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Stunted Cloud-forest in Taveuni, Fiji[1]

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ABSTRACT: The vegetation and microclimate of a stunted ridge-top cloud-forest on Mt. Koroturanga (1210 m), Taveuni, Fiji (Lat. 17°S, Long. 180°) is described. Canopy heights decreased from about 30 m at sea level to 10 m at 1140 m altitude and to 3–7 m on the ridge and upper windward slopes. The stunted trees were of low height for their stem diameter, and had abundant epiphytic bryophytes. The upper windward slopes and ridge were usually cloud enveloped and had low temperature (*c* 17°C), high relative humidity (*c* 94%) and high wind speed (*c* 5 $\mathrm{m\,s^{-1}}$ at 15 m height). Canopy height was closely correlated with estimated rates of leaf transpiration. The cloud-forest had abundant *Freycinetia urvilleana* in the upper canopy and included species restricted to this environment on a few peaks in Fiji, e.g. *Ascarina swamyana* and *Medinilla waterhousei*.

STUNTED, OR ELFIN, RIDGE-TOP FORESTS (thickets, shrublands or woodlands) are recorded from cloudy montane environments throughout the wet tropics and sub-tropics, especially where humid onshore winds rise over coastal ranges (Howard 1968, Grubb 1977). These forests, also called "moss forests", are recognized by both the low height of the tree canopy and the abundance of epiphytic bryophytes. The canopy height varies from 1 m to 18 m in different localities, and the abundance of bryophytes ranges up to a cover of 10–20 cm depth, (Howard 1968, Russell and Miller 1977). Despite the lack of a precise structural definition, these forests are inevitably associated with sites frequently enveloped in clouds, and the trees are stunted in comparison with most other sites at similar altitudes. Severely stunted forests occur above *c* 600–800 m altitude, the height at which rising maritime air masses start to form clouds, and the lower limits rise away from the coast, an aspect of the massenerhebung effect (Grubb 1971). These stunted forests are not simply the result of greater altitude, though tropical forests at *c* 3000–4000 m altitude also typically have a low canopy and abundant bryophytes.

Hypotheses to explain the stunted trees and abundant bryophytes have involved most of the peculiar aspects of the microclimate and soils. Wind speeds on ridges are generally higher than those on lower slopes (Grace 1977, Bradley 1980). It has been suggested that this could cause a thigmomorphogenetic response which produces stunting (Lawton 1982), that the wind damages buds and new leaves thereby reducing growth (Weaver, Byer and Bruck 1973), or that dessicating winds reduce growth (Beard 1944, Grace 1977). There is, however, little evidence of wind-clipping in tropical forests (Baynton 1968, Grubb 1977) and the winds are typically very humid (Baynton 1968, 1969, Weaver et al. 1973). The cloudy conditions result in at least a 40–60% reduction in solar radiation (Baynton 1968, Gates 1969) reducing the rate of photosynthesis (Grubb 1977, Roth, and de Bifano 1980), lowering temperatures, and reducing growth rates (Beard 1944, Grubb 1947). Through a combination of microclimatic conditions, clouds greatly reduce transpiration (Beard 1944), and rates of only 3–10 × $10^{-7}\,\mathrm{g\,cm^{-2}\,s^{-1}}$ were calculated by Gates (1969) for canopy leaves. Rates of about 0.4 × $10^{-7}\,\mathrm{g\,cm^{-2}\,s^{-1}}$ were measured with potometers for lower canopy leaves

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(Weaver et al. 1973) in Central American cloud-forests. During a summer season in a New Zealand cloud-forest the shoot water potentials ranged from −0.1 to −1.2 Mpa (Green and Jane 1983), indicating little water stress. Stomata closed as the saturation deficit increased when the enveloping cloud cleared (Jane and Green 1985), possibly a consequence of poor root development in waterlogged soils. The significance of very low transpiration rates is uncertain: Grubb (1977) contends that they are probably not limiting growth, but Weaver et al. (1973) suggests that they may result in nutrient deficiency which causes stunting. Grubb (1971, 1977) also suggests that stunting is related to nutrient deficiency, especially of nitrogen and phosphorous, because of the low rate of mineralization and nutrient release in the soils. A further characteristic of the soils is a probable high rate of leaching and high soil-water content, resulting in a low soil nutrient concentration; factors which would contribute to nutrient deficiency (Grubb 1977). A shallow soil may also be the cause of stunting in some situations (Gleason and Cook 1926, Grubb 1977, Kirkpatrick, and Hassall 1985).

