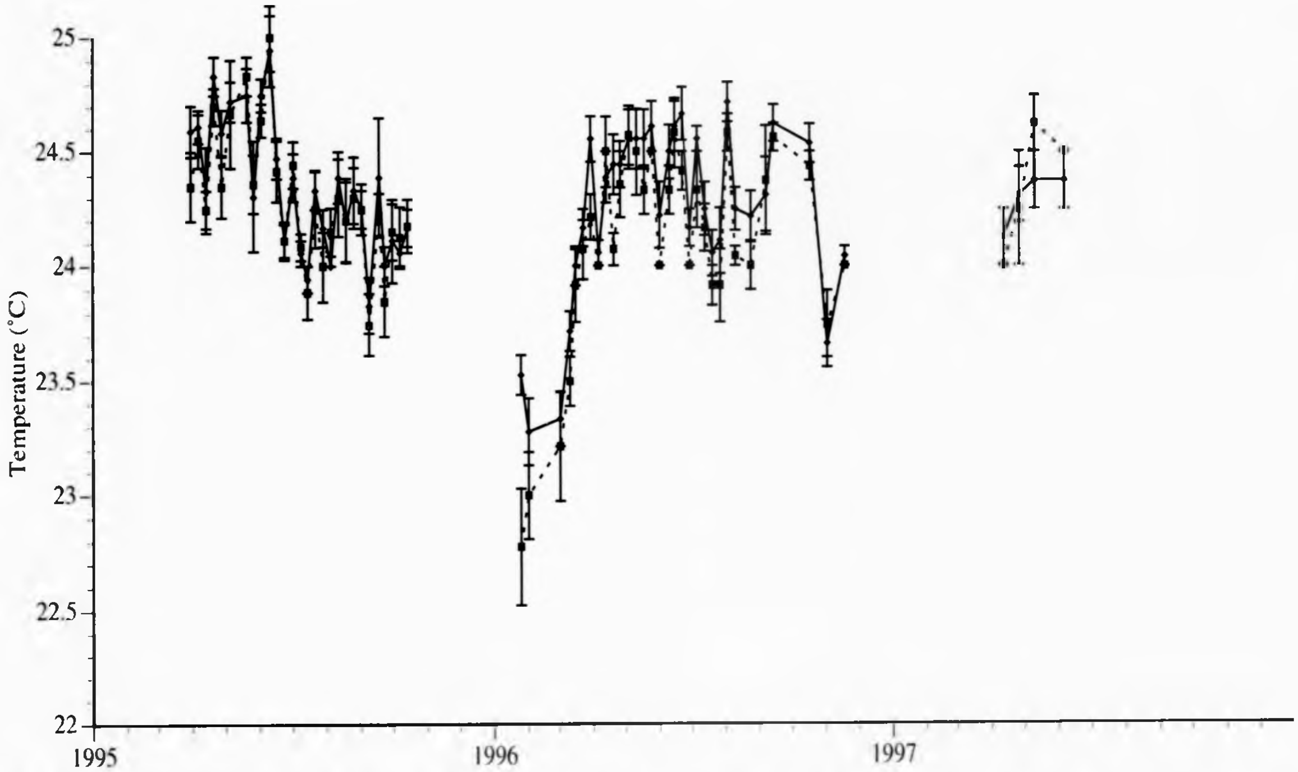

Figure 3-4. Soil temperature at 20 cm depth on ridge (—◆—) and lower slope (---■---) sites, 1995-1997. Error bars are standard errors of the mean.

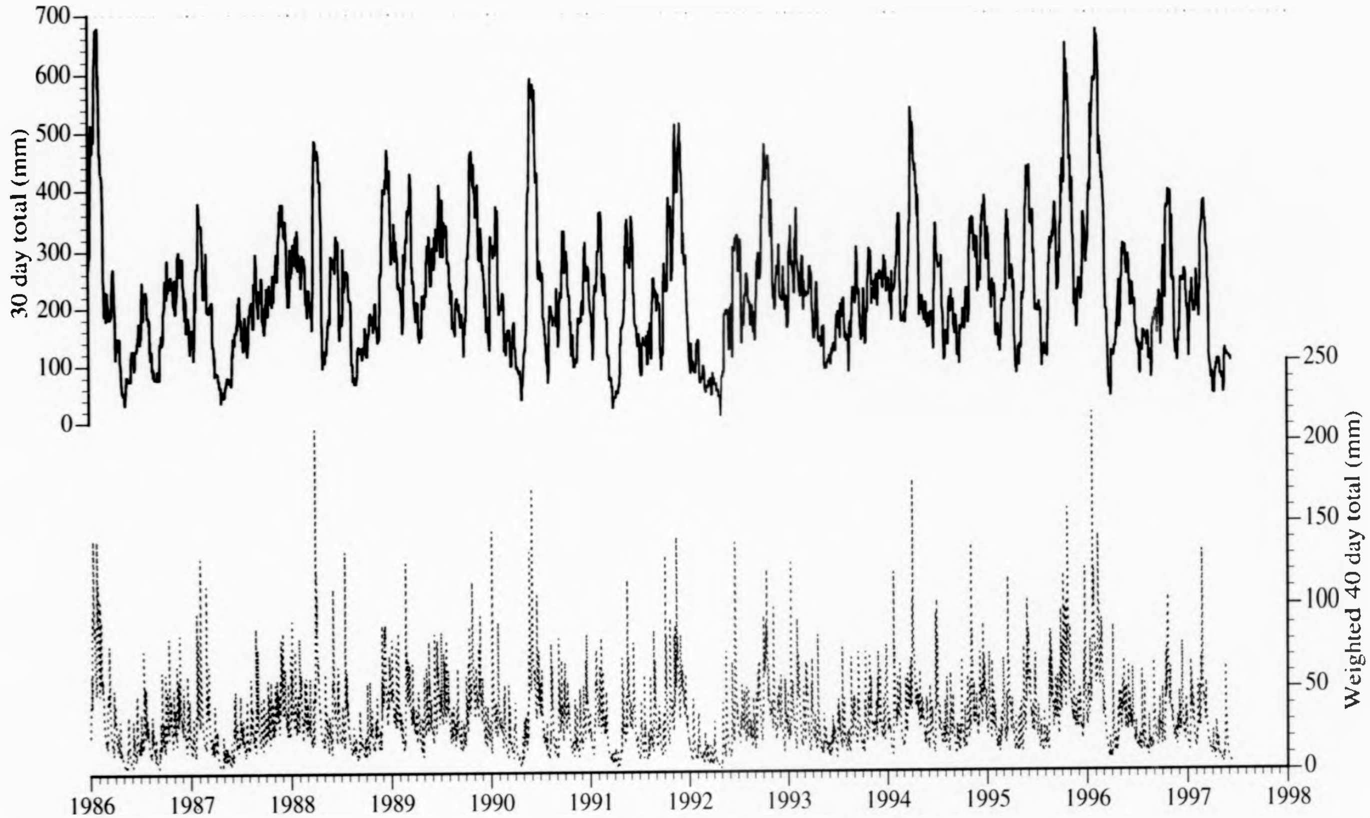

Figure 3-5. 30-day rainfall totals (—) and 40-day weighted rainfall totals (W40) (---) for 1986-1997.

Table 3-5. Fitted estimates in water potential estimation equation (Equation (3-2)) for ridge and lower-slope sites. R is the equation slope and is the same for both ridge and lower-slope sites because parallel curves were fitted.

Site	R (±S.E.=0.0086)	A (MPa)	B (MPa)
Ridge	0.7554	-0.0525	-2.0280
Lower slope	0.7554	-0.0096	-1.4070

The formula and calculated estimates can be used to estimate soil water potentials in other years in the climate record (Table 3-6). The discrepancy between estimated and actual mean lowest values is partly a result of values being estimated at times where water potentials were not measured i.e. drier points may have occurred between weekly measurements. Of great interest is 1992, the driest year on record (Figure 3-6). Then, water potentials remained above the permanent wilting point, the lowest estimated values being -1.2 MPa (ridge) and -0.8 MPa (lower slope) (W40=2.01 mm). The only other year to have similar lowest estimated values is 1986. Therefore, the estimates suggest that average soil water potentials have never fallen below permanent wilting point during the DVFC climate record. As with the running totals, 1995 and 1996 were wetter than the long term average.

The lowest possible estimates of soil water potential, when W40=0 mm, are -2.1 MPa (ridge) and -1.4 MPa (lower slope). Therefore, a period of complete drought greater than 40-days is necessary before lower-slope sites reach permanent wilting point (-1.5 MPa), but ridge sites will reach this level even if some rain falls. When the estimate of ridge water potential is -1.5 MPa, lower slope water is estimated as -1.09 MPa (W40 = 0.95 mm).

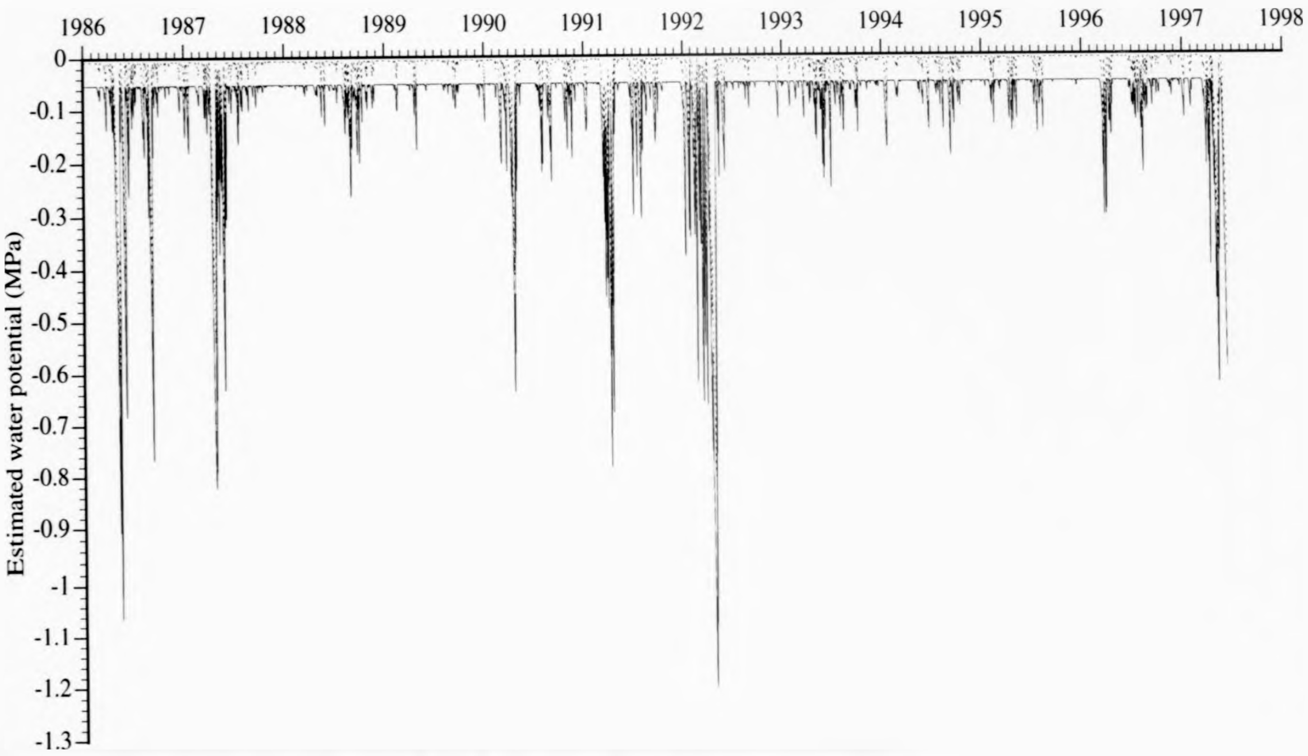

Figure 3-6. Estimated ridge (—) and lower slope (---) soil water potentials for 1986-1997.

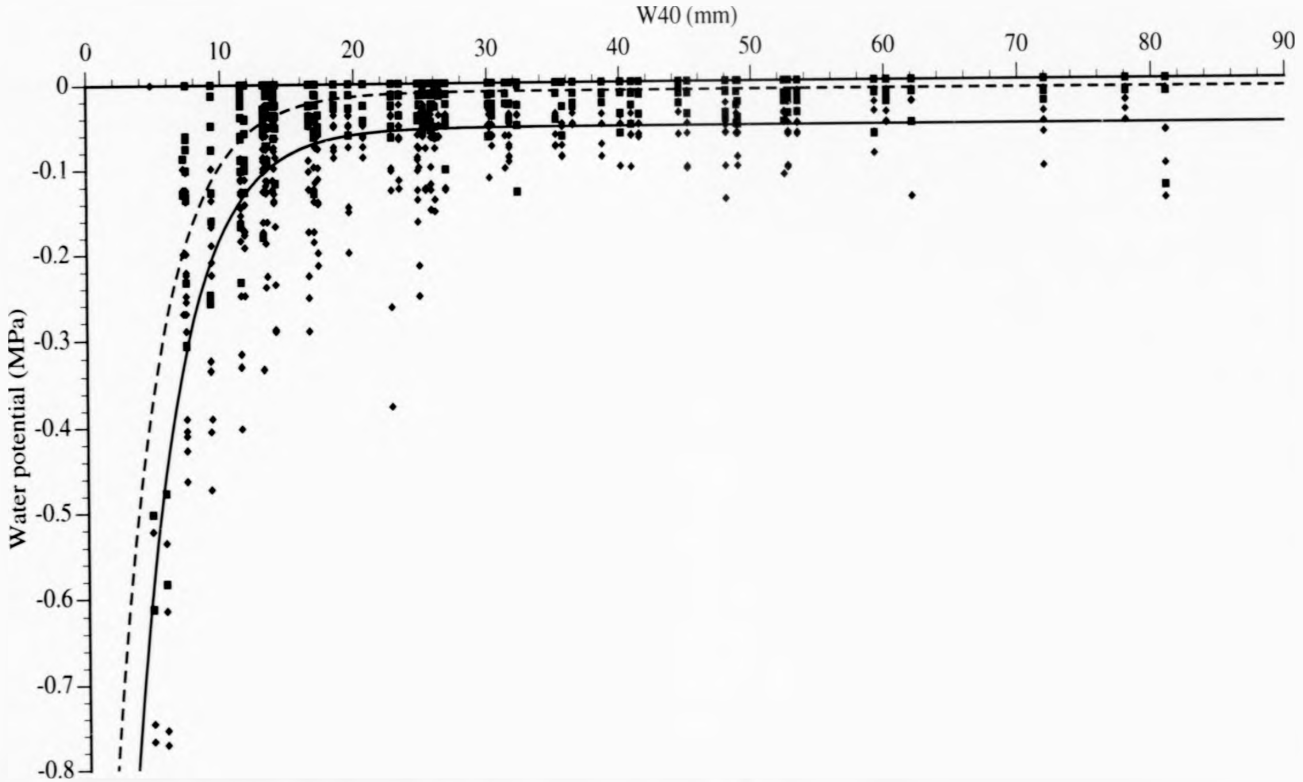

Figure 3-7. Ridge (—◆—) and lower slope (--■--) W40 to water potential fitted curves.

Table 3-6. Lowest values of soil water potential (MPa) estimated from equation (3-2) for each year of the climate record, from ridge and lower-slope sites, 1985-1997. Actual measured values are in brackets.

Year	Ridge	Lower slope	Difference
1985	-0.1092	-0.0460	0.0632
1986	-1.0647	-0.7089	0.3558
1987	-0.8219	-0.5404	0.2815
1988	-0.2637	-0.1532	0.1105
1989	-0.1785	-0.0940	0.0845
1990	-0.6396	-0.4140	0.2256
1991	-0.7858	-0.5154	0.2704
1992	-1.2059	-0.8069	0.3990
1993	-0.2520	-0.1451	0.1069
1994	-0.1942	-0.1049	0.0893
1995	-0.1513 (-0.1140)	-0.0752 (-0.0292)	0.0761 (0.0848)
1996	-0.3059 (-0.2589)	-0.1825 (-0.1111)	0.1234 (0.1478)
1997	-0.6290 (-0.6686)	-0.4066 (-0.5299)	0.2224 (0.1387)
MEAN	-0.5078	-0.3225	0.1853

Soil depth

Soil pits were dug at a ridge and lower-slope site, and a road cutting was examined. With the ridge pit bedrock was reached at 2.1 m, and from a depth of 0.85 m the soil was a mixture of friable rock and heavy clay. In the case of the lower-slope subplot bedrock was not found at the maximum depth augered (2.9 m), friable rock was encountered from a depth of 2.3 m. Along the road cutting bedrock often was not visible, where it was it was at a depth of 2-3 m. At no point during excavations was evidence of anaerobic soil conditions found. The local heavy clay soil turns blue when saturated and anaerobic (pers. obs.) all soil excavated at all depths was red-brown.

DISCUSSION

Characterising the DVFC climate record

Mean monthly rainfall totals are inadequate for characterising the DVFC climate, both the totals themselves, and any indicator calculated from the totals (e.g. PI), suggest that that dry periods do not occur, while both monthly and running totals show that dry periods have occurred in most years of the record, as Walsh (1992) writes *the use of averages* [monthly means] *tends systematically to understate the frequency of dry periods in wetter tropical areas*. Monthly totals and the PI_i index of Walsh (1992) provide easily calculated ways of comparing different years and when the CRD value (Walsh, 1996) is also calculated the severity of any drought is also estimated. However, monthly totals do underestimate the number of dry spells at DVFC especially those occurring during the second inter-monsoon period in August/ September. The D-indices of Nieuwolt (1982) are a poor measure of the magnitude of dry periods at DVFC because values are calculated for each month are independent of any dry periods that occurred in previous months. Also, the occurrence of dry periods is underestimated because a series of six or nine day dry periods, separated by one day of rain (>1 mm) will not register in D7 and D10 indices respectively. Therefore, to fully represent any dry periods 30-day running totals must be calculated.

Dry periods and droughts

While early studies of the regional climate classed Northern Borneo as ever-wet and non-seasonal (Köeppen, 1918), more recent studies have shown that dry periods occur, can be very severe, and are an annual event at many locations. Brünig (1969) studied rainfall data from stations in Sarawak, monthly totals (four stations) from a 71- to 7-year period and running totals (five stations) from a 2-year period. At three stations monthly totals <100 mm were less frequent than at DVFC, and at all stations running totals <100 mm were less frequent than at DVFC. Brünig concluded that the dry periods were of sufficient duration to be of ecological significance. Baillie (1976), also in Sarawak, calculated water balances and concluded that moisture stress regularly occurred on shallow soils (75 mm water capacitance) but was rarer on deeper soils (150 mm water capacitance). It is difficult to compare these data directly with the available DVFC data, but as Brünig's Sarawak stations were wetter than DVFC it would be expected that water stress developed more often at DVFC than at Baillie's sites. Becker (1992) calculated running totals for sites in Brunei and concluded that at two sites dry periods greater than a month in duration occurred once every two years. Walsh (1992) presented PI and PI_i values for Sandakan, Sabah (for location see Figure 2-1) for a 111 year period (1879-1989). The mean PI was 15.1 but the annual PI_i varied hugely, the lowest value, in 1906, was 0. The PI_i values for the years that overlap with the DVFC record (1985-1989) are lower than those recorded at DVFC but appear uncorrelated. In a more comprehensive review, Walsh (1996) examined rainfall records for the whole of Sabah and adjacent areas, including DVFC (1985-1994) and calculated CRDs for dry periods. At most stations a regular dry period occurred. Dry periods were more frequent in east Borneo compared with west Borneo and at coastal stations compared with inland stations.

In east Borneo, as well as annual dry periods, occasional extreme drought events occur (Walsh, 1996). These 'supra-annual' droughts are linked to the complex El Niño-Southern Oscillation phenomenon (ENSO). Any reduction of rainfall in Sabah occurs in January to May in the second year or the event (Walsh, 1996). The data available for Brunei (Becker, 1992) and Sarawak (Brünig, 1969) suggest that extreme drought events do not occur in western parts of north Borneo.

The most recent extreme drought event in Sabah was 1982-1983 when the CRD for Sandakan was between 200 and 299 mm (four dry months) and for Tawau between 400 and 499 mm (seven dry months) (Walsh, 1996). In April and May, 1983 large patches of forest became dry enough to burn (Beaman, 1985). Most fires occurred in previously logged forest (including the DVCA) and had largely spread from fires set to clear land for agriculture. The magnitude of the drought varied between stations, Sandakan had similar or greater CRDs in 1986, 1987 and 1992 (Walsh, 1996), which correspond to the driest years in the DVFC record, but in Tawau the drought was the longest dry period on record. In Sabah, previous to this event, droughts of similar or greater magnitude occurred in 1915, 1903 and 1878 (Walsh, 1996). The DVFC climate record does not cover the 1982-1983 drought and the variability between stations makes it impossible to predict the magnitude of any drought experienced. Newbery *et al.* (1996) suggest that some of the 11 large trees ha^{-1} standing dead or recently fallen recorded in the 1985/86 LPP enumeration may have been killed by recent dry conditions and that fluctuations in tree frequencies in the 90-160 cm gbh class may have resulted from previous droughts. However, 50 km east on the coastal mountain Gunung Silam, Proctor *et al.* (1989) recorded no increase in mortality following the 1982/83 drought. As an interior station, Walsh (1996) predicts that DVFC will experience a severe drought every 100-200 years. Therefore, it would seem safe to conclude that more extreme drought events have occurred at DVFC than are currently represented in the climate record.

Soil water potentials during dry periods and droughts

Soil water potentials were measured over a 25-month period, and these data extrapolated to the whole of the climate record. Given the data available, fitting rainfall data to measured soil water potentials is the only way of estimating soil water potentials in other years in the climate record. The approach appears to give reasonable estimates although estimated values outside the range of fitted values must be considered approximations. There appear to be no previous attempts to using weighted totals in this manner. It would be desirable to measure soil water contents over a long time period to establish the relationship between soil water content and W40.

In Borneo, there are few data available on what level of soil water potential or soil water content develop during dry periods. At DVFC, Green (1992) measured weekly gravimetric soil water contents, at three depths (5-10, 10-15 and 25-30 cm), from December, 1990 to December, 1991 and converted them manually to matric potential using moisture-release curves. Green's sites are roughly 500 to 1500 m north of the LPPs. Release curves were different at different depths, and although measured water contents were lower at greater depths, estimates of water potentials were greater at greater depths. At the wetter times of year his values are similar to those recorded by the psychrometers in this study, however, at drier times of year his estimates are much lower. During April, 1991 his estimates of soil water potential are well below -1.5 MPa at all depths. Although 1991 is one of the drier years in the climate record (Table 3-1, Table 3-2) Green's values are well below what might be expected from values estimated from the data above. His soil water release curves have no values between -0.2 and -1.5 MPa and because between these points large changes in water potential occur for very small changes in water content, extremely accurate weighing of soil samples would have been required to get accurate estimates of water potential. Therefore, these estimates should be considered approximations, although the possibility exists that Green's sites are drier than the LPPs.

Elsewhere, in terms of the occurrence of dry periods <100 mm rainfall the four Jamaican montane sites of Kapos and Tanner (1985) are similar to DVFC, although evapotranspiration is lower and there is no evidence for the occurrence of more extreme dry periods. Soil moisture contents were measured at different sites, at 0-10 and 10-20 cm, and critical moisture contents (-0.2 and -1.5 MPa) were calculated from moisture release curves. The possibility of inaccuracy at low soil water potentials is acknowledged, and disturbed soil cores yielded different estimates than intact soil cores. All the sites had different water release curves, estimated soil water potential never fell below -1.5 MPa, but for two sites, at 10-20 cm depth was below -0.2 MPa for some of the time. The lowest estimated soil water potential was -0.8 MPa. For comparison in Panamanian moist forest soil water potentials, measured with psychrometers, fall as low as -2.3 MPa at 20 cm depth during the dry season (Becker *et al.*, 1988). Similarly in Ghanaian moist forest, soil water potential during the dry season (Total 11.5 mm rain, 12 November to 5 March) fell to below -2.5 MPa at 20 cm depth (Veenendaal *et al.*, 1995). Without knowing how the occurrence of dry periods varies from year to year at the sites of these other studies it is difficult to say how typical the reported values are. However, the lowest values measured for DVFC are similar to those experienced near the beginning of a moist forest dry season and the lowest estimated values are similar to those that occur during the middle of the dry season of moist forests. If DVFC is affected by extreme drought events, soil water potentials might be expected to fall to, or below, water potentials measured at the end of the dry season in seasonal tropical forests.

Topographic variation in soil water availability

Soil water potentials on ridge sites were lower than lower-slope sites and the difference became greater during drier times. Studies on the local variation in soil water availability have looked at topography (e.g. this study; Ashton *et al.*, 1995; Poulsen, 1996), compared gaps and understorey sites (e.g. Becker *et al.*, 1988) and different soil types (e.g. Kapos and Tanner, 1985). The present finding of a ridge/ lower slope difference is supported by previous studies and agrees with theories predicting a gradient of decreasing soil moisture upslope from stream channels (Carson & Kirkby, 1972). Other reasons suggested for differences are differences in soil water capacity (Kapos & Tanner, 1985; Barnes & Harrison, 1982), differences in subsoil permeability (Becker *et al.*, 1988), differences in air current exposure (Becker *et al.*, 1988) and differences in soil depth (Nelson & Anderson, 1983; Mishio, 1992). Soil depth does vary between ridge and lower-slope sites, but limited studies suggest that the soils are not shallow, soil particle size is unrelated to topography (Newbery *et al.*, 1996) and it seems unlikely that the ridge and lower-slope sites here would be differently exposed to air currents. During logging more large trees are taken from ridges than elsewhere (Pinard, pers. comm.) and it often suggested that, at DVFC, because of increased stability, large canopy trees are more common on ridge sites than elsewhere. Dry soil is stronger than wet soil so any differences in water potential found between sites will also reduce the likelihood of canopy trees falling on ridge sites compared to elsewhere. Gale (1997) found more fallen trees on lower-slope and mid-slope transects than ridge transects at DVFC. It is possible that the transpiration of these large trees contributes to the topographic difference in soil water.

Elsewhere, Poulsen (1996) measured gravimetric soil water content at locations within a 1 ha lowland dipterocarp forest plot at Kuala Belalong, Brunei. Samples taken from higher elevations had lower water contents than those samples from lower elevations, over a 60 m elevation difference there was a 7 % moisture content difference. In the present study the maximum elevation difference between subplots is about 35 m which would correspond to a 4.5 % moisture content difference at Poulsen's site. Similarly Ashton *et al.* (1995) found differences in soil moisture content in Sri Lanka from ridge-tops to valley sites, midslope sites being intermediate. Becker *et al.* (1988) in moist forest in Panama, measured soil water potentials, with psychrometers, at gap, understorey, plateau lip and slope sites (plateau higher than slope, maximum elevation difference 18 m), over a period of one year. Gap sites had higher water potentials than understorey sites and plateau sites lower water potentials than slope sites. However, unlike this study, the authors conclude that the differences between sites did not significantly increase at drier times of year, although the presented data suggests that there is no difference between sites at wetter times of year.

Differences were greater (maximum difference 1 MPa, 50 % of lowest value) on a north-south slope compared with an east-west slope (maximum 0.5 MPa, 25 % of lowest value). As all subplots in this study were on east-west slopes it is not possible to say whether water potentials vary with slope orientation. The low lying sites of Rogstad (1990) in Peninsula Malaysia were regularly inundated and it is suggested that anaerobic soil conditions develop. There is no evidence that such conditions develop at the lower-slope sites at DVFC, although no detailed investigation has taken place. Green (1992) dug soil pits to 2 m and found no evidence of anaerobis, and soil surface puddles never form (pers. obs.).

In conclusion, soil water variation related to topography means that trees growing <20 m apart will experience different soil water regimes. During dry periods it seems likely soil water potentials on ridge sites will be low enough to result in plant water stress while lower-slope trees have sufficient soil water available. During droughts ridge water potentials may be sufficiently low to cause tree death.

Chapter Four. Plant water relations

INTRODUCTION

Measurement of plant water status

Water moves from soil to plant to atmosphere down a water potential gradient (Elfving *et al.*, 1972) and therefore, measurement of water potential has gained acceptance as the most useful approach to quantification of water status (Pallardy *et al.*, 1991). Plant water potential (ψ) has three components, osmotic or solute potential (ψ_π), turgor or pressure potential (ψ_p) and gravitational potential (ψ_g). Osmotic potential arises both from dissolved cell solutes, and the interaction of water with charged surfaces, and this latter is sometimes referred to as matric potential (ψ_τ). Pressure potential arises both from xylem tension and positive internal cell pressure, caused by cell membranes pressing against cell walls. Gravitational potential varies at a rate of 0.1 MPa per 10 m height.

While leaf water potential is usually measured (e.g. Fetcher, 1979), stem (e.g. Kaufmann & Kramer, 1967) and root (e.g. Slavikova, 1967) potentials have also been measured. The most widely used methods of water potential measurement are vapour pressure and pressure equilibration. Vapour pressure is measured with thermocouple psychrometers or thermocouple dewpoint hygrometers. Pressure equilibration is carried out with a pressure chamber. Unfortunately, there is considerable evidence that values produced by these two different methods do not always agree (e.g. Boyer, 1967; Kaufmann 1968). For field measurements of plant water potential the preferred method is that of pressure equilibration (Pallardy *et al.*, 1991). For leaf measurement, an excised leaf is placed in the chamber head such that only the petiole protrudes from the chamber. Once sealed, the chamber is pressurised with compressed nitrogen or air, until water appears at the cut surface. The pressure of the chamber at this point is assumed to be equal to the average water potential for the entire leaf. It is important to ensure both that, water loss during measurement, and the length of petiole protruding is minimised (Turner, 1987).

Water potential measurements with a pressure chamber can be used to separate water potential into its osmotic and pressure potential components, by the use of pressure volume curves. Leaf turgor loss point is the point at which the cell membrane ceases to exert pressure on the cell wall and hence ψ_p=0. The relationship between $1/\psi_\pi$ (and hence $1/\psi$ at ψ_p=0) and relative leaf water content (R^*) is linear. So several measurements of ψ at a range of leaf water contents below turgor loss point can be extrapolated to give an estimate of ψ_π at leaf saturation ($\psi_{\pi,sat}$). Once the relationship between water content and ψ_π is known, ψ_p can also be calculated. Plant osmotic adjustment, a decrease (more negative) in $\psi_{\pi,sat}$, will reduce the water content at which turgor is lost and hence is a possible drought adaptation. Another possible drought adaptation is the alteration of cell wall elasticity, inelastic cell walls will result in a larger change in turgor pressure for a give change in cell water content than elastic cell walls. Turgor potential is related to cell volume changes by a proportionality factor, the elastic modulus, ε. The bulk, weighted-average value of elasticity, ε', is calculated as in Equation (4-1). Cells with elastic walls will have a lower value of ε than inelastic cells.

$$\varepsilon' = \frac{d\psi_p}{dR^*} R^* \tag{4-1}$$

At low water potentials both photosynthesis and growth are inhibited. However, care needs to be taken in interpreting plant water potentials, as instantaneous measurements are inadequate measure of plant stress (Pallardy *et al.*, 1991). The same ψ values may be related differently to stomatal conductance, or may represent different values of component potentials and rates of leaf expansion. Also ψ varies during the day, and ψ in a transpiring plant is related not only to soil water potential but to other factors such as plant resistance, soil resistance and vapour pressure deficit (Elfving *et al.*, 1972). To avoid these difficulties pre-dawn water potentials are measured. In principle, the hydraulic system equilibrates with the soil overnight when the stomata are closed. Pre-dawn ψ is therefore useful as a measure of baseline water stress at the whole plant level (Pallardy *et al.*, 1991). However, plants in a heterogenously moist soil with only a partly droughted root system may not have different pre-dawn ψ values from well watered controls but have a larger daily amplitude in leaf water potential. Therefore, it is useful as well as pre-dawn measurements to measure values at mid-day, when the lowest water potential values are expected.

Drought adaptation

Studies on plants growing in dry regions have identified two plant types, drought escaping, and drought resisting (Fahn & Cutler, 1992). Drought escaping plants complete their life-cycle at times of high water potentials, not relevant when woody plants are being considered, but a species confined to sites where low soil water potentials did not occur would also be a drought escaper. Drought resisting plants have been further subdivided into drought evaders (or avoiders) and drought endurers (or toleraters). Drought evaders restrict water expense, or develop extensive root systems, or both. Drought endurers remain alive when practically no root absorption of water can take place. Water storage is a drought endurance adaptation, as is osmotic adjustment, discussed above.

Short term response to drought stress is mediated by abscisic acid (ABA) whose formation is induced by drought. ABA is transported to the guard cells where it brings about stomatal closure (Hiron & Wright, 1973). There is a threshold response to ABA levels which results in stomata being closed for several hours. Any ABA effect is reversed by cytokinin.

The seasonal and site differences in found soil water potential (Chapter 3) are expected to result in seasonal and site differences in plant water status. As an extrapolation of the soil water data to drier years suggests that droughts occur on ridge sites, trees growing on these sites are expected to show greater drought adaptation than trees growing on lower-slope sites.

MATERIALS AND METHODS

Selection of individuals

A subset of the individuals used in the phenology survey were (see chapter 5 for details). Ideally individuals from all four study species in all size classes at the different sites would have sampled at regular intervals. However use of the Scholander pressure chamber imposes restricted maximum possible sample size because of the long time required to take one measurement. This restriction is especially severe for pressure volume curves where only 6-8 leaves can be processed during one day, even when the bench dehydration technique is employed (Turner, 1987). While not as restricted, pre-dawn readings also create problems in that leaves have to be cut and processed within a limited time frame (the ‘pre-dawn window’, in this case two hours). Also, both *Cleistanthus glaber* and *Ardisia colorata* petioles were too short to be inserted into the pressure chamber, although *C. glaber* leaves were sufficiently small for a twig to be used. As a result of these restrictions only one size class (10-24.9 mm DBH) and two species (*Mallotus wrayi* and *Dimorphocalyx muricatus*) were studied. Samples were taken over a range of soil water potentials (Figure 4-1). A summary of the surveys is shown in Table 4-1.

Table 4-1. Dates of, and soil water potentials during, plant leaf water measurements. Soil water potentials are means of previous and subsequent week's measurements.

Dates	No.	Mean ridge WP (MPa)	Mean lower-slope WP (MPa)	Pre-dawn	Mid-day	Pressure-volume curves
2-4/5/95	1	-0.08	-0.02	+	-	-
7-9/6/95	2	-0.03	-0.01	+	-	+
19-21/9/95	3	-0.03	-0.01	+	-	+
16-18/4/96	4	-0.19	-0.07	+	-	+
23-26/7/96	5	-0.08	-0.01	+	+	-
13-14/5/97	6	-0.51	-0.55	+	+	-

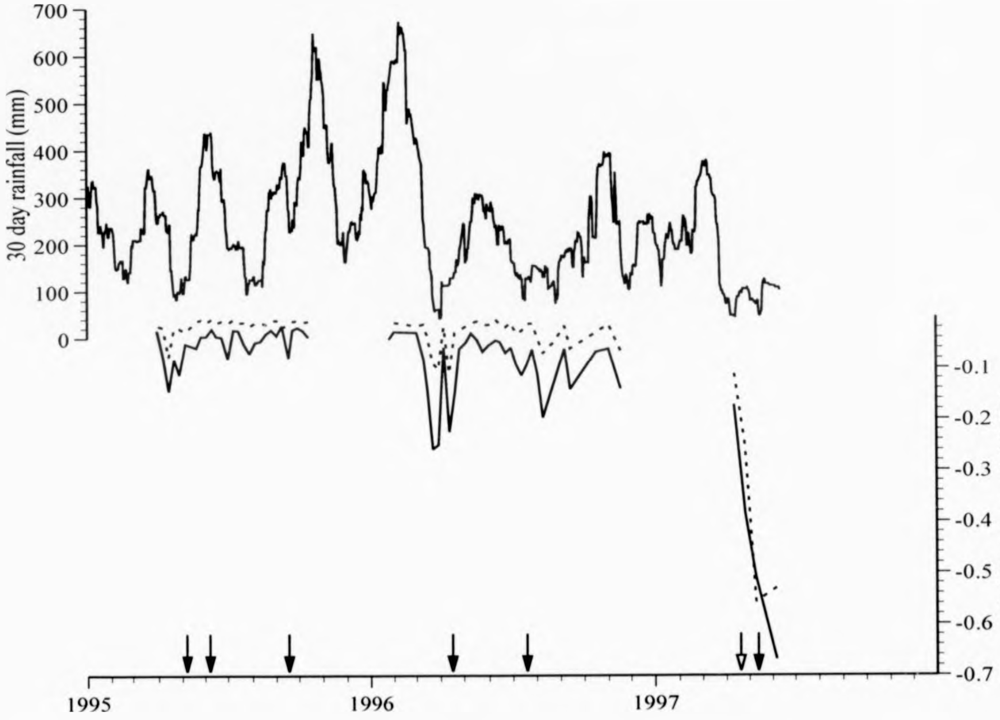

Figure 4-1. 30-day rainfall totals and ridge (—) and lower-slope (---) soil water potentials. Filled arrows indicate point of plant water status survey, the hollow arrow a leaf assimilation and conductance rate study.

Pre-dawn measurements

From the set of phenology individuals 12 individuals were selected per LPP, four each of *D. muricatus* ridge, *M. wrayi* ridge and *M. wrayi* lower-slope. The selection was at random from the 10-24.9 mm size class, but any individuals sampled in the previous pre-dawn measurements were excluded. The day before sampling each individual was visited, a sample branch selected and the branch height recorded. The branch selected was the one nearest to the phenology survey branch. Owing to the difficulty of locating trees in the dark and the restricted sampling time, each LPP was sampled on separate days, one day apart. Sampling usually started at 04:00 and was normally completed by 05:15. Two leaves were cut from each sample branch and immediately placed in a ziplock bag with a humidified atmosphere and then placed in an insulated, chilled bucket. Pre-dawn water potentials were not taken immediately, the sample trees were scattered throughout the 4 ha plot and it would not have been feasible to transport the pressure chamber to each tree in time. All leaves were sampled first and the pre-dawn water potential was later measured for each leaf using a Skye SKPM1400 pressure chamber (Skye Instruments, UK) at the field centre. Thereby sample sizes were increased. Cold storage in humidified plastic bags is effective in minimising changes in leaf water potential (Parker & Pallardy, 1985). Compressed air was used to pressurise the leaf chamber. On reaching the field centre all the bags containing the leaves were placed in a fridge. Before measurement each leaf was wrapped in polythene film to prevent water loss. During measurement petioles were inserted so that <1 cm was outside the chamber, to minimise exclusion error. Pressurisation rates were <0.025 MPa s^{-1}. Water potential measurements were always completed by 07:00, and the maximum interval between a leaf being cut and its water potential being recorded was 2 h. The data used in the analysis were the means of the water potentials for the two leaves cut for each individual.

Elfving *et al.* (1972) suggest that the relationship between pre-dawn leaf and soil water potential is linear. Therefore, in principle, an ANCOVA could be carried out with soil water potential as a covariate. However, this assumes that the soil water potential measured is the same as the soil water potential available to the tree. Plant water potentials were regressed on soil water potentials, if a relationship existed an ANCOVA was carried out, if not an ANOVA with collection as a fixed factor was carried out. The values of soil water potentials used were the means in Table 4-1, it would have been possible to use the measured value from the psychrometer in the subplot where each tree grew, but although values between subplots varied, there was no evidence to suggest that within subplot variation was less than among subplot variation. As there were no *D. muricatus* individuals from lower-slope sites two separate analyses were carried out, comparing *D. muricatus* with *M. wrayi* from ridge sites, and *M. wrayi* from ridge and lower-slope sites.

Mid day water potentials

Mid day water potentials were taken in exactly the same manner as pre-dawn water potentials, from the same individuals, on the same day, but leaf collection commenced at 12:00 and was completed by 13:30.

The relationship between mid-day plant water potentials and soil water potential is complex and related to soil resistance, plant resistance and vapour pressure deficit (Elfving *et al.*, 1972). Therefore, it is not possible to carry out an ANCOVA as with the pre-dawn measurements. Rather two ANOVAs were carried out, with collection and either species or site as fixed factors.

Pressure volume curves

Pressure volume curves were constructed for leaves sampled the previous day for pre-dawn measurements. The leaves were rehydrated for roughly 24 h in deionized water. Only six leaves could be processed in one day and were selected thus, two each of, *D. muricatus* ridge, *M. wrayi* ridge and *M. wrayi* lower-slope. Selection was not random, rather undamaged leaves of a suitable size were selected, and two leaves cut from the same tree were never used. This selection method was used because the pressurisation/ de-pressurisation cycles and handling, meant that an already damaged leaf would not have lasted through the whole procedure. Each leaf was weighed on a TS120S balance (Ohaus Corporation, USA), to an accuracy of 1 mg, then wrapped in polythene film, and the water potential determined with a Skye SKPM1400 pressure chamber, then reweighed. Between each reading the leaves were allowed to dry out on a bench top. Trial studies showed that the leaves dried out very quickly, therefore, between measurements, leaves were placed in a plastic bag, open at one end to slow down the drying rate. A sufficiently slow rate of drying was required to ensure several measurements were made before the turgor loss point. Eight measurements were taken per leaf. The leaves were then dried for 24 hours at 80 °C and reweighed. Moisture content, at each measurement point, was calculated as in Equation (4-2). Where, $Weight_a$ is weight after water potential measurement, $Weight_b$ is weight before water potential measurement, $Weight_h$ is hydrated weight and $Weight_d$ is dry weight. Unfortunately, the balance failed after the fourth collection and, since accurate weighing was no longer possible, pressure volume curves were not constructed for the fifth and sixth collections.

$$MoistureContent = \frac{\left(\frac{Weight_b + Weight_a}{2}\right) - Weight_d}{Weight_h - Weight_d}$$

(**4-2**)

Water potential parameters were obtained from the data using a non-linear regression technique that avoids the subjective nature of graphical analysis (Schulte & Hinckley, 1985). The fitted equation had two components representing turgor and osmotic pressure. Schulte & Hinckley suggest several alternative turgor potential models, the modified exponential function (PVC) was selected because it had the fewest parameters of the models that provided a good fit to Schulte & Hinckley's test data. Note that Schulte & Hinckley's table summarising the models and the text contain several errors, and the model fitted has been corrected. The fitted model is shown in Equation (4-3) where, ψ is water potential, $\Psi_{\pi,sat}$ is osmotic potential at saturation, R^* is relative water content, R^*_0 is the relative water content at zero turgor, X is the symplastic fraction of total water content and a is a parameter to be estimated. The data for each site species combination were grouped for each collection, plotted and obvious outliers removed, and the model fitted using SPSS (release 7.5, SPSS Inc, USA). Both symplastic water fraction and relative water content at zero turgor were constrained between one and zero, while $\psi_{\pi,sat}$ was constrained to be less than zero. Other values for these parameters would have been biologically impossible. The pressure potential model allows negative turgor pressure, but, using a conditional model, pressures were set to zero below zero turgor. The estimated parameters and the fitted equation were then used to calculate water potential at zero turgor (ψ_0). Bulk modulus of elasticity at full hydration (ε'_{sat}) was calculated as Equation (4-1).

$$\psi = \frac{\psi_{\pi,sat}}{1 - \left[\frac{1 - R^*}{X}\right]} - \psi_{\pi,sat}\left\{\exp\left[a\left(R^* - R_0^*\right)\right] - 1\right\}$$

(**4-3**)

Root depth

Initial observations were carried out where roots had been exposed, either by the action of animals (wallows), or by road building. Unfortunately no exposed *D. muricatus* could be located as wallows are rarely found on ridges. However, several *M. wrayi* of different sizes were located. At the cut surface excavations were carried out to determine the depth of the tap root and the distribution of laterals down it. It proved difficult to determine the length of the laterals as few were in the same plane as the cut. While yielding some information no comparisons of ridge and ubiquitous species was possible.

In a more complete study the complete root systems of two species, *M. wrayi* and *D. muricatus* were excavated and measurements taken of the excavated systems. As far as possible all roots >2 mm in diameter were recovered. To allow comparison, representative ridge and lower-slope sites were selected. These sites were, out of necessity, outside, but adjacent to, the LPPs (see Figure 2-7 for location). At the ridge site five each of *M. wrayi* and *D. muricatus* individuals were excavated, while at the lower-slope site five *M. wrayi* were excavated. All individuals were 25-45 mm DBH, the largest size class in the phenology study. The height and DBH of each tree was recorded, the tree was then felled at roughly 30 cm above ground level. Before excavation proceeded the position of ground level and magnetic north, were marked on the trunk. The tree was then dug up using a combination of a small trowel and fingers; secateurs were used to cut roots from neighbouring trees. Excavation was carried out 20-24 March, 1996, root systems were removed to the field centre and all measurements carried out within one week of excavation. Starting at ground level, for each lateral, the diameter (at tap root join), soil depth, and total length were measured. The lateral was then cut off and discarded. The procedure was the repeated until all laterals had been measured. The depth of the now lateral-less tap root was then measured. For comparison in November, 1997 one *A. colorata* and one *C. glaber* tree was excavated from the ridge site.

As with the analyses above *D. muricatus* and *M. wrayi* ridge, and *M. wrayi* ridge and *M. wrayi* lower-slope groups were compared separately. For each lateral the cross-sectional area at the tap-root join was calculated, this value was used as a relationship between cross-section and water conducting capacity was expected. ANOVAs were carried out comparing tap-root length, lateral cross-sectional area and lateral depth (weighted by cross-sectional area) between groups. As a relationship between tree height and tap-root depth seemed likely, where a significant difference in tree heights existed between groups, tree height was used as a covariate.

Photosynthesis and stomatal conductance rates

A limited investigation of photosynthetic and stomatal conductance rates was carried out with an IRGA (LCA4, ADC Ltd, UK) and a 20 W tungsten-halogen lamp powered by a 12 V lead-acid battery. Reference air was drawn in 1.5 m above the ground. Measurements were carried out between 24 and 28 April, 1997, at three sites, each site on a separate day, a LPP ridge subplot, a LPP lower-slope subplot and a gap site at the end of the crane access road (Figure 2-2). At each site eight seedlings were measured, at the ridge site four *D. muricatus* and four *M. wrayi*, at the lower-slope four *M. wrayi* and four *A. colorata* and at the gap site four *M. wrayi* growing in direct sunlight and four growing in shade immediately adjacent to the gap. Seedlings were selected at random from those present <30 cm in height. Measurements commenced between 08:30 and 09:00 and were always completed by 11:00, and alternated between species or environment. Conductance and assimilation rate were measured for each seedling at 300 and 600 µmol m^{-2} s^{-1} PPFD. These light levels are similar to those at which dipterocarp seedling assimilation rates saturate (Zipperlen & Press, 1996). Light levels during measurement were adjusted by altering the distance between the lamp and leaf, and were measured with a Quantum PAR sensor and hand-held meter (Skye Instruments, UK). Five minutes were allowed for leaf acclimation, both between inserting the leaf in the cuvette, and upon increasing the illumination level, before readings were taken. Each datum recorded was the mean of four immediately consecutive readings. Light levels at each site were measured at 1 min intervals, on different days (19-23 June, 1997), with a randomly placed pair of Quantum sensors and a Datahog2 logger (Skye Instruments, UK).

As above separate ANOVAs were carried out for each site, plus one ANOVA comparing *M. wrayi* seedlings among sites.

RESULTS

Pre-dawn leaf water potentials

Pre-dawn potentials were measured for *Dimorphocalyx muricatus* and *Mallotus wrayi* individuals growing on ridge and lower-slope sites, over a range of soil water potentials. All leaves were cut from branches 2-4 m above ground level. Measured leaf water potentials (Figure 4-2) were lower at low soil water potentials than at higher soil water potentials. An exception is April, 1996 where it appears that sampling may have taken place during a wet period between two dry periods. At the wettest point, June, 1995, the leaf water potential of *D. muricatus* was -0.09 MPa, and that of *M. wrayi* -0.26 MPa (ridge) and -0.11 MPa (lower-slope), at the driest point, May, 1997, these fell to -0.21, -0.50 and -0.57 MPa respectively. However, measured *M. wrayi* water potentials fluctuated more than those of *D. muricatus* and are different among times where soil water potentials were similar. It is notable how at the driest time *D. muricatus* water potentials remain well above soil water potential at 20 cm, while *M. wrayi* potentials are similar to those found in the soil. There was a poor relationship between plant pre-dawn water potential and soil water potential at 20 cm depth (plant wp=-0.13+0.54soil wp, r^2=0.14; $F_{1,187}$=32.35, p<0.001) so ANOVAs were carried out with collection as a fixed factor rather than ANCOVAs. Comparing *D. muricatus* and *M. wrayi* ridge, there was a significant difference in collection time ($F_{5,82}$=6.60, p=0.001), *M. wrayi* water potentials were significantly lower than *D. muricatus* ($F_{1,82}$=6.57, p=0.012) and there was a significant interaction between collection time and species ($F_{5,82}$=2.54, p=0.034). Specifically, the difference was bigger at drier times. Comparing *M. wrayi* between sites there was a significant difference in collection time ($F_{5,81}$=7.37, p<0.001), but not between sites ($F_{1,81}$=0.49, p=0.486), nor was there a collection time site interaction ($F_{5,81}$=0.49, p=0.725).

Mid-day leaf water potentials

For two leaf collections mid-day water potentials were measured, on the same day, for the same trees as pre-dawn water potentials. In July, 1996 soil water potentials were much higher than in May, 1997 (Figure 4-3). Each of the study group water potentials fell below those found in the soil at 20 cm depth, both at the wet and dry collection times (wet, *D. muricatus* ridge, -0.12 MPa, *M. wrayi* ridge, -0.88 MPa and *M. wrayi* lower-slope, -0.90 MPa; dry -0.59 MPa, -1.64 MPa and -1.77 MPa, respectively). Plant water potentials were significantly lower at the dry collection time compared to the wet (*D. muricatus v. M. wrayi* ridge, $F_{1,27}$=24.59, p<0.001; *M. wrayi* ridge *v. M. wrayi* lower-slope, $F_{1,27}$=26.82, p<0.001). As with the pre-dawn data, leaf water potentials of *D. muricatus* were significantly higher than those of *M. wrayi* on ridge sites ($F_{1,27}$=53.47, p<0.001) but there was no significant difference between *M. wrayi* individuals growing at different sites ($F_{1,27}$=0.26, p=0.612).

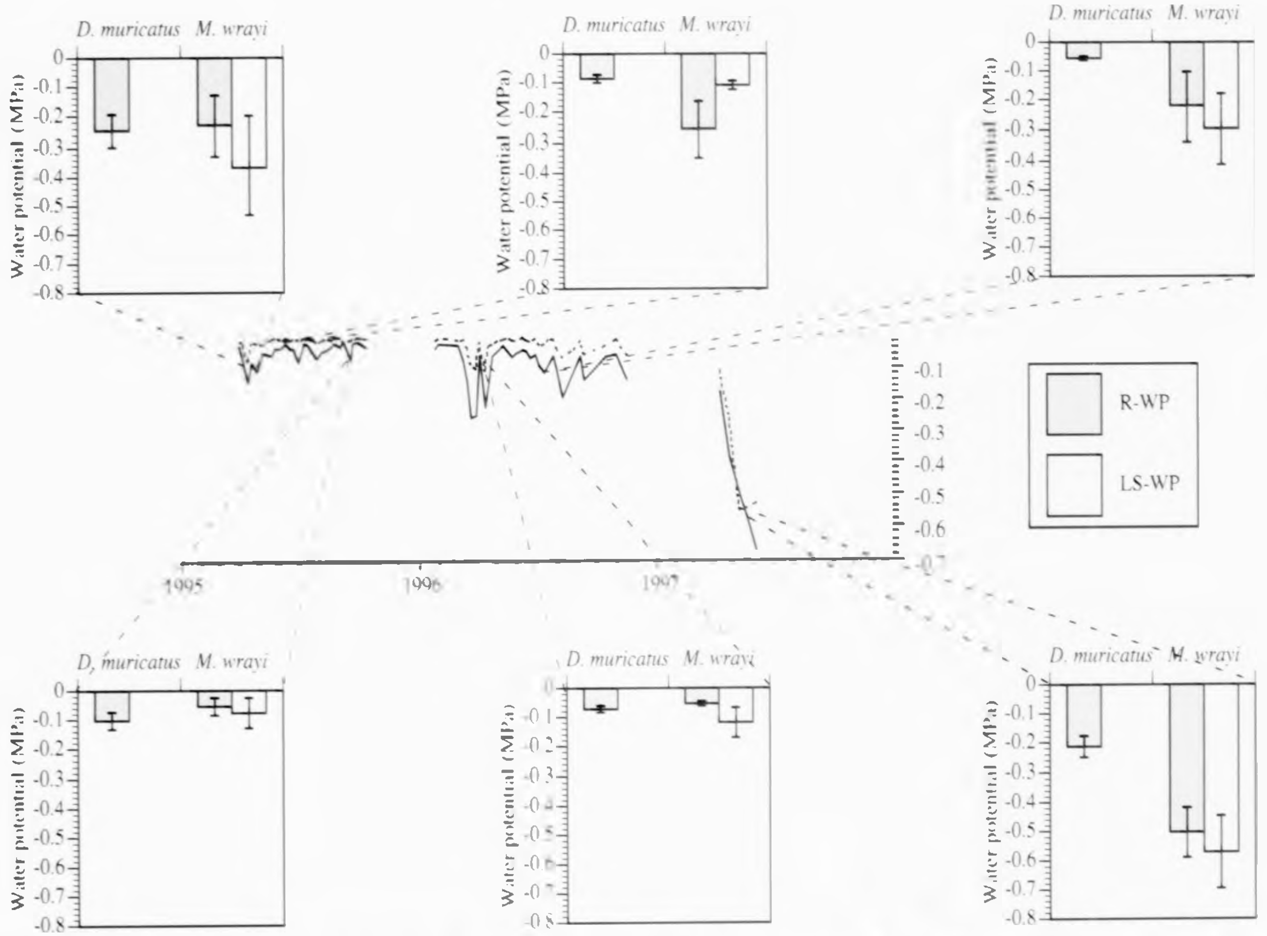

Figure 4-2. Pre-dawn *Dimorphocalyx muricatus* and *Mallotus wrayi* leaf water potentials, from ridge (R) and lower-slope (LS) sites, at dates and soil water potentials indicated on central graph. Error bars are the standard error of the mean, n=8.

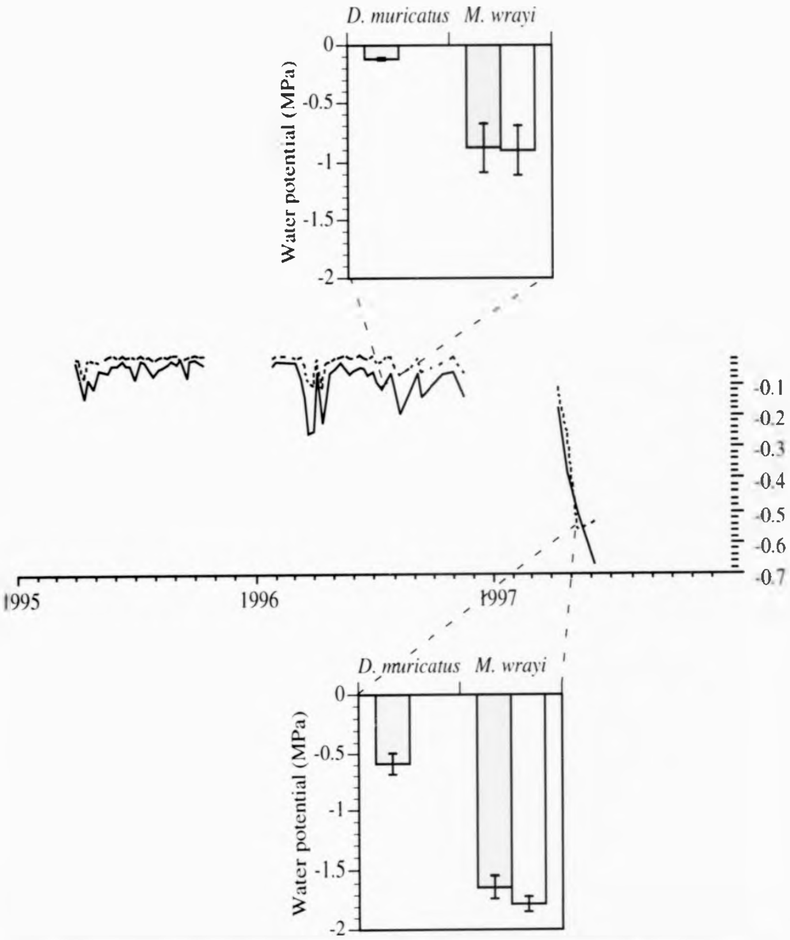

Figure 4-3. Mid-day *Dimorphocalyx muricatus* and *Mallotus wrayi* leaf water potentials, from ridge and lower-slope sites, at dates and soil water potentials indicated on central graph. Error bars are the standard error of the mean, n=8. Legend as Figure 4-2.

Pressure-volume curves

A non-linear model consisting of an osmotic and pressure function was fitted to pressure-volume curve data, obtained at three different dates, from *D. muricatus* and *M. wrayi* trees, on ridge and lower-slope sites. For collections two and four the model converged and r^2 values are high (Table 4-2). Unfortunately, for all of the collection three groups the model failed to converge and the estimated values must be treated with caution, although they are similar to the other estimated values. Soil water potentials were high for a period before collection two and relatively low for a period before collection four (Figure 4-1) so useful comparisons can be made between the estimates at these points. At collection two, leaf osmotic potentials at full hydration ($\psi_{\pi,sat}$) were the same for *D. muricatus* and *M. wrayi* lower-slope but lower for *M. wrayi* ridge, while leaf water potentials at zero turgor (ψ_0) were highest for *D. muricatus*, and lowest for *M. wrayi* ridge, with *M. wrayi* lower-slope in between. *D. muricatus* loses turgor at a high water content (R^*) so there is little difference between $\psi_{\pi,sat}$ and ψ_0. At the drier collection time, four, both $\psi_{\pi,sat}$ and ψ_0 are lower for *D. muricatus* and *M. wrayi* ridge while the values for *M. wrayi* lower-slope are similar. Values of bulk modulus of cell elasticity at full hydration (ε'_{sat}) are similar for *D. muricatus* and *M. wrayi* at both collection times excepting the very high value for *D. muricatus* at the wet collection time. All three groups have lower R^* values than at the wetter collection time. At both collection times ψ_0 values are much lower than recorded pre-dawn water potentials (Figure 4-2) for both those collection points and the other times surveyed. However, recorded mid-day values for *M. wrayi* for both sites (Figure 4-3) during dry periods approach estimates of ψ_0 suggesting that *M. wrayi* leaves have low turgor pressures during the day.

Table 4-2. Non-linear regression estimates of osmotic potential at full hydration ($\psi_{\pi,sat}$), relative water content at zero turgor (R^*), water potential at zero turgor (ψ_0) and bulk modulus of elasticity (ε'_{sat}) for *Dimorphocalyx muricatus* and *Mallotus wrayi* leaves from ridge (R) and lower-slope (LS) sites. Collections 2 & 3 are wet times of year, 4 is a dry time of year.

Species	$\psi_{\pi,sat}$ (MPa)	R^*	ψ_0 (MPa)	ε'_{sat} (MPa)	r^2
Collection 2					
D. muricatus	-1.12	0.95	-1.38	17.47	0.90
M. wrayi (R)	-1.56	0.81	-2.07	5.94	0.82
M. wrayi (LS)	-1.12	0.85	-1.56	7.28	0.91
Collection 3					
D. muricatus [1]	-1.09	0.87	-1.38	7.35	0.68
M. wrayi (R) [1]	-1.07	0.82	-1.42	4.12	0.52
M. wrayi (LS) [1]	-1.31	0.89	-1.50	8.42	0.36
Collection 4					
D. muricatus	-1.45	0.83	-1.75	7.90	0.77
M. wrayi (R)	-1.69	0.73	-2.32	6.41	0.95
M. wrayi (LS)	-1.05	0.71	-1.48	3.64	0.60

[1] Model did not converge

Root depth

Root depths and lateral distributions were measured for *D. muricatus* trees on ridge sites and *M. wrayi* on ridge and lower-slope sites. *M. wrayi* ridge trees were significantly shorter than and *M. wrayi* lower-slope trees ($F_{1,8}$=5.32, p=0.050) but *M. wrayi* ridge trees were not significantly different in height from *D. muricatus* trees ($F_{1,8}$=0.57, p=0.473). Both species had tap-roots, and the tap-roots branched in some trees from each of the groups. Tap-root length and lateral root cross-sectional area are shown in Figure 4-4. *D. muricatus* was significantly more deeply rooted than *M. wrayi* on ridge sites ($F_{1,8}$=20.74, p=0.002), but while it appears that *M. wrayi* ridge and *M. wrayi* lower-slope means differ, the difference is not significant if height is included as a covariate ($F_{1,7}$=1.59, p=0.284). Mean *M. wrayi* ridge lateral root cross-section area (10.29 cm^2) was significantly higher ($F_{1,8}$=8.62, p=0.019) than that of *D. muricatus* (3.23 cm^2) but there was no significant difference ($F_{1,7}$=2.84, p=0.136) between *M. wrayi* ridge and *M. wrayi* lower-slope (5.59 cm^2). However, mean *D. muricatus* lateral depth (311.9 cm), weighted by cross-sectional area, was significantly higher ($F_{1,121}$=55.70, p<0.001) than *M. wrayi* ridge (116.5 cm), while there was no significant difference ($F_{1,132}$=0.08, p=0.782) between *M. wrayi* ridge and *M. wrayi* lower-slope (137.9 cm^{-2}). Although fine roots were not measured *D. muricatus* fine roots were much thicker than *M. wrayi* fine roots. For comparison excavation of a *C. glaber* and *A. colorata* tree suggests that both these species have a similar root structure, and rooting depth, to *M. wrayi* (data not shown).

Assimilation and conductance rates

Assimilation and conductance rates of *Ardisia colorata*, *D. muricatus*, and *M. wrayi* seedlings, in gap, ridge and lower-slope sites, at 300 and 600 µmol m^{-2} s^{-1} PPFD were measured (Figure 4-5). Seedlings growing in full sun at the gap site received most sunlight (Table 4-3), followed by those in adjacent shade, then those growing at the ridge site, while the seedling growing at the lower-slope site received least light. As light measurements only took place on one day at each site, measured values are unlikely to be truly representative of the long-term average. Mean soil water potentials were -0.38 MPa, ridge and -0.25 MPa, lower-slope at the time of measurement, soil water potentials at the gap site were not measured.

Table 4-3. Measured PPFD during one day at each of the IRGA sites. For the ridge and lower-slope sites values are the mean of two sensors, for the gap site one sensor measured in full sun (FS) the other in adjacent shade (Sh).

Site	Total (mol m^{-2})	Maximum (µmol m^{-2} s^{-1})
Gap (FS)	9.41	1415
Gap (Sh)	1.57	348
Ridge	0.36	275
Lower-slope	0.03	34

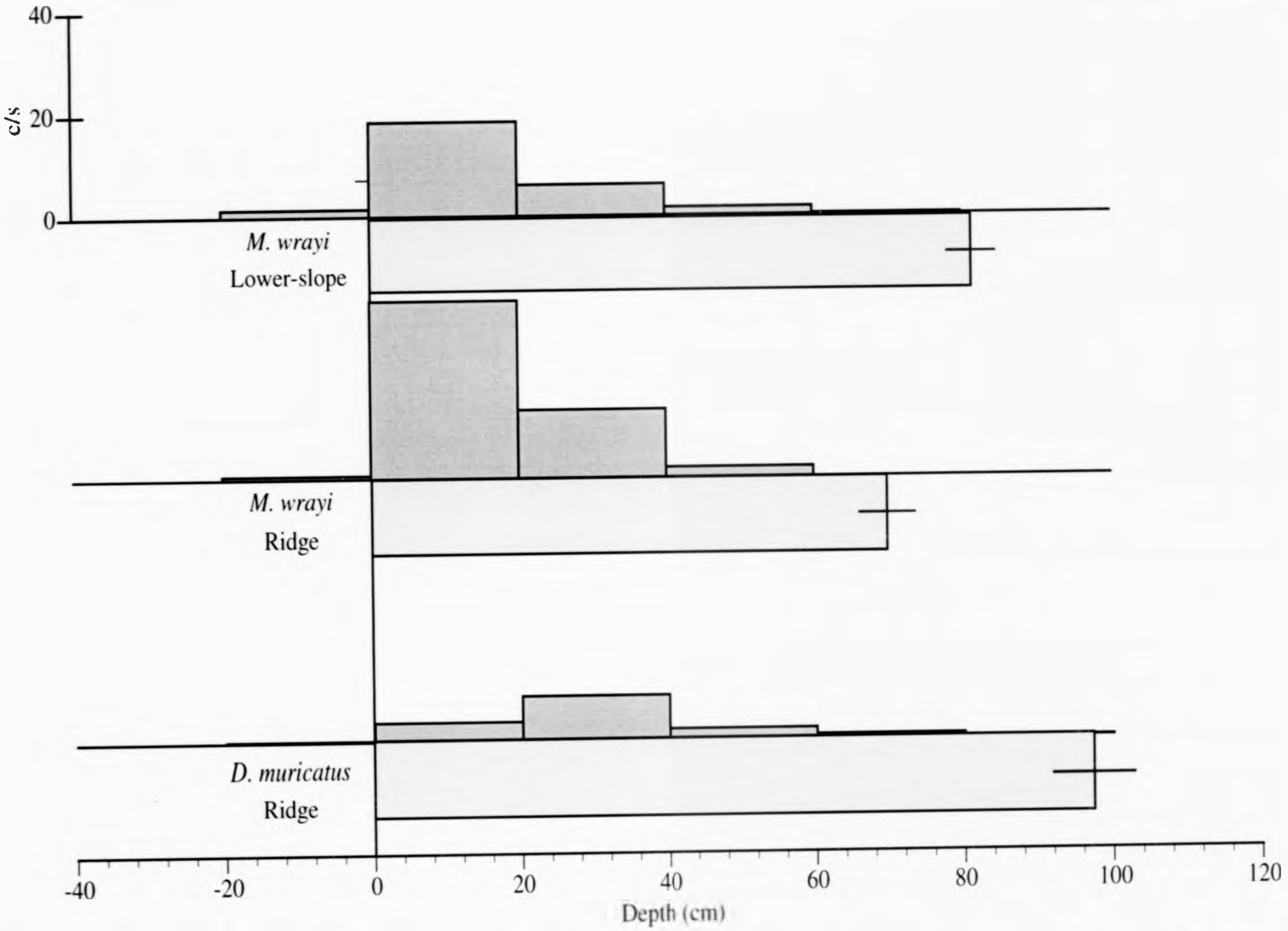

Figure 4-4. **Root depths of *Dimorphocalyx muricatus* and *Mallotus wrayi* from ridge and lower-slope sites. Horizontal bars are mean tap-root depth. Error bars are standard error of the mean, *n*=5. Vertical bars are total lateral root cross-sectional area at each depth (cm^2).**

At the gap site *M. wrayi* assimilation rate was significantly higher in full sun ($F_{1,12}=5.33$, $p=0.040$) than in the shade but there was no significant difference between illumination levels ($F_{1,12}=1.45$, $p=0.251$), there was no significant difference in conductance rate between environments ($F_{1,12}=0.837$, $p=0.378$) or illumination levels ($F_{1,12}=1.556$, $p=0.236$). At the ridge site there were no significant differences in assimilation rate or conductance rate, between *D. muricatus* and *M. wrayi* ($F_{1,12}=0.19$, $p=0.670$; $F_{1,12}=2.634$, $p=0.131$, respectively), or between illumination rates ($F_{1,12}=0.02$, $p=0.906$; $F_{1,12}=0.05$, $p=0.821$; respectively). At the lower slope site *M. wrayi* assimilation rate was significantly higher than *A. colorata* ($F_{1,12}=27.98$, $p<0.001$) and the difference between illumination levels was also significant ($F_{1,12}=4.80$, $p=0.040$), *A. colorata* assimilation rate was significantly lower at 600 μmol m^{-2} s^{-1} than at 300 μmol m^{-2} s^{-1} (Tukey compromise post-hoc, $p<0.05$). There was no significant difference in conductance rate between species ($F_{1,12}=2.45$, $p=0.144$) or illumination levels ($F_{1,12}=0.01$, $p=0.936$). Comparing *M. wrayi* among sites there was a significant difference in assimilation rate ($F_{2,18}=5.25$, $p=0.016$) with the rate at the ridge site being significantly lower than both the gap and lower-slope sites (Tukey compromise post-hoc, $p<0.05$), but there was no significant difference in conductance rate among sites ($F_{2,18}=5.33$, $p=0.256$).

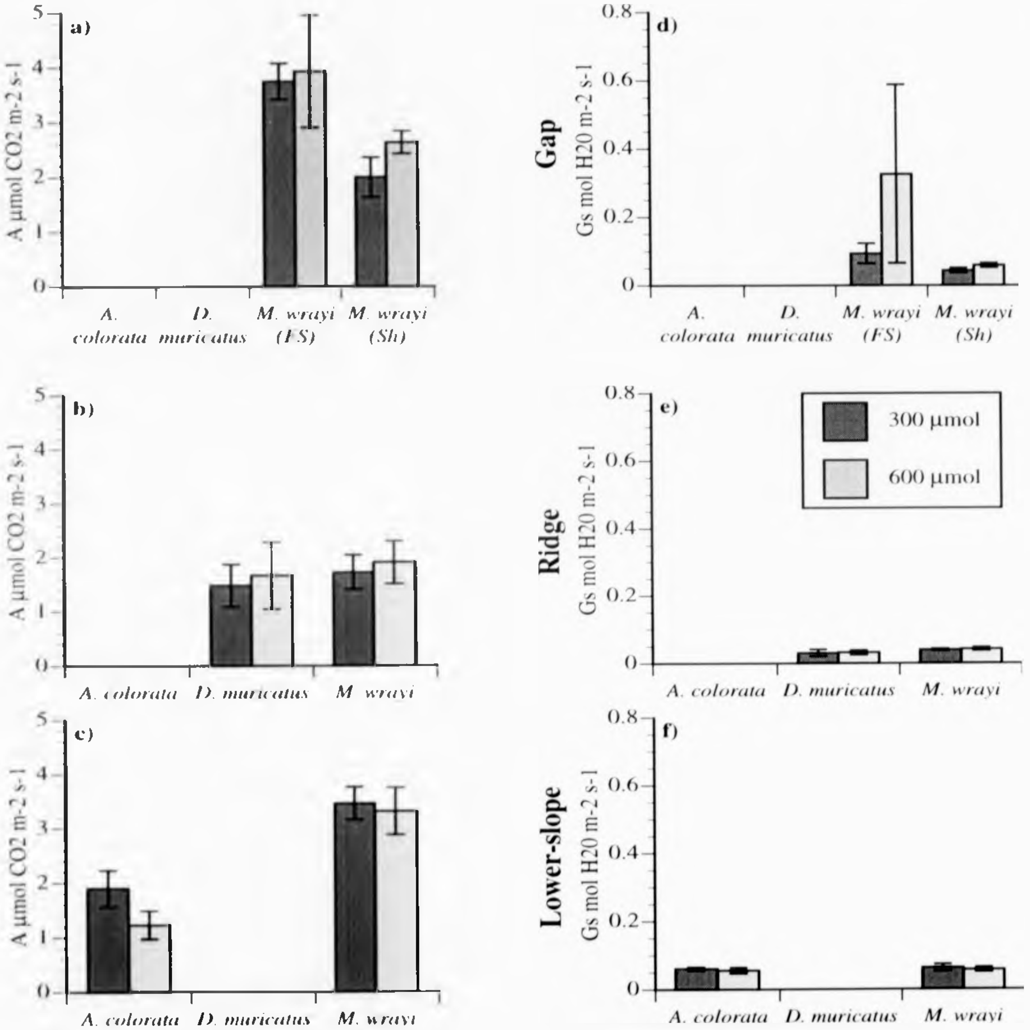

Figure 4-5. Assimilation (a-c) and conductance rates (d-f) for *Ardisia colorata*, *Dimorphocalyx muricatus* and *Mallotus wrayi* at 300 and 600 µmol m^{-2} s^{-1} PFD measured at gap (a,d), ridge (b,e) and lower-slope (c,f) sites in full sun (FS) and shade (Sh). Error bars are standard errors of the mean, *n*=4.

DISCUSSION

Plant water potential, assimilation and conductance

There was a poor relationship between pre-dawn water potentials and soil water potential at 20 cm depth, although plant water potentials were lower at drier times than wetter times. Pre-dawn plant water potentials were also usually higher than soil water potentials. These findings suggest that both *D. muricatus* and *M. wrayi* root into soil with greater water potentials than those found at 20 cm. Measured root depths confirm that both species root to well below 20 cm.

Despite differences in soil water potential between ridge and lower-slope sites (Chapter 3) there were no differences in *M. wrayi* pre-dawn or mid-day water potentials between sites, while there was a difference between *M. wrayi* and *D. muricatus* on ridge sites. The pre-dawn water potential values measured here for *M. wrayi* are similar to those found both in the wet and moist tropics (Table 4-4). Mid-day values are lower than all of the other tropical wet forest species. *D. muricatus* pre-dawn and mid-day values are higher, the mid-day water potential at the wet time of year very much so.

It is interesting to note the variation in published values (Table 4-4) for the same species, all three Panamanian studies were carried out at the same site (Barro Colorado Island) but the values of Becker *et al.* (1988) and Wright *et al.* (1992) for *Psychotria horizontalis*, and Fetcher (1979) and Wright *et al.* (1992) for *Trichilia tuberculata* differ markedly. This variation suggests that either there is year to year, or an extremely local site variation in plant water potential. The results from the present study also demonstrate that measured plant water potentials vary at times when soil water potentials are similar.

Measured assimilation rates for all species are similar to those measured in dipterocarp seedlings at DVFC (Zipperlen & Press, 1996), as with the dipterocarps it appears that photosynthesis rates saturate at roughly 300 µmol m^{-2} s^{-1} PPFD. The reduction in rate for *A. colorata* at 600 µmol m^{-2} s^{-1} suggests that photoinhibition occurs. Conductance rates are similar to those found at other tropical sites (e.g. Wright *et al.*, 1992).

Table 4-4. Published values of water potential (ψ), osmotic potential at full hydration ($\psi_{\pi,sat}$), water potential at zero turgor (ψ_0), bulk modulus of elasticity (ε_{sat}) and root depth, for understorey or small stature trees, from ridge (R) and lower-slope (LS) sites (or equivalent), at wet and dry times of year, in the wet and moist tropics. Numbers to one decimal place precision have been estimated from figures. Wet and dry points are the extremes for each site, a dry time at a wet forest site would be wetter than a dry time at a moist forest site.