In the Pacific region stunted ridge-top forests occur on most mountainous islands, e.g. New Guinea (Paijmans 1976), Samoa (Banks 1982), Kosrae (Maxwell 1982), Cook Islands (Merlin 1985), and the Fiji islands (Smith 1979, Kirkpatrick and Hassall 1985). Kirkpatrick and Hassall (1985) describe the flora of a stunted forest at about 400–420 m altitude near the summit of Mt. Korobaba in Viti Levu, stunting which they attribute to shallow soils and windiness. Stunted cloud-forest is apparent on the high ridges in Viti Levu, Vanua Levu, and Taveuni above about 900 m altitude and is most extensive on the ridges about Mt. Koroturanga (1210 m) and Mt. Uluingalau (1241 m) in Taveuni. The ridge-top forests in Taveuni described in this paper apparently have the highest rainfall and cloud cover of any sites in Fiji and may be considered as an extreme type of stunted forest. Microclimatic observations were made to determine how transpiration rates vary between the lowland, upland, and ridge-top forests.

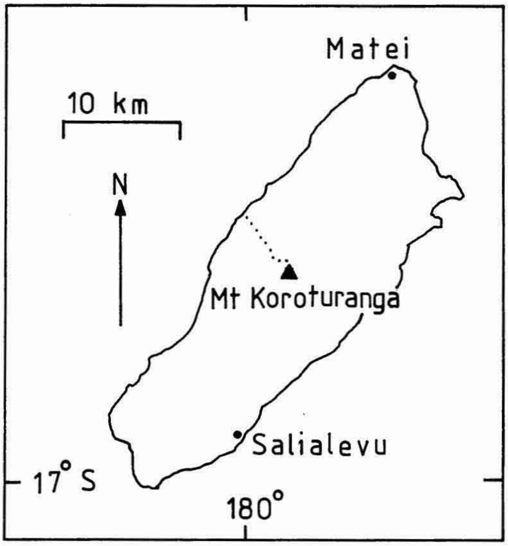

FIGURE 1. Map of Taveuni showing localities mentioned in the text. The altitudinal transect is indicated by the dotted line.

STUDY AREA

Taveuni is 42 km long (N.E.–S.W.) and 10–14 km wide (S.E.–N.W.) with a central mountain range rising to 900–1241 m over much of its length (Figure 1) (Lat. 16°50′S., Long. 180°). The landforms are volcanic in origin, ranging from Tertiary lavas in the north-east to mid-Holocene eruptions in the south-west (Fiji Geological Survey, pers. comm.). Up to about 800 m altitude there are relatively uniform slopes of 10–14° dissected by river gorges, giving way to steeper slopes of 15–35° on the pyroclasts which comprise the higher ranges. The study area is the ridge 800 m north of Mt. Koroturanga (Des Veoux Peak) at an altitude of about 1200 m. The substrate is a clayey soil of 10–30 cm depth passing into pyroclasts with a coarse sand-sized texture. The pyroclasts are dipping at about 25–35° on the north-west slope, virtually parallel with the hill slope. Excavations, e.g. roadworks, tend to induce instability and scree formation, but natural landslides were not apparent in the study area although they were observed on other slopes.

The rainfall at the summit of Mt. Koroturanga is recorded daily by the Department of Public Works and averages 9970 mm year^{-1} (5 years) and 27 mm day^{-1}, with no obvious seasonal trend except for higher rainfall associated with cyclones, typically between December and April. There is a daily cycle of increasing cloud cover over the main range and the study area is reported to be enveloped in cloud during many mornings (5:00–8:00 am) and intermittently during the rest of most days. Pilots routinely flying to Matei (Figure 1) indicated that the peak was only visible, from a similar altitude, about once every 20–30 flights, and sometimes not for several months in succession.

Rainfall on the southeast coast of Taveuni is about 5000 mm year^{-1} (e.g. Salialevu), while rainfall on the northwest coast is about 2800 mm year^{-1} (e.g. Matei). Evidently the prevailing southeast trade winds rise over the central ranges causing orographic rainfall on the eastern slopes and peaks, but there is a rainshadow on the western slopes. On the drier western slopes the rainfall pattern is more seasonal and monthly rainfall is only about 100–200 mm between April and October. Average wind velocities are about 2–3 m s^{-1} at southeast coastal recording stations in Fiji. Wind velocity is not recorded on the west coast of Taveuni but is evidently much less, and the sea surface is often smooth. The average daily range of air temperatures at Matei is 24–30°C in January and 21–27°C in July, and relative humidity at 9:00 am is about 80% in the wet season and 75% in the drier months, declining by about 5% in the early afternoon and increasing by about 5% at night.

The central part of the southeast coast is uninhabitated and forest occurs from sea level up to the highest peaks, while on the other coasts there are gardens and plantations up to about 350 m altitude. The flora, fauna, and water chemistry of a crater swamp 3 km northeast of the ridge has been described by Southern, Ash, Brodie and Ryan (1986), and the vegetation is otherwise poorly known except for notes in the floras by Brownlie (1977), Parham (1972), and Smith (1979, 1981, 1985).

METHODS

The study area was visited on several occasions during 1982–1983 and a vegetation transect was examined across the island (N.E.–S.W.) via Mt. Koroturanga. Canopy heights were noted and herbarium specimens collected. At several localities transects of 100 canopy trees were recorded including their identity, canopy height, and stem diameter. The results of transects on the summit-ridge of Mt. Koroturange (1200 m), and at 1000 m and 800 m altitudes on the northwestern slopes are presented in this paper. Specimens were identified at the Suva herbarium and nomenclature follows Smith (1979, 1981, 1985) and Brownlie (1977), or Parham (1972) for other dicotyledons. Mean stem diameter for each species was calculated from mean basal area.

Meteorological observations were made from 8 am to 12 pm on 17 November 1983, which had the typical daily weather pattern of continual high-level clouds over the mountains and intermittent enveloping clouds on the upper windward slopes and ridge top. Similar weather occurred on succeeding days, so no contrasting sunny periods were observed. Observations were made on a lattice tower up to 15 m in height on the summit, and repeatedly at several sites in the forest, forming a transect across the ridge. Observations were also made at altitudes of 800 m and at sea level, combined with sea-level records taken at Matei Airfield. Wind velocity was measured with a Wallac thermoanemometer, leaf temperatures and cloud temperatures with a Barnes Instantatherm infrared thermometer, and other temperatures were recorded with thermocouples connected to a Conmark electronic thermometer. Relative humidity was estimated from a whirling hygrometer and light intensity was estimated with a camera photocell.

RESULTS

Vegetation

The composition of the vegetation is indicated by the transects on the ridge-top (1200 m) and at 1000 m and 800 m altitude (Table 1).

TABLE 1

CANOPY AND EPIPHYTIC SPECIES RECORDED ON TRANSECTS IN FOREST AT THREE ALTITUDES, MT. KOROTURANGA, TAVEUNI. + = present nearby