		Pre-dawn ψ (MPa)		Mid-day ψ (MPa)		$\psi_{\pi,sat}$ (MPa)		ψ_0 (MPa)		ε_{sat} (MPa)		
Site	Species	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Root depth (cm)
Wet Forest												
Costa Rica [1]	*Pentaclethra macroloba* [11]	-0.3	-0.33	-1.2	-1.2	-1.13	-1.21	-	-	12.7	9.8	-
Hawaii [2,10]	*Dubantia ciliolata*	-	-0.61	-1.13	-1.57	-	-1.08	-	-1.5	-	2.22	-
	Dubantia scabra	-	-0.11	-0.50	-0.78	-	-0.81	-	-0.9	-	10.23	-
Jamaica [3]	*Chaetocarpus globosus*	-0.66	-	-0.74	-	-	-	-	-	-	-	-
	Cyrilla racemiflora	-	-0.38	-	-0.74	-	-	-	-	-	-	-
	Ilex macfadyenii	-0.28	-	-1.10	-	-	-	-	-	-	-	-
	Podocarpus urbanii	-0.68	-	-1.30	-	-	-	-	-	-	-	-
	Vaccinium meridinale	-0.50	-	-1.70	-	-	-	-	-	-	-	-
Malaysia [4]	*Dimorphocalyx muricatus*	-0.09	-0.21	-0.12	-0.59	-1.11	-1.44	-1.38	-1.75	17.47	7.90	97.4
	Mallotus wrayi (R)	-0.26	-0.50	-0.88	-1.64	-1.58	-1.69	-2.07	-2.32	5.94	6.41	69.8
	Mallotus wrayi (LS)	-0.11	-0.57	-0.90	-1.77	-1.20	-1.05	-1.38	-1.47	7.28	3.64	81.4

[1] Oberbauer *et al.* (1987); [2] Robichaux (1984); [3] Tanner & Kapos (1985); [4] this study; [10] two species from different sites; [11] understorey saplings of a canopy species

Table 4-4 continued

Site	Species	Pre-dawn ψ (MPa)		Mid-day ψ (MPa)		$\psi_{\pi,sat}$ (MPa)		ψ_0 (MPa)		ε_{sat} (MPa)		Root depth (cm)
		Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Moist forest												
Australia [5]	*Castanospermum australe*	-	-0.4	-	-0.9	-	-0.80	-	-1.01	-	-	-
Ghana [6]	*Entandrophragma utilo* [12]	-0.9	-2.7	-1.4	-3.1	-	-	-	-	-	-	-
	Terminalia superba [12]	-1.0	-2.5	-1.3	-3.0	-	-	-	-	-	-	-
Panama [7]	*Psychotria chagrensis*	-0.1	-1.1	-0.8	-1.7	-0.9	-1.3	-0.9	-1.3	10	14	51
	Psychotria furcata	-0.2	-0.7	-0.7	-1.7	-0.9	-1.7	-1.0	-2.1	5	18	29
	Psychotria horizontalis	-0.1	-0.8	-0.7	-1.4	-1.1	-1.4	-1.3	-1.6	6	20	33
	Psychotria limonensis	-0.1	-0.7	-0.4	-1.0	-1.0	-1.1	-1.1	-1.2	8	12	92
	Psychotria marginata	-0.1	-0.6	-0.6	-1.3	-1.3	-1.5	-1.4	-1.7	13	27	38
Panama [8]	*Psychotria horizontalis (R)*	-1.7	-2.5	-	-	-	-	-1.88	-2.29	-	-	30 [12]
	Psychotria horizontalis (LS)	-0.6	-0.9	-	-	-	-	-1.67	-1.95	-	-	30 [12]
	Trichilia tuberculata (R)	-1.1	-2.0	-	-	-	-	-	-	-	-	80 [13]
	Trichilia tuberculata (LS)	-0.6	-1.1	-	-	-	-	-	-	-	-	80 [13]
Panama [9]	*Cordia alliodora*	-0.1	-0.6	-1.0	-2.0	-	-	-	-	-	-	-
	Trichilia cipo (= T. tuberculata)	-0.4	-2.5	-1.5	-4.0	-	-	-	-	-	-	-

[5] Myers *et al.* (1987); [6] Veenendaal *et al.* (1995); [7] Wright *et. al.* (1992); [8] Becker *et al.* (1988); [9] Fetcher (1979); [12] seedlings; data from Becker & Castillo (1990)

Water stress and drought adaptation

At all times measured both species maintained pre-dawn water potentials well above the turgor loss point (ψ_0). At mid-day, at low soil water potentials, *M. wrayi* leaves will have turgor potentials which may be low enough to reduce assimilation rate on ridge sites. The *M. wrayi* seedlings growing at the ridge site had lower assimilation rates than both gap and lower-slope sites even though light levels at the gap site were higher than the ridge site which were higher than the lower-slope site. So assimilation rates were unrelated to light levels and if, as other studies suggest, gap sites are wetter than understorey sites (e.g. Becker *et al.*, 1988), it seems likely that *M. wrayi* seedling assimilation rate is periodically limited by water availability on ridge sites. Zipperlen (1997) found that soil water potentials as high as -0.08 MPa were sufficient to reduce stomatal conductance in dipterocarp seedlings. *D. muricatus* mid-day water potentials never approached the estimated ψ_0, but *D. muricatus* seedlings on the ridge site had a similar assimilation rate to *M. wrayi*. Either the seedlings were more drought stressed than the mature trees or *D. muricatus* has a lower maximal rate of photosynthesis than *M. wrayi*.

D. muricatus was deeper rooted than *M. wrayi* and had a greater proportion of lateral root cross-sectional area at greater depths, although total *D. muricatus* cross-sectional area was lower than that of *M. wrayi*. The difference in pre-dawn water potentials is, probably, accounted for by *D. muricatus* rooting into soil with higher water potentials than *M. wrayi*. The difference in mid-day values and root cross-sectional area suggests that either *D. muricatus* has a higher root and shoot conductivity or reduced desiccation rate, or both, compared with *M. wrayi*. In the limited leaf conduction rate study at a dry time of year, there was no difference between *D. muricatus* and *M. wrayi* on ridge sites, although measurements were not carried out at mid-day. Differences in hydraulic architecture have previously been found between other species and high conductance proposed as a drought adaptation (e.g. Tyree *et al.*, 1991).

The findings of Wright *et al.* (1992) confirm the importance of root depth, of their study species the deepest rooted species *P. limonensis* has water potential values (Table 4-4) the most similar to *D. muricatus*. Jackson *et al.* (1995), in Panamanian moist forest, found differences in stable hydrogen composition (δD) of xylem water between species, and as δD values declined with soil depth, it is suggested that different species were utilising water from different depths. δD of xylem water was negatively correlated with stomatal conductance rate and leaf water potential indicating that species using deeper water had higher rates of water use and higher leaf water potentials. Little information is available on rooting depth for individual tropical species. Becker & Castillo (1990) measured root lengths and areas, in Panamanian moist forest, the results are not partitioned by root depth, although the pictures of the species presented suggest that there are differences. Canopy species saplings were more deeply rooted than understorey species of the same height. In Borneo, Baillie & Mamit (1983) observed roots along a road cutting in Sarawak. Most of the trees measured were canopy species and had root depths of up to 4 m, although most trees were in the 1-2 m range. Beneath forests of seasonally dry Amazonia, root systems extend to >15 m depth (Nepstad *et al.*, 1994), but soil at the present site is probably much shallower than this (Chapter 3).

Both *D. muricatus* and *M. wrayi* osmotically adjusted cell solutes between wet and dry times. Estimated values of osmotic potential at full hydration ($\psi_{\pi,sat}$), for both species, are similar to other published values (Table 4-4). Becker *et al.* (1988) found similar differences in $\psi_{\pi,sat}$ to *M. wrayi* for *P. horizontalis* between plateau and slope sites. Although *M. wrayi* had similar values of ψ, at pre-dawn and mid-day, on ridge and lower-slope sites differences in $\psi_{\pi,sat}$ between sites suggest that trees on the ridge sites experience lower-soil water potentials at other times.

There was no clear pattern in change in bulk modulus of elasticity at full hydration (ε'_{sat}) between wet and dry times. In contrast Wright *et al.* (1992) found a clear increase in ε'_{sat} between wet and dry times of year. Differences in ε'_{sat} may be accounted for by leaf age. Both the species in this study (Chapter 5) and the species of Wright *et al.* produce new leaves during or immediately after the annual dry spell. Therefore, if new, fully expanded leaves are selected, leaves sampled during the dry period will be almost 1 y old whereas leaves sampled during a wet period will be younger. In this study, for water potential parameters, it is likely that the age of leaves compared was similar because newly flushed leaves during the wet sample time were not fully expanded so older leaves were used. Stomatal function and water status of tropical tree species leaves have been shown to change with leaf age (Reich & Borchert, 1988). Wright *et al.* found a decrease in stomatal conductance with leaf age. It is possible that loss of stomatal function may be a result of an increase in ε'_{sat}. In studies of temperate deciduous species, where maximum leaf age is <1 y, seasonal increases in ε'_{sat} have been attributed to tissue maturation and development (e.g. Parker *et al.*, 1982). Therefore, where comparisons between wet and dry periods are required, it would seem desirable to sample during and immediately after of before the dry period, to avoid leaf age being a confounding factor.

At drier times than occurred during this study it seems likely that *M. wrayi*, on ridge sites, will suffer severe drought stress. Drier times have occurred at DVFC in the previous ten years (Chapter 3) and there is strong evidence that severe droughts occur less frequently. Although *M. wrayi* trees could maintain turgor by further increasing cell solute concentrations, the values of $\psi_{\pi,\mathrm{sat}}$ measured are already towards the lower range found in tropical moist forest species (Table 4-4), so further adjustment may not be possible. The low leaf water potentials that develop in *M. wrayi* during the day suggest that there is a high water potential gradient between leaf and stem, which may result in xylem cavitation (Schultz & Matthews, 1997). The deeper rooted *D. muricatus* would be less vulnerable to drought stress at these drier times. As well as accessing deeper water it appears that *D. muricatus* is able to maintain high water potentials during the day. Therefore, during a severe drought it is predicted that *M. wrayi* on ridge sites will have a higher mortality rate than both *D. muricatus* and *M. wrayi* on lower slope sites. However, if a drought occurred that was severe enough to dry the deeper soil both species would be equally vulnerable on ridge sites. Mortality of both slope and generalist species increased during a severe drought in Panamanian moist forest (Condit *et al.*, 1995). Condit *et al.* expected a higher mortality of slope specialists than generalists, but if as here (Chapter 3), during droughts, slopes stay wetter than other sites and the difference becomes greater as the drought develops, mortality would not be expected to be higher.

Implications for the distribution of the study species

Although there is some evidence that *D. muricatus* is more drought tolerant than *M. wrayi* (difference in mid-day and pre-dawn water potentials at dry times and increased rooting depth) and that droughts occur on ridge sites, *M. wrayi* trees are still found on ridge sites albeit less commonly than lower-slope sites (Chapter 2). Therefore, either severe droughts do not occur with sufficient regularity to completely exclude *M. wrayi* or *M. wrayi* trees grow in wet microsites on the ridges, or both. Mishio (1992) attributed some of the difference in the distribution of shrub species, on ridges, in Japan, to very small scale (<1 m) heterogeneity in soil depth. Both study species, when seedlings and shallowly rooted, would be vulnerable to drought, but both species fruit after a dry spell (Chapter 5) and probably can root to a sufficient depth before the next severe drought occurs.

The differences in water relations between *M. wrayi* from ridge and lower-slope sites suggests a high degree of physiological plasticity. Abrams (1986) found a similar degree of plasticity between understorey and open-grown *Cercis canadensis* in north-eastern Kansas, USA. Alternatively there could be genetic differences between populations. Tognetti *et al.* (1997) attribute physiological difference in *Pinus halepensis* seedlings from different Italian provenances to ecotypic variation. However, the populations here are very close together and not isolated, *M. wrayi* occurs throughout the LPPs. Further *M. wrayi* on ridge sites also shows great plasticity. *M. wrayi* is the commonest species ≥10 cm gbh in the LPPs (Newbery *et al.*, 1992) and this 'success' may be the result of the physiological plasticity.

It is possible that *D. muricatus* is excluded from lower-slope sites by competition for nutrients. Although *D. muricatus* root architecture is well adapted for water uptake at depth, it seems poorly adapted for nutrient uptake. At DVFC most total nitrogen is present in the upper 20 cm of soil (Green, 1992; Nussbaum, 1995) but most *D. muricatus* roots are below this depth, and there are few of them. However, extractable phosphate does not vary with root depth (Green, 1992). Rogstad (1990), in Peninsular Malaysia, found differences in distribution between *Polyalthia* species. He suggests that species confined to ridge sites are unable to tolerate anaerobic soil conditions that occurred on his lower-slope sites. However, *D. muricatus* is deeper rooted than *M. wrayi*, so that it roots into deeper, and hence wetter soil, and there is no evidence that soil anaerobis occurs at DVFC (Chapter 3), also *D. muricatus* seed is able to establish on lower-slope sites (Chapter 7).

Chapter Five. Phenology, leaf life-span, and leaf structure

INTRODUCTION

It has been proposed that in weakly and strongly seasonal tropical forests leaf and flower production coincide with seasonal peaks in irradiance except where limited by water stress (van Schaik *et al.*, 1993; Wright & van Schaik, 1994). Light periods coincide with dry periods, and in strongly seasonal forests drought sensitive species produce leaves during the wet season (Reich & Borchert, 1984). However, there is considerable within site variation among species flowering and leaf production patterns (Medway, 1972; Frankie *et al.*, 1974; Newstrom *et al.*, 1994) and not all tropical forests have a peak in production correlated with the timing of solar maxima (Reich, 1995). Various mechanisms for the synchrony of leaf and flower production among species have been proposed. Studies have identified external environmental cues such as minimum night temperature (Ashton *et al.*, 1988) or irradiance (Wycherley, 1973) while Wright (1991) and Reich (1995) suggest that endogenous rhythms may also be important. Identifying any proximal cue is problematic because environmental variables covary in the field (Wright, 1991).

Leaf structure can be a strong indicator of water availability across sites (e.g. Abrams *et al.*, 1990). Species growing on dry sites have been shown to produce more xeromorphic leaves, leaves that have a greater thickness and lower specific area, than species on moist sites (e.g. Abrams, 1986), and Abrams *et al.* (1994) found relationships between leaf ecophysiology and leaf structure. In contrast, sub-montane tropical tree species have xeromorphic leaves but appear not to suffer from drought stress (Sugden, 1985; Tanner & Kapos, 1982; Kapos & Tanner, 1985). Cost benefit models of leaf life-span predict that leaf longevity is long when construction costs are large (e.g. Kikuzawa, 1991). Leaves with low specific areas have higher construction costs than those with high specific areas (Chabot & Hicks, 1982), so xeromorphic leaves are predicted to live longer than mesomorphic leaves. However, some studies have shown otherwise (Williams *et al.*, 1989) and other factors beside water stress determine leaf life-span (reviewed in Chabot & Hicks, 1982).

Seasonality at DVFC varies from year to year (Chapter 3), some years have no or an abbreviated dry period, while other years may have >90-day period with 30-day rainfall totals <100 mm. There is also evidence for more severe droughts occurring less frequently.

There are differences in the soil water potentials that develop during these dry periods between ridge and lower-slope sites. Differences in drought sensitivity have been found between a ridge and ubiquitous species (Chapter 4). This chapter investigates the seasonality of leaf and flower production, leaf structure and leaf life-span of two ridge and two ubiquitous understorey species, whether there are differences between groups and whether there are difference in ubiquitous species between sites. Leaf-structure is also investigated for other common species.

MATERIALS AND METHODS

Phenology and leaf life-span

Individuals were selected from the enumeration data set (Chapter 2). Three size classes were chosen, 0-9.9 (class 1), 10-24.9 (class 2) and 25-44.9 mm (class 3) dbh for each of *Ardisia colorata*, *Cleistanthus glaber*, *Dimorphocalyx muricatus* and *Mallotus wrayi*. Therefore, a range of sizes from small seedlings to reasonably large mature trees (up to roughly 8 m in height) were covered. While larger individuals are present in the plots, their branches would have been both unreachable and unviewable. The enumeration data were subsetted into these size classes for each plot. From these subsets individuals were selected, at random, in the numbers shown in Table 5-1. Differences in numbers selected reflect the different numbers enumerated. For example there were only four *C. glaber* individuals in the 0-9.9 mm size class in each plot.

Table 5-1. The number of individuals per LPP used for each species, in three size classes, on ridge (R) and lower-slope (LS) sites in the phenology survey.

	<10 mm		10-24.9 mm		25-44.9 mm	
Species	R	LS	R	LS	R	LS
Ardisia colorata						
LPP 1	5	12	5	12	5	12
LPP 2	5	12	5	12	5	12
Cleistanthus glaber						
LPP 1	4	-	4	-	7	-
LPP 2	4	-	4	-	7	-
Dimorphocalyx muricatus						
LPP 1	20	-	20	-	20	-
LPP 2	20	-	20	-	20	-
Mallotus wrayi						
LPP 1	15	20	15	20	15	20
LPP 2	15	20	15	20	15	20

For each of the selected trees in the 10-24.9 and 25-44.9 mm categories one healthy, undamaged branch >1 m in height was selected to be monitored. In the case of the trees in the 0-9.9 mm category all of the plant was monitored.

Monthly, from April to September, 1995, for each selected branch or individual the number of leaves, the number flushing leaves, the number of inflorescences, and the number of fruits were counted. The survey normally took place over two or three consecutive days though occasionally a longer time was required. During this initial period it was realised that it was not always possible to be completely certain that a leaf counted as flushing in the current month had not in fact flushed the previous month and been counted then. This uncertainty created problems in the attempt to generate estimates of leaf turnover. Some of the larger individuals also proved problematic in that their branches were partially obscured by other trees. Therefore, the methodology was modified to take account of these problems.

The modified monitoring utilised the same individuals as before. However, branches of those large individuals that were difficult to see were excluded. To be sure that a leaf had in fact flushed that month a tagging procedure was adopted. The leaf or stem below a group of flushing leaves was tagged, initially with expandable plastic rings, later with coloured string. Different markers were used each month, so later it could be determined when a group of leaves had flushed. The new leaves themselves were not marked to avoid damaging the delicate unexpanded tissue. Unfortunately this procedure could only be adopted with the individuals whose monitored branch was within reach. Rather than exclude those individuals who could not be reached they were retained and monitored using the original methodology. It was important to retain these larger trees in the data set to ensure that flowering and fruiting was recorded. While many understorey species flower and fruit at a small size it was better to include trees that could said to be mature with a high degree of certainty. The flushing data from these trees was not included in the estimates of leaf turnover, but the data was accurate enough to include in the proportion of leaves flushing analysis. The modified methodology commenced in April, 1996 and continued until December, 1996. A final survey was also carried out in April, 1997 during a lighter, drier period.

The proportion of leaves flushing was calculated by dividing the number of leaves flushing by the total number of leaves for each branch. Leaf life-span estimates were calculated as Williams *et al.* (1989), modified from Jow *et al.* (1980). Equation (5-1) gives the expected leaf life-span (L) of leaves produced at some arbitrary time (t_α), where b is the number of leaves flushed, d the number of leaves dropped, between two census dates t_1 and t_2, $N_{t\alpha}$ is the number of leaves present at t_1 plus the number produced between t_1 and t_α. When evaluated at $t_\alpha=t_1$, L is simply the interval between census dates divided by the proportion of leaves lost during that interval. Evaluation of L at $N_{t\alpha}=d$ minimises the use of extrapolated data in estimates.

$$L = \left(\frac{N_{t\alpha}}{d} + \frac{N_{t1} - N_{t\alpha}}{b}\right)(t_2 - t_1) \qquad (5\text{-}1)$$

Proportion flushing data were tested for heterogeneity of variance with Cochran's C test (using mean number of replicates), where heterogeneity existed, the data were arc-sin transformed, appropriate where data are proportions (Underwood, 1997). ANOVAs were calculated for each collection separately, the lack of balance meant that a RM ANOVA could not be carried out. To see if there was a significant difference between months data were lumped and an ANOVA, with month as the only factor, calculated. As there were no *C. glaber* or *D. muricatus* lower-slope trees separate ANOVAs were calculated comparing *A. colorata*, *C. glaber*, *D. muricatus*, and *M. wrayi* on ridge sites and *A. colorata* and *M. wrayi* between ridge and lower-slope sites.

Leaf structure

Rather than just look at leaf structure of the core study species, the scope of the study was extended to include the 20 most numerous species in the LPPs (Table 5-2), which comprise 48.4 % of total stems >10 cm gbh (calculated from Newbery *et al.*, 1996). To allow an objective separation into ridge and lower-slope sites collection took place in the ridge and lower-slope subplots in the LPPs (Chapter 2). Using the subplot co-ordinates, the 85-86 enumeration data, and FoxPro (version 2.6, Microsoft Corp., USA), a list of all individuals of the target species in the subplots was extracted. A 50 cm gbh cut-off point was then applied to try and ensure that leaves would be within the maximum reach of a pruning pole (roughly 6 m). The resulting list was then sorted by species and subplot and individuals randomly selected. Where possible, for each species, three individuals from a lower-slope and three individuals from a ridge site were selected. As lower-slope subplots were defined by their absence, there were no lower-slope *C. glaber*, *D. muricatus*, or *Lophopetalum beccarianum* individuals. Also, there were no ridge *Baccaurea stipulata* or *Pentacae laxifolia* individuals. In other cases there were fewer than three individuals available per site, in that case collection took place from all the trees available.

Leaf collection took place 9-11 October, 1996. A pair of leaves were collected from each selected individual. The leaves were cut from a healthy well lit branch and immediately placed in a ziplock plastic bag to prevent drying and shrinkage. For some species collection from the selected trees was not possible because of tree death or tree branches being out of reach, where alternative trees existed they were collected instead. The number of individuals collected from each species, at each site, are shown in Table 5-2.

One leaf from each pair was photocopied, dried and weighed. Each photocopied image was then scanned and its area determined with a PowerBook 5300 (Apple Inc., USA) computer using the public domain NIH Image program (version 1.59, developed at the US National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). A correction factor was determined for the process using an image of known size. The leaf was then dried for 24 h at 80 °C. The specific leaf area (SLA) for each leaf was then calculated by dividing the area by the dry weight.

A 1 cm section across the midrib was cut from the second leaf of each pair and fixed in FAE (2 % formalin, 45 % ethanol, 5 % acetic acid). A 4 mm x 10 mm piece, including the midrib, of each section was dehydrated in ethanol and embedded in wax (ParaPlast Plus, Sigma, UK). The wax blocks were sectioned using a rotary microtome (Cambridge Scientific, UK) at 7 µm thickness and the sections stained with safranin and counter-stained with fast green.

Measurements of the leaf sections took place with a light microscope and closely followed those of Tanner & Kapos (1982). Blade thickness, midrib thickness, thickness of the adaxial and abaxial epidermis (excluding cuticle), thickness of the adaxial and abaxial cuticle, thickness of palisade and non-palisade mesophyll, avoiding exceptionally wide or narrow portions were all measured. The presence of a hypodermis, transcurrent sclerenchyma and crystals was noted.

Table 5-2. Species collected for leaf structure study, their rank and peaks in distribution in the LPPs, and the number of trees sampled from ridge (R) and lower-slope (LS) sites.

Species	Family	Rank[1]	Peaks[2]	R	LS
Aglaia dubia (Merr.) Kosterm.	Meliaceae	12	-	2	3
Aporusa acuminatissima Merr.	Euphorbiaceae	11	-	-	3
Ardisia colorata Roxb.	Myrsinaceae	3	-	3	3
Baccaurea stipulata J.J.Sm.	Euphorbiaceae	13	-	-	3
Cleistanthus glaber Airy Shaw	Euphorbiaceae	10	+	3	-
Dimorphocalyx muricatus (Hk.f.) Airy Shaw	Euphorbiaceae	2	+	3	-
Fordia splendidissima (Miq.) Buijsen	Leguminoseae	4	-	3	3
Litsea caulocarpa Merr.	Lauraceae	9	-	2	1
Lophopetalum beccarianum Pierre	Celastraceae	16	+	3	-
Madhuca korthalsii (Pierre) Lam.	Sapotaceae	5	-	3	3
Mallotus penangensis Muell. Arg.	Euphorbiaceae	18	+	3	3
Mallotus wrayi King ex Hk.f.	Euphorbiaceae	1	-	3	3
Maschalocorymbus species 1 Bremek.	Rubiaceae	6	-	3	3
Pentace laxiflora Merr.	Tilliaceae	15	-	-	1
Polyalthia cauliflora Hk.f. & Thoms	Annonaceae	8	-	2	1
Polyalthia sumatrana (Miq.) Kurz	Annonaceae	17	-	3	3
Polyalthia xanthopetala Merr.	Annonaceae	14	-	3	1
Shorea fallax Meij.	Dipterocarpaceae	7	+[3]	3	3
Shorea johorensis Foxw.	Dipterocapaceae	20	(+)	-	1
Shorea parvifolia Dyer	Dipterocarpaceae	19	(+)	-	1

[1] Ranked by density ha^{-1}, from Newbery *et al.* (1996);

[2] - no peaks in distribution, + distinct peaks in distribution (Type A), (+) irregular distribution (Type B) from Newbery *et al.* (1996);

[3] Type A distribution in LPP 1, Type B in LPP 2.

RESULTS

Leaf production

New leaves, as a proportion of total leaves, were counted monthly for *Ardisia colorata*, *Cleistanthus glaber*, *Dimorphocalyx muricatus* and *Mallotus wrayi*, from ridge and lower-slope sites, in three size classes. All the species except *A. colorata* showed an increase in leaf production in April and May, with a smaller increase later in each of the years studied (Figure 5-1). Peaks in leaf flushing coincided with periods shortly after those of high sunshine hours and low soil water potentials (Figure 5-2). Sunshine hours were similar in April, 1995 and April, 1996, but sunshine hours in the immediately previous months were lower in 1996 than 1995. Sunshine data are not available after May, 1996. Soil water potentials were much lower in April, 1997 than 1995 and 1996, but 1996 was lower than 1995. April, 1996 had a lower minimum temperature than 1995 and 1997. Although surveys were not carried out January-March, few leaves were produced by the study species during this time (pers. obs.).

Unexpanded and partially expanded *M. wrayi* leaves are fragrant and appear to have two extra-floral nectaries where the petiole is inserted into the lamina. These structures are visited by ants and persist in mature leaves as glands, a taxonomic feature of the species (Airy Shaw, 1975). Unexpanded *D. muricatus* leaves are purple, and while no extra floral nectaries were observed, *D. muricatus* stems are frequently hollow and contain ant colonies. It is unclear whether these ants are pathogenic, have no effect, or are beneficial. Unexpanded leaves of *A. colorata* are red, and those of *C. glaber* white. While no measurements on leaf herbivory were made, observations suggest that herbivory of *A. colorata* leaves was low, compared with *D. muricatus* and *M. wrayi* which had similar levels of herbivory while herbivory of unexpanded *C. glaber* leaves was relatively high.

Considering only trees growing on ridge sites (Table 5-3), the proportion of leaves flushing in the April of each year studied was significantly higher than at other times of year. There were also differences from year to year, significantly more leaves were flushed in April, 1996 than in April, 1995 or April, 1997. With the exception of May, 1995, the proportion of leaves flushing at other times of year did not differ significantly. While there were significant differences among species during most months measured (Table 5-3) means at times when few leaves were produced are similar (Figure 5-1). There are interesting year to year differences among species at times of greatest leaf production. In May, 1995 *M. wrayi* trees produced significantly more leaves than the other species. In April, 1996 *C.*

glaber produced significantly more leaves than *D. muricatus* and *M. wrayi* which produced a similar number of leaves, while *A. colorata* did not increase in leaf production compared with other times of year. In April, 1997 *C. glaber*, *D. muricatus*, and *M. wrayi* all produced significantly more leaves than *A. colorata*. There were no significant differences between size classes. In summary, in the years measured *M. wrayi* trees consistently increased in leaf production in April or May, while *C. glaber* and *D. muricatus* trees increased leaf production in April in two out of three years, *A. colorata* never increased in leaf production.

Considering *A. colorata* and *M. wrayi* trees growing on ridge and lower-slope sites (Table 5-4) there are similar differences among years and within years as above. Leaf production was higher in April, 1996 and 1997 than April, 1995, *M. wrayi* trees increased leaf production at these times while *A. colorata* did not. There was no significant difference in leaf production between sites, and, again there are no consistent difference between size classes. However, although not significant, there are interesting site and size class differences for *M. wrayi* in April, 1997, in the two smaller size classes, trees on lower-slope sites produced more leaves than those on ridge sites, this situation was reversed in the largest size class. At this point there was a significant weak negative correlation between *M. wrayi* tree basal diameter and the proportion of leaves flushing on lower-slope sites (-0.23, p=0.019) but not on ridge sites (-0.11, p=0.346).

Table 5-3. Significance of difference between means of arc-sin transformed proportion of leaves flushing for *Ardisia colorata*, *Cleistanthus glaber*, *Dimorphocalyx muricatus*, and *Mallotus wrayi* trees on ridge sites from three size classes.

Month [1]	Species [2]	Size [3]	Species.Size
1995			
April ^{c}	0.399	**0.014** $^{\mathrm{I}}$	0.135
May ^{b}	**<0.001** $^{\mathrm{I}}$	0.716	0.981
June ^{a}	**<0.001** $^{\mathrm{II}}$	0.271	0.091
July ^{a}	**<0.001** $^{\mathrm{II}}$	0.177	0.199
August ^{a}	0.089	0.656	**0.019**
September ^{ab}	**0.005** $^{\mathrm{II}}$	0.561	0.229
1996			
April ^{c}	**<0.001** $^{\mathrm{III}}$	0.262	**0.011**
May ^{ab}	**<0.001** $^{\mathrm{IV}}$	0.360	0.179
June ^{a}	**<0.001** $^{\mathrm{III}}$	0.636	0.829
July ^{a}	**<0.001** $^{\mathrm{IV}}$	0.677	0.177
August ^{a}	**<0.001** $^{\mathrm{III}}$	0.882	0.615
September ^{a}	**<0.001** $^{\mathrm{II}}$	0.912	0.055
October ^{ab}	**<0.001** $^{\mathrm{II}}$	0.475	0.500
November ^{ab}	**<0.001** $^{\mathrm{IV}}$	0.498	0.351
December ^{a}	**<0.001** $^{\mathrm{III}}$	0.777	0.863
1997			
April ^{d}	**<0.001** $^{\mathrm{V}}$	0.973	0.987

[1] Months with same letters are not significantly different (Tukey compromise post-hoc, $p<0.05$);

[2] Species groups (Tukey compromise post-hoc, $p<0.05$);

$^{\mathrm{I}}$ *A. colorata* ^{a}, *C. glaber* ^{b}, *D. muricatus* ^{ab}, *M. wrayi* ^{c};
$^{\mathrm{II}}$ *A. colorata* ^{a}, *C. glaber* ^{b}, *D. muricatus* ^{a}, *M. wrayi* ^{a};
$^{\mathrm{III}}$ *A. colorata* ^{a}, *C. glaber* ^{b}, *D. muricatus* ^{c}, *M. wrayi* ^{c};
$^{\mathrm{IV}}$ *A. colorata* ^{ac}, *C. glaber* ^{b}, *D. muricatus* ^{a}, *M. wrayi* ^{c};
$^{\mathrm{V}}$ *A. colorata* ^{a}, *C. glaber* ^{b}, *D. muricatus* ^{b}, *M. wrayi* ^{b}.

[3] Size groups (Tukey compromise post-hoc, $p<0.05$);

$^{\mathrm{I}}$ Class 1 ^{a}, Class 2 ^{b}, Class 3 ^{ab}.

Table 5-4. Significance of difference between means of arc-sin transformed proportion of leaves flushing for *Ardisia colorata* and *Mallotus wrayi* trees on ridge and lower-slope sites from three size classes. Other factor interactions were not significant.

Month [1]	Site	Species	Size [2]	Species.Size
1995				
April ^{c}	0.927	0.645	0.122	0.465
May ^{c}	0.343	**0.005**	0.564	0.575
June ^{a}	0.834	**0.001**	**0.007** [1]	**0.001**
July ^{a}	0.699	**<0.001**	0.136	**0.011**
August ^{a}	0.785	**0.020**	0.595	**<0.001**
September ^{ab}	0.978	0.816	0.233	0.094
1996				
April ^{d}	0.623	**<0.001**	**0.050**	**0.037**
May ^{bc}	0.734	0.491	0.516	**0.013**
June ^{a}	0.299	**<0.001**	0.550	**0.034**
July ^{a}	0.840	**<0.001**	0.024	**0.004**
August ^{a}	0.582	**<0.001**	0.059	**0.005**
September ^{a}	0.818	**0.001**	**0.033**	**0.014**
October ^{ab}	0.683	0.052	0.957	0.434
November ^{ab}	0.351	**<0.001**	0.082	0.087
December ^{a}	0.596	**<0.001**	0.208	0.280
1997				
April ^{d}	0.245	**<0.001**	0.818	0.223

[1] Months with same letters are not significantly different (Tukey compromise post-hoc, $p<0.05$);

[2] Size groups (Tukey compromise post-hoc, $p<0.05$);

[1] Class 1 ^{a}, Class 2 ^{b}, Class 3 ^{ab}.

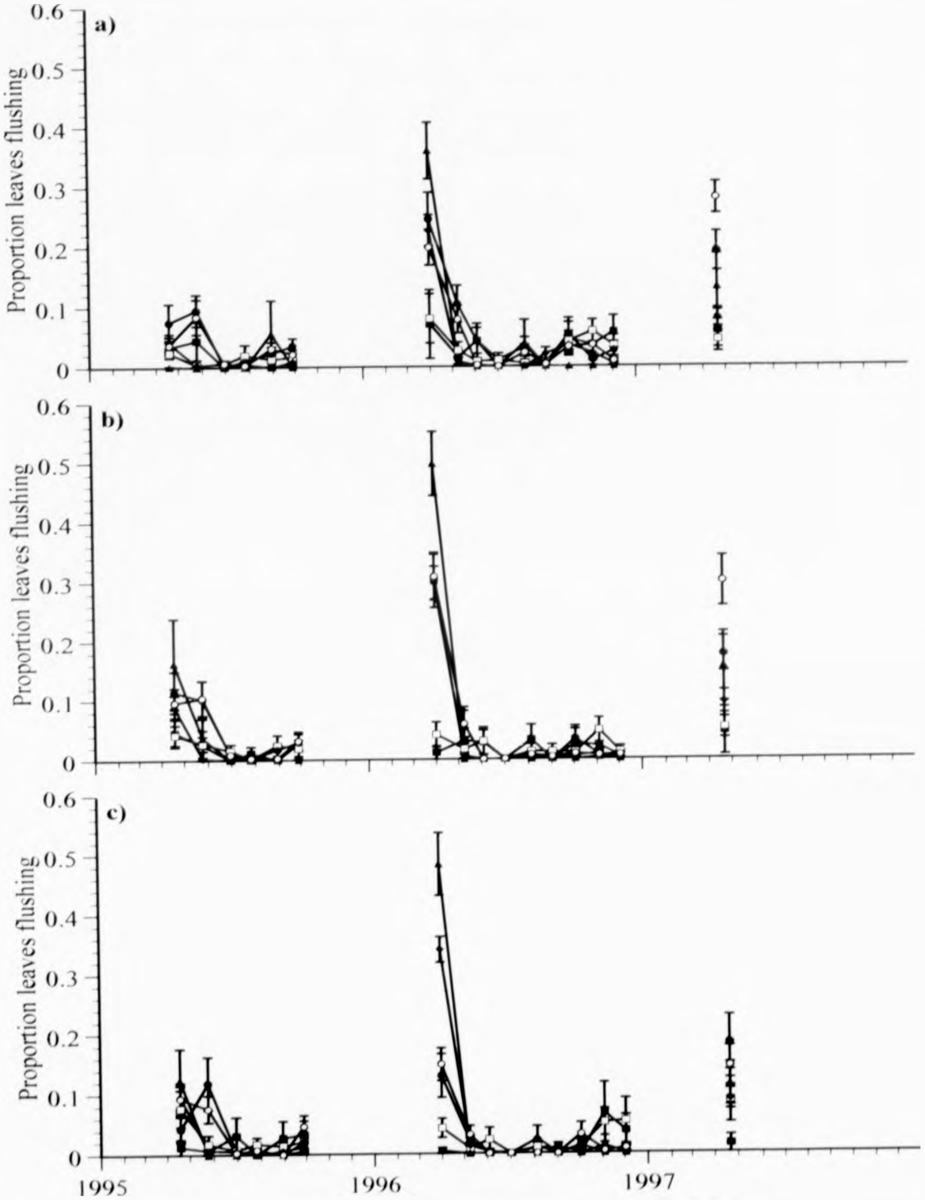

Figure 5-1. Monthly proportion of leaves flushing, for a) 0-9.9 mm, b) 10-24.9 mm and c) 25-44.9 mm dbh, *Ardisia colorata* (■), *Cleistanthus glaber* (▲), *Dimorphocalyx muricatus* (◆) and *Mallotus wrayi* (●), filled symbols are ridge sites, hollow lower-slope. Error bars are standard error of the mean.

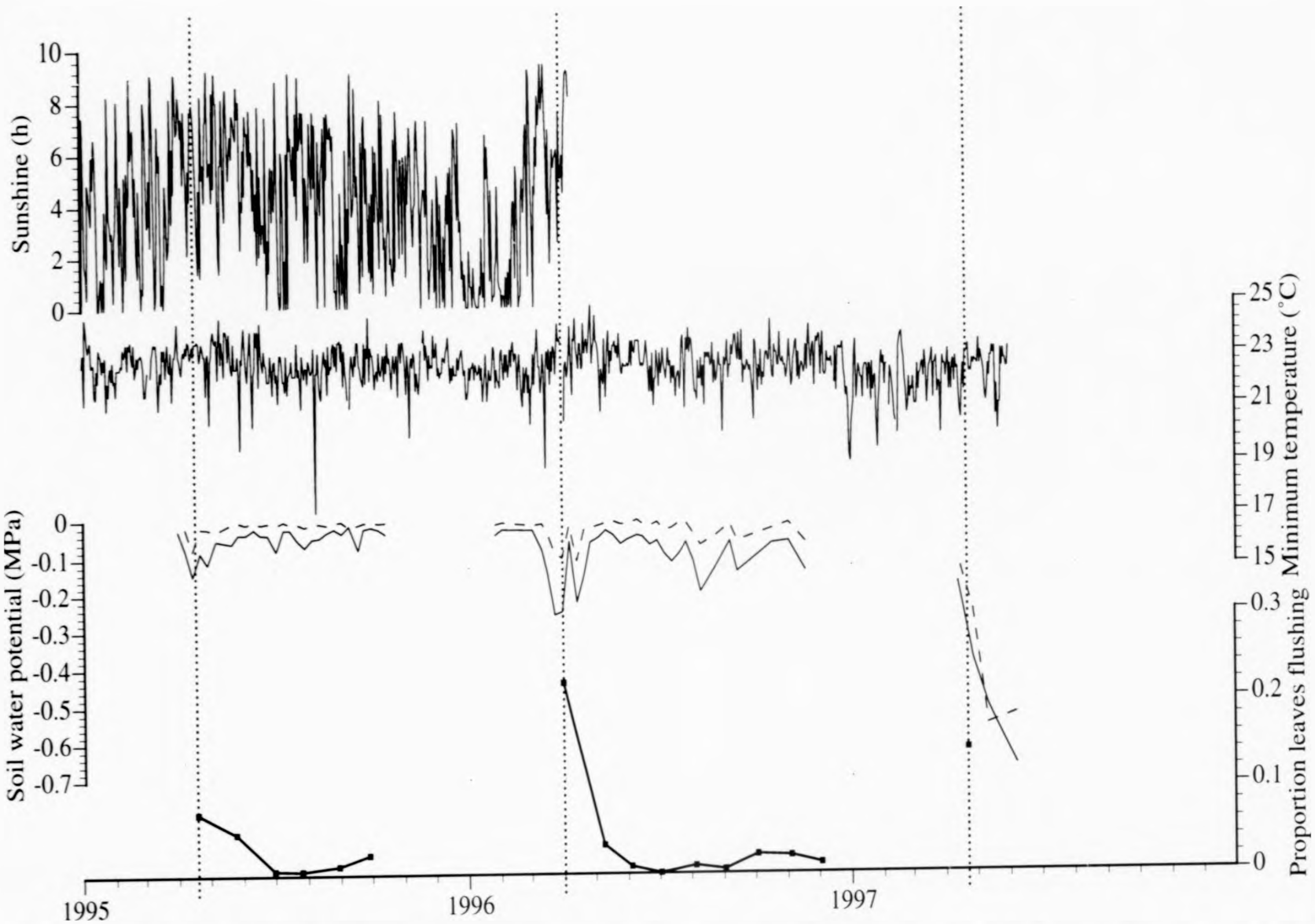

Figure 5-2. Daily sunshine and minimum temperature, weekly soil water potential on ridge (—) and lower-slope (---) sites and the mean proportion of all leaves flushing. Reference lines are at times of peak flushing for each year.

Flowering and fruiting

The number of *A. colorata*, *C. glaber*, *D. muricatus*, and *M. wrayi* trees flowering and fruiting, as a proportion of total trees, were counted monthly, from ridge and lower-slope sites, in three size classes. Peaks in flower production occurred at the same time as peaks in leaf production, April and May. Few trees flowered in 1995 compared to 1996, while no trees flowered in April, 1997 (Figure 5-3). 1996 was a 'mast flowering' year when many canopy species also flowered. *A. colorata* trees in the study group were never observed to flower. Elsewhere, during the whole period of study, one 30 cm tall *A. colorata* was observed fruiting and one small tree flowering. Therefore, *A. colorata* trees studied were large enough to be mature. *C. glaber*, *D. muricatus*, and *M. wrayi*, in all size classes, flowered, but few *D. muricatus* and *M. wrayi* in the smallest size class, hence it appears that *C. glaber* becomes mature at a smaller size. During both flowering years more *C. glaber* trees flowered than *D. muricatus* and *M. wrayi* trees. More *M. wrayi* trees on ridge sites flowered than on lower-slope sites and the difference was greater for size class two than three. Euphorbiaceae flowers are unisexual, and observations on the flowering trees suggest that all the study species are monoecious. Flowering *D. muricatus* branches stagger male and female flower opening, male flowers opening first. Both *D. muricatus* and *M. wrayi* flowers were seen to be visited by small bees, visitors to *C. glaber* flowers were not observed.

Fruit set in 1995 was lower than that in 1996 (Figure 5-4). In 1995 and 1996 fruit set for *D. muricatus* and *M. wrayi* was lower in the in the two smaller size classes compared to the larger size class, but similar in all size classes for *C. glaber*. While more *M. wrayi* trees on ridge than lower-slope sites produced flowers, more trees on lower-slope sites set fruit. Fruit on *M. wrayi* trees disappears faster than on *D. muricatus* and *C. glaber* trees suggesting that *M. wrayi* fruit ripens faster. Both *D. muricatus* and *M. wrayi* fruit are explosively dehiscent, but differ in their fruit structure. *D. muricatus* fruit have an additional outer fleshy layer surrounding a hard tri-valved capsule, this outer layer dries out and falls off before dehiscence occurs. *C. glaber* fruit are fleshy and indehiscent and so may be animal dispersed. *M. wrayi* trees set more fruit per tree than *D. muricatus* or *C. glaber* (data not shown).

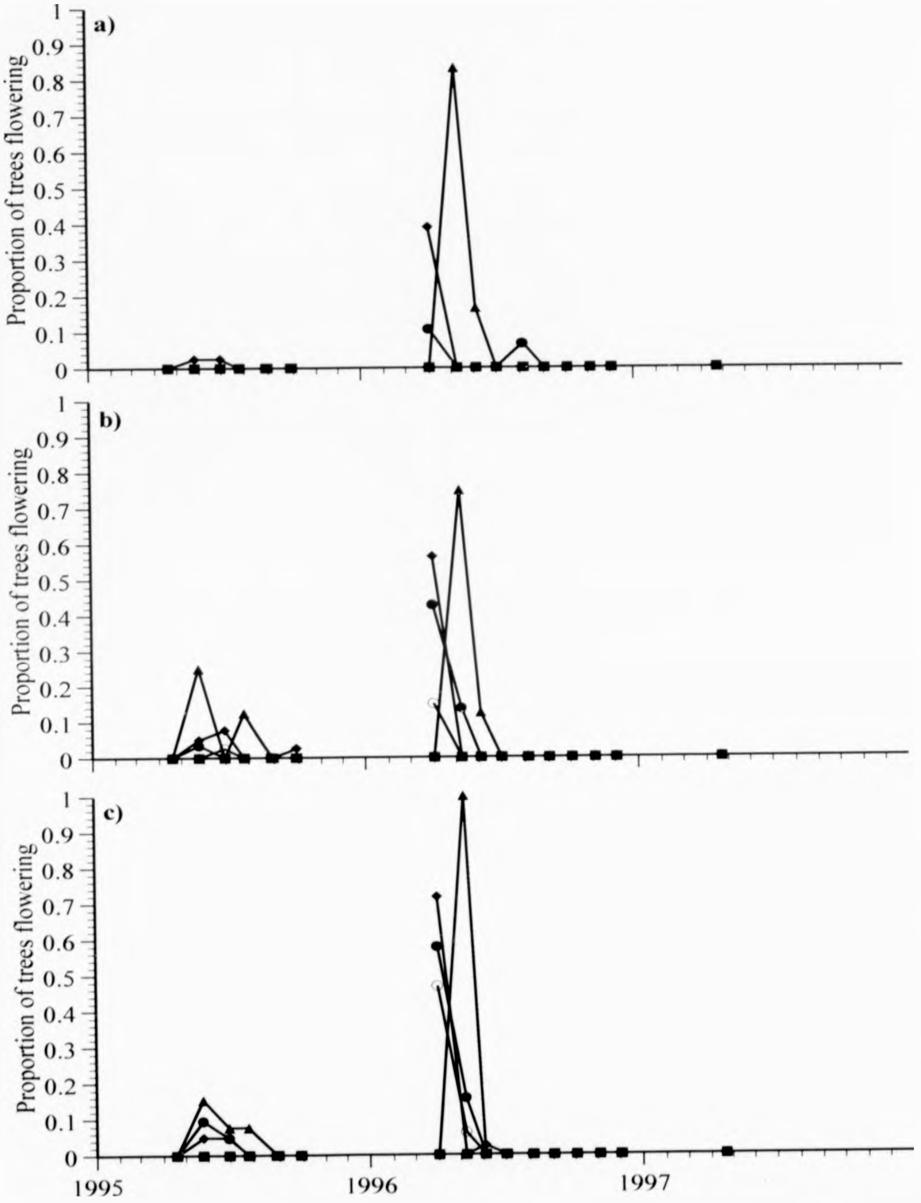

Figure 5-3. Proportion of trees flowering. Symbols and size classes as Figure 5-1.

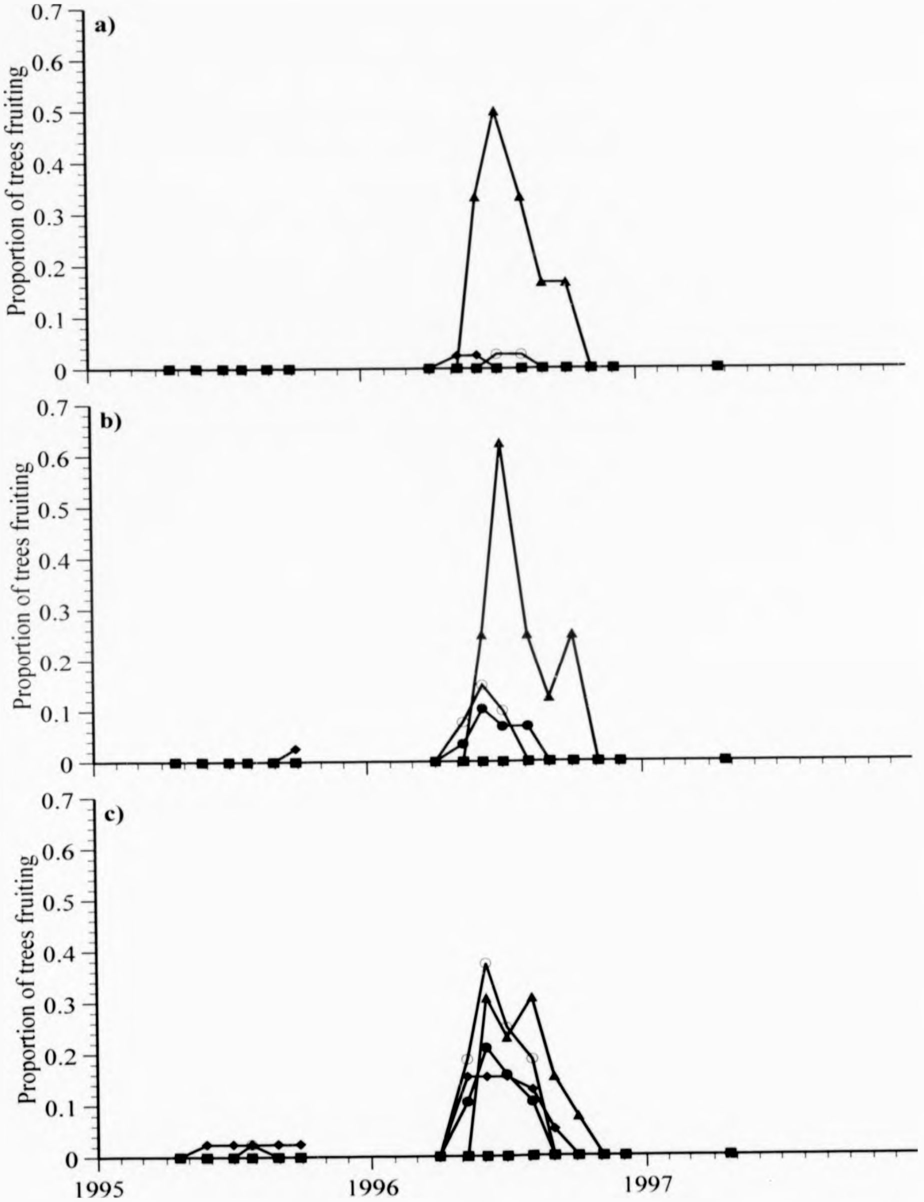

Figure 5-4. Proportion of trees fruiting. Symbols and size classes as Figure 5-1.

Leaf life-span

Leaf life-span for *A. colorata*, *D. muricatus*, and *M. wrayi* was estimated using the leaf production data for 1996. There were too few complete records for *C. glaber* in size class one and two, and for *M. wrayi* ridge in size class three for reliable estimates to be calculated (Figure 5-5). All estimates in size class three are probably biased because only those trees with branches within reach were included. Of the study trees 22.9 % *A. colorata*, 0 % *C. glaber*, 8.5 % *D. muricatus* and 14.5 % *M. wrayi*, did not produce any new leaves during 1996 and were excluded from the calculation.

On ridge sites there was a significant difference between species ($F_{3,153}$=5.15, p=0.020) with *A. colorata* leaves significantly longer lived, than *D. muricatus* and *M. wrayi* leaves, but there was no significant difference between *C. glaber* and the other species (Tukey compromise post-hoc, $p<0.05$). There was no significant difference between size classes ($F_{2,153}$=1.02, p=0.363).

Comparing *A. colorata* and *M. wrayi* between sites, there was no significant difference between sites ($F_{1,157}$=0.36, p=0.550) or size classes ($F_{2,157}$=2.03, p=0.134) but again *A. colorata* leaves were significantly longer lived than *M. wrayi* leaves ($F_{1,157}$=44.46, $p<0.001$).

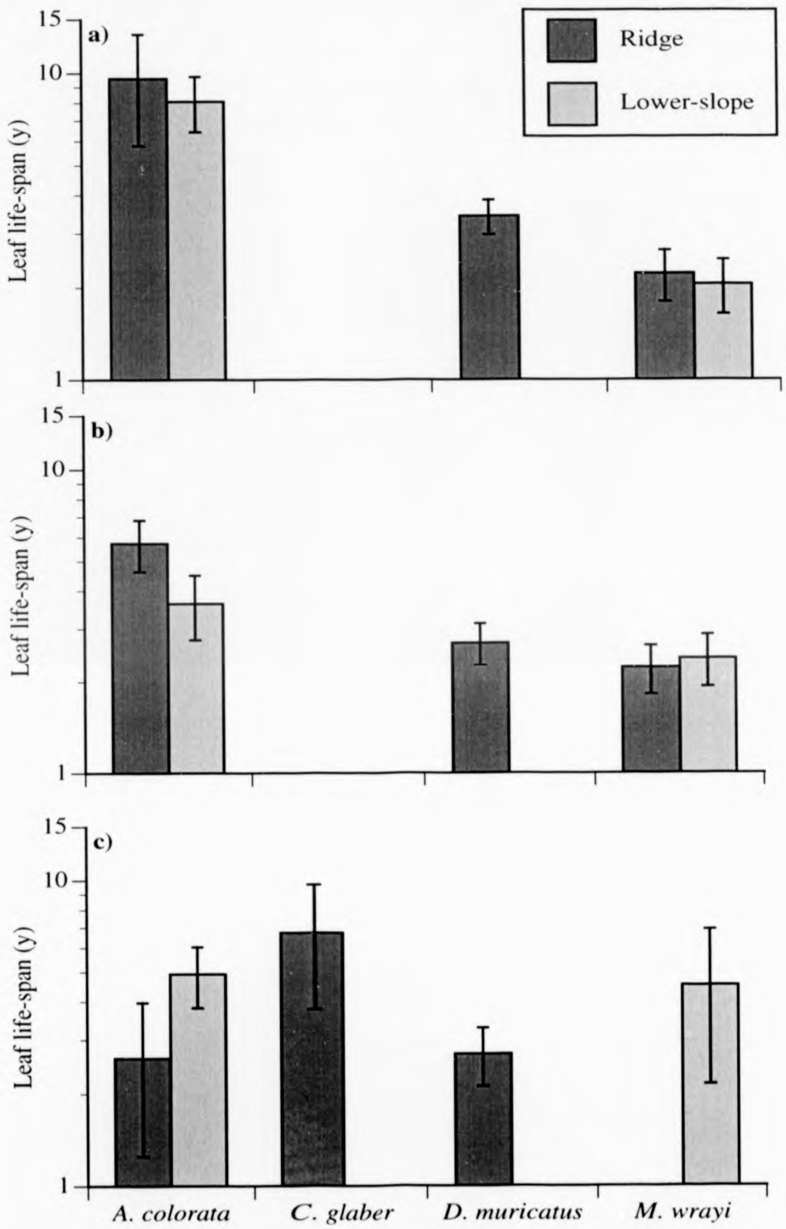

Figure 5-5. Leaf life-span of *Ardisia colorata*, *Cleistanthus glaber*, *Dimorphocalyx muricatus* and *Mallotus wrayi* trees from ridge and lower-slope sites. Size classes as Figure 5-1.

Leaf structure

Leaf characters of the 20 most common species in LPPs were measured. Leaves of all species had sclerenchyma while none had a hypodermis layer. Only *Polyalthia sumatrana* had transcurrent sclerenchyma and only *Baccaurea stipulata* and *Polyalthia sumatrana* crystals. Other measurements are shown in Table 5-5.

Comparing the phenology study species, *A. colorata*, *D. muricatus* and *M. wrayi* have similar sized leaves, bigger than *C. glaber*. *C. glaber* has the largest specific leaf area (SLA), followed by *M. wrayi* then *D. muricatus* then *A. colorata*. *A. colorata* leaves are thickest, followed by *D. muricatus* then *C. glaber* then *M. wrayi*. *A. colorata* and *D. muricatus* have a similar palisade to mesophyll ratio, smaller than *M. wrayi* and *C. glaber*. *D. muricatus* and *A. colorata* leaves have thicker cuticles than *C. glaber* and *M. wrayi* leaves.

Comparing the 20 most common species, means for ridge species, ubiquitous species and lower-slope species are similar for all characters and within group variation of characters is high. For example, excluding compound leafed species, leaf area ranges from 89.4-347.7 cm^2 for ridge species, 47.4-364.0 cm^2 for ubiquitous species, and 18.3-196.4 cm^2 for lower-slope species. With the exception of *Litsea caulocarpa*, ubiquitous trees, of the same species, from lower-slope sites have a greater leaf area than trees from ridge sites. Excluding *A. colorata* and *M. wrayi* there is also a corresponding increase in SLA. For the ubiquitous species, between sites, other leaf characters are similar, and where there are differences, including for lamina thickness, they are not consistent among species.

There are significant correlations between SLA and lamina, palisade and mesophyll thickness (Table 5-6). There is also a significant correlation between lamina thickness and cuticle thickness, the correlation between epidermis thickness and lamina thickness is lower. So thicker leaves have proportionally thicker epidermal cuticles, than thinner leaves.

Table 5-5. Leaf characters of the 20 most common species in the LPPs. Ridge species are confined to ridge subplots, lower-slope species to lower-slope subplots and ubiquitous species are found in both ridge (R) and lower-slope (LS) subplots. For families, authorities and replication see Table 5-2.

									Adaxial epidermis		Abaxial epidermis	
Species	Leaf area (cm^2)	Specific leaf area ($cm^2 g^{-1}$)	Lamina thickness (µm)	Midrib thickness (µm)	No palisade cell layers	Palisade thickness (µm)	Mesophyll thickness (µm)	Palisade: mesophyll ratio	Thickness (µm)	Cuticle thickness (µm)	Thickness (µm)	Cuticle thickness (µm)
Ridge												
Cleistanthus glaber	89.4	363.6	121.0	522.8	1	29.3	57.5	0.55	12.6	1.0	10.9	1.1
Dimorphocalyx muricatus	347.7	286.0	212.3	1895.0	1	19.5	190.2	0.11	18.4	3.9	17.2	4.1
Lophopetalum beccarianum	257.9	290.1	199.0	1153.0	1	30.5	103.6	0.30	16.7	3.2	9.2	4.6
Mean	231.7	313.2	177.4	1190.3	1	26.4	117.1	0.24	15.9	2.7	12.4	3.3
Ubiquitous												
Aglaia dubia (R) [1]	96.6	276.6	137.0	632.4	2	25.3	102.9	0.24	9.2	3.2	6.9	2.9
Aglaia dubia (LS) [1]	116.0	310.2	133.6	452.1	2	22.4	82.8	0.27	8.2	4.7	6.9	4.3
Ardisia colorata (R)	247.8	240.7	308.2	1750.0	1	44.8	238.8	0.29	15.5	4.7	11.2	4.3
Ardisia colorata (LS)	304.3	187.2	315.1	1815.1	1	43.1	251.7	0.17	16.1	4.6	11.5	5.1
Fordia splendidissima (R) [1]	861.3	193.3	137.0	756.9	2	51.7	62.9	0.96	13.8	1.7	7.8	1.7
Fordia splendidissima (LS) [1]	1180.0	286.9	132.4	698.6	1	29.3	67.8	0.43	16.1	1.4	9.2	1.2
Litsea caulocarpa (R)	254.0	441.2	222.6	969.2	2	44.8	126.7	0.35	17.2	1.1	12.1	1.1
Litsea caulocarpa (LS)	138.2	287.9	212.3	1164.4	1	36.2	69.0	0.53	20.7	1.7	17.2	1.7
Mallotus penangensis (R)	248.2	257.2	132.4	867.6	1	35.6	71.8	0.54	14.9	2.3	8.6	1.9
Mallotus penangensis (LS)	344.3	274.1	121.0	819.6	1	31.6	62.7	0.51	11.5	2.3	7.2	3.0

Table 5-5 continued

Species	Leaf area (cm^2)	Specific leaf area (cm^2 g^{-1})	Lamina thickness (µm)	Midrib thickness (µm)	No. palisade cell layers	Palisade thickness (µm)	Mesophyll thickness (µm)	Palisade: mesophyll ratio	Adaxial epidermis		Adaxial epidermis	
									Thickness (µm)	Cuticle thickness (µm)	Thickness (µm)	Cuticle thickness (µm)
Ubiquitous (continued)												
Mallotus wrayi (R)	236.6	344.9	78.8	739.7	1	16.4	43.1	0.39	6.9	1.5	7.8	1.1
Mallotus wrayi (LS)	306.7	318.7	77.6	835.6	1	19.5	44.2	0.45	6.6	0.9	6.8	1.0
Maschalocorymbus species 1 (R)	355.9	301.9	137.0	1180.3	1	21.3	75.3	0.30	28.7	2.0	8.6	1.3
Maschalocorymbus species 1 (LS)	362.9	337.8	155.3	1207.8	2	26.4	74.7	0.38	31.0	1.7	14.9	1.4
Polyalthia cauliflora (R)	47.4	381.0	140.4	404.1	1	33.6	67.2	0.50	17.2	1.1	13.8	1.1
Polyalthia cauliflora (LS)	54.4	425.3	150.7	479.5	1	24.1	62.0	0.39	13.8	0.9	13.8	0.9
Polyalthia sumatrana (R)	126.0	244.4	242.0	662.1	1	41.7	160.9	0.26	14.9	4.0	9.2	4.6
Polyalthia sumatrana (LS)	127.2	261.4	278.5	687.2	1	42.5	181.6	0.23	14.3	4.6	8.1	5.2
Polyalthia xanthopetala (R)	161.4	284.6	132.4	847.0	1	35.6	65.5	0.55	12.6	1.7	11.5	1.0
Polyalthia xanthopetala (LS)	364.0	288.9	150.7	876.7	1	34.5	69.0	0.50	13.8	0.9	10.3	0.9
Shorea fallax (R)	220.9	309.6	130.1	840.2	1	18.4	75.9	0.24	16.1	2.9	6.9	1.4
Shorea fallax (LS)	230.9	339.0	95.9	995.4	1	25.9	32.8	0.84	14.9	2.2	8.6	1.0
Mean (R)	266.0	295.4	163.5	877.2	1.2	33.6	99.2	0.41	15.2	2.4	9.5	2
Mean (LS)	320.8	301.6	165.7	912.0	1.1	30.5	90.8	0.43	15.2	2.4	10.4	2.3

Table 5-5 continued

Species	Leaf area (cm^2)	Specific leaf area ($cm^2\ g^{-1}$)	Lamina thickness (µm)	Midrib thickness (µm)	No. palisade cell layers	Palisade thickness (µm)	Mesophyll thickness (µm)	Palisade: mesophyll ratio	Adaxial epidermis Thickness (µm)	Adaxial epidermis Cuticle thickness (µm)	Adaxial epidermis Thickness (µm)	Adaxial epidermis Cuticle thickness (µm)
Lower-slope												
Aporusa acuminatissima	90.6	263.9	154.1	866.4	1	22.4	81.9	0.27	18.1	1.3	6.9	1.3
Baccaurea stipulata	67.1	241.7	319.6	1002.3	2	47.1	158.1	0.30	33.9	1.6	15.5	1.4
Madhuca korthalsii	676.1	200.4	315.1	2328.8	2	37.9	215.5	0.18	15.5	1.7	10.3	1.7
Pentace laxiflora	18.3	304.3	130.1	417.8	1	31.0	53.5	0.58	22.4	1.7	15.5	1.7
Shorea johorensis	196.4	311.8	116.4	726.0	2	32.8	60.3	0.54	13.8	2.2	10.3	2.2
Shorea parvifolia	61.0	406.4	109.6	616.4	1	25.9	63.8	0.41	22.4	0.9	8.6	0.9
Mean	184.9	288.1	190.8	993.0	1.5	32.9	105.5	0.38	21.0	1.6	11.2	1.5
Overall weighted mean	266.4	297.9	170.9	942.3	1.2	31.7	99.2	0.39	16.4	2.2	10.4	2.2

[1] compound leaf

Table 5-6. Correlations between leaf characters. Values in bold are significant at the 95 % level.

	Specific leaf area	Lamina thickness	Palisade thickness	Mesophyll thickness	Adaxial epidermis	Abaxial epidermis	Adaxial cuticle thickness
Lamina thickness	**-0.50**	-	-	-	-	-	-
Palisade thickness	**-0.44**	**0.65**	-	-	-	-	-
Mesophyll thickness	**-0.52**	**0.92**	**0.49**	-	-	-	-
Adaxial epidermis	-0.02	0.33	0.18	0.14	-	-	-
Abaxial epidermis	0.14	**0.36**	0.22	0.21	**0.55**	-	-
Adaxial cuticle thickness	**-0.49**	**0.48**	0.17	**0.65**	-0.16	-0.13	-
Abaxial cuticle thickness	**-0.49**	**0.55**	0.26	**0.68**	-0.16	-0.07	**0.93**

DISCUSSION

Timing and magnitude of leaf and flower production

The bulk of previous tropical studies have been qualitative or semi-quantitative (e.g. Medway, 1972; Frankie *et al.*, 1974). Previous quantitative phenology studies (e.g. Reich & Borchert, 1984; Wright, 1991; Aide, 1993) have presented the results as the proportion of the total annual production for each species so differences in production between years and species are masked. The use of the proportion of leaves flushing at each time avoids this difficulty and allows statistical analyses to be carried out. A further advantage is that a complete years data is not required. Another important point is that the individuals here were selected at random from an unbiased population, rather than those visible from some location (e.g. Medway, 1972; Putz, 1979), along transects (e.g. Wong, 1983) or selected by some undisclosed procedure (e.g. Frankie *et al.*, 1974; Reich & Borchert, 1984).

Cleistanthus glaber, Dimorphocalyx muricatus and Mallotus wrayi.

Cleistanthus glaber, *Dimorphocalyx muricatus* and *Mallotus wrayi* each had a peak in leaf and flower production at the driest and sunniest time of each year studied. The magnitude of the peak in production varied from year to year, production was low in the wettest year, high in the moderately dry year and intermediate in the driest year. South-East Asian phenology studies are few. In West Malaysia, both Putz (1979), looking at canopy species, and Wong (1983), looking at understorey species, conclude that phenology is aseasonal. These findings are possibly a result of qualitative sampling, the species here produced most of their leaves during one month, but also produced a few leaves at other times, so simply scoring trees as 'flushing' or 'not-flushing' would suggest aseasonality. Further, in other studies, sample sizes were low with often only one individual per species. Medway (1972) looking at canopy species also in West Malaysia over a nine year period found that most species showed a seasonality in leaf and flower production. Heideman (1989), in the central Philippines found a peak in flowering during the dry season and early wet season for both canopy and understorey trees.

Flower production was different in the two years surveyed. Flowering of Dipterocarpaceae and most other canopy trees in the region is a super-annual event ('mast' flowering) that occurs every two to ten years (Ashton *et al.*, 1988 and references therein). Although the maximum observed peak in flowering here coincided with a mast year (1996), the study species flowered in two out of three years of the study, and other common understorey species such as *Baccaurea stipulata*, and *Polyalthia spp.* were observed to flower in all three study years. Hussin (1994) observed flowering of many understorey species in both 1990 (a mast year) and 1991 (a non-mast year). Therefore, it seems that the majority of understorey species flower far more frequently than canopy species.

In other locations, Gentry & Emmons (1987) examined understorey flower and fruit phenology from 13 neotropical sites in 6 countries plus African and Australasian localities. Areas with weak dry seasons and rich soils had more fertile plant species than those with strong dry seasons and poor soils. Frankie *et al.* (1974) compared wet and dry Costa Rican sites and found that at the dry site most leaf production occurred at the onset of rains while at the wet site most leaf production occurred during the dry season. However, reinterpretation of the data by Reich (1995) shows that wet forest production is less seasonal than Frankie *et al.*'s figures suggest. Species at the dry site were more seasonal than those at the wet site in flower production. In Panamanian moist forest four out of five shrub species had a seasonal peak in leaf production (Wright *et al.*, 1992) At the same site, Aide (1993), reports marked variation in synchrony among 32 understorey species. In

Rwandan montane forest Sun *et al.* (1996) found that leaf production peaks in the dry season.

The findings for these three study species are consistent with the hypothesis of Wright & van Schaik (1994), that light limited species in seasonal environments have been selected to coincide with seasonal peaks of irradiance. Aide (1993), in Panamanian moist forest, also demonstrated that species with synchronous leaf flushing suffered less leaf predation than asynchronous species. No quantitative measurements were made on herbivory, but observations suggest that herbivory was high on *C. glaber*, low on *D. muricatus* and *M. wrayi* and very low on *A. colorata* so there is not a clear relationship between seasonality and leaf predation. Observations also suggest that all species except *C. glaber* have chemical or ant defence against herbivory.

There is evidence that *M. wrayi* trees on ridge sites suffered some diurnal drought stress in April, 1997, and that seedling assimilation was water limited (Chapter 4). The reduction in leaf production for *M. wrayi* on ridge sites in the smaller and more shallowly rooted size classes compared with the largest size class suggests that leaf production may have been water rather than light limited at this time. Wright *et al.* (1992) found that only the most deeply rooted of five shrub species produced leaves in the dry season, while drought reduced leaf production in a more shallowly rooted species.

Timing of fruit production and ripening was largely determined by timing of flower emergence, and there were little differences among the study species. The difference in fruit set for *M. wrayi* between ridge and lower-slope sites suggests that *M. wrayi* fruit production may be limited by water stress on ridge sites. Fruit set could also be pollen limited but Niessenbaum (1993) found that fruit set of an understorey shrub in the USA was light and not pollen limited. Timing of fruit ripening (fruit disappearance), in 1996, coincided with a minor dry period. A dry spell may be required to dry the dehiscent fruit. In dry forest in Ghana dry-fruited species fruited in the dry season and fleshy fruited species in both wet and dry seasons (Lieberman, 1982).

Ardisia colorata

Ardisia colorata trees did not flower and had no strong peak in leaf production. Observations on other understorey species at DVFC suggest that this behaviour is atypical. Most other understorey species were seen to flower (see above) at some point and produce many new leaves, especially in April, 1996. *A. colorata* leaves have one of the lowest SLAs and are longer lived than the other species studied. Assimilation rates of *A. colorata* leaves are lower than those of *M. wrayi* (Chapter 4) and photoinhibition occurs at high light levels.

Generally long-lived leaves have lower photosynthetic rates than shorter lived leaves (Reich *et al.*, 1992). Therefore, *A. colorata* leaves may not have the photosynthetic capacity to respond to increased sunlight. Alternatively *A. colorata* may be very drought sensitive and hence does not produce leaves at times of year when drought is more likely to occur. Reich & Borchert (1984) in tropical dry forest found that drought sensitive species produced leaves in the wet season, but their drought sensitive species leaves were mesomorphic, while *A. colorata* has xeromorphic leaves.

While differences in phenology were found among species, there were no clear differences found between ridge and ubiquitous species. In terms of timing and degree of leaf production *D. muricatus* and *M. wrayi* were similar to each other, while *A. colorata*, with lower leaf production, and *C. glaber*, with higher leaf production were different.

Proximal cues and other mechanisms

When considering the mechanism for the synchrony of leaf and flower production it is important to distinguish between the timing and magnitude of production. Even if endogenous rhythms determine timing, the differences in production between years found here suggest that that an environmental factor determines magnitude. It is also important to distinguish between bud initiation (the development of buds), and bud break (the release of buds from dormancy), and to consider bud development time. There are three points where environmental cues or endogenous rhythms may be important, the initiation of buds, the differentiation of buds into flowers of leaves, and bud break. Ashton *et al.* (1988) conclude that the proximal cue for dipterocarp mast flowering is unusually low minimum night temperatures which results in the initiation of flower rather than leaf buds 9-16.5 weeks before bud break and flower emergence. In tropical dry forest in Costa Rica leaf and flower bud dormancy is broken by rain or irrigation (Borchert, 1994). Wycherley (1973) found that flower bud break in orchids was a result of the sudden decrease in temperature associated with storm events. There is evidence that flower bud break in coffee is a result of water stress (Alvim, 1960) but buds initiate in response to photoperiod (Piringer & Borthwick, 1955). In weakly seasonal tropical forests increases in plant growth at times of high irradiance or changes in water relations at times of low water potentials and the associated physiological changes could break bud dormancy. A possible hypothesis is that the year to year variation in any proximal cue may mean that in some years when seasonality, and the cue, are weak some buds remain dormant for longer than others, hence the magnitude of the bud break cue also determines magnitude of any peak in production. It is suggestive that in 1995, when flower and leaf production was low, the production peak was spread over a longer period than 1996 when production was high. Differences in rainfall patterns have been found to affect the within population variation of flowering time of a Mexican tropical shrub (Domínguez & Dirzo, 1995).

What is the mechanism for the synchrony of flower and fruit production at DVFC? The present data do not allow a definitive answer, for which experimental manipulation of environmental factors would be required. Also required is more knowledge about the development of the study species. However, remembering that trees on ridge sites experience more drought stress and, possibly, higher light levels and lower humidities, than trees on lower-slope sites, and that trees in smaller size classes are more shallowly rooted, and hence experience greater drought stress than larger trees, some interesting points can be raised. A greater number of *M. wrayi* trees flowered on ridge than lower-slope sites. The differences among size classes and between years suggest that plant water stress may break flower bud dormancy. During 1995, most trees in a *D. muricatus* population growing on a chert outcrop (Figure 2-2) flowered, while few trees elsewhere in the forest flowered (pers. obs.). It is likely that the trees growing on this loose rock experience greater drought stress than elsewhere. No size or site differences were found in leaf production, suggesting that water stress is not important, Wright (1991) found that in Panamanian moist forest irrigation of shrubs disrupted the timing of, but did not delay, nor affect the magnitude of, leaf production. A drop in minimum temperature was observed each year before the leaf production peak but drops at other times did not precede leaf production and it seems unlikely that minimum temperature is important in the buffered understorey environment. Incidentally, in 1996, the period of low temperatures before a mast fruiting predicted by Ashton *et al.* (1988) was not observed. If light is the proximal cue for bud break there is an apparent contradiction between the finding that leaf production increases at sunnier times and the finding that there is no relationship between individual tree leaf production and light environment. Bentley (1979), reported a similar lack of relationship between light measurements and past leaf production. This contradiction is resolved if trees are responding to the seasonal increase in light, which would be the same for ridge and lower-slope sites, rather than the magnitude. The increase in sunshine hours from March to April was greatest in the year with the biggest proportion of leaves flushing. Wright (1991) suggests that the gradual breakdown in synchrony in irrigated shrubs is a result of the disruption of endogenous rhythms entrained to a water stress cue, and it is possible that endogenous rhythms are important here in bud initiation. Loubry (1994), in seasonal forest in French Guiana, concluded that there were both endogenous and exogenous components to the leaf-fall periodicity. Wright & Cornejo (1990) and Wright (1991) also propose that atmospheric factors like humidity may be important in the timing of leaf fall and production but again here there were no differences between sites while the data available (Chapter 2) suggests that there are differences in humidity.

In summary, the hypothesis that the environmental cue for bud break is the increase in bright sunshine and the resulting increase in plant production, or mild drought stress, is attractive because these cause well understood changes in plant hormone distribution which could cause bud break. There is evidence here that drought stress causes flower bud break and seasonal increases in bright sunshine leaf bud break. However, the data available does not make it possible to completely rule out other cues like short term temperature changes or atmospheric humidity changes, or endogenous rhythms. The current data and lack of knowledge about the species development mean that no conclusions can be reached about but initiation or differentiation.

Leaf structure, life-span and drought adaptation

Few previous studies have examined community leaf structure in tropical lowland rain forest sites, and there are a disproportionate number of studies in other, less extensive, tropical habitats (Table 5-7). Also note the monograph of Roth (1995) which reports much detailed information of leaf structure for many montane Venezuelan species, but unfortunately fails to summarise the data succinctly. In comparison with other lowland forest the leaves of the study species are of similar thickness but have higher specific leaf areas (SLA). However, the mean SLA values are within the range of the species of Wright *et al.* (1992). The cuticles alone of the study species were similar in thickness to the cuticles plus cell walls of Grubb (1974). As here, in most broad leafed woody vegetation sites there is a negative correlation between SLA and lamina thickness and a positive correlation between lamina thickness and cuticle thickness (Turner, 1994). The study species are more mesomorphic than species from both montane and heath forest habitats. Note though that the SLA values of Tanner & Kapos (1982) and Sugden (1985) are underestimates because dried (and hence shrunk) herbarium specimen leaves were used. Other studies have also measured stomatal density and guard cell length, unfortunately facilities were not available to do this at DVFC. Jansen & Baas (1973) found that the leaf vascular system of *Lophopetalum beccarianum* was very complex. There seem to be no published accounts of the leaf anatomy of the other study species. As the species sampled were ranked by abundance rather than basal area, there is a bias against canopy species. Also, the morphology of the leaves produced by canopy species in an understorey environment (as sampled here) is different from those produced in the canopy (Meijer & Wood, 1964). Roth (1984) found that many Venezuelan lowland rain forest species had a wide variation in leaf anatomy within individual trees.

There were no clear differences in leaf structure among species groups. Abrams *et al.* (1994), in central Pennsylvania, found differences in species leaf structure between sites of different water availability, but there was no overlap in species composition between sites.