SPECIES	1200 m	1000 m	800 m
	(% STEMS AND MEAN STEM DIAMETER, cm)		
Antrophyum smithii C. Christensen	+		
Ardisia brackenridgei (A. Gray) Mez	1%(8)		
Ascarina swamyana A. C. Sm.	+		
Blechnum milnei (Carruthers) C. Christensen	+		
Cyathea medullaris (Forst. f.) Sw.	1%(6)		
Cyrtandra tempestii C. B. Clarke	1%(3)		
Dysoxylum lenticellare Gillespie	1%(15)		
Fagraea vitiensis Gilg et Benedict	2%(14)		
Faradaya ovalifolia (A. Gray) Seem.	1%(3)		
Ficus barclayana Miq.	3%(14)		
Freycinetia urvilleana Hombr. et Jacq.	3%(3)		
Grammitis hookeri (Brackenridge) Copeland	+		
Hymenophyllum flabellatum Labill.	+		
Hymenophyllum javanicum Sprengel	+		
Macropiper vitiense (A. C. Sm.) A. C. Sm.	1%(2)		
Maesa insularis Gillespie	3%(4)		
Medinilla waterhousei Seem.	+		
Pipturus argenteus Wedd.	1%(2)		
Randia vitiensis (Seem.) Fosberg	5%(5)		
Scaevola floribunda A. Gray	3%(11)		
Timonius affinis A. Gray	3%(15)		
Trimenia weinmanniifolia Seem.	1%(12)		
Weinmannia sp	1%(20)		
Astronidium parviflorum (Gillespie) A. C. Sm.	11%(10)	1%(8)	
Citronella vitiensis Howard	2%(7)	1%(14)	
Clinostigma exorrhizum (Wendl.) Martelli	1%(10)	8%(15)	
Cryptocarya sp	1%(4)	3%(13)	
Ficus vitiensis Seem. (?)	11%(10)	2%(11)	
Geissois ternata A. Gray	3%(8)	1%(45)	
Rapanea myricifolia (A. Gray) Mez	1%(15)	2%(23)	
Spireanthemum serratum Gillespie	19%(19)	7%(26)	
Cyathea alata Copel.	7%(8)	4%(8)	2%(8)
Dysoxylum gillespieanum A. C. Sm.	4%(21)	15%(26)	9%(48)
Macaranga seemannii (Muell. Arg.) Muell. Arg.	5%(12)	10%(24)	6%(22)
Syzygium sp	4%(16)	6%(22)	3%(31)
Elaeocarpus chelonimorphus Gillespie		1%(25)	
Flacourtia sp		1%(17)	
Garcinia sessilis (Forst. f.) Seem.		1%(25)	
Hedycarya dorstenioides A. Gray		1%(27)	
Litsea sp		2%(26)	
Neuburgia corynocarpa (A. Gray) Leenhouts		4%(22)	
Sterculia vitiensis Seem.		1%(45)	
Aglaia sp		2%(18)	2%(19)
Calophyllum vitiense Turrill		15%(27)	13%(49)
Decaspermum vitiense (A. Gray) Niedenzu		1%(10)	1%(17)
Dysoxylum richii (A. Gray) C. DC.		1%(16)	20%(45)
Omolanthus nutans (Forst. f.) Guill.		1%(15)	1%(20)
Planchonella pyrulifera (A. Gray) van Royen		4%(19)	1%(45)
Trichospermum richii (A. Gray) Seem.		2%(12)	3%(36)
Alphitonia zizyphoides (Spreng.) A. Gray			6%(36)
Alstonia vitiensis Seem.			1%(18)
Arytera concolor (Gillespie) A. C. Sm.			1%(40)
Bischofia javanica Blume			1%(35)
Calophyllum neo-ebudicum Guillaumin			4%(47)
Capparis quiniflora DC.			1%(45)

TABLE 1 (continued)

SPECIES	1200 m	1000 m	800 m
	(% STEMS AND MEAN STEM DIAMETER, cm)		
Cupaniopsis amoena A. C. Sm.			1%(35)
Cynometra insularis A. C. Sm.			1%(35)
Elattostachys falcata (A. Gray) Radlk.			3%(34)
Endospermum macrophyllum (Muell. Arg.) Pax et Hoffm			6%(59)
Heritiera ornithocephala Kosterm.			2%(42)
Hernandia olivacea Gillespie			1%(18)
Palaquium hornei (Baker) Dubard			5%(43)
Parasponia andersonii (Planch.) Planch.			1%(20)
Parinari insularum A. Gray			3%(36)

Although a few species occur in the canopy at all three altitudes, e.g. *Dysoxylum gillespianum*, *Macaranga seemannii* and *Syzygium* sp., most species are apparently restricted in altitudinal range. The ridge-top cloud-forest includes trees such as *Spireanthemum serratum* and *Ascarina swamyana* which are rarely observed in other habitats. Several epiphytes are similarly restricted to cloud-forests, e.g. *Medinilla waterhousei* and ferns such as *Antrophyum smithii*, *Grammitis hookeri*, *Hymenophyllum flabellatum* and *H. javanicum*. Epiphytic bryophytes were abundant at the ridge top. Climbing *Freycinetia* spp occur at all sites, and on the upper windward slopes and ridge top *F. urvilleana* forms about 40% of the upper leaf canopy and their stems form a dense tangle.

Tree canopy height and trunk diameter decline with altitude, (Figure 2, Figure 3), and from Table 1 it is apparent that this trend also occurs within species. The reduction in canopy height is greater than the reduction in maximum stem diameters, giving the ridge-top trees a stunted appearance.

Leaf and leaflet size in the cloud-forest ranged from the tiny leaflets of bryophytes and ferns to tree leaves of about 6 × 4 cm to 12 × 8 cm, and *Freycinetia* leaves of about 30–40 × 3–5 cm. At lower altitudes there was an increasing proportion of larger-leaved trees, ranging from about 6 × 4 cm to 30 × 20 cm at sea level.

Micrometeorology

The spatial pattern of observations across the ridge top is indicated in Figure 3. Wind speeds increased with elevation above the canopy surface, reaching about 5 m s^{-1} at 15 m height. Wind velocity fluctuated greatly over periods of 1–30 s and the values shown in Figure 2 indicate intermediate values between lulls of about half that velocity and gusts of twice that velocity. The wind velocity around the upper canopy was about 0.8–1.5 m s^{-1} on the windward side of the ridge and 0.5–1.0 m s^{-1} on the lee side. Canopy leaf surface temperatures were similar in different species and continually varied by about ±1°C over a period of 1–2 minutes, decreasing during periods of enveloping cloud. On average, leaf temperatures were about 17°C on the windward slopes and ridge top, increasing to about 19°C on lee slopes at similar altitude, and increasing to about 20°C at 40 m below the ridge on the lee side. Relative humidities were all high, and successive estimates indicated values of about 90–96% on the windward slopes and ridge top, declining to about 84–92% on the lee slopes. A fine mist of cloud water droplets formed intermittently over the upper windward slope and ridge top but rarely extended more than about 20 m down the lee slope. The infrared temperature of this cloud was 16–17°C. In comparison with sunny sites, light intensity fluctuated with cloud cover from about 15% to 40%, with a typical value of about 30%. This corresponds to about 1.5–4.0 × 10^7 erg. cm^{-2} s^{-1} (12–33 mW cm^{-2}) solar radiation.

During the same period at Matei, wind velocity was about 2–3 m s^{-1} (10 m height), air temperatures reached 28°C, relative humidity was 75–81%, and there were intermittent

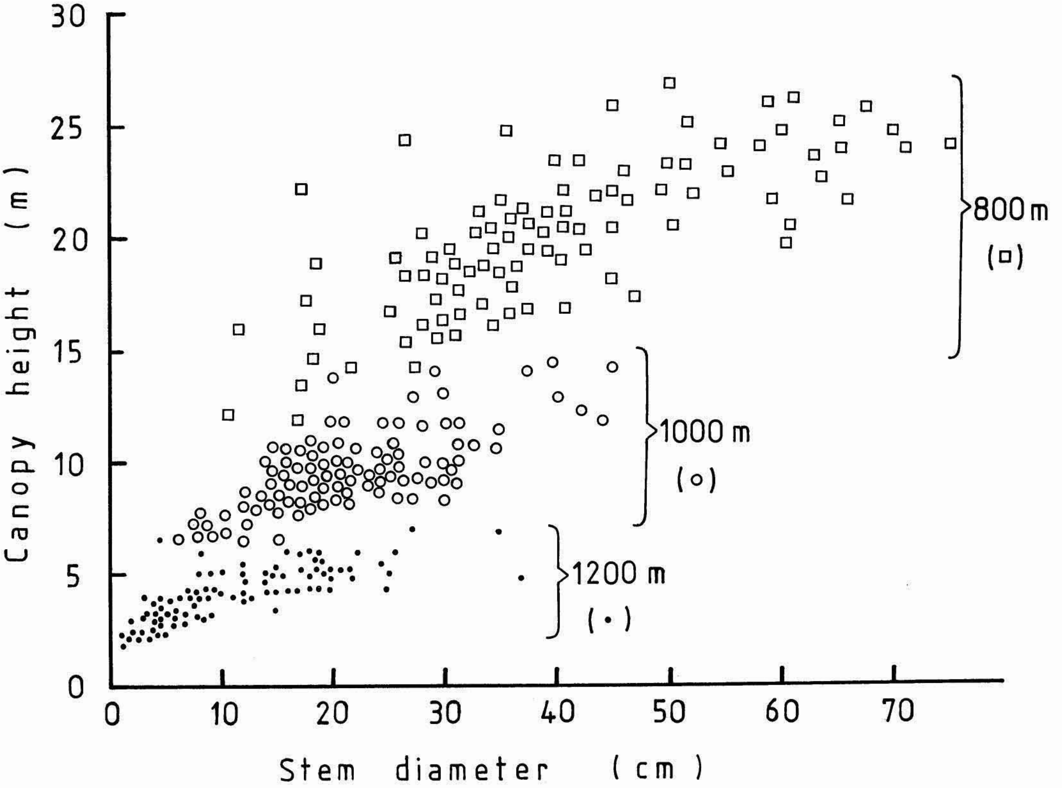

FIGURE 2. Scatter diagram showing the canopy height and stem diameter of canopy trees from transects at 800 m, 1000 m and the ridge top at 1200 m on Mt. Koroturanga, Taveuni.