Mulkey *et al.* (1992) found that there were differences in leaf structure between leaves produced by a Panamanian shrub between wet and dry seasons. It is therefore possible that the species at DVFC may produce more xeromorphic leaves in drier years. It would be interesting to see if there is a difference in leaf morphology between shallowly rooted seedlings and larger trees. Within the ubiquitous species group it appears that trees from ridge sites have smaller leaves and a lower SLA than trees of the same species from lower-slope sites. Similarly, Zipperlen (1997) at DVFC found that dipterocarp seedlings growing in an exposed site had a lower SLA in an 'exposed' logged forest site compared to a primary forest site. Abrams *et al.* (1990) found differences in leaf morphology of *Fraxinus pennsylvanica* grown from seed from sites of different water availability. This finding suggests that the differences between *Fraxinus* populations were genetic and leaf morphology was not plastic. It is likely that here gene mixing occurs between ridge and lower-slope sites at DVFC, so the differences found here may be a result of phenotypic plasticity. Although differences in water availability between sites may result in the differences in leaf structure, there is also evidence that ridges are lighter than lower-slope sites. As there are plastic differences in morphology between sun and shade leaves (e.g. Abrams & Kubiske, 1990) the differences in light may confound any differences in water availability.

Estimates of *A. colorata* leaf life-span are longer than those of *D. muricatus* and *M. wrayi*. The estimates are an average at the whole plant or branch level rather than leaf level. Therefore, it is not possible to distinguish between a tree that produces leaves, some of which are eaten immediately the rest of which are relatively long lived and a tree that produces intermediately lived leaves on which predation is low. Observations suggest that *C. glaber* may be in the former class. As wet forest species are not deciduous estimates of leaf life-span are longer than in moist and dry forest sites (Reich, 1995). Bentley (1979), in Costa Rica, found for 40 understorey species 39 % of leaves were retained for > 2 y but that there was considerable variation among species. In Mexico mean lifespan for different *Piper* species varied from 0.2-2.2 y, with gap species at the lower end and understorey species at the upper end of the range (Williams *et al.*, 1989). Reich (1995) calculated the mean for all tropical wet sites to be 2.1 y, similar to the values for *D. muricatus* and *M. wrayi*, but *A. colorata* estimates are considerably higher. There is not a clear relationship between estimated life-span and leaf morphology. *M. wrayi* leaves have a higher SLA than *D. muricatus* but a similar estimated life-span. In a comprehensive review of leaf life-span in relation to leaf and plant characteristics across diverse ecosystems Reich *et al.* (1992) found that generally SLA does decrease as leaf life-span increases. However as Williams *et al.* (1989) point out it is important to distinguish between 'cheap' cellulose and 'expensive' leaf protein and variation in both affects SLA. For example, *D. muricatus* leaves may have a similar amount of protein as *M. wrayi* leaves but more cellulose so construction costs could be similar.

Taking the species for which water relations data are available (Chapter 4) *D. muricatus*, a ridge species, which is more drought tolerant, has more xeromorphic leaves than the less drought tolerant species, *M. wrayi* a ubiquitous species. Abrams *et al.* (1994) demonstrated that both midday water potential and ψ_{π} at zero turgor decrease with decreasing SLA. However, using leaf structure alone as a measure of drought tolerance is inadvisable. Differences in leaf structure among species will reflect taxonomic differences as well as adaptation to the environment. Drought evaders, species that access water unavailable to other species, might be expected to have mesomorphic rather than xeromorphic leaves. Trees in montane forest with xeromorphic leaves are not drought tolerant (Kapos & Tanner, 1985). So in terms of phenology, leaf structure and life-span ubiquitous, ridge and lower-slope species cannot be separated into clear guilds.

Table 5-7. Published leaf structure data means from different tropical forests and one temperate forest. Within study groups are different sites (roman) or different species groups (italic).

	Specific leaf area ($cm^2 g^{-1}$)	Lamina thickness (μm)	Adaxial outer wall thickness (μm)	Abaxial outer wall thickness (μm)	Palisade non-palisade ratio
Tropical lowland rain forest					
Indonesia [1]	82.3	99.4	3.6	2.9	0.27
New Britain [2]	-	230	3.8	2.2	0.40
Malaysia [3]					
ridge	313.2	177.4	2.7 [11]	3.3 [11]	0.24
ubiquitous	298.5	164.6	2.4 [11]	2.2 [11]	0.43
lower-slope	288.1	190.8	1.6 [11]	1.5 [11]	0.38
Mexico [4]					
obligate gap	163.8	182.9	-	-	0.80
gap-dependent	106.1	228.8	-	-	0.69
gap-independent	144.5	188.0	-	-	0.60
Panama [5]	240.4	-	-	-	-
Tropical heath forest					
Malaysia [6]	-	475	9	6	0.51
Tropical montane forest					
Jamaica [7]	81.3 [10]				
mor ridge	-	295	7.3	5.5	0.48
mull ridge	-	247	5.5	4.2	0.48
wet slope	-	229	6.0	4.5	0.48
gap	-	247	4.9	4.2	0.45
Venezuela [8]					
transition	95.5	284	5.7	5.7	0.68
cloud	70.9	300	6.2	6.2	0.79
wet	68.6	397	8.5	8.5	0.71
Temperate forest					
USA [9]					
xeric	155.3	145.6	-	-	-
mesic	137.6	136.4	-	-	-
wet-mesic	242.1	109.7	-	-	-

[1] Gosling (1991); [2] Grubb (1974); [3] this study; [4] Popma *et al.* (1992); [5] Wright *et al.* (1992); [6] Peace & Macdonald (1981); [7] Tanner & Kapos (1982); [8] Sugden (1985); [9] Abrams *et al.* (1994); [10] mean for all species; [11] cuticle thickness excluding cell wall.

Chapter Six. An experiment to manipulate soil water potentials in the field

INTRODUCTION

Previous studies of seedling growth and survival in S.E. Asia have, almost entirely, concentrated on dipterocarps (e.g. Turner, 1989; Ashton *et al.*, 1995; Pinard *et al.*, 1996; Zipperlen & Press, 1996) with a smaller amount of work on pioneer species (e.g. Nussbaum *et al.*, 1995). Studies on understorey species are few (Rogstad, 1990; Burslem *et al.*, 1995; Burslem *et al.*, 1996) and there appear to be no previous S.E. Asian studies that include field manipulation of soil water.

Trees of *Mallotus wrayi* ≥10 cm gbh are found throughout the LPPs while trees of *Dimorphocalyx muricatus* are confined to ridge sites (Newbery *et al.*, 1996; Chapter 2). *D. muricatus* trees show greater adaptation than *M. wrayi* to the drier soil conditions periodically found on ridge sites (Chapter 4). Root depth and distribution are an important part of this adaptation, and, therefore, any selection for *D. muricatus* on ridge sites will be strongest at the shallowly rooted seedling stage. *D. muricatus* root structure seems poorly adapted for nutrient uptake and may require greater investment (i.e. higher light levels) than that of *M. wrayi*. *D. muricatus*, may, therefore, be excluded from lower-slope sites by competition for light, nutrients or both.

This chapter attempts to test the predictions that growth of *D. muricatus* seedlings would be lower on lower-slope sites and that *M. wrayi* seedling mortality increases in droughted areas compared to that of *D. muricatus*. Seedlings of *D. muricatus* and *M. wrayi* were planted in ridge and lower-slope sites and their soil water environment manipulated. Mortality and growth of these seedlings was then measured over a 19-month period.

MATERIALS AND METHODS

Plot and subplot selection

In primary forest the SPPs and in logged forest the SLPs were used (Chapter 2). As the plots had been established for other purposes, only one half of each SLP was used, and the other half left completely undisturbed. In the SLPs, each selected half (40 m x 20 m) plot was divided into 32 possible 5 m x 5 m subplots and, from these, three subplots were selected at random. Contiguous subplots were rejected, so subplots were >5 m apart. In the logged forest plots only one subplot was selected. Any subplot that contained a tree >50 cm dbh was moved to exclude that individual, so large trees with extensive root systems were not present in any subplot. (see Figure 6-1.) Each subplot was then delimited with a white painted PVC tube at each corner and string. As with the subplots in the LPPs a survey of individuals was then conducted >1 cm basal diameter. Four species were enumerated, *Ardisia colorata*, *Cleistanthus glaber*, *Dimorphocalyx muricatus* and *Mallotus wrayi*. As before each individual was tagged with an aluminium tag secured with fishing line.

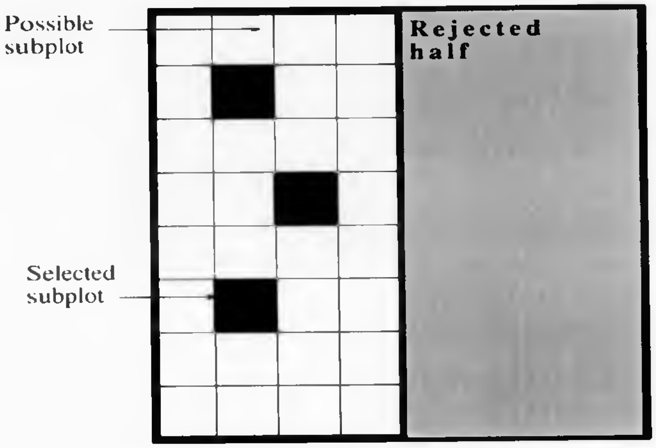

Figure 6-1. Layout of primary forest SPP used for field manipulation experiment.

Application of treatments to primary forest plots

Treatment application took place in March and April, 1996. Two treatments plus a control (no treatment) were applied, the imposition of artificial drought with polythene at ground level, and trenching. The treatments were randomly assigned to the three subplots selected per plot.

Each drought subplot was covered at ground level with 0.125 μm high impact transparent polythene sheeting. To reduce the number of perforations in the sheeting all trees and herbs below breast height (1.3 m), excepting the study species, were removed. The polythene was then laid down in 2 m x 5 m strips, 2.5 strips per plot. Holes were cut around any trees present in the subplots. The strips were secured together at the seams using a combination of laminated plastic adhesive (Sime-Derby, Malaysia), applied to both surfaces, and staples.

To provide a good seal the plastic was folded over itself before stapling, the seal was thereby raised and shed water. The original intention had been to then seal the sheeting around the remaining trees with silicone rubber, however, the number of perforations was small and the holes provided ventilation and prevented anaerobic conditions forming in the soil. Around each trench subplot, a trench roughly 40 cm deep and 20 cm wide was excavated, and all roots within the trench cut. The trench was then back filled with the excavated soil.

Measurement of soil water potential

Soil water potential was measured directly in some subplots, and indirectly in all subplots. On 26 April, 1996, 12 soil psychrometers (P55, Wescor Inc., USA) were installed, at 20 cm depth, in two pairs of plots in the primary forest. Measurement then took place weekly as in the LPPs (Chapter 3). Hence the soil water potential of each treatment was directly measured in ridge and valley sites, replicated twice. In these subplots, plus the remaining subplots, at irregular intervals, a soil sample was taken with an auger at 18-22 cm depth. For the drought plots a hole was cut in the polythene, and resealed with silicone rubber. The soil samples were weighed, dried at 105 °C, reweighed, and gravimetric soil moisture content calculated. At each of the sample sites a further soil sample was taken and its sand-silt-clay composition determined using the pipette method.

An exponential calibration curve was fitted between the moisture content points of known water potential with Genstat 5 (release 3.1, NAG, UK). The curve was used to convert the moisture contents of all the subplots at each measurement point to water potential. The water potential data were then analysed using a repeated measures ANOVA model with treatment as a split plot factor.

Soil water gradient

On 1 May, 1997 soil samples were taken at 20, 40, 60, 80 and 100 cm depth from control, trench and lower-slope plots from two ridge and two lower slope SPPs. The samples were weighed, dried and reweighed. Volumetric soil moisture was calculated using soil bulk densities of Green (1992).

Source of seedlings

In September, 1995 seed collection took place in the primary forest adjacent to but outside the LPPs. A limited quantity of *D. muricatus* seed was available while few individuals of *M. wrayi* had set fruit but none ripened. As many *D. muricatus* seed as possible were collected from the primary forest and germinated on a moist sand bed in the DVFC nursery. To supplement these seedlings and to provide *M. wrayi* seedlings for comparison, cuttings were propagated. A primitive high humidity chamber was set up in the DVFC nursery with a polythene dome over a sterilised sand bed to provide the high humidity atmosphere required. *M. wrayi* cuttings were taken from a large population of individuals adjacent to the gap site (Figure 2-2), *D. muricatus* cuttings were taken from the chert-spillerite area. Younger 'more juvenile' material is far more likely to strike cuttings (G. Reynolds pers. comm.) therefore, the ends of branches from small individuals were selected. Branches were cut, placed in plastic bags, and taken to the nursery as soon as possible. Here each cutting was cut through a node, dipped in hormone rooting powder, its leaf area reduced and inserted in moist sand. The cuttings were then watered twice daily. Callus and root formation in both species was roughly 50 %, far less than the over 90 % attained in a commercial nursery (G. Reynolds pers. comm.). In November, 1996 the rooted cuttings and seedlings were potted into a blend of 10 % sand and 90 % forest top-soil, in black oil-palm seedling bags, and grown under two layers of shade netting until planted out.

Planting of seedlings

Owing to the limited seed availability, relatively poor cutting success and disappointing nursery survival there were fewer seedlings than desired. Therefore, a compromise design was reached, see Table 6-1 for summary. In each primary forest control subplot four each of *D. muricatus* seedlings, *D. muricatus* cuttings and *M. wrayi* cuttings were planted. In each drought subplot four each of *D. muricatus* seedlings and *M. wrayi* cuttings were planted. In each trench subplot four *D. muricatus* seedlings were planted. In each logged forest plot four each of *D. muricatus* cuttings and *M. wrayi* cuttings were planted. Each seedling was planted in a pre-augured hole. In the drought plots each plant was sealed with an additional 30 cm square of polythene and silicone rubber. Seedlings were planted in a 'chessboard' pattern of alternating species roughly 75 cm apart and a > 1 m away from the subplot edge. Primary forest seedlings were planted 2-5 May, 1996 and logged forest seedlings 31 May, 1996. The height and number of leaves of each seedling was recorded at planting. Two weeks after planting the seedlings were surveyed and any dead seedlings replanted. The seedlings were then remeasured in October, 1996, June, 1997 and November, 1997.

The experiment was analysed using height increase and net leaf production from May, 1996 to November, 1997. In the primary forest three separate analyses were carried out, comparing a) *D. muricatus* seedlings and cuttings and *M. wrayi* cuttings within the control subplots, b) *D. muricatus* seedling and *M. wrayi* cuttings between drought and control subplots and c) *D. muricatus* seedlings among all subplots. A blocked ANOVA was used with treatment as a split plot factor and species as a split-split plot factor.

Table 6-1. Summary design for planting of seedlings in field manipulation experiment. (Number planted per ridge or lower-slope subplot.)

Treatment	Primary forest	Logged forest
Control	4 *D. muricatus* seedlings	
	4 *D. muricatus* cuttings	4 *D. muricatus* cuttings
	4 *M. wrayi* cuttings	4 *M. wrayi* cuttings
Drought	4 *D. muricatus* seedlings	
	4 *M. wrayi* cuttings	
Trench	4 *D. muricatus* seedlings	

Measurement of seedling light environment

During June, 1997 one measurement was taken above each seedling with a Quantum sensor (Skye Instruments, UK) attached to a hand held meter. Simultaneously the light at the meteorology station at the field centre was logged with a Datahog2 (Skye Instruments, UK). All individuals within a subplot were measured sequentially, but ridge and lower-slope plots were alternated. The percentage photosynthetically active radiation (% PAR) was then calculated for each seedling. These light measurements are inadequate to represent the seedling light environment. Ideally they would have been supplemented by long-term data logging and hemispherical photographs (see Brown & Whitmore, 1992).

Harvest of seedlings

At the end of the experiment in November, 1997 a random sample of the surviving primary forest individuals were harvested. Owing to differences in mortality between treatments the number of individuals sampled varied. Where possible all treatment combinations were sampled with replication. Each seedling was excavated with a trowel and fingers and transported as quickly as possible to the field centre. There the seedlings were washed and divided into leaf, stem and root fractions. For each seedling, leaf area determined using the same methods as before (Chapter 5). All fractions were then dried at 80 °C for > 24h and weighed.

RESULTS

Pre-treatment enumeration

Within each treatment subplot all study species were tagged and their diameter measured. Of the ridge species *Cleistanthus glaber* was absent from all subplots and *Dimorphocalyx* *muricatus* was only present in six out of twelve ridge subplots. Of the lower-slope species *Mallotus wrayi* was present in all subplots, while *Ardisia colorata* was present in half. Owing to the patchy distribution of these trees they were ignored for the rest of the experiment.

Subplot soil water potential

Gravimetric soil water content was measured, at 20 cm, in all control, trench, and drought subplots, on three occasions, and converted to water potential using an exponential calibration curve (Figure 6-2; variance accounted for 69.2 %, $F_{2,17}=22.33$, $p<0.001$). Soil particle size varied among subplots but was unrelated to soil water content.

Considering primary forest subplot soil water potential (Figure 6-3) there was no significant difference between ridge and lower-slope sites (split plot RM-ANOVA, $F_{1,12}=0.91$, $p=0.411$) nor did trenching significantly affect water potential ($F_{1,12}=0.88$, $p=0.367$) although the mean values for trenched subplots are intermediate between control and drought subplots. The drought treatment significantly decreased soil water potential ($F_{1,12}=6.19$, $p=0.029$) but there was not a significant drought time interaction ($F_{2,24}=1.20$, $p=0.320$) although at the wettest measurement point there was no difference between treatment means.

In the logged forest sites (Figure 6-5) there was no significant difference between ridge and lower slope water potential ($F_{1,5}=0.03$, $p=0.869$). There was also no significant difference between primary control plots and logged forest water potentials ($F_{1,11}=1.66$, $p=0.264$).

Soil water gradient

Volumetric water contents were measured at 20, 40, 60, 80, and 100 cm in all treatments during a dry spell. Generally there was an increase in moisture content with soil depth (Figure 6-4), although in several treatments there was a decrease in soil moisture from 80 to 100 cm. At the point of measurement ridge sites appear drier than lower-slope sites.

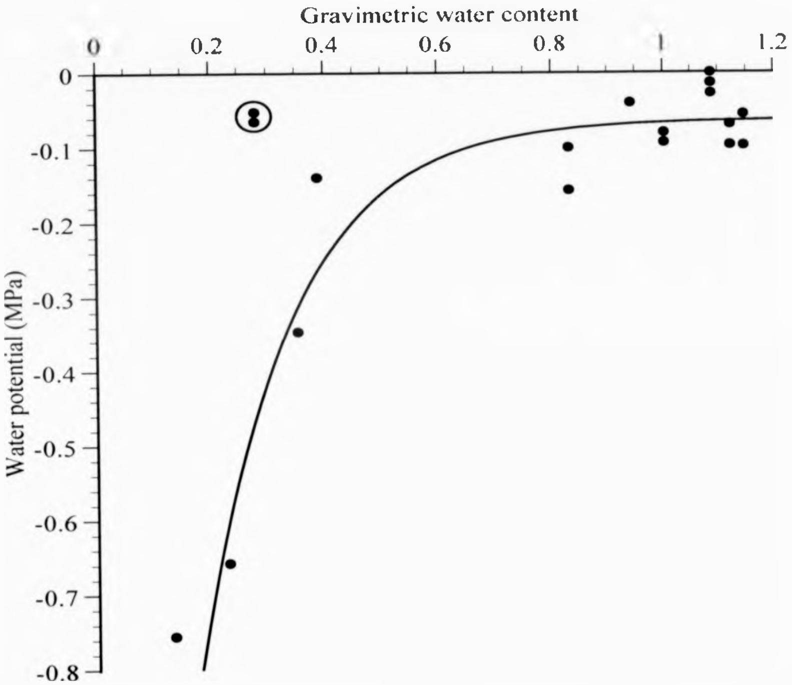

Figure 6-2. Curve fit of subplot soil water content on water potential. $WP = -0.063-2.32x0.0018^{MC}$. The circled points, included in the fit, are from the same subplot.

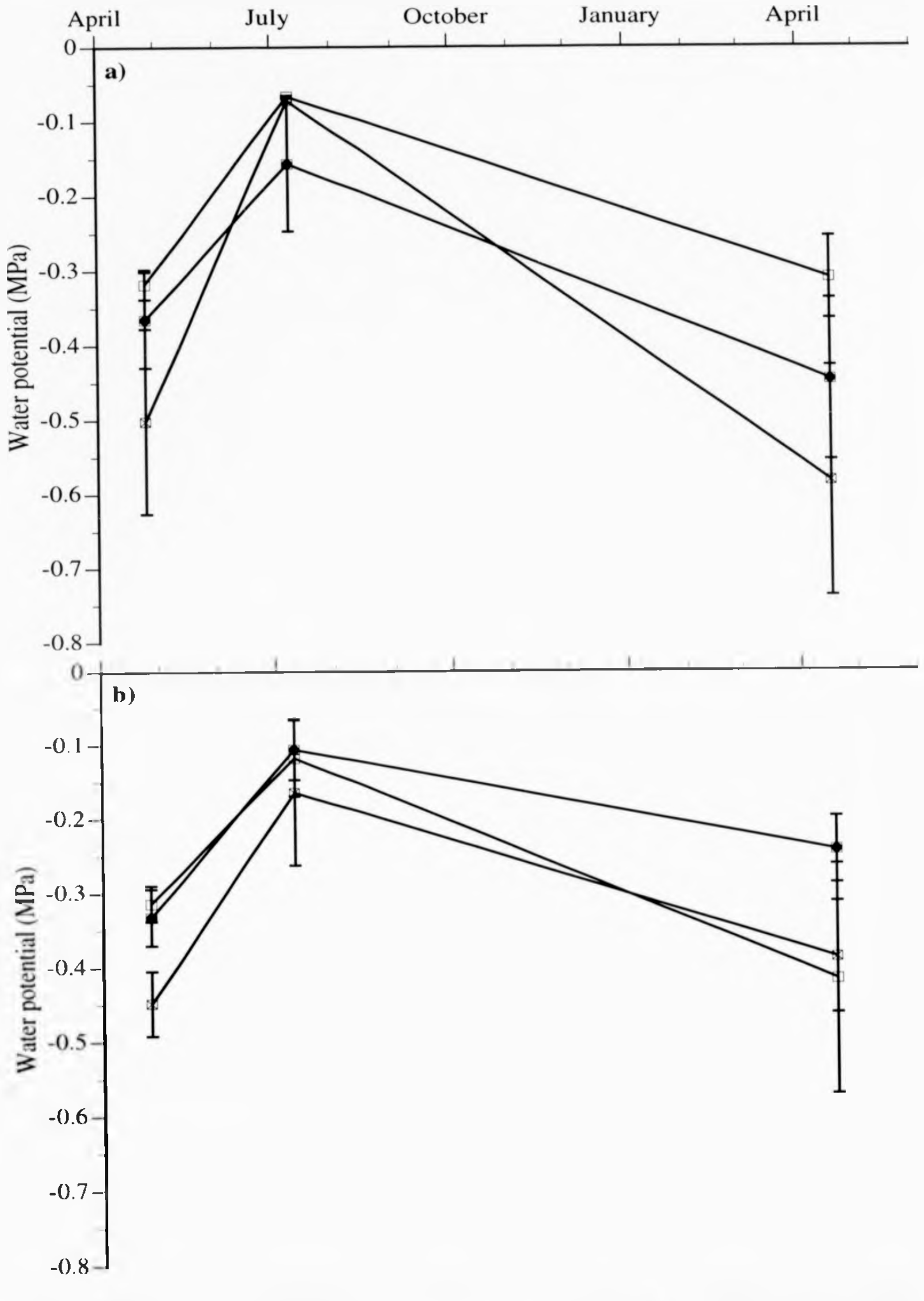

Figure 6-3. Soil water potentials of primary forest a) ridge and b) lower slope control (□), trench (■) and drought (⊠) subplots.

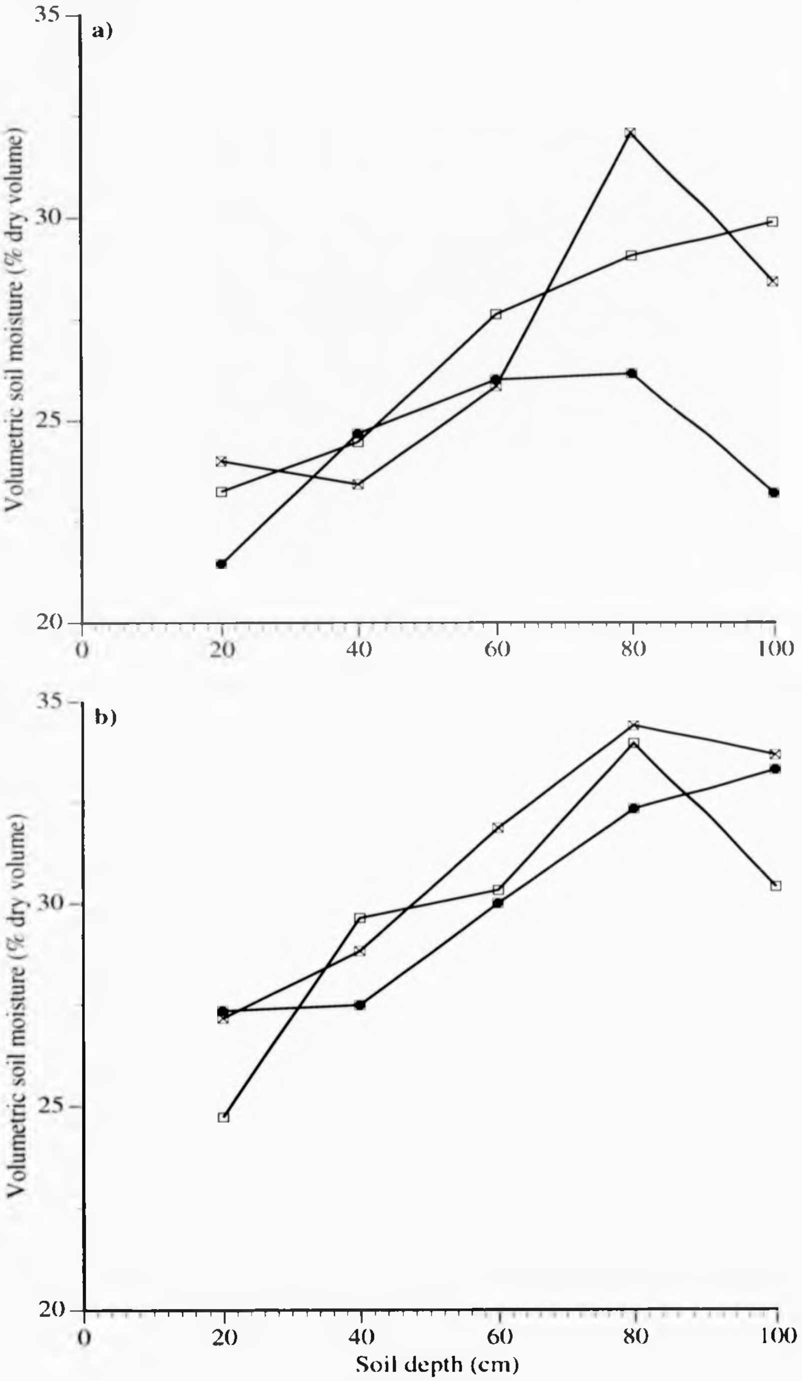

Figure 6-4. Volumetric soil water gradients on a) ridge and b) lower-slope sites, May 1, 1997. Symbols as Figure 6-3.

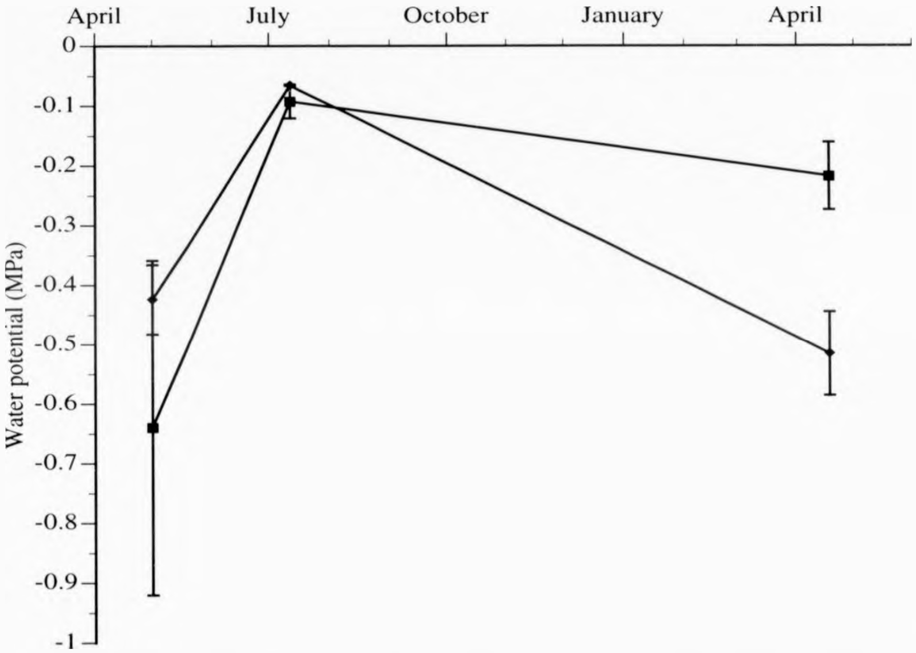

Figure 6-5. Soil water potentials of logged forest ridge (◆) and lower slope (■) subplots.

Subplot and seedling light environment

Light as percentage of full PAR was measured above each seedling during June, 1997. There was no significant difference between logged and primary forest light ($F_{1,252}$=0.48, p=0.482) nor between ridge and lower-slope sites ($F_{1,252}$=3.18, p=0.76). However, primary forest ridge seedlings received significantly more light than primary forest lower-slope seedlings (means comparison $F_{1,191}$=5.62, p=0.019).

Seedling growth and mortality in primary forest sites

Height increase, leaf production, and mortality of seedlings and cuttings growing in control, trench, and drought subplots was recorded over an 18 month period. There were significant differences in initial leaf number and height of the seedlings and cuttings (Table 6-2). *D. muricatus* seedlings were intermediate in height between *D. muricatus* cuttings and *M. wrayi* cuttings. *D. muricatus* seedlings had more leaves than *M. wrayi* cuttings which had more leaves than *D. muricatus* cuttings.

Table 6-2. Initial heights and leaf numbers of seedlings and cuttings. Means with different letters are significantly different (p<0.05, Tukey compromise post-hoc).

	N	Mean height (cm) ±S.E.	Mean leaves ±S.E.
D. muricatus cutting	64	6.9 ±0.4 ^{a}	2.7 ±0.2 ^{a}
D. muricatus seedling	96	8.4 ±0.2 ^{b}	5.5 ±0.1 ^{b}
M. wrayi cutting	96	11.8 ±0.4 ^{c}	4.9 ±0.2 ^{c}

Causes of seedling/cutting mortality were not formally determined. Observations suggested that shorter seedlings and cuttings were frequently smothered by leaf litter. *D. muricatus* cuttings were significantly shorter than both *D. muricatus* seedlings and *M. wrayi* cuttings and especially vulnerable to this smothering. No evidence of browsing or large scale insect infestation were observed for either species, in unsmotherered seedlings that died leaves browned and fell.

Mortality rates of both *D. muricatus* and *M. wrayi* cuttings were high compared with *D. muricatus* seedlings (Figure 6-6). There are interesting differences in the degree and timing of mortality among treatments and between sites (Table 6-3). Between May and October, 1996, mortality of *M. wrayi* cuttings for both drought and control treatments was higher in lower-slope sites than ridge sites. In contrast between October, 1996 and June, 1997 mortality of *M. wrayi* in control sites was similar while in drought sites mortality on lower-slope sites was greater than ridge sites. While between June and November, 1997 mortality of *M. wrayi* cuttings was higher in ridge sites for both treatments. However, mortality for the whole period of the experiment was similar for *M. wrayi* from both treatments and sites.

Growth and leaf production of surviving individuals was low, and for most treatment combinations negative (Figure 6-7, Figure 6-8). *D. muricatus* seedlings maintained a positive height increase in all treatments but only in trenched plots on lower-slope sites did an increase in the number of leaves occur. *M. wrayi* leaf production was consistently negative, i.e. a net loss of leaves, for all treatments. Only those *M. wrayi* cuttings in drought plots registered an increase in height by November, 1997. Comparing drought and control subplots (Table 6-4) there was a significant difference between species for both height increase and leaf production, and between droughted and control plots for leaf production. Within control subplots (Table 6-5) there was a significant difference between species for both height increase and leaf production. Comparing *D. muricatus* among treatments (Table 6-6) there were no significant differences in leaf production and height increase.

Logged forest mortality was higher than in the primary forest sites (Figure 6-9) with near to or 100 % for all treatment combinations by the end of the experiment. The chief cause of mortality appeared to be smothering by the very large *Macaranga gigantea* leaves. Of those seedlings surviving, as in the primary forest, leaf production and height increase were low or negative. There were too few surviving cuttings in November, 1997 to carry out ANOVAs on growth or leaf production.

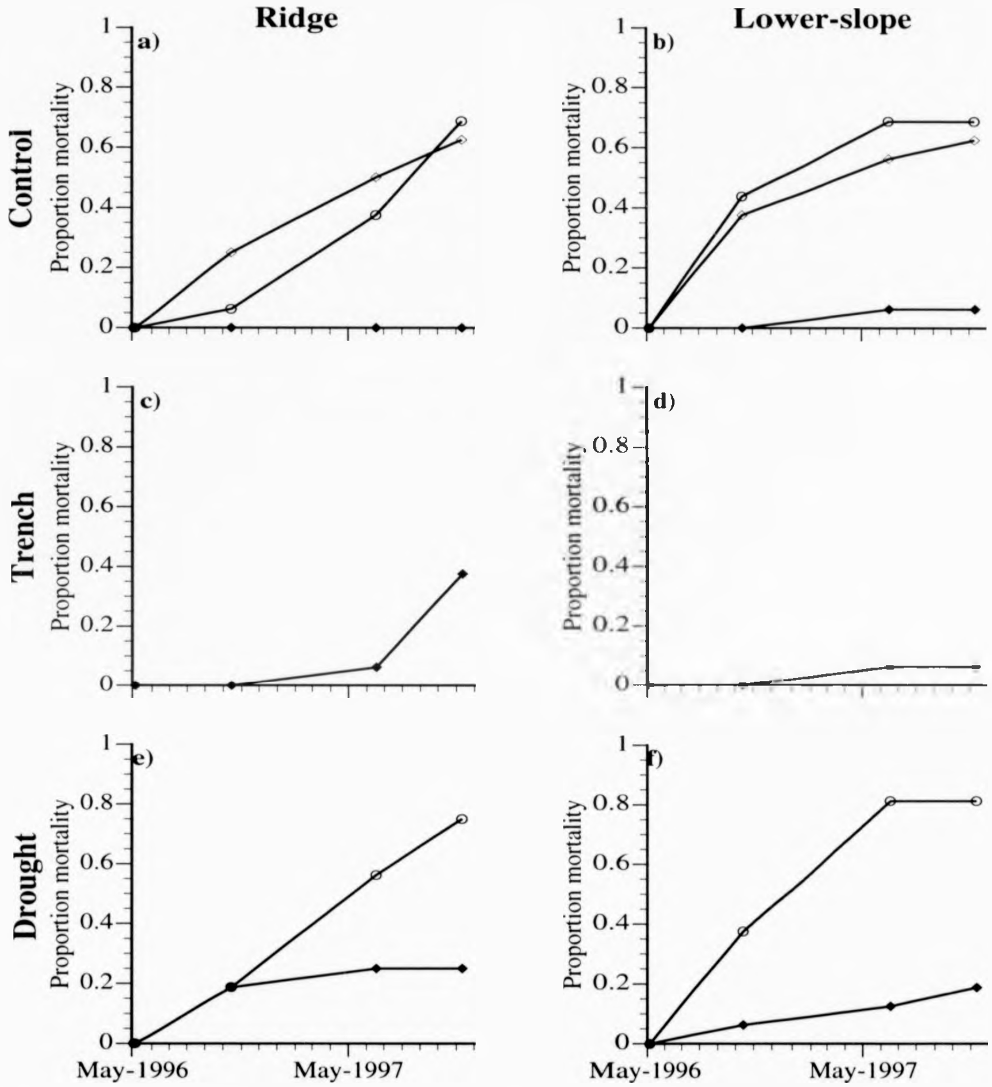

Figure 6-6. Cumulative primary forest seedling mortality for *Mallotus wrayi* cuttings (○), *Dimorphocalyx muricatus* seedlings (◆) and *D. muricatus* cuttings (◇) from control (a, b), trench (c, d) and drought (e, f) subplots on ridge (a, c, e) and lower slope (b, d, f) sites.

Table 6-3. Percentage mortality rates, between measurement points, for *Dimorphocalyx muricatus* seedlings and cuttings, and *Mallotus wrayi* cuttings from control, trenched and drought subplots on ridge and lower-slope sites in primary forest.

	Control		Trench		Drought	
	Ridge	Lower slope	Ridge	Lower slope	Ridge	Lower slope
May-October, 1996						
D. muricatus cuttings	25.0	37.5	-	-	-	-
D. muricatus seedlings	0.0	0.0	0.0	0.0	18.8	6.3
M. wrayi cuttings	6.3	43.8	-	-	18.3	37.5
October, 1996-June, 1997						
D. muricatus cuttings	33.3	30.0	-	-	-	-
D. muricatus seedlings	0.0	0.0	6.3	6.3	15.4	6.7
M. wrayi cuttings	33.3	43.8	-	-	46.1	70.0
June-November, 1997						
D. muricatus cuttings	25.0	14.3	-	-	-	-
D. muricatus seedlings	0.0	0.0	33.3	0.0	0.0	7.1
M. wrayi cuttings	50.0	0.0	-	-	42.6	0.0
May, 1996-November, 1997						
D. muricatus cuttings	62.5	62.5	-	-	-	-
D. muricatus seedlings	0.0	6.25	37.5	6.3	25.0	18.8
M. wrayi cuttings	68.8	68.8	-	-	75.0	81.3

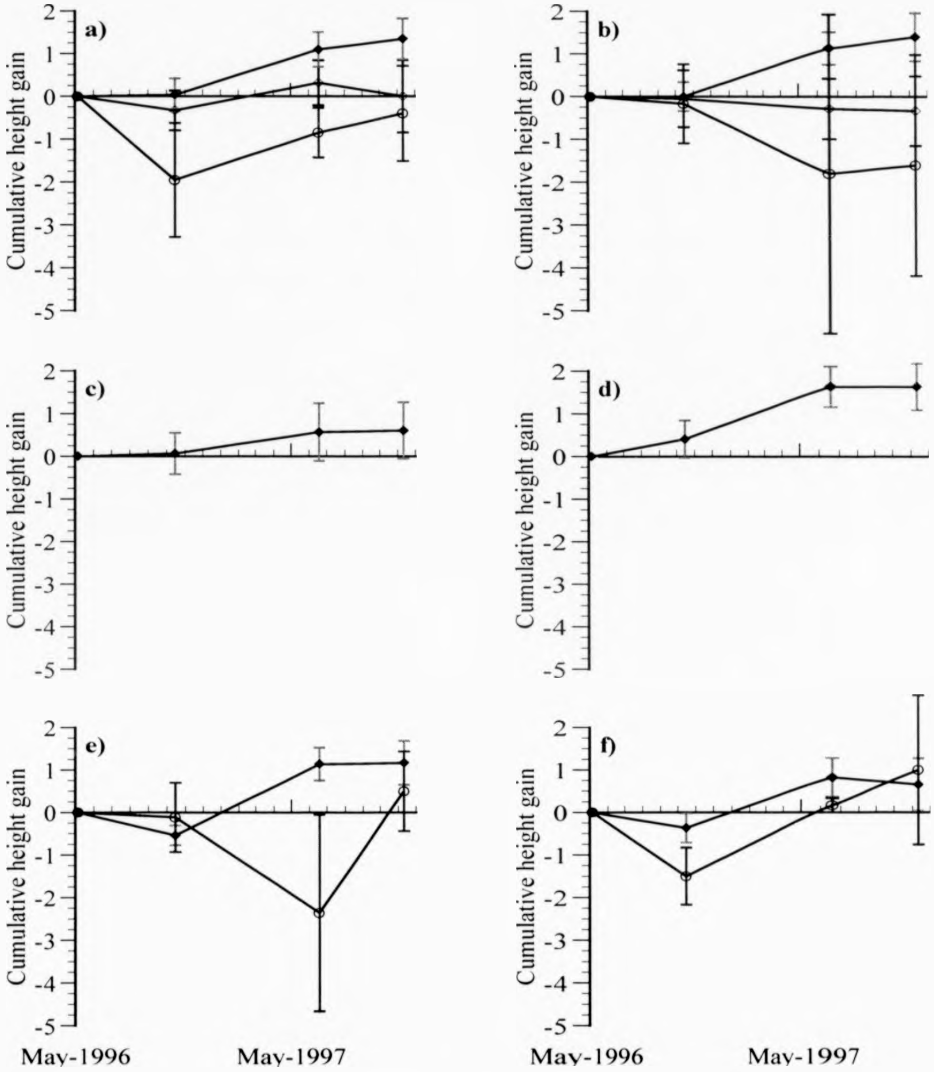

Figure 6-7. Primary forest cumulative height increments (cm). Symbols and letters as Figure 6-6. Error bars are standard error of the mean.

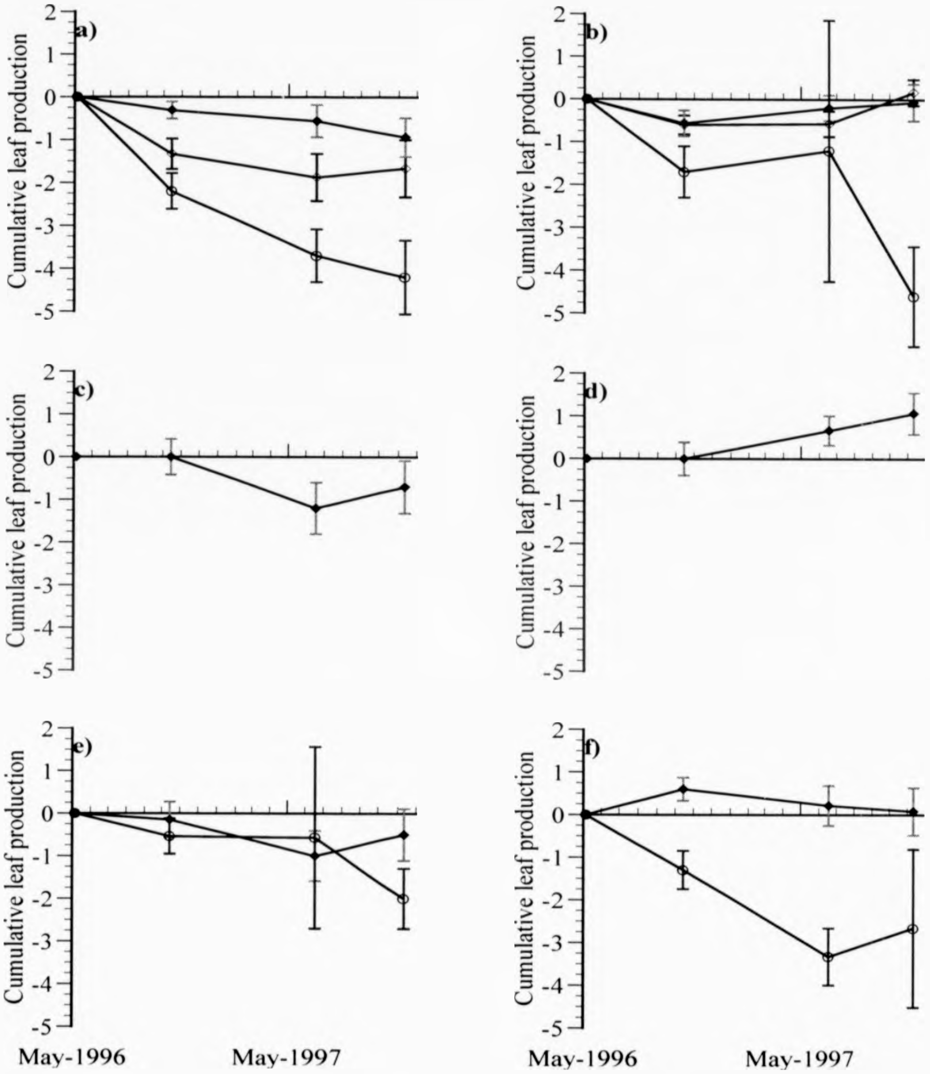

Figure 6-8. Primary forest leaf production. Error bars are standard errors of the mean. Symbols and letters as Figure 6-6.

Table 6-4. ANOVA of *Dimorphocalyx muricatus* seedlings and *Mallotus wrayi* cuttings surviving until November, 1997 a) height increase and b) leaf production, in control and drought subplots.

a)

Source of variation	d.f. (missing)	SS	*F*	*p*
block stratum	3	111.36	1.61	
block.site stratum				
site	1	2.14	0.09	0.781
Residual	3	69.10	3.38	
block.site.treat stratum				
drought	1	1.61	0.24	0.629
site.drought	1	11.15	1.64	0.207
Residual	47 (7)	320.22	0.92	
block.site.treat.units stratum				
species	1	92.61	12.45	**0.004**
site.species	1	0.247	0.03	0.858
species.drought	1	9.59	1.29	0.278
site.species.drought	1	1.81	0.24	0.630
Residual	12 (48)	89.29	7.44	
Total	72 (55)	452.69		

Table 6-4 b)

Source of variation	d.f. (missing)	SS	*F*	*p*
block stratum	3	31.14	1.35	
block.site stratum				
site	1	0.50	0.06	0.816
Residual	3	23.10	1.38	
block.site.treat stratum				
drought	1	38.70	6.93	**0.011**
site.drought	1	18.26	3.27	0.077
Residual	47 (7)	262.53	0.90	
block.site.treat.units stratum				
species	1	299.86	48.54	**<0.001**
site.species	1	14.05	2.27	0.157
species.drought	1	17.40	2.82	0.119
site.species.drought	1	14.06	2.28	0.157
Residual	12(48)	74.13	6.18	
Total	72 (55)	413.12		

Table 6-5. ANOVA of *Dimorphocalyx muricatus* seedlings and cuttings and *Mallotus wrayi* surviving until November, 1997 a) height increase and b) leaf production in control subplots.

a)

Source of variation	d.f. (missing)	SS	*F*	*p*
block stratum	3	116.95	1.31	
block.site stratum				
site	1	1.37	0.05	0.844
Residual	3	89.15	5.35	
block.site.units stratum				
species	2	38.50	3.47	**0.041**
site.species	2	0.07	0.01	0.993
Residual	41 (43)	227.54		
Total	52 (43)	377.20		

b)

Source of variation	d.f. (missing)	SS	*F*	*p*
block stratum	3	7.736	0.58	
block.site stratum				
site	1	17.96	4.01	0.139
Residual	3	13.45	1.35	
block.site.units stratum				
species	2	304.75	45.85	**<0.001**
site.species	2	20.40	3.07	0.057
Residual	41 (43)	136.24		
Total	52 (43)	281.17		

Table 6-6. ANOVA of *Dimorphocalyx muricatus* seedlings surviving until November, 1997 a) height increase and b) leaf production among subplots.

a)

Source of variation	d.f. (missing)	SS	*F*	*p*
block stratum	3	16.98	0.40	
block.site stratum				
site	1	1.34	0.09	0.779
Residual	3	42.68	3.63	
block.site.units stratum				
trench	1	0.73	0.18	0.669
drought	1	2.51	0.64	0.427
site.trench	1	10.85	2.77	0.101
site.drought	1	2.33	0.59	0.444
Residual	69 (15)	270.55		
Total	80 (15)	330.15		

b)

Source of variation	d.f. (missing)	SS	*F*	*p*
block stratum	3	6.73	0.45	
block.site stratum				
site	1	30.41	6.08	0.090
Residual	3	15.01	1.39	
block.site.units stratum				
trench	1	5.19	1.44	0.234
drought	1	1.56	0.43	0.512
site.trench	1	0.574	1.59	0.211
site.drought	1	0.311	0.09	0.770
Residual	69 (15)	248.47		
Total	80 (15)	306.22		

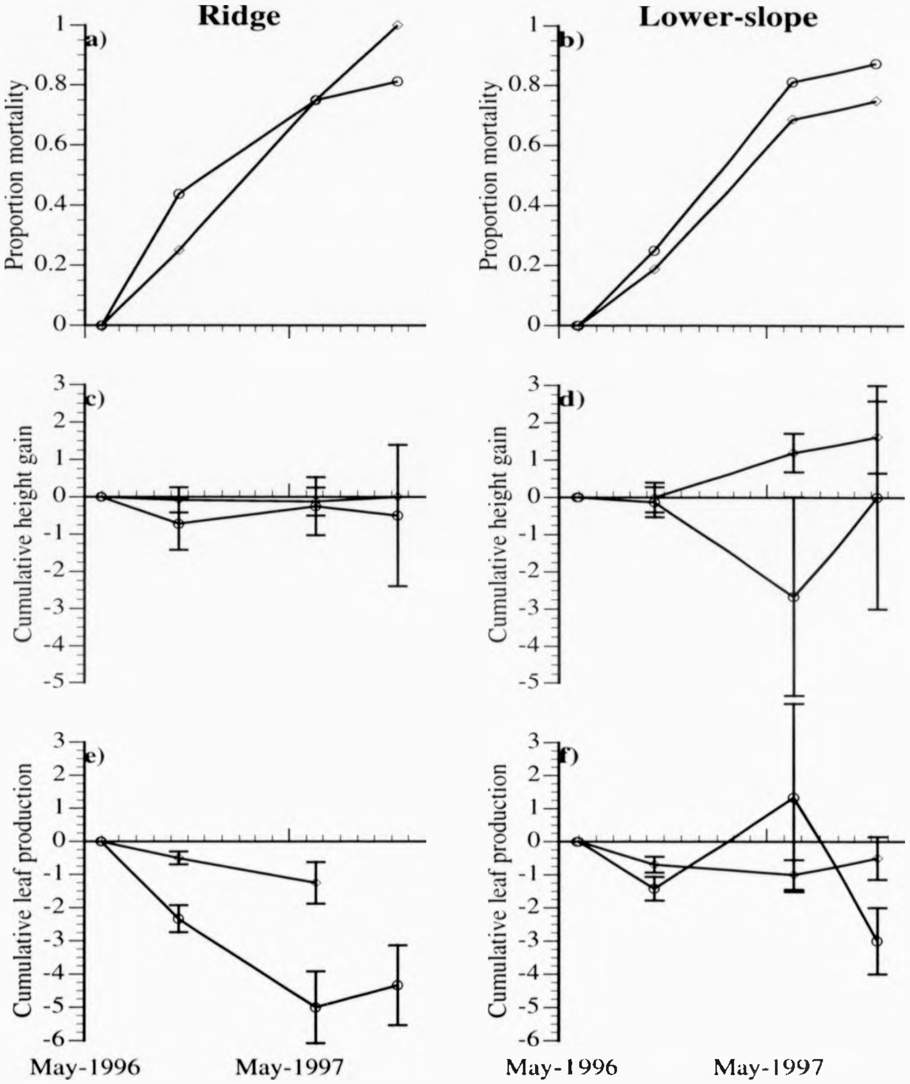

Figure 6-9. Logged forest *Dimorphocalyx muricatus* (◇) and *Mallotus wrayi* (○) cutting mortality (a, b), height increase (c, d) and leaf production (e, f) from ridge (a, c, e) and lower slope (b, d, f) sites.

Seedling harvest

A sample of the cuttings and seedlings surviving in November, 1997 were harvested. There were too few individuals surviving to analyse by treatment except for *D. muricatus* seedlings, for which there were no significant differences among treatments. Therefore, the harvested plants were lumped and analysed by type (Table 6-7). *D. muricatus* cuttings had a significantly lower specific leaf area (SLA) than both *D. muricatus* seedlings and *M. wrayi* cuttings which had a similar SLA. There was no significant difference in root:shoot ratio among type although *D. muricatus* cuttings had a lower mean than *D. muricatus* seedlings and *M. wrayi* cuttings. *D. muricatus* roots were more fragile than those of *M. wrayi* so root:shoot ratios of *D. muricatus* are probably an underestimate.

Table 6-7. Specific leaf area and root:shoot ratio of *Dimorphocalyx muricatus* seedlings and cuttings, and *Mallotus wrayi* cuttings at harvest in November, 1997. Means with different letters are significantly different (*p*<0.05 Tukey compromise post-hoc).

	N	Specific leaf area ($cm^2 g^{-1}$) ±S.E.	Root:shoot ratio ±S.E.
D. muricatus cuttings	5	182.85 ±9.14 ^{a}	0.33 ±0.04 ^{a}
D. muricatus seedlings	17	234.86 ±5.64 ^{b}	0.56 ±0.06 ^{a}
M. wrayi cuttings	10	254.45 ±15.72 ^{b}	0.46 ±0.05 ^{a}

DISCUSSION

Differences in water and light environment among plots

Application of polythene sheeting at ground level was successful in reducing soil water potential at 20 cm depth. Unexpectedly, the trenching treatment did not significantly affect plot water potential, and the trend was a reduction in water potential, contrary to the expected increase. Water is extracted by some understorey trees at soil depths >1 m and it is probable that canopy trees extract water from greater depths (Chapter 4). The reduction in soil moisture from 80 to 100 cm observed, may be the result of water extraction by canopy trees. It is therefore likely that trenching to 40 cm depth is insufficient to prevent water extraction by canopy trees. Elsewhere trenching studies have demonstrated both an increase in available soil water (Toumey & Kleinholz, 1931; Gerhardt, 1996) and no effect (Christy, 1986). Trenching has been also shown to increase nutrient availability (Watt & Fraser, 1933) and to decrease mycorrhiza richness, diversity and eveness (Simard *et al.*, 1997). As soil nutrients and mycorrhiza were not measured in the present study it is not possible to say whether these effects occurred.

Again contrary to expectations, there was no significant difference in soil water potential between the ridge and lower slope SPPs. This lack of difference between sites suggests that the difference found in chapter 3, remembering that the LPP subplots were selected by presence or absence of ridge species not topography, may be the result of more than just topography. However, the soil moisture gradient study did indicate a ridge/ lower slope difference at a very dry measurement time. It is perhaps important that two out of the four ridge SPPs used did not have populations of *Dimorphocalyx muricatus* and the gradient study was conducted in the blocks that did have populations. In the control subplots water potentials measured were similar to those measured on lower slopes in the LPPs and in the drought subplots similar to those measured on ridges in the LPPs (Chapter 3). However, ridge SPPs were significantly lighter than lower slope SPPs. Therefore, useful comparisons can be made between the relatively high light ridge plots and low light lower-slope plots, and relatively high water potential control plots and low water drought plots.

Seedlings *v.* cuttings: interpreting the results

Interpretation of the results depends on whether the results for *Mallotus wrayi* cuttings are representative of *M. wrayi* seedlings. There are clear differences between *D. muricatus* seedlings and cuttings, but the poor performance of these cuttings appears to be the result of short initial height (resulting in smothering by leaf litter) and poor root development. Brown and Whitmore (1992) at DVFC, Swaine *et al.* (1990) in Ghana and Gerhadt (1996) in Costa Rica have all found that seedling mortality decreases with seedling height. *M. wrayi* cuttings were not short and had similar root:shoot ratios to both *D. muricatus* seedlings and *M. wrayi* wildings grown for over 1 year in pots (Chapter 8). It seems likely, therefore, that the results for *M. wrayi* cuttings give an indication of those results that might have been obtained were *M. wrayi* seedlings used. However, the harvested seedlings were those that survived, those that died my have had different root:shoot ratios.

The comparison between cuttings of one species and seedlings of another species is probably of equal validity as a comparison between wildings of one species and seedlings grown from seed of another species, commonly reported (e.g. Ashton *et al.*, 1985; Burslem *et al.*, 1996). Gerwing (1995) compared the growth of seedlings of *Piper auritum* with cuttings of *P. phytolaccaefolium* without commenting on possible cutting/ seedling differences. It would be desirable to repeat this experiment, with *M. wrayi* seedlings, and with greater replication.

Seedling mortality and growth in the primary forest

Seedling and cutting growth (measured as height increase) was frequently negative, suggesting seedling die-back. However, the range of measured values was small and measured negative growth may simply indicate accumulation of leaf litter at the seedling base and inaccuracy of seedling measurements. No such problems exist with leaf production, although the negative production of *D. muricatus* is partly accounted for by loss of seedling cotyledons. With so few *M. wrayi* and *D. muricatus* cuttings surviving to the end of the experiment relative mortality among the treatments is of greater interest than growth.

As for the species here Zipperlen & Press (1996) found that two species of dipterocarp seedling planted in a 'low-light' (≡ understorey) environment, at DVFC, over a similar time period, grew little or not at all. Mortality rates were higher than *D. muricatus* seedlings but lower than *D. muricatus* and *M. wrayi* cuttings. Mortality was reduced and growth rate increased in higher light environments. Similarly Still (1993), also at DVFC, within the LPPs found that mean growth of several species of dipterocarp seedlings was low, although variable within species. Mortality ranged from 0-16 % y^{-1} and was often a result of litter fall. Osunkjoya *et al.* (1992), in Australian rain forest, found that uncaged seedling suffered 35 % higher mortality (75 *v.* 40 %) than caged seedlings, but the low mortality of *D. muricatus* seedlings in this study suggests that mammal predation is low at DVFC.

The slow growth of dipterocarps under forest understorey conditions is not surprising as it is well known that many species require canopy gaps to reach maturity (Whitmore, 1984). What is remarkable is that the species here, confined to the understorey, show similar slow rates of growth. With no comparable S.E. Asian studies (none with understorey species under field conditions) it is not possible to say how representative these results are. However, it is clear that it is not simply a matter of the seedlings acclimating to the higher light nursery conditions prior to planting out as seedlings germinated from seed in the field showed similar low growth rates (Chapter 7). It is also clear that the study species are capable of much higher rates of growth than observed here (Chapter 8). It seems probable that *D. muricatus*, while being able to persist in understorey conditions requires higher light levels to grow. These increased light levels would occur both in very small (e.g. branch fall) and larger gaps. All the understorey species studied showed evidence of scarring (Chapter 2) and are therefore able to resprout following damage sustained in gaps, provided they are not smothered. It seems likely that what is true for *D. muricatus* will also be true for other common understorey species (*M. wrayi*, *B. stipulata*), although *Ardisia colorata* seems poorly adapted to higher light levels (Chapter 4). Some support for this hypothesis is provided by Primack & Lee (1991) who observed an increase in growth of *Mallotus* spp.

(including *M. wrayi*) trees following logging, the increase in growth was, however, greater for pioneer *Macaranga* spp.

Despite the problems discussed above it is clear that, while *D. muricatus* trees >10 cm gbh (Newbery *et al.*, 1996) and smaller trees (Chapter 2), on lower-slope sites are absent, *D. muricatus* seedlings planted on ridge and lower-slope sites grow equally well. Although, in terms of soil water potential, the ridge and lower-slope sites in the SPPs are not representative of the LPPs, there was also no difference in growth between the drought and control treatments. Mortality of *D. muricatus* seedlings was actually higher in the drought subplots than the control subplots, the reverse of what might be predicted. This finding suggests that *D. muricatus* seedlings can grow in wet soil and are not excluded from lower-slope sites by anaerobic conditions unlike the *Polyalthia sumatrana* of Rogstad (1990). The lack of difference in *D. muricatus* performance between control and trench plots suggests that any nutrient or mycorrhiza effects were also not important.

Although there were differences in light environment between ridge and lower-slope sites it is not possible to discount light as an important factor in *D. muricatus* distribution. Prior to the start of the experiment the seedlings had been grown in a higher light environment (DVFC nursery) than that found in the SPPs. As growth over the experimental period was negligible, it seems likely that the seedlings at the end had a similar root:shoot ratio as at the start of the experiment, plus there was no significant difference among treatments. Therefore, a sufficient investment in roots may have already occurred to allow *D. muricatus* seedlings to tolerate dry conditions.

The differences in mortality of *Mallotus wrayi* cuttings among treatments are of great interest, especially for the first two measurement periods. Between May and October, 1996, a largely wet period, mortality in the control and drought subplots was similar, but much greater in lower slope than ridge sites. While between October, 1996 and June, 1997, including a severe dry period, mortality was again higher in lower-slope plots, but also, the mortality in the drought lower-slope plots was almost twice that in the drought ridge plots. This result indicates a light drought interaction and suggests that under low light conditions *M. wrayi* cuttings are unable to invest enough in root growth to tolerate or evade drought. Similarly, in Panamanian moist forest, *Virola surinamensis* (a canopy species), cannot persist in the understorey during the dry season unless supplied with additional water (Fisher *et al.*, 1991). It also appears that, unlike the *D. muricatus* seedlings, the *M. wrayi* cuttings grown under the same light environment prior to planting out had not 'defaulted' to a sufficient root allocation to tolerate or evade drought, i.e. *M. wrayi* shows plasticity in root shoot allocation whereas *D. muricatus* does not.

The findings above are supported by Ashton *et al.* (1995), in Sri Lanka, who found differences in mortality among species (four *Shorea* species), site (ridge, midslope and valley = dry to wet), and light environment (from understorey to gap centre). Two species (both 'valley' or 'midslope species'), as with *M. wrayi*, had high mortality rates in low light, dry conditions, and lower mortality in high light, dry conditions. The other two species (both 'ridge' or 'midslope' species) were similar to *D. muricatus* in that mortality rates were similar across all the study conditions. Unlike here, growth of all four *Shorea* species was positive at all sites, and greatest at the lightest sites. Also, all the species showed plasticity in root and shoot allocation among sites, but, unfortunately, root:shoot ratios are not given. Gerhardt (1996) found, in Costa Rican seasonal forest, that trenching increased both soil moisture and the survival of tree seedlings. In addition both trenching and thinning (increased light) had a positive effect on growth but there was no interactive effect. Burslem *et al.* (1996), in a pot experiment, found that while simulated drought did not affect overall height increment of two dipterocarp and one understorey species there were significant differences in leaf area and root:shoot ratios between treatments. Simulated drought also caused an increase in lateral roots as a proportion of total root mass. However, this may be a pot artefact, pots may not have pronounced gradient of water availability with depth, and maximum root depth is confined, thus droughted pot plants increased root area rather than root depth. In the field water availability does increase with soil depth so seedlings may increase root depth rather than root area.

Logged forest seedlings

Performance of both *D. muricatus* and *M. wrayi* cuttings in the logged forest was poorer than that found in the primary forest. There was no significant difference in soil water potential between forest types and the increased mortality of the seedlings may be a result of smothering by *Macaranga gigantea* leaves. It is likely, therefore, that regeneration of these common understorey species is suppressed in logged forest, under pioneer species.

Chapter Seven. Seed establishment in the field

INTRODUCTION

Most previous tropical studies of seed establishment have concentrated on testing the Janzen-Connell model (Janzen, 1970; Connell, 1971), that differences in dispersal distance from the parent tree affect seed and seedling survival (see Notman *et al.*, 1996 and references therein). However, other tropical experiments have found differences in seed germination and establishment both among habitats and among species, independent of distance from parent trees (e.g. Schupp & Frost, 1989; Rogstad, 1990; Gerhardt, 1996; Forget, 1997; see also review by Vázquez-Yanes & Orozco-Segovia, 1993). More specifically Rogstad (1990) attributed the absence of *Polyalthia hypoleuca* from wet sites to poor seed germination under wet soil conditions.

Although mature *Dimorphocalyx muricatus* trees are absent from lower-slope sites, *D. muricatus* seedlings planted in these sites survive and grow (Chapter 6). Mature *D. muricatus* on ridges grow close to lower-slope sites and *D. muricatus* fruit is explosively dehiscent so seed must reach these sites. This chapter tests the hypothesis that *D. muricatus* seed is unable to germinate and establish on lower-slope sites. A ubiquitous species (*M. wrayi*) and a lower-slope species (*B. stipulata*) are included for comparison. A secondary hypothesis is that the lower numbers of the ubiquitous species and absence of lower-slope species on ridges is explained by a lower seed germination and establishment rate than on lower-slopes.

MATERIALS AND METHODS

Seed collection

Seed collection took place from 8 August to 28 August, 1996. Prior to collection, a survey was conducted along Main Trail West (Figure 2-2), and the position of heavily fruiting trees noted. The only relevant species from which seed was available were *Mallotus wrayi*, *Dimorphocalyx muricatus* and *Baccaurea stipulata*. This last species was not sufficiently common in the LPPs to include in previous parts of the study but is a possible lower-slope specialist (Newbery *et al.*, 1996). As seed availability was limited no attempt was made to randomise the trees from which seed was collected.

The different species and individuals did not ripen exactly simultaneously. Ripeness was easily determined for both *B. stipulata* and *D. muricatus*. *B. stipulata* has fleshy, animal dispersed fruits which turn red upon ripening. *D. muricatus* produces explosively dehiscent fruit, and before dehiscence the outer part of the seed dries and falls off leaving a woody capsule. *M. wrayi* also produces dehiscent fruit, but there is little indication that dehiscence is about to occur. *M. wrayi* seed was only collected from those individuals on which some fruit had already dehisced. Fruits were collected by hand when within reach and with a pruning pole for bigger individuals. Following collection, the dehiscent fruit were air dried, in a net bag, until dehiscence occurred. To avoid seed drying out further they were them placed in airtight jars and placed in the field or nursery as soon as possible. *B. stipulata* seed were separated from the outer part of the fruit and inner aril by hand. The seed was then washed to remove any sugary residue, attractive to ants. When attempting to germinate *B. stipulata* seed in the nursery the previous year predation by ants had been very high. For all species hollow and predated seed were discarded.

The design of the field experiment

The same SPPs as for the field manipulation experiment were used (Chapter 6). Four ridge and four lower-slope plots, each 40 x 40 m. For each plot one 40 m east-west edge was selected to be a transect for the experiment. The edge selected was that one that was most characteristic of the site i.e. for the ridge plots the upper, and in the valley plots the lower edge. At 5 m intervals along each transect groups of seed were placed (Figure 7-1). Each group consisted of five *B. stipulata*, five *D. muricatus*, and five *M. wrayi* seed. The seed was placed at randomly assigned positions on a wire metal grid. Grouping was chosen both to facilitate the relocation of the seed and to reduce the likelihood of 'trap-lining' by seed predators. It was hoped that the wire grid would prevent seed being washed away. In total there were 9 groups and 45 seed of each species per plot. Not all the seed was placed in the field simultaneously, but as it became available, 13-28 August.

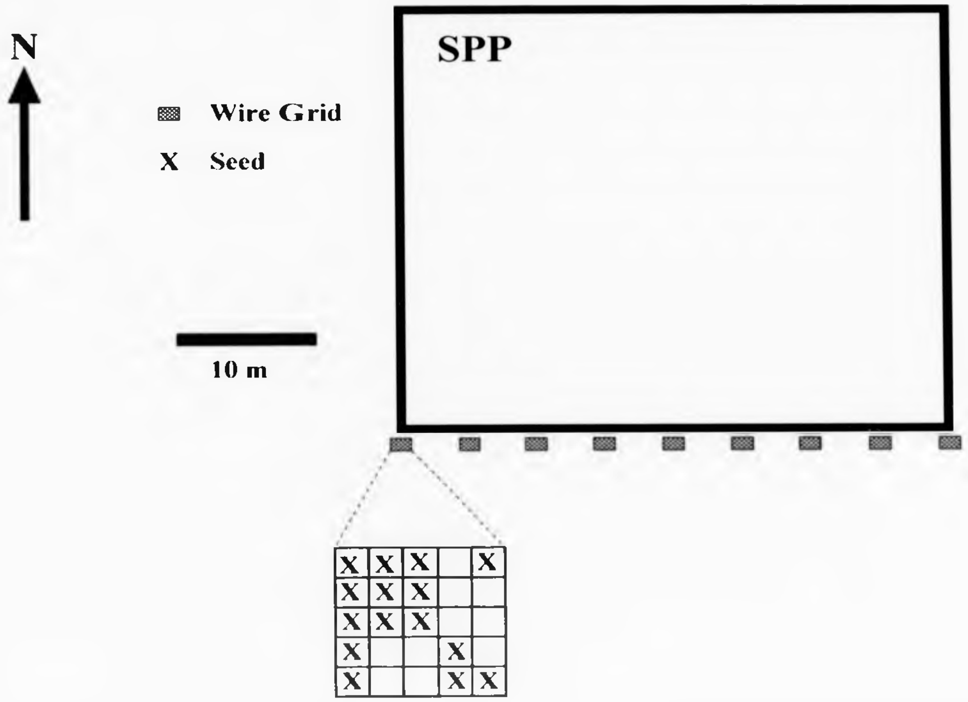

Figure 7-1. Design of seed establishment experiment.

Monitoring of seed establishment

Commencing 23 August and initially weekly, but less frequently after the first eight weeks, the status of each seed was assessed. Each seed was scored as absent, rotten, eaten, radicle visible, cotyledon visible or new leaf produced. Eaten seed were present and obviously ‘gnawed’, but where seed fragments existed all missing seed were scored as eaten. Absent seed may have been eaten or washed away. Any seed that had moved were put back into position on the grid. The final survey took place 6 May, 1997.

Time to germination was calculated as time from placement in the field until time when germination was observed. A repeated measures split plot ANOVA model was use to analyse the numbers of germinated seed present at each survey time. The fate data were analysed as a split plot MANOVA, excluding absent seed as the fate categories are compositional (sum to 100 %). Forget (1997) analysed a similar experiment with fate and site as whole plot factors, but it is unclear how fate, a result, can be treated as a factor.

Nursery control

Concurrently with the field experiment 50 seed of each species were placed on a moist sand bed in the Padang Baru nursery (Figure 2-2) and for the first eight weeks their status monitored in the same way as the field seed.

RESULTS

Germination time and rate

Baccaurea stipulata, *Dimorphocalyx muricatus* and *Mallotus wrayi* seed were collected and placed along ridge and lower-slope transects, and their fate followed over a nine month period. For *M. wrayi*, fruiting individuals tended to be clustered, possibly corresponding to lighter patches. Fruiting *B. stipulata* were more common close to the Segama river and by small streams. The only individuals of *D. muricatus* along Main Trail West are on the chert-spillerite outcrop (Figure 2-2). As with *M. wrayi* fruiting was patchy, again possibly corresponding to lighter areas. *M. wrayi* and *B. stipulata* seeds were of similar size roughly 5 mm in diameter while *D. muricatus* seed was larger roughly 10 mm in diameter.

Germination rate of *B. stipulata* was highest, followed by *D. muricatus*, *M. wrayi* seed had a very low germination rate (Table 7-1). All three species had a higher germination rate on ridge sites than lower-slope sites. For comparison nursery germination rates over the same period were *B. stipulata* 70 %, *D. muricatus* 32 % and *M. wrayi* 6 %. It is curious that while the nursery germination rates of *B. stipulata* and *M. wrayi* are higher, but similar to those found in the field, the rate of *D. muricatus* is much lower.

Time to seed germination (Table 7-1) was significantly shorter for *D. muricatus* compared with *B. stipulata* (ANOVA, $F_{1,397}$=397.28, p=0.001; *M. wrayi* excluded owing to small sample size). There was also a significant difference in germination time between sites ($F_{1,397}$=5.01, p=0.026) although the means are similar. There was no significant site species interaction ($F_{1,397}$=0.33, p=0.391).

Table 7-1. Percentage germination and mean time to germination of *Baccaurea stipulata*, *Dimorphocalyx muricatus*, and *Mallotus wrayi* seed on ridge and lower-slope sites. Where N is the number of seed germinating with the percentage in brackets.

	N (%)	Time to germination ± S.E. (days)
B. stipulata		
ridge	117 (65)	34.7 ±0.7
lower-slope	103 (57)	32.7 ±0.7
D. muricatus		
ridge	95 (53)	21.4 ±0.6
lower-slope	89 (49)	20.3 ±0.6
M. wrayi		
ridge	2 (1)	21.0 ±0.0
lower-slope	1 (1)	28.0 ±0.0

Although, on average, *B. stipulata* seed take longer to germinate than *D. muricatus* seed, the peaks in germinated seed present of both species coincide (Figure 7-2), but the peak for *B. stipulata* is of a longer duration. The data were analysed with a split-plot RM ANOVA (Table 7-2), excluding *M. wrayi*, and the first survey point, when no seed had germinated. Significantly more *B. stipulata* germinated seed were present than *D. muricatus* seed, and there was no significant interaction between species and time. Nor was there a significant difference in the number of germinated seed between ridge and lower-slope sites. However, it is interesting to note the steeper decline in *B. stipulata* numbers from November to April on ridge rather than lower-slope sites.

Table 7-2. RM ANOVA of number of germinated seed present.

	df	SS	F	p	$p_{\varepsilon\alpha}$[1]	$p_{\varepsilon\beta}$[2]
Site	1	156.03	0.65	0.452		
Residual	6	1448.78				
Species	1	1246.23	10.35	**0.018**		
Species.Site	1	10.00	0.48	0.833		
Residual	6	1243.78				
Time	9	6810.10	61.96	**<0.001**	**<0.001**	**<0.001**
Time.Site	9	155.23	0.96	0.482	-	-
Residual	54	969.48				
Time.Species	9	325.03	2.96	0.063	-	-
Time.Species.Site	9	31.50	0.29	0.976	-	-
Residual	54	659.48				

Epsilon correction as estimated by [1] Geisser & Greenhouse, 1958 (0.160); [2] Huynh & Feldt, 1970 (0.511).

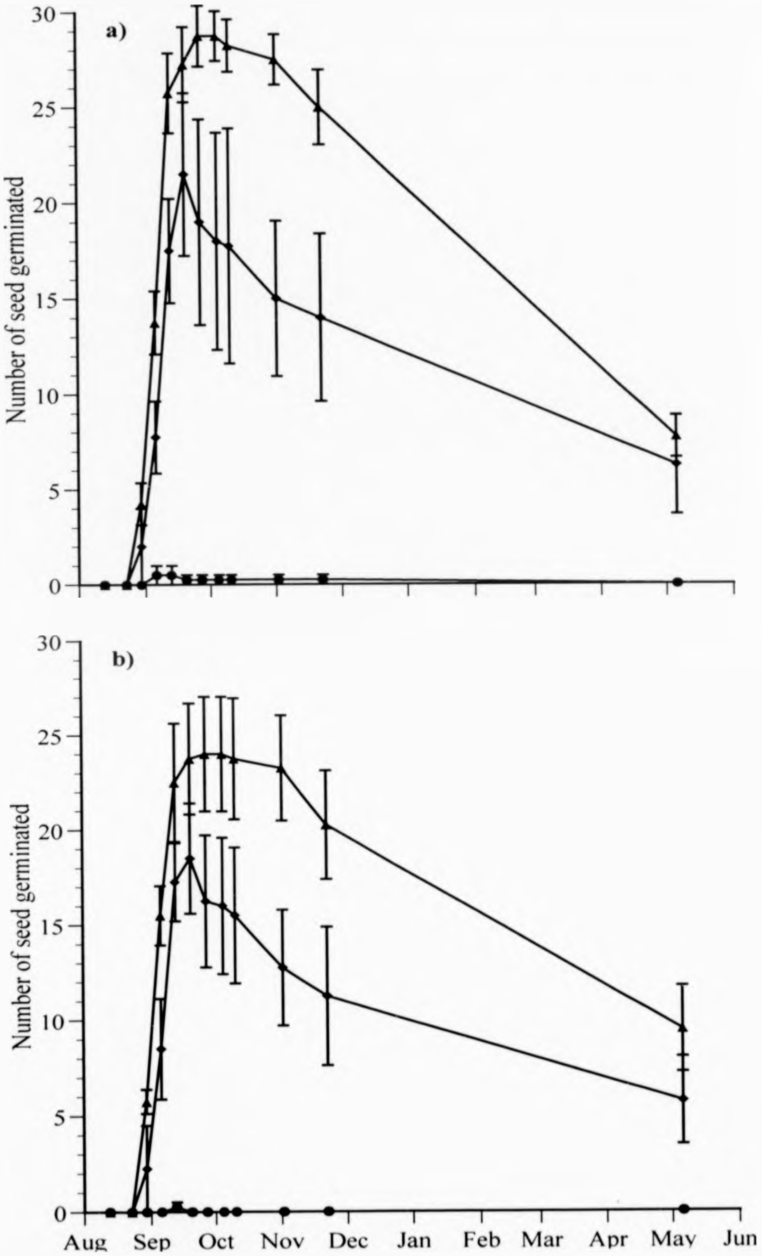

Figure 7-2. Number of *Baccaurea stipulata* (▲), *Dimorphocalyx muricatus* (◆) and *Mallotus wrayi* (●) germinated seed present in ridge (a) and lower-slope (b) transects. Total seed per transect=45. Error bars are standard errors of the mean, *n*=4.

Seed fate

Seed establishment and, where possible, the cause of seed disappearance was recorded. At the end of the experiment no seed remained dormant (Figure 7-3). However, on 22 November, 1996 58 % of *M. wrayi* seed remained dormant, compared with 3 % *B. stipulata* and 13 % *D. muricatus* seed. The next survey was not until 6 May, 1997 so these dormant seed may have been unretrievably dispersed by then. Few seed of each species were classified as eaten or rotten, although the absent class probably includes some eaten seed. There was no significant difference in seed fate between ridge and lower-slope transects (MANOVA, $F_{4,3}$=4.54, p=0.122) nor was there a significant difference between *B. stipulata* and *D. muricatus* ($F_{4,3}$=1.88, p=0.315). Again *M. wrayi* seed were excluded as so few seed germinated.

Growth of the established seedlings was not measured. However, of the seedlings established in May, 1997, 49 % *B. stipulata* had produced a new leaf compared with 23 % *D. muricatus*. The date of the last seedling survey coincided with a severe dry spell, and it was noted that many *B. stipulata* seedlings were wilted, especially on the ridge transects while *D. muricatus* seedlings were not visibly affected.

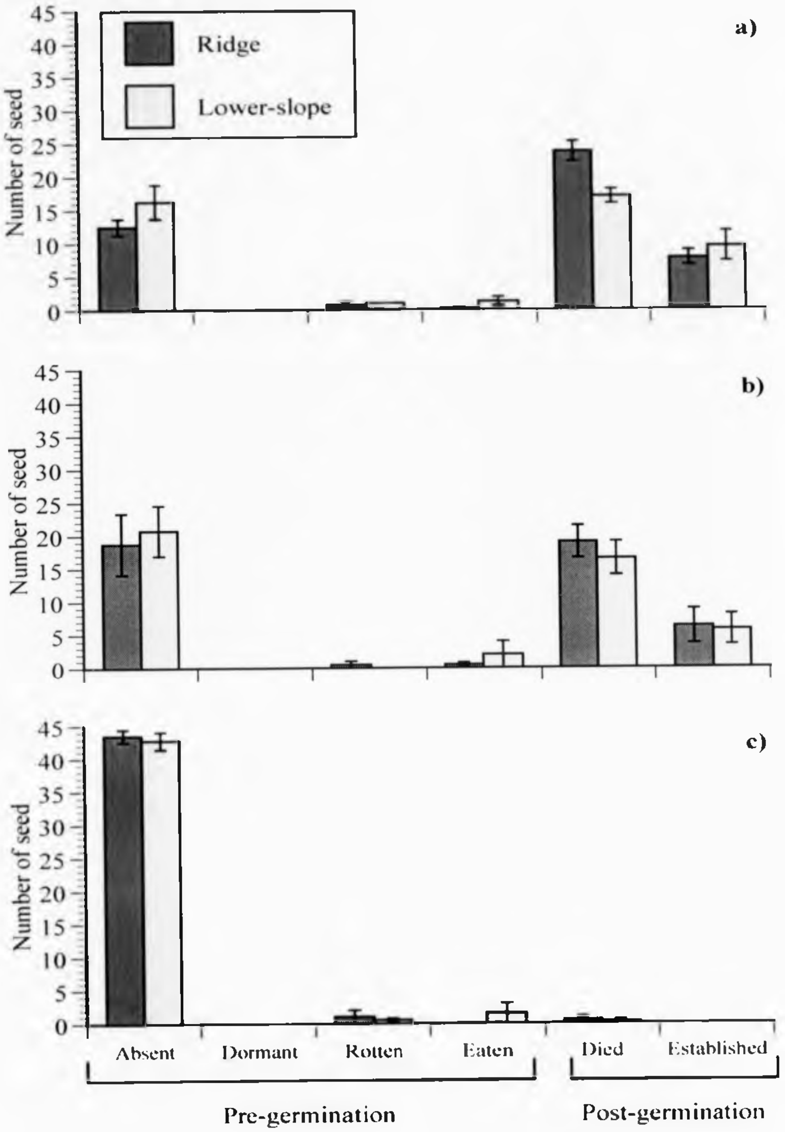

Figure 7-3. Fate of a) *Baccaurea stipulata*, b) *Dimorphocalyx muricatus* and c) *Mallotus wrayi* seed on ridge and lower-slope transects. Error bars are standard errors or the mean, *n*=4.

DISCUSSION

Seed germination rate

It is notable how low the germination rate of *Mallotus wrayi* seed was compared with *Baccaurea stipulata* and *Dimorphocalyx muricatus* seeds. As mature *M. wrayi* fruit were collected from trees with dehiscing fruit, it is unlikely that the seed were unripe. Although no *M. wrayi* seed were present at the end of the experiment it is probable then many of the ungerminated seed had been dispersed. Therefore, either a high proportion of *M. wrayi* seed are inviable or remain dormant for a period greater than three months, or both. Ng (1980), under nursery conditions, found a similarly low germination rate for *M. phillipensis* (5 %). However, germinating *Macaranga* spp. seeds can be observed in leaf litter six months after dispersal (B. Howlett, *pers. comm.*) and as genera *Macaranga* and *Mallotus* are closely related (Airy Shaw, 1975) ungerminated *Mallotus wrayi* seed may be dormant rather than inviable. Liew (1973), in Sabah, found both *Mallotus pinangensis* (sic, probably *M. penangensis*) and *M. ricinoides* in the soil seed bank, again suggesting dormancy.

More generally, Ng (1980) studied germination ecology of 335 Malaysian woody plants and found a continuum from complete germination within two weeks to dormancy of several years. Primary forest species largely germinated immediately but some did remain dormant. Hopkins & Graham (1987) examined seed germination rates of 50 Australian pioneer, secondary and primary forest species. Of the primary forest species the soft coated seeds were obligate immediate germinators and the hard coated seeds showed variably delayed germination. In contrast, many of the secondary and pioneer species showed facultative dormancy if buried. *M. wrayi* seed was not noticeably more hard coated than *B. stipulata* or *D. muricatus* but may have been more impermeable, another factor in delayed germination (Vázquez-Yanes & Orozco-Segovia, 1993).

Also striking is the poor germination rate of *D. muricatus* seed under nursery compared with field conditions. Nursery seed were placed on a perpetually moist sand bed, and the low viability of *D. muricatus* seed under these conditions suggests intolerance of permanent dampness. Under nursery conditions Rogstad (1990) found a similar intolerance for *Polyalthia hypoleuca* seed, plants of which are not found in inundated areas of Pasoh, West Malaysia. In contrast *P. glauca* (a species found in inundated areas) seed germinated under wet conditions. As *D. muricatus* seed germinated and established on lower-slope sites where adult trees were absent, the wet conditions of the nursery may not be representative of field conditions. Further, *D. muricatus* seed is dispersed during dry spells (Chapter 5) evading wet conditions. However, the August-September dry spell is unreliable (Chapter 3), and while *D. muricatus* trees apparently fruit regularly (Chapter 5), the stand size distribution is skewed towards larger trees (Chapter 2). These facts suggest that post-dispersal seed establishment is unreliable, and pre-germination seed death may be an important cause.

Eversham III *et al.* (1996) found that high temperatures, high light environments, low soil moisture and leaf litter promoted germination of Puerto Rican early successional and late successional montane forest species. Similarly Vázquez-Yanes & Orozco-Segovia (1982) found that high temperatures promoted germination of a Mexican pioneer species. Here there was a slight increase in germination rate in ridge sites compared with lower-slope sites, which may be attributable to the higher light, and presumably, higher temperatures found on ridge sites.

Seed germination time

Mean germination time of *B. stipulata* seed was longer than that of *D. muricatus*. This difference is a result of a longer spread of germination times for *B. stipulata*. The narrow spread and short germination times of *D. muricatus* seed may be an adaptive mechanism to ensure germination takes place during a post-dispersal dry spell, as discussed above. Conversely the longer germination times for *B. stipulata*, more drought sensitive than *D. muricatus*, may be an adaptive mechanism to evade any post-dispersal dry spell. If *M. wrayi* seed are dormant rather than inviable they will also evade the normal short duration, and any unusually long dry spell. This hypothesis is supported by Augspurger (1979), who, in Panamanian moist forest, found that seed germination and seedling survival of a shrub species were affected by post-dispersal rainfall. Low rainfall post-dispersal resulted both in low germination and low establishment rates for her study species.

Seed fate and seedling survival

For all the study species a small proportion of the ungerminated seed rotted. This low proportion is partly a result of the exclusion of hollow seed, which would otherwise of rotted, at the start. Where no selection is carried out the proportion of rotten seed can exceed 30 % (e.g. Forget, 1997). The low rate of rotting in *M. wrayi* provides some support for the suggestion that the seed may be dormant rather than inviable.

As absent seed may have been eaten or merely dispersed, the low proportion of seed scored as eaten must be treated with caution. There is however, no evidence for discrimination by seed predators among the study species and, while *B. stipulata* is a scatter- and *D. muricatus* a clump-disperser (*sensu* Howe, 1989) no differences were found in seed establishment. Observed post seed germination insect and mammal predation was low in both species, although cause of death was not formally attributed. Without knowing relative positions of conspecifics it is difficult to comment further on the Janzen-Connell hypothesis. The steeper decline of *B. stipulata* numbers on ridge sites than lower-slope sites and the observed wilting of *B. stipulata* seedlings suggest that *B. stipulata* seedlings may be more vulnerable to drought than *D. muricatus* seedlings (confirmed in Chapter 8). This difference may be the result of the generally higher leaf area of *B. stipulata* seedlings (more seedlings produced an additional leaf than *D. muricatus*).

To conclude, under the conditions of this experiment *D. muricatus* seed is able to germinate and establish on lower-slope sites. However, the low rate of germination under nursery conditions suggests that in wetter years *D. muricatus* establishment rate may be lower on lower-slope sites than on ridge sites. Coupled also to the low production of seed per tree, compared with *M. wrayi*, if seed establishment were a reliable indicator of mature tree distribution, *D. muricatus* should be present but less common on lower-slope sites than ridges. Clearly this is not the case so some other mechanism may also be important in the exclusion of *D. muricatus*. It seems possible that *B. stipulata* seedlings are excluded from ridge sites by drought. It is perhaps important the dry years tend to be grouped (Chapter 3), while *B. stipulata* seedlings survived up until the end of the experiment a series of dry years may kill any ridge seedlings. There is strong evidence both here and in the literature that *M. wrayi* seed remains dormant, thus evading immediate and later dry spells, possible long enough to germinate in a group of wet years.

Chapter Eight. Experiments to manipulate soil water potential in pots

INTRODUCTION

There is strong evidence that at DVFC growth of understorey seedlings is light limited (e.g. Zipperlen & Press, 1996) and periodically drought limited (Chapters 4,6). While at high light levels growth of dipterocarp seedlings may be nutrient limited (e.g. Nussbaum *et al.*, 1995), there is little evidence that such limitation occurs in the understorey. However, Burslem *et al.* (1996) present evidence of drought nutrient interactions under understorey light conditions. The small difference in light levels between ridge and lower-slope sites affect seedling survival and growth (Chapter 6). It seems possible that light levels, and nutrient and water availability, all interact, and affect understorey seedling survival and growth.

It is likely that lower-slope species are excluded from ridge sites by high mortality rates during severe droughts. If soil water increase with depth, this selection will be strongest at the shallowly rooted seedling stage. Ridge species should, therefore, remain un-wilted and live for longer during a severe drought.

While results of pot experiments can differ from field experiments (see Grubb, 1994 and references therein) they enable application of treatments not possible in the field. With the resources available manipulation of light environment and nutrient availability was not possible in the field. It was also not feasible to reduce soil water availability to that found during a severe drought. Two experiments were carried out, the first investigated the interactive effect of drought, light and phosphate on *Mallotus wrayi* wildings, the second droughted *Dimorphocalyx muricatus* and *Baccaurea stipulata* until death occurred. In both experiments field conditions were replicated as closely as possible.

MATERIALS AND METHODS

Experiment 1. *Mallotus wrayi*: interaction of drought, light, and phosphate

Collection of plant material

No understorey seed was available at the time of experiment set-up so wildings were used. Of the study species only *M. wrayi* wildings were available in sufficient numbers. Wildings were collected early morning while humidity was high, wrapped in damp newspaper and placed in a plastic bucket. Seedlings <30 cm height were selected to avoid having to cut the tap root upon planting. As soon as possible after collection (<1 h) the wildings were planted in a 12 inch circumference (roughly 9 cm diameter) oil palm seedling bag. The soil used was forest top soil (0 to 15 cm) collected from near the East Ridge Trail (Figure 2-2) mixed, and sieved through a 1 cm mesh. Roughly 240 seedlings were collected, their height and number of leaves measured and left under 4 layers of shade netting for two weeks. After this period all those seedlings that had died were removed and the remainder ranked and numbered by height multiplied by the number of leaves. These ranked plants were then randomly assigned to the treatments on 31 May, 1995.

Treatments

Plants were grown under two light levels (high light = 2.7 % PAR full daylight (HL); low light = 1.2 % PAR full daylight (LL)), with (+D) and without (-D) artificial drought, and with (+P) and without (-P) phosphate addition. Light values are the mean of four spot measurements taken with a Quantum sensor (Skye Instruments Ltd., UK) while daylight was simultaneously logged outside, as previously (Chapter 5). Artificial drought was imposed by polythene below leaf level, intercepting water but not affecting light (Figure 8-1). Droughted plants were watered once per week, un-droughted plants twice daily. Phosphate was added as rock phosphate ($\equiv$ 56 kg ha^{-1}) once every six months, total addition over the course of the experiment was roughly 80 mg P per pot. For each addition the rock phosphate powder was suspended in 10 ml of water to improve distribution in the pots. Initially there were 18 plants per treatment combination, 144 plants in total. Within each light level plants were re-randomised monthly.

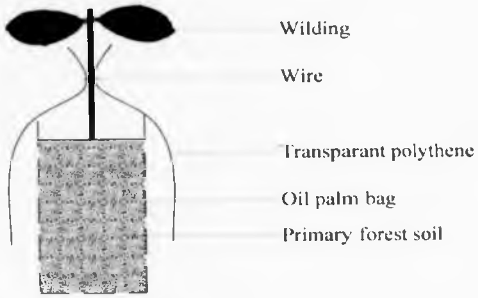

Figure 8-1. Schematic of droughted wilding.

Measurement of soil water potential

Pot soil water potential was measured indirectly, using a similar approach to that in the field (Chapter 6). An oil palm bag was filled with the same soil as used to plant the seedlings, and psychrometers (P55T, Wescor Inc., USA) placed at 10 and 14 cm soil depth. The pot was then saturated with water until field capacity, and air dried over a period of one week. At regular intervals over the week dewpoint readings (see Chapter 3 for methods) were made. Before each reading the pot was weighed and place in a sealed, insulated bucket for 1 h to allow soil water equilibration and temperature stabilisation. The mean of readings at each depth was taken and a calibration curve of soil water potential against soil water content (as proportion of total saturated weight) plotted and an exponential equation fitted. Soil water content as total saturated weight was used because the weight of soil for each pot in the experiment was unknown.

Measurement of wilding growth

Initially on a monthly, later at three monthly intervals, height, and number of leaves were measured. Destructive harvests were carried out prior to treatment application and then on 10 October, 1995 and 18 June, 1996. A further harvest had been planned but failure of the nursery watering system prevented measurements after 8 October, 1996. The water supply may have been unreliable from the end of July, so results beyond this date are treated with caution.

At each destructive harvest, for each treatment, six wildings were selected at random. For two of these plants pre-dawn water potential was measured and pressure volume curves constructed. The water potential measurements were made on whole plants as leaf petioles were too short for insertion into the pressure chamber. The plants were harvested at 06:00, and measurements immediately taken with a pressure bomb, the plants were then rehydrated for 24 hours and pressure volume curves constructed (see Chapter 4 for more detailed methods). For each plant the pot was weighed, saturated with water, reweighed and water potential estimated using the calibration curve. The plant leaves were then removed and photocopied. Each wilding was split into leaf, stem, fine root (excluding taproot) and coarse root (taproot), these fractions dried at 80 °C for >24 h, and weighed. Each photocopied image was scanned and the leaf area determined with a Macintosh PowerBook 5300 computer using the public domain NIH Image program (version 1.59, developed at the US National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). A correction factor was determined for the photocopier using an image of known size. The specific leaf area (SLA) for each individual was then calculated by dividing leaf area by leaf dry weight.

Experiment 2. *Baccaurea stipulata* and *Dimorphocalyx muricatus*: time to drought death

Plant material

Seedlings of *Baccaurea stipulata* and *Dimorphocalyx muricatus* were used. The plants were all grown from seed collected in August, 1996, germinated on a moist sand bed, and planted in 8 inch circumference (6.5 cm diameter) oil palm bags. The soil used was forest top soil (collected as above) blended with 10 % sand to improve drainage. The seedlings were grown under one layer of shade netting (26.7 % PAR full daylight) in the DVFC nursery until the experiment commenced in April, 1997.

Treatments

All plants were placed under one layer of shade netting in a polythene tunnel, on a raised concrete bench (light = 3.6 % full daylight PAR). One treatment was applied, daily watering (+W), and no water (-W).

Measurements

At regular intervals (usually daily, but never less than once every three days) the status of each seedling was assessed. Any seedling that was severely wilted (all leaves dropped below horizontal) or dead (no green remaining on leaves) was scored as wilted or dead respectively. The experiment ceased when all the seedlings in the -W treatment had died.

One week after the experiment started the stomatal conductance and assimilation rate of the seedlings was measured with an portable leaf chamber (PLC4, ADC Ltd, UK) attached to an infra-red gas analyser (LCA-4, ADC Ltd., UK). The air intake of the IRGA was placed approximately 2 m above the ground in the centre of the nursery. Four randomly selected plants of each species in each treatment were measured. Replicates alternated between treatments and species, making four blocks of one replicate for each combination. This blocking structure was used because humidity levels fell in the nursery over the course of the measurements. For one leaf, for each selected individual, assimilation and conductance rates were measured at 300 µmol s^{-1} m^{-2} light. The light was provided by a halogen bulb connected to a lead-acid battery and light levels were adjusted by altering the distance between the lamp and leaf surface. Light was measured using a Skye Quantum sensor attached to a hand-held meter. Before each measurement, to allow acclimation, the leaf was placed in the leaf chamber for at least 5 minutes. Four immediately sequential measurements were than taken. The mean of these measurements was then used in subsequent analysis.

Following the death of all the -W treatment seedlings a destructive harvest was carried out on the +W treatment seedlings. Six individuals of each species were randomly selected. As above the seedlings were split into leaf, stem and root fractions, the leaf area determined, the fractions dried at 80 °C for >24 h, and weighed.

RESULTS

Experiment 1. Light, drought and phosphate.

Soil water potential calibration and pot water potential

An exponential calibration curve of soil water potential against moisture was constructed (Figure 8-2; variance accounted for 99.1 %, $F_{2,26}$=1534.21, $p<0.001$). Water potential varies little between 81 and 100 % moisture content (as proportion of saturated weight). While, because differences in the calculation method, the curve here cannot be directly compared with the field calibration curve (Figure 6-2), it is notable how abrupt and steep the decline in water potential is compared with the field curve. This difference suggests an important change in soil structure between the nursery and field soil. This abrupt change is characteristic of soils with large particles, and perhaps indicates the formation of clay aggregates when the soil dried, prior to potting.

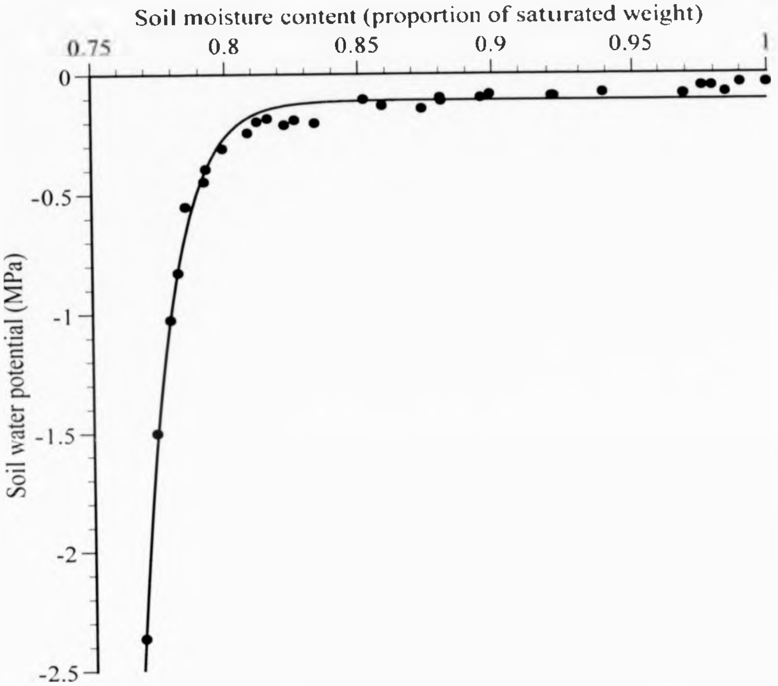

Figure 8-2. Soil water potential calibration curve for nursery soil.

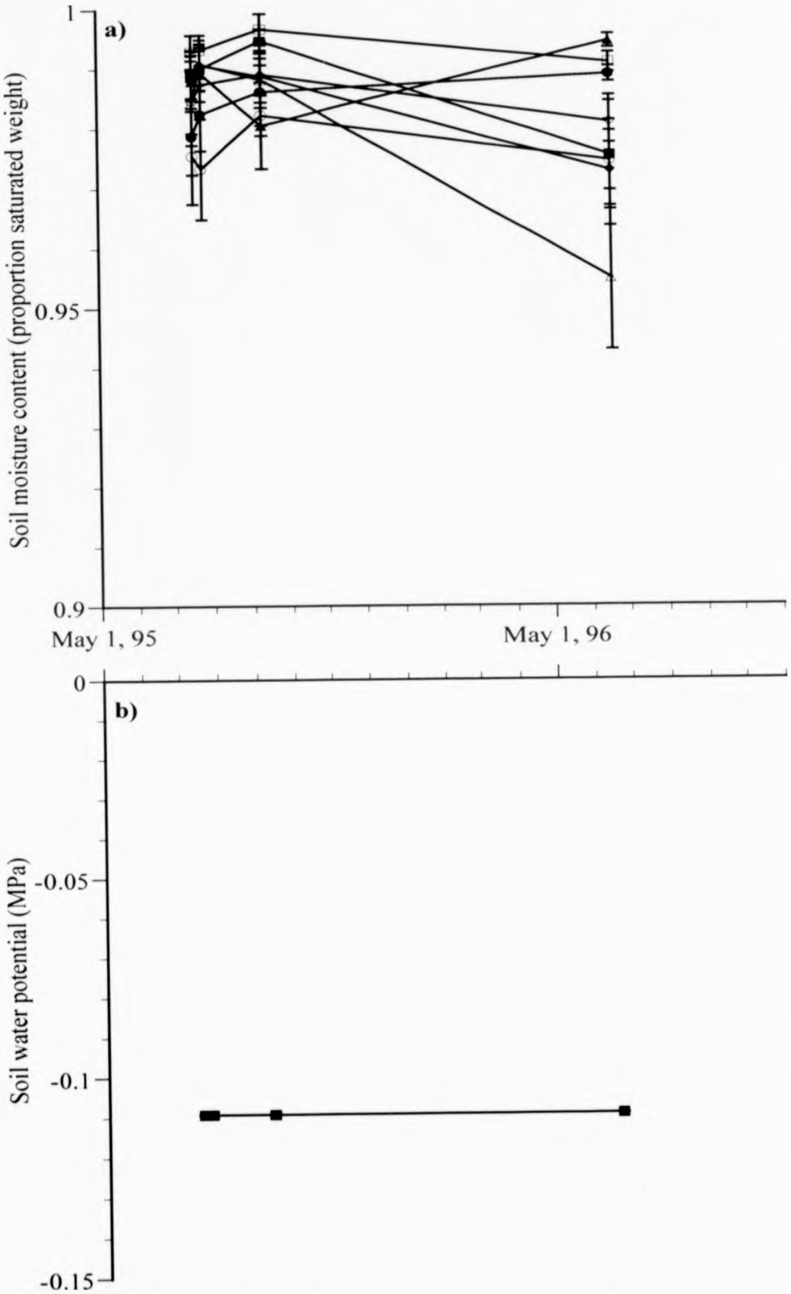

Figure 8-3. Pot soil a) moisture content and b) estimated water potential. Filled symbols LL, hollow symbols HL, -P-D (■), -P+D (●), +P-D (▲), +P+D (◆).

Soil moisture content (Figure 8-3a) varied little and estimated soil water potential (Figure 8-3b) not at all among treatments and measurement dates. Therefore, the drought treatment was not successful in reducing soil water potential. The estimated soil water potential of the pots is similar to that found on lower-slope and valley sites during wet periods (Chapter 3). However, the measurements of +D and -D plants have not been lumped because of differences in soil anaerobis observed on harvest (see below).

Growth of wildings

Non-destructive and destructive measurements of *Mallotus wray* wilding growth under different light, drought, and phosphate levels were made over a 17 month period. On harvesting towards the centre of many pots blue, sulphurous, soil, was observed, indicating anaerobis. It is possible that the less frequently watered pots were less prone to this condition. It is apparent from the reduction in height increase (Figure 8-4a) and negative leaf production (Figure 8-4b) post June 1996 that the seedlings were droughted beyond this point.

All treatments increased height and leaf number to June, 1996. Comparing height increase among treatments up to June 1996, HL plants grew significantly more (ANOVA, $F_{1,85}$=17.85, p<0.001) than LL plants but differences among the other treatments and combinations were not significant. Up to October, 1996, including a possible drought period, there was a significant difference in height increase between HL and LL plants ($F_{1,40}$=15.86, p<0.001) and between +D and -D plants ($F_{1,40}$=5.15, p=0.029). Comparing leaf number increase up to June 1996, there was a significant +P+D interaction ($F_{1,85}$=4.83, p=0.031). Up to October, 1996 there was a significant difference between +D and -D plants ($F_{1,40}$=16.54, p<0.001). These results suggest that the drought treatment was effective once watering became more intermittent. For both leaf number and height increase, while there is not a significant light drought interaction, the LL+D plants show the biggest reduction in growth. Similarly the -P plants show a bigger reduction in growth than the +P plants.

Between the first and second harvests (Figure 8-5a-g) there were significant increases in leaf area (LA) (ANOVA, $F_{1,77}$=26.27, p<0.001), leaf weight (LW) ($F_{1,77}$=10.14, p=0.002), specific leaf area (SLA) ($F_{1,77}$=310.66, p<0.001), leaf area to fine root ratio (LA:FR) ($F_{1,77}$=24.18, p<0.001), coarse roots (CR) ($F_{1,77}$=4.85, p=0.031), and fine roots (FR) ($F_{1,77}$=6.40, p=0.014). There was no significant change in root:shoot ratio (R:S) ($F_{1,77}$=1.62, p=0.205) and the decline between the pre-treatment harvest and first harvest is probably a result of recovery of leaf area following transplant shock.

There were significant differences in LA ($F_{1,77}$=9.21, p=0.003), LW ($F_{1,77}$=9.08, p=0.004), SLA ($F_{1,77}$=9.35, p=0.003), CR ($F_{1,77}$=4.86, p=0.031) and FR ($F_{1,77}$=6.37, p=0.014) between HL and LL plants. There were also harvest light interactions for LA ($F_{1,77}$=9.36, p=0.003) LW ($F_{1,77}$=9.66, p=0.003), SLA ($F_{1,77}$=14.83, p<0.001), and CR ($F_{1,77}$=4.79, p=0.032). The +D plants had a significantly higher R:S than the -D plants ($F_{1,77}$=4.00, p=0.049), although the means are similar. There was also significant harvest light drought interaction for R:S ($F_{1,77}$=5.06, p=0.027) and by the second harvest the HL plants had a lower R:S then the LL plants. There was no significant differences in LA between +P and -P plants, nor a HL+P interaction, although the plants in the high light treatment with phosphate addition had the largest mean LA values. However, for LA:FR there was a significant light phosphate interaction ($F_{1,77}$=4.11, p=0.046). For all measurements all other treatment interactions were not significant.

Wilding water relations

Pre-dawn water potentials were measured and pressure volume curves constructed at each harvest. Considering the lack of difference in soil water potential among treatments it is unsurprising that there were also no significant differences in pre-dawn water potential among the wildings at harvest (Figure 8-5h).

Owing to the lack of difference in plant water potential among treatments, data for each harvest were lumped, and analysed together (Table 8-1). There was a reduction in osmotic potential pre-treatment to the first harvest, although the leaf relative water content at zero turgor remained similar.

Table 8-1. Non-linear regression estimates of osmotic potential at full hydration ($\psi_{\pi,sat}$), relative water content at zero turgor (R^*), water potential at zero turgor (ψ_0), and bulk modulus of elasticity (ε'_{sat}) of *Mallotus wrayi* wildings.

	$\psi_{\pi,sat}$ (MPa)	R^*	ψ_0 (MPa)	ε'_{sat} (MPa)	r^2
31/5/95	-1.17	0.81	-1.45	5.14	0.95
10/10/95	-0.76	0.78	-0.97	3.27	0.69
18/6/96	-	-	-	-	-

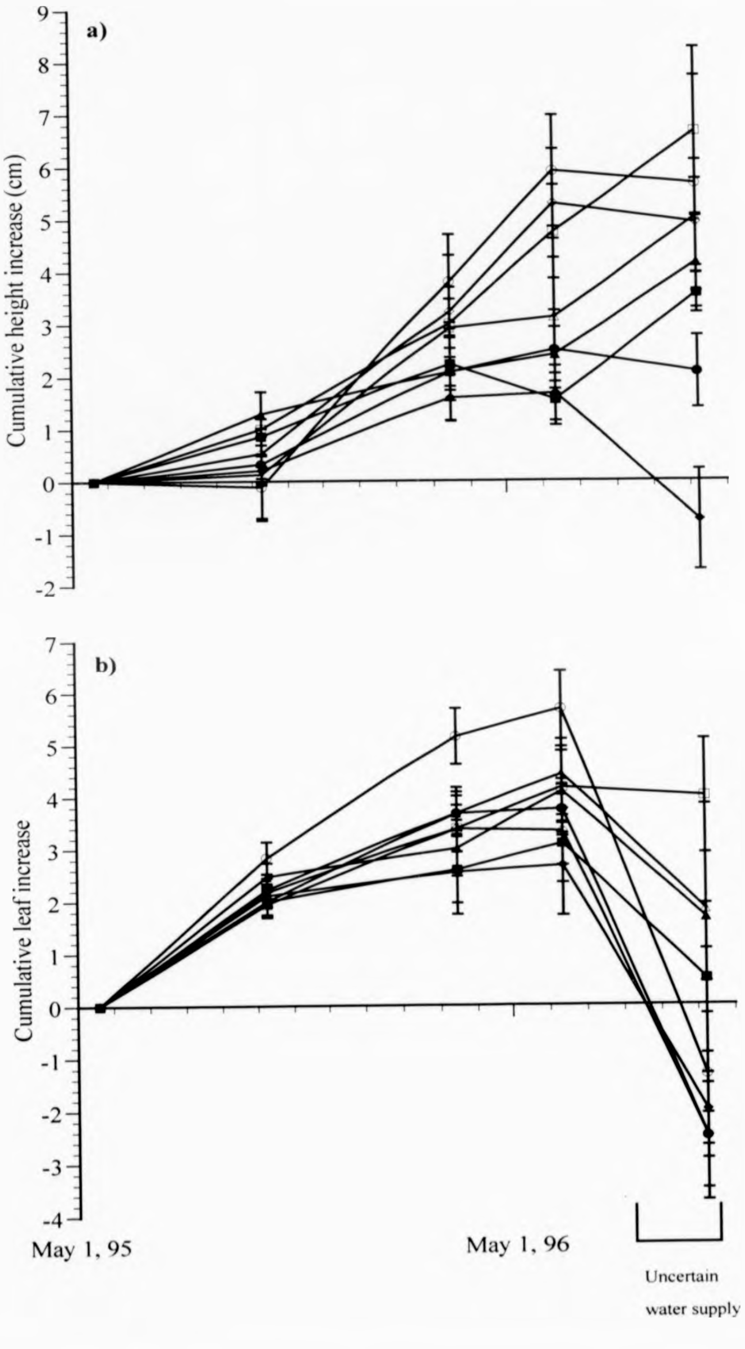

Figure 8-4. Seedling height and leaf no. increase. Symbols as Figure 8-3.

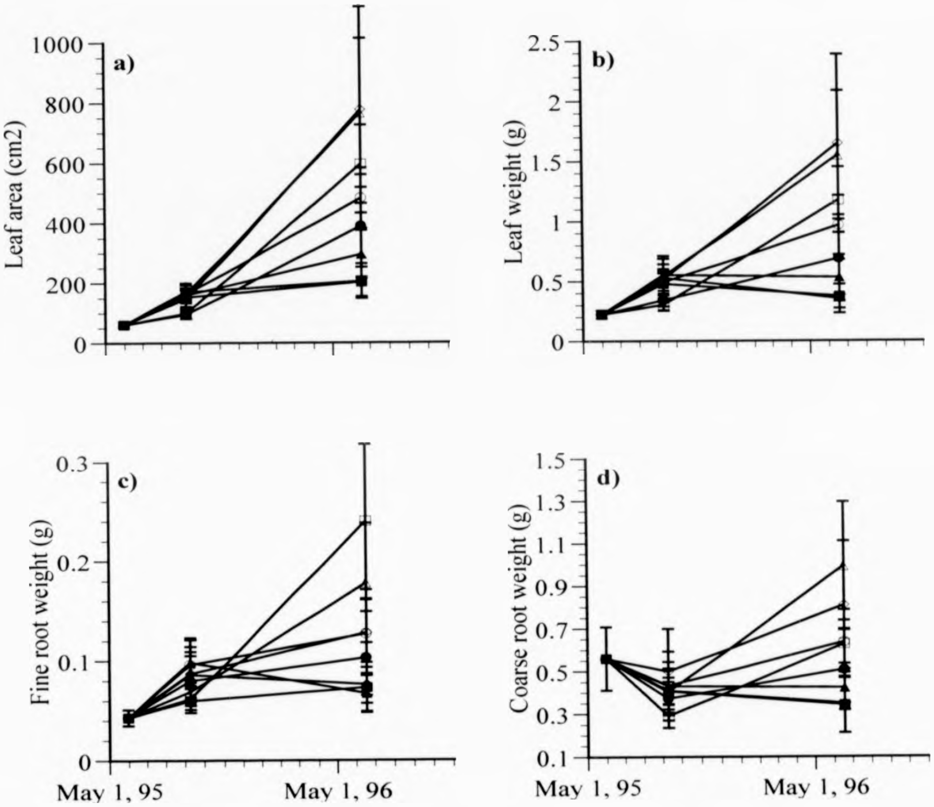

Figure 8-5. Harvest a) leaf area, b) leaf weight, c) fine root weight, and d) coarse root weight. Symbols as Figure 8-3.

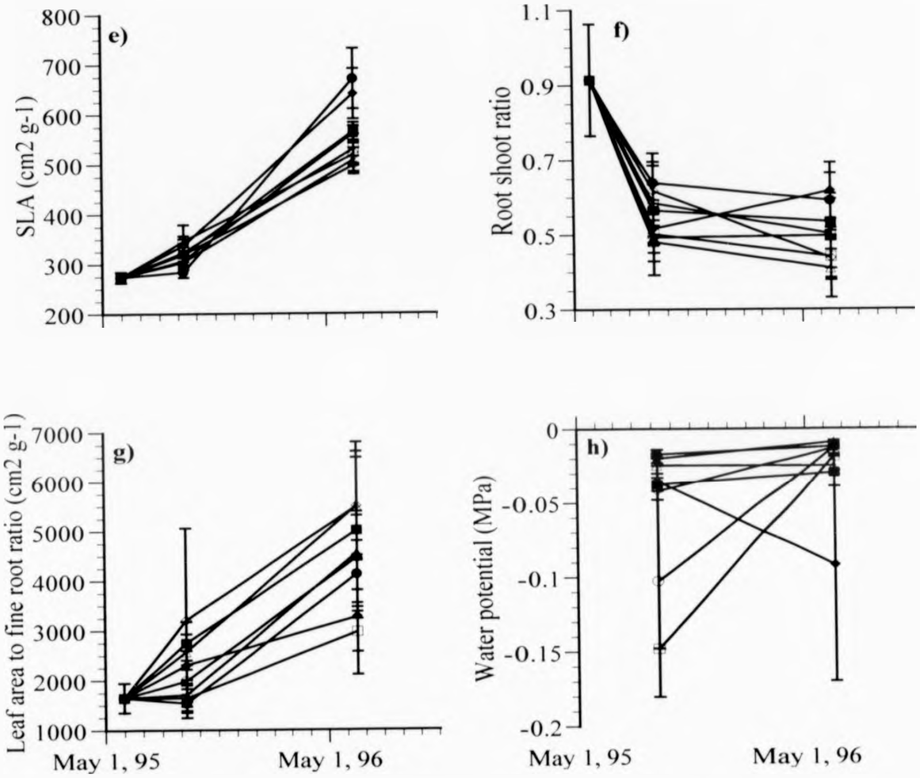

Figure 8-5 continued. e) Specific leaf area, f) root:shoot ratio, g) leaf area to fine root ratio, and h) pre-dawn water potential. Symbols as Figure 8-3.

Experiment 2. Time to drought death.

Initial measurements

Prior to the start of the experiment *Baccaurea stipulata* and *Dimorphocalyx muricatus* seedlings were allocated to treatments and measured. *B. stipulata* seedlings were significantly taller and had significantly more leaves than *D. muricatus* seedlings (Table 8-2).

Table 8-2. Initial heights and leaf numbers of *Baccaurea stipulata* and *Dimorphocalyx muricatus* seedlings. Means with different letters are significantly different (ANOVA, $p<0.05$).

	N	Mean height (cm) ±S.E.	Mean leaves ±S.E.
B. stipulata	30	19.8 ±0.8 ^{a}	9.4 ±0.4 ^{a}
D. muricatus	30	11.8 ±0.7 ^{b}	7.8 ±0.3 ^{b}

Time to wilting and death

Half the seedlings of each species received no water (-W) until they died, time of severe wilting was also noted. No measurements of soil water content were taken, but after roughly two weeks soil in the -W pots had set into a solid block. All droughted seedlings were dead by day 55 and no seedlings of the control group (+W) died over the same period. *D. muricatus* seedlings took significantly longer to wilt (ANOVA, $F_{1,29}$=45.57, $p<0.001$) and die ($F_{1,29}$=32.45, $p<0.001$) than *B. stipulata* seedlings (Figure 8-6).

Assimilation and conductance rates

After one week the assimilation and conductance rates of the +W and -W seedlings were measured. The assimilation rate of *B. stipulata* seedlings was significantly greater (Blocked ANOVA, $F_{1,9}$=5.23, p=0.048) than that of *D. muricatus* seedlings, and there was no significant difference between +W and -W seedlings (Figure 8-7a). There was no significant difference in conductance rate between *B. stipulata* and *D. muricatus* seedlings, nor between +W and -W seedlings (Figure 8-7b).

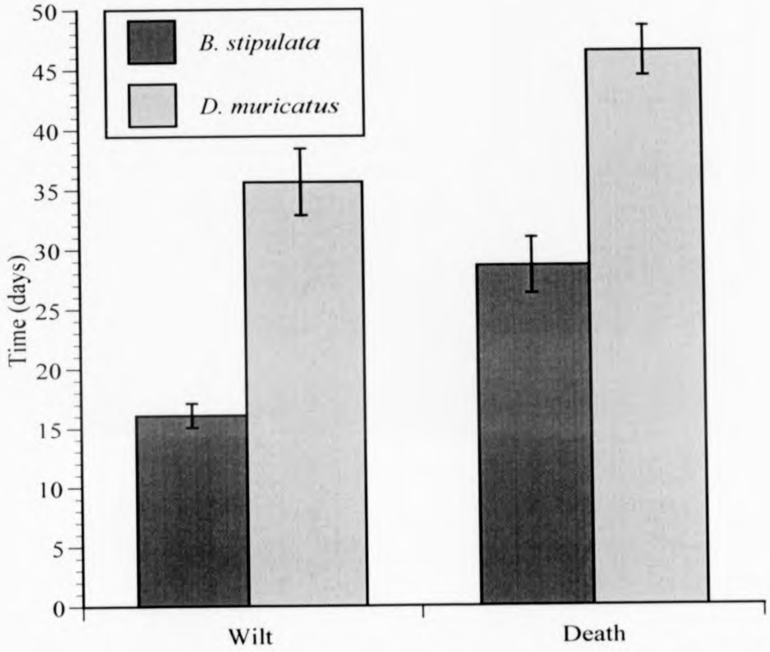

Figure 8-6. Time to wilting and death of *Baccaurea stipulata* and *Dimorphocalyx muricatus* seedlings.

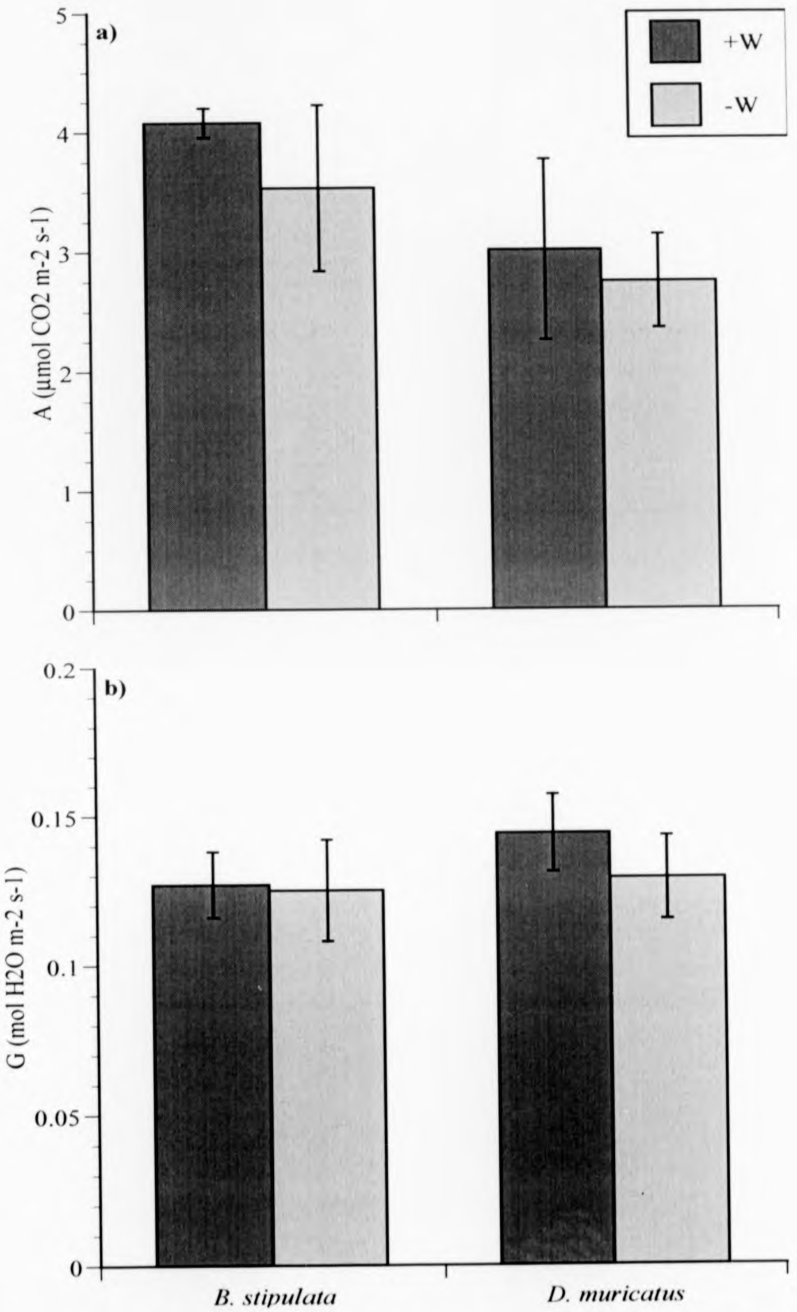

Figure 8-7. a) Assimilation rates and b) conductance rates of watered (+W) and un-watered (-W) *Baccaurea stipulata* and *Dimorphocalyx muricatus* seedlings.

Destructive harvest

Following the death of the -W seedlings, a sample of the +W seedlings were harvested. There were no significant differences in leaf area, specific leaf area, root weight or root:shoot ratio between *B. stipulata* and *D. muricatus* seedlings (Table 8-3). As previously (Chapter 6) it was noticeable how much thicker *D. muricatus* fine roots were than *B. stipulata* or *M. wrayi* fine roots.

Table 8-3. Leaf area, specific leaf area (SLA), root weight and root:shoot ratio of +W plants. ±S.E. Means with the same letter are not significantly different from each other (ANOVA, p<0.05).

	N	Leaf area (cm^2)	SLA ($cm^2\ g^{-1}$)	Root weight (g)	Root:shoot ratio
B. stipulata	6	373.4 ±64.1 ^{a}	207.1 ±8.5 ^{a}	0.94 ±0.15 ^{a}	0.36 ±0.06 ^{a}
D. muricatus	6	383.1 ±89.9 ^{a}	219.1 ±15.9 ^{a}	0.83 ±0.21 ^{a}	0.38 ±0.05 ^{a}

DISCUSSION

Experiment 1

Treatment success

The ineffectiveness of the drought treatment is unfortunate, but even if the treatment had successfully reduced the soil moisture content, the change in soil structure means that it would have been very difficult to maintain a low, but un-catastrophic soil water potential. The fortunate failure of the nursery water supply does provide some data on the effect of drought on the wildings and is probably a more accurate simulation of a field drought than artificially maintaining an arbitrary low soil water potential.

Shade cloth provides a more spatially and temporally even light distribution than found in the field (see review by Chazdon, 1988). However, the two light environments are similar to the mean values found on ridge (HL) and lower-slope (LL) sites (Chapter 6). There appear to be no comparable S.E. Asian nursery studies that have used two 'low-light' levels, the similar study of Burslem *et al.* (1996) used one level, 0.9 % daylight, while Turner (1989) compared dipterocarp growth at 1, 6 and 12 % daylight. Unlike these studies no attempt was made here to reduce the red/far red quotient to that of the understorey. Elsewhere Kolb *et al.* (1990) compared the interactive effect of light, soil moisture, and nutrients on the growth response of *Quercus rubra* and *Lirondendron tulipifera*, but at 20 and 100 % full sun.

While phosphorus addition rates were similar to that of Burslem *et al.* (1996), they are probably not comparable because of the different forms of phosphate used (Na_2HPO_4 and rock phosphate, respectively).

Treatment affect on growth

Plants in the HL treatment grew taller, increased leaf area and increased coarse and fine root weight more than plants in the LL treatment. The lack of a significant difference in leaf number suggests that the HL treatment resulted in bigger leaves rather than more leaves. Turner (1989) found a similar increase in growth of dipterocarps from 1 to 6 % daylight. There were no differences in growth between the +P and -P treatments. So, at these light levels, the wildings were predominately light, not phosphate limited. The trend towards increased leaf area with phosphate addition at the HL levels suggests that at higher light levels than here the wildings may be phosphate limited.

Once watering became erratic there was a clear difference in growth between +D and -D plants. As in the field (Chapter 6), the plants most vulnerable to drought were those grown under LL conditions. The most likely explanation for this difference is the low root weight of the LL plants, reducing their water uptake capability. There is also some evidence that phosphate addition provides some drought protection. As there was no differences in fine root mass between +P and -P plants, addition may have affected the distribution or function rather than weight of fine roots. In contrast Burslem *et al.* (1996) found no difference in growth of +P and -P seedlings (two dipterocarp and one understorey) under drought conditions. It is possible that this difference in finding is explained by the difference in drought treatments, Burslem *et al.* maintained the droughted seedlings at low soil water potentials, but not low enough to result in leaf loss. Response of phosphate addition in the field, where there is root competition, may differ from pots (Grubb, 1994).

Treatment effect on dry mass allocation

Over the course of the experiment there was a remarkable increase in specific leaf area (SLA) in all treatments. The pre-treatment SLA value is similar to that found for *M. wrayi* trees and other tropical tree species (see Table 5-5, Table 5-7). However, for all treatments, by the second harvest, the SLA value had increased to well above that normally found in the tropics. All the wildings received a plentiful water supply and grew in pots with no root competition. The increase in SLA under these conditions indicates both high plasticity, and, by implication, that *M. wrayi* trees and seedlings growing under field conditions regularly experience drought conditions. This degree of plasticity does not appear typical of other species, the seedlings of Burslem *et al.* (1996), showed a slight decrease in SLA when droughted, but not to the same extent. The temperate tree species of Jarvis & Jarvis (1963) showed a greater decrease in SLA when droughted than those of Burslem *et al.* (1996), but the change was smaller than that here. However, droughting has been shown to decrease expanded leaf area, and thereby SLA, in *Eucalyptus globulus* seedlings (Metcalfe *et al.*, 1990). The high SLA values here may have made the wildings especially vulnerable to drought once the water supply became erratic. The significant difference in SLA between HL and LL plants suggests a greater investment in leaf area for LL plants, and photosynthetic machinery for HL plants. This difference may have also made the LL plants more vulnerable to drought. Similarly Fetcher *et al.* (1983) found that leaves of two Costa Rican forest species were thinner when grown in full shade, compared with full sun.

Root:shoot ratios had, by the second harvest, significantly decreased in HL plants compared with LL plants. As both root and shoot weight increased in the HL plants over the LL plants, the decrease in root:shoot ratio indicates a proportionally greater increase in leaf weight. Despite this increase, and an increase in leaf area to fine root ratio, the HL plants were less affected by the erratic watering regime. It seems here that the absolute root weight was more important in surviving drought than the relative root weight. In contrast the droughted plants of Burslem *et al.* (1996) had a lower leaf area to fine root weight than the un-droughted plants and the more drought tolerant *Populus* clones of Mazzoleni & Dickmann (1988) a higher root:shoot ratio than the less drought tolerant clone. If gradients of soil water with depth develop in pots, and plants with larger roots also rooted deeper, the importance of absolute root weight is explained.

Experiment 2

As predicted *Dimorphocalyx muricatus*, a ridge species survived for longer than *Baccaurea stipulata*, a lower-slope species, when un-watered. Mean time to wilting of the species of Burslem *et al.* (1996) was 67-100 d, much longer than observed here. However, although the pots were of a similar size, the figures are probably not directly comparable, the soils are different and Burslem *et al.*'s was not mixed with sand.

Dry mass allocation does not provide a simple explanation for the difference between the two species, there was no apparent difference between *D. muricatus* and *B. stipulata*. It has been previously demonstrated that *D. muricatus* is a drought evader (Chapter 4) and this experiment provides evidence of drought tolerance. It is likely that the soil used had a similar water release curve to that of the *M. wrayi* soil, and observations on soil structure suggest that the rapid decline in soil water potential had occurred after two weeks, *D. muricatus* seedlings remained un-wilted beyond this point. Thick fine roots are a possible drought adaptation, soil will take longer to shrink away from thick roots than thin roots. The thick roots and relatively thick leaves of *D. muricatus* may also store water. It is also probable that, as previously suggested (Chapter 4), *D. muricatus* plant conductance resistance is low and that leaf osmotic adjustment occurs.

It is clear that, unlike *M. wrayi* (see above), *B. stipulata* and *D. muricatus* SLA is not very plastic. SLA of the +W plants, with a watering regime similar to that of the *M. wrayi* wildings was similar to that found in the field (Table 5-5). It is important for a drought tolerant plant not to have a very plastic dry mass allocation response to varying water conditions. While droughts are not as immediate or catastrophic as, for example, a cyclone, once a drought has occurred the only way (assuming growth stops) a plant is able to increase root: shoot relative allocation is to shed parts (e.g. leaves). Hence, if previous to any drought a plant has increased shoot allocation, or increased SLA it will be at risk of drought damage. However, the root:shoot ratio of well watered *D. muricatus* here was lower than *D. muricatus* grown in the field (Chapter 6).

D. muricatus assimilation rate was lower than that of *B. stipulata* but higher than observed for seedlings growing on ridge sites (Figure 4-5). This difference in assimilation rate may account for the difference in seedling height and leaf number between the species. At harvest leaf areas were similar, but *D. muricatus* would have a lower total assimilation rate than *B. stipulata*. After one week without water neither *B. stipulata* nor *D. muricatus* had any reduction in assimilation or conductance rate compared with watered plants. It seems that, as with the *M. wrayi* experiment, even though here the pots were smaller and the soil mixed with sand, one week without water was not long enough for low soil water potentials to develop.

Conclusions

Both experiments illustrate the difficulties in simulating drought under nursery conditions, at least with the soil at DVFC. The apparent change in soil structure means that an abrupt change in pot soil water potential occurs over a relatively small change in soil water content. It would be very hard to maintain an intermediate soil water potential, such as occurs on ridge sites, under these conditions. At higher water contents, measuring soil water content alone provides a poor indication of the soil water deficit experience by the plant. Care would have to be taken in any future experiments to minimise the disruption of soil structure. Alternatively, it might be possible to use an inert polymer such as polyethylene glycol to reduce soil osmotic potential.

The *M. wrayi* experiment demonstrates that, under understorey light conditions, a relatively small increase in light level leads to a large increase in growth. In the field, with root competition for water and nutrients, and the occurrence of drought, this small difference in light may be critical for survival. *M. wrayi* cutting survival was lower on droughted lower-slope sites than droughted ridge sites (Chapter 6). The plasticity of *M. wrayi* dry mass allocation makes it vulnerable to infrequent droughts.

D. muricatus seedlings appear to have drought adaptations beyond deep rooting. These adaptations would enable shallowly rooted *D. muricatus* seedlings to survive droughts on ridge sites. It is not clear whether adult *D. muricatus* trees have similar adaptations.

Chapter Nine. General Discussion

REVIEW OF METHODS

Length of study and frequency of measurements

The total length of the study was 36 months, of which 25 months were spent at DVFC. This length of time was sufficient to include years of different rainfall, but few dry spells. The year-to-year differences found illustrate the importance of covering an adequate time span. A study solely carried out in 1996 would have produced different results from 1997.

Weekly psychrometer measurements and monthly phenology measurements were sufficient to characterise soil water and leaf production variation. The failure of so many psychrometers was disappointing, but seems typical of psychrometers under tropical field conditions (e.g. Becker *et al.*, 1988), so alternatives should be investigated for future work. Soil water measurements outside the LPPs were relatively infrequent and perhaps should have been more frequent, although the sampling of soil would make this difficult. The field-plant-water-relations study would have benefited from more mid-day measurements and a water-potential-component measurement at the driest point (prevented by equipment failure). Measurement of seedling and cutting growth and mortality in the field could have been more frequent, and measurement immediately before and after dry periods would have been desirable. Similarly during the seed establishment experiment later measurements were infrequent and not carried out before and after a dry period.

Scope of study and sample sizes

Most of the study compared *Dimorphocalyx muricatus* and *Mallotus wrayi* as representative ridge and lower-slope species, with *Ardisia colorata*, *Baccaurea stipulata* and *Cleistanthus glaber* also included in some parts. The leaf morphology of the 20 most common species was also studied. This narrow scope does make generalising the results to all ridge, ubiquitous and lower-slope species difficult. However, together the five species named above account for 25.6 % of the stems ≥10 cm gbh, compared with 48.4 % for the twenty most common species. Increasing the number of species studied would have a relatively poor return in terms of number of stems studied, and would have made adequate sample sizes for the rarer species difficult. It would also be difficult to carry out an adequate water relations study on more than two species simultaneously. Future studies should consider replicating by measuring different species at different times with similar soil water potentials.

The phenology study was possibly over-replicated for *D. muricatus* and *M. wrayi*, and it may have been better to study fewer trees in detail to get estimates of leaf life-span, and more trees (and more species) in less detail for timing of leaf and flower production. The field manipulation experiment was under-replicated, but constrained by the lack of seeds and wildings, a problem that is difficult to overcome.

Measurements taken

Water relations, root depth, phenology, leaf morphology, seed establishment and seedling growth of *D. muricatus* and *M. wrayi* were measured. A subset of these measurements was carried out on other species. Areas neglected include growth of trees, detailed conductance and assimilation rates, and rates of herbivory. Under a separate study the growth, mortality, and recruitment of all trees in the LPPs has recently been measured (D.N. Kennedy, D. M. Newbery, G.H. Petol, C. Ridsdale, R. Ong & L. Mandani, unpublished data) and these results will be of great interest. The results of the water relations study implied differences in conductance rates among species. An increased knowledge of conductance, sap flow and assimilation rates would be desirable. Observations suggest there are differences in herbivory rates which may warrant further investigation. Apart from soil water and soil temperature, measurements of subplot physical environment were lacking. Measurements of light, air temperature and humidity would have all benefited from being logged for several days at several locations within each subplot.

Nursery and field experiments

Nursery and field experiments were both handicapped by the dearth of viable seeds and seedlings at most times during the study. Nursery experiments were further impeded by a change in soil properties making it difficult to simulate drought conditions, accurately. Although dipterocarp seedlings are commercially available from the InFaPro project, and pioneer species seeds are plentiful, neither are acceptable alternatives for the study of understorey ecology. The use of cuttings did provide some useful results, but the differences found between cuttings and seedlings mean that cuttings are not adequate substitute for seedlings. Any future study would be advised to take advantage of seed production and maintain a 'seedling bank' in a nursery. Reducing nursery soil osmotic potential with polyethylene glycol may be an alternative way of maintaining low soil water potentials in nursery experiments.

DISCUSSION POINTS

Do droughts occur at Danum?

Soil water potential measurements spanned a period greater than two years and only at one point did low water potentials occur. At this point water potentials were high compared with those found in other tropical moist (forests intermediate between rain and dry forests, defined in the introduction) and dry forests. However, even though the DVFC climate record covers little over ten years (1985-present), one dry period, much drier than any in the study period, has previously occurred (in March, 1992). Estimated soil water potentials during this period approached those found in moist forest in Panama (Becker *et al.*, 1988) and Ghana (Veenendaal *et al.*, 1995), mid-dry season. The extensive review of over 100 years of Sabah climate records by Walsh (1996), provides strong support for more severe dry periods having occurred prior to 1985. Unfortunately, the local variation in rainfall in Sabah means that it is not possible to say how frequently, and how regularly such droughts occur at DVFC. Future rainfall measurements will provide more information over the scale of years, but information for decades and centuries will be more difficult to acquire. The finding of Burgess (1966), that some of the study species have growth rings, may be of use here. It is possible that these rings are caused by slow growth during droughts. Comparison of the spacing and number of rings among sites may allow comparison with sites with more extensive rainfall records.

Are droughts more severe on ridge sites?

In the LPPs, ridge sites were drier than lower-slope sites and this difference became bigger during dry spells. However, there was not a clear difference between the less extensively measured ridge and lower slope SPPs. Therefore, it seems probable that sites where ridge species occur are drier than elsewhere, and experience more severe droughts, but factors other than topography may also be important. In drier spells than measured, here estimates demonstrate that droughts of greater magnitude and duration do occur on ridges than lower-slope sites.

How big an effect do canopy trees have on soil water; how does the total transpiration rate vary among sites?

The majority of soil water measurements took place at 20 cm depth. Cutting all roots entering 5 m x 5 m subplots down to 40 cm depth did not affect soil water at 20 cm. However, observations here and elsewhere in Borneo (Baillie & Mamit, 1983) suggest that both canopy and understorey species root to well below these depths. Water content generally increased with depth, but at some sites decreased between 80 and 100 cm, suggesting extraction of water by trees. Water *usage* may be greater when water *availability* is greater, so measurement of soil water while extraction is occurring may be misleading.

Mature canopy trees will have a much larger leaf area, exposed to lower humidities, than other trees. Consequently, their total transpiration rates will be greater than other trees in the forest and may be an important determinant of soil water potential. In the tropics, soil water potentials have been demonstrated to be higher in gap sites, i.e. sites without canopy trees, than understorey sites (Becker *et al.*, 1988; Veenendaal *et al.*, 1995). If distribution of these large trees was uneven, areas where clusters occurred would be drier than elsewhere. It is possible that ridge sites are more stable than elsewhere, and hence large trees are more common, which may reinforce any differences in soil water availability.

Are tree species affected by drought at DVFC? At what size are they most vulnerable?

During the study period, as discussed above, an extreme dry period did not occur. However, on the ridge sites, during the driest spell, there was some evidence for species being affected by drought. *M. wrayi* seedlings growing on ridge sites had lower assimilation rates than elsewhere. Both *M. wrayi* and *D. muricatus* trees osmotically adjusted leaf cell solutes between wet and dry periods, and *M. wrayi* mid-day leaf water potentials approached their turgor loss point. Leaf production was lower in the dry year compared with the previous wet year, but was also low in a very wet year, so factors other than drought may have been important here. *M. wrayi* wildings showed a marked increase in SLA once freed from root competition and regularly watered, and similarly, lower-slope individuals of ubiquitous species generally had a higher SLA than ridge individuals. Finally, *M. wrayi* cutting mortality was highest during a dry period. Excepting the cutting mortality -cuttings are more likely to die than seedlings- these observed effects are weak and would not have a big influence on species distribution or composition. However, during a drier period the magnitude of these effects would increase. For example, general understorey wilting and some bare canopy crowns were observed during the 1992 drought (K. Bidin, pers. comm.). During a more extreme 'once a century drought', predicted by Walsh (1996) the effects may be more severe and tree death could occur. Forest structure at DVFC (uneven size-class distribution, relative species paucity and high liana density) suggests that such events may have occurred (Newbery, 1992).

The observed leaf loss by canopy species compared with understorey wilting during the 1992 dry period suggests that mature canopy trees are more vulnerable to drought than other trees. As mentioned above, they will have a large total transpiration rate. In addition, because of gravity, a 40 m tall tree will need to keep leaf water potential roughly 0.3 MPa below that of a 10 m tall tree to maintain the same water potential gradient (Hinckley *et al.*, 1978). There will also be increased xylem resistance and an increased likelihood of embolism because of the long xylem pathway. Hence, canopy trees may be more droughted than understorey trees at similar soil water potentials. However, canopy trees have more extensive root systems and root into deeper soil than other trees, and as Newbery *et al.* (1996) suggest those growing on ridges may root into lower-slope sites, although there will be root competition from lower-slope trees. Further, as canopy trees will be exposed to drought more often, they may have a greater drought resistance than other trees. If this resistance is not plastic, immature canopy trees growing in the understorey will also be relatively drought resistant. This inference is supported by canopy tree saplings being more deeply rooted than understorey trees and shrubs in Panamanian forest (Becker & Castillo, 1990). Understorey trees will be exposed to dry conditions less frequently and selection pressure for drought adaptation will be weaker than for canopy trees, hence they may be more vulnerable to drought than canopy trees. This suggestion is supported by the findings of Condit *et al.* (1996), that, in Panama, following a 25-year drying trend the numbers of small stature species slope specialists declined but that of larger species slope specialists did not.

The limited soil-water-gradient-with-depth study, and the work of Green (1992) both show that soil water increases with soil water depth, even though water extraction by trees may be greater at greater depths. Consequently newly established, shallowly rooted seedlings, with little secondary growth to resprout from, will be the most vulnerable to drought. The relative rareness of ubiquitous seedlings on ridge sites compared with lower-slope sites supports this conclusion. Similarly Still (1993), at DVFC, found that dipterocarp seedling mortality was high during a dry period compared with a wet period. If seedlings are the most vulnerable stage there are implications for interpreting enumeration studies that measure only established trees. There may not be differences in mortality between the measured trees, but fewer trees of one species may be recruited into the measurement size-class because of seedling mortality. For example, Condit *et al.* (1995), in Panama, found no difference in mortality between 'generalists' (≡ ubiquitous) and slope specialists during a drought period, but it is possible that there were differences in smaller size-classes.

Are understorey ridge species more drought adapted than other species? What are the adaptations?

In the field, during dry spells, *D. muricatus* trees maintained higher pre-dawn and mid-day water potentials than *M. wrayi* trees. Analysis of leaf osmotic and turgor potentials suggested that *D. muricatus* would have a greater capacity for osmotic adjustment during drier spells. *D. muricatus* trees were deeper rooted than *M. wrayi* trees growing at the same site. Mortality of *D. muricatus* seedlings was lower than that of *M. wrayi* cuttings in droughted subplots. In a nursery drought experiment, *D. muricatus* seedlings took longer to wilt and die then *B. stipulata* seedlings, and there were no apparent differences in dry mass allocation between the species. These findings are evidence for *D. muricatus* being more drought resistant than other ubiquitous and lower-slope species. However, it is not clear whether the other ridge species of Newbery *et al.* (1996), *C. glaber* and *L. beccarianum*, share this drought resistance. Root structure of *C. glaber* is more similar to that of *M. wrayi* than *D. muricatus*, but it may share other drought adaptations. The similar spatial and size-class distribution of the ridge species does suggest that they all share similar ecological characteristics, but further investigation would be desirable.

The field studies of *D. muricatus* suggested that it was primarily a drought evader (deeply rooted), although the results also implied low stomatal conductance rates and low xylem resistance. However, the nursery experiment also provided evidence of drought tolerance. The thick leaves and fine roots suggest a possible water storage capacity. Dry mass allocation, which was less plastic than *M. wrayi*, may also be important. The plastic allocation of *M. wrayi*, in the predominately wet climate, will result in high specific leaf area and low root:shoot ratio, thereby increasing vulnerability to drought.

Why are ridge species not found on lower-slope sites?

Over the course of the study several hypotheses were considered to explain the absence of *D. muricatus* and other ridge species from lower-slope sites. There is little evidence that the species are unable to grow in wet soils, as found by Rogstad (1990) for a *Polyalthia sumatrana* in Pasoh, *D. muricatus* seedlings planted into lower-slope sites survived, and regularly watered *D. muricatus* seedlings in the nursery grew well. The possibility remains of occasional inundation as proposed by Ho *et al.* (1987), but *D. muricatus* seedlings, established since the last flooding event, should then be found on lower-slope sites.

There is some evidence that *D. muricatus* seed germination is reduced under wet soil conditions, and the uneven size-class distribution of the ridge species, despite regular fruiting, is also suggestive of infrequent seed establishment. The root structure and dry mass allocation of *D. muricatus* may also be important. The root system of trees seems ill-adapted for nutrient uptake, lateral roots are few, and occur at relatively deep depths, and fine roots are coarse. Greater investment in roots will reduce investment in leaf area, important if, as light measurements suggest, lower slopes are darker than ridges. Ridge species may, therefore, be excluded from lower-slope sites by low light levels and competition for nutrients. These hypotheses are not exclusive, and none of the proposed mechanisms seems powerful enough alone to explain the complete absence of ridge species from lower-slope sites. However, these mechanisms together could exclude *D. muricatus*.

If drought and drought adaptation is important, why are ubiquitous species found on ridge sites?

Of key importance is the frequency and severity of the droughts. Between any drought events, lower slope and ubiquitous species will be able to establish on ridge sites, which, if lighter, may be more favourable for growth than elsewhere. Once establishment has occurred, a long period to the next drought will enable the seedlings to root deeper and thus become more drought resistant. The more frequent and more severe droughts are, the more probable that ubiquitous species will be killed on ridge sites. It appears that at DVFC droughts occur sufficiently often and are sufficiently severe to exclude lower-slope species such as *B. stipulata* and to reduce ridge populations of ubiquitous species like *M. wrayi*. It is interesting to note that in Panamanian moist forest, with a strong dry season, there is a clear group of species associated with wet slopes (Condit *et al.*, 1996), while in the wetter forest at Danum, there is a clear group associated with dry ridges. Other possibilities are that *M. wrayi* may also evade drought with dormant seed, and there may be wet microsites on ridge sites, but these suggestions were not confirmed.

Drought frequency and intensity increases towards the eastern coast of Sabah (Walsh, 1996) so it would be expected that towards the coast, populations of ridge species become more extensive, and populations of ubiquitous and lower-slope species less so. Unfortunately, logging operations have moved in an east to west direction, so there are few areas of coastal primary lowland forest intact to test this idea. On the coastal mountain Gunung Silam, 50 km east of DVFC, Proctor *et al.* (1989) recorded an increase in litterfall, but no increase in mortality in plots 280-700 m altitude following the 1982/83 drought. Bruijnzeel *et al.* (1993) dismiss drought as an important factor on Gunung Silam at 870 m, but the possibility remains that, at lower altitudes, trees are exposed to drought more regularly than at DVFC thus affecting drought resistance and species composition.

Are the populations of ridge species relics?

Although the uneven size-class distribution of the ridge species does suggest infrequent establishment, the species do fruit regularly, and seedlings are present so the populations are not moribund. However, the seed dispersal mechanism of *D. muricatus* does require a relatively strong dry spell. *Lophopetalum* and *Dimorphocalyx* species related to those found at DVFC occur in wet evergreen forest, with a strongly seasonal climate, in Uppangala forest, Western Ghats, India (Pascal & Pelissier, 1996). The glacial reduction in rainfall would favour any drought resistant species, so their distribution would become more extensive during glacial periods. During interglacials these populations would then retract, but the rate of decline may be slow. (Condit *et al.*, (1995) estimate the cohort life-span for some Panamanian tree species to be >1000 years.) Therefore, the current population distributions may be beyond the ecological range of the species, i.e. the forest is in dis-equilibrium.

Differences in drought resistance among species, topographic variation in soil water, and differences between glacial and inter-glacial rainfall have implications for long term forest dynamics. As discussed above, the range of ridge species may extend during glacials and retract during inter-glacials, and the reverse might be expected for ubiquitous and lower-slope species. Thus, just as it has been proposed that drought sensitive species persist in refugia during glacials, ridge sites may be refugia for ridge species during inter-glacial periods. In both cases isolation of small populations would occur, though whether speciation could occur over relatively small time periods (about 100,000 years) is doubtful. However, Ashton (1969) does suggest that rain forest dipterocarp species have radiated from a dry or moist forest ancestors. While the glacial reduction in rainfall is not in doubt, there is considerable biogeographical, geomorphological and paleoecological evidence that Amazonian glacial refugia did not occur (see review by Bush, 1994). Any differential drought resistance between canopy and understorey will mean that the communities may be uncoupled during long term changes in rainfall. Changes in rainfall patterns caused by global warming will also affect the distribution of tree species with different drought resistances. Survival of populations will be affected by speed of migration and the presence of any barriers to migration.

Are species within topographic guilds ecologically similar?

Few species were studied, so a complete answer of this question is impossible. In the most complete study, that of leaf morphology, there were not clear differences in leaf structure among guilds. However, differences in leaf structure may not be adaptive. In terms of leaf production and flowering patterns *A. colorata* is different from *C. glaber*, *D. muricatus*, and *M. wrayi*. Similarly the limited assimilation study found differences between *A. colorata* and *M. wrayi* seedlings. This limited evidence suggests that Hubbell & Foster (1986), are incorrect when they suggest that within guilds adaptive convergence has occurred.

Equilibrium or dis-equilibrium?

Baillie *et al.* (1987) draw attention to the apparent difference in views between workers in West Malaysia, who favour a stochastic view of the forest, and those in East Malaysia (Sabah and Sarawak), who consider there to be a stronger element of edaphic determinism. However, demonstration of site specificity only implies lack of stochasity if site conditions are constant over time. If the above analysis is correct it seems that at DVFC variation in rainfall, over different time scales, prevents equilibrium. Statements such as 'we will soon be able to make a worldwide assessment on the lability of the species composition of tropical forests' (Condit *et al.*, 1996) should be treated with caution as difference in the timing and frequency of plot enumerations relative to the timing and frequency of any extreme events may suggest different labilities.

What cues flowering and fruiting of understorey trees at DVFC?

See Chapter 5 for a more extensive discussion of this question. In summary it was concluded that the best explanation for seasonal differences in leaf and flower production was that mild water stress cued flower bud break, and seasonal light increase leaf bud break. These conclusions were tentative and experimental manipulation would be required to confirm them. The seasonality in leaf production of three out of four of the study species may also be an adaptation to increased seasonality during glacial periods.

How does logging affect understorey species?

D. muricatus and *M. wrayi* cuttings planted in logged forest did not grow well and mortality was higher than in primary forest sites. The chief cause of mortality appeared to be litter-fall from pioneer species, especially *Macaranga gigantea*. The ability of the study species to resprout from the base means that trees will survive logging damage, and they may be able to respond to higher light levels. However, the poor growth of *M. wrayi* under low light conditions suggests that growth of understorey species under climbing bamboo will be suppressed. There was no measured difference in soil water between logged and primary forest sites; any increase in air exposure may be balanced by the removal of canopy trees. The more frequent fruiting of understorey species may mean that there is a larger seedling bank than for dipterocarps. Overall, understorey species do not seem to be at an especial advantage or disadvantage compared with canopy species in logged forest.

FURTHER WORK

The within-site soil water variation, variation of soil water with depth, and interaction with canopy tree distribution should be investigated further. For example, are ubiquitous trees on ridge sites associated with wet microsites? Trenching to greater depths than here would be labour-intensive but provide valuable information about how water availability and water extraction varies with soil depth. Analysis of xylem-water-stable-hydrogen composition, as described by Jackson *et al.* (1995), would allow comparisons of depth of soil water extraction between trees of different sizes and species to be made, without root excavation. As mentioned above a more detailed comparison of light, air temperature and humidity between sites would also be desirable.

The water relations of other ridge, ubiquitous and lower slope understorey species should be studied to see if the differences found between *D. muricatus* and *M. wrayi* are general. It would also be interesting to compare understorey water relations with canopy saplings and mature trees, although this last would be difficult. As well as the water-potential measurements here, assimilation, conductance and sap flow should also be measured.

Experimental manipulations not carried out here include irrigation and opening the canopy. Both would be helpful in determining the cues for leaf and lower bud break, but they would also be difficult to implement, and probably have to be carried out outside the conservation area. It would also be hard to find a nutrient free source of water. If a reliable source of seedlings and pot droughting method could be found, further experiments could be carried out. Competition experiments, growing seedlings of different species in the same pots under different water and light environments, would also be useful. Following cohorts of seedlings in the field under different water and light regimes could provide valuable information.

The results of the most recent LPP enumeration will help confirm or refute some of the ideas above. The previous enumeration was 1986/7, so the period between the two enumerations includes the 1992 dry period. How does the growth and mortality of the ubiquitous species compare between sites? How does the growth and mortality of ridge, ubiquitous and lower-slope species compare? How do recruitment patterns vary between sites and among species groups?

If intact patches of primary forest near, or on, the east coat (e.g. Sepilok Jungle Reserve, Sandakan) could be found, a comparison of their species composition and distribution would be interesting. As discussed above, ridge species distribution would be expected to be more extensive in coastal forest.

Finally, is there gene flow among the isolated ridge species patches? RAPD (random amplification of polymorphic DNA) could be used to 'fingerprint' ridge species and the within and among patch variation compared with that of ubiquitous species from the same sites. Is there evidence that now isolated populations have been contiguous in the past?

SUMMARY CONCLUSIONS

- The infrequent dry and drought periods that occur at DVFC have an important effect on understorey tree ecology.
- Areas where ridge species occur are drier than elsewhere, and the difference becomes greater during dry periods.
- *D. muricatus* has a greater drought resistance than ubiquitous and lower-slope species. Other ridge species are expected to have a similar resistance. The drought resistance is a combination of drought evasion and drought tolerance.
- Drought resistant species will be favoured during glacial periods which may partly determine their current distribution.
- Drought species may be excluded from lower-slope sites by some combination of competition for light and nutrients and poor seed germination under wet conditions.
- Droughts are sufficiently frequent to exclude lower-slope species but not frequent enough to exclude ubiquitous species.

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