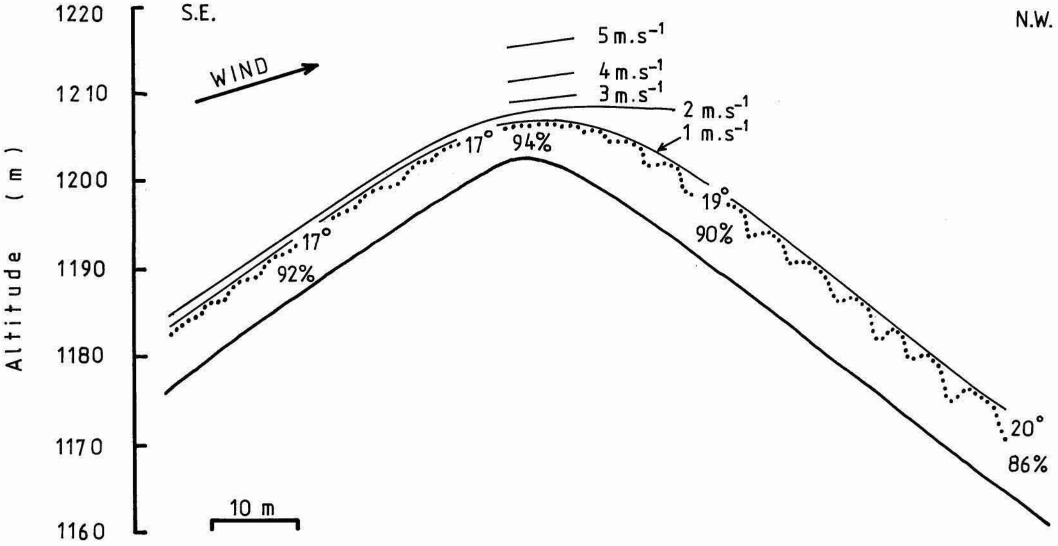

FIGURE 3. Profile diagram across the ridge north of Mt. Koroturanga, Taveuni, showing average micro-climatic parameters at 9 am–12 pm, 17 Nov. 1983: winds, m s^{-1} × 0.5–2; Leaf temperature, °C ± 1°C; relative humidity, % ± 2%. The tree canopy height is shown by the dotted line, and the prevailing wind direction is indicated (S.E. to N.W.).

TABLE 2

MICROCLIMATE AND ESTIMATED TRANSPIRATION RATES AT FOUR SITES ON OR NEAR MT. KOROTURANGA, TAVEUNI, WITH LEAVES OF 5 × 5 CM, LEAF RESISTANCE OF 5 S CM^{-1}, AND A WIND VELOCITY OF 1 M S^{-1}. Calculations based on Gates and Papain (1971)

SITE	ALTITUDE (m)	AIR TEMP. (°C)	REL: HUMID. (%)	RADIATION (10^{-7} erg cm^2 s^{-1})	TRANSPIRATION (10^{-7} g cm^{-2} s^{-1})
Ridge-top	1200	17	93	3	2
Lee slope	1160	20	86	6	12
Lee slope	800	24	80	8	24
Matei	0	28	75	8	29

cloudy periods and no rainfall. Wind velocity above the ridge was evidently nearly twice that at sea level. At 800 m altitude on the western slopes there was intermittent sunshine and air temperatures reached 24°C. Air temperatures apparently declined by 0.5°C 100 m^{-1} altitude up to 800 m, but much more rapidly on the cloudy upper slopes. In the absence of clouds it was estimated that the air temperature at the altitude of the ridge would be about 22°C, indicating that the cloud caused a 4–6°C lowering of temperature. Relative humidity increased with altitude, most rapidly towards the cloud-enveloped ridge (Table 2).

On the basis of the meteorological observations, rates of transpiration were calculated at four sites for a leaf of 5 × 5 cm effective diameter (an actual diameter of about 7 × 7 cm), a leaf resistance of 5 s cm^{-1}, and a wind velocity of 1 m s^{-1} (Table 2), using the equations of Gates and Papain (1971). Even though these assumptions and the observations may be inexact, the trend between the sites is clear. Transpiration rates declined gradually with altitude up the sunny lee slopes to 83% at 800 m and then declined more rapidly to 40% at the cloudy site on the lee slope at 1160 m and to about 7% on the cloud-enveloped ridge. When the rates of transpiration are plotted against corresponding canopy heights (Figure 4), it is apparent that these two parameters are almost directly proportional, suggesting that there may be a direct causal relationship.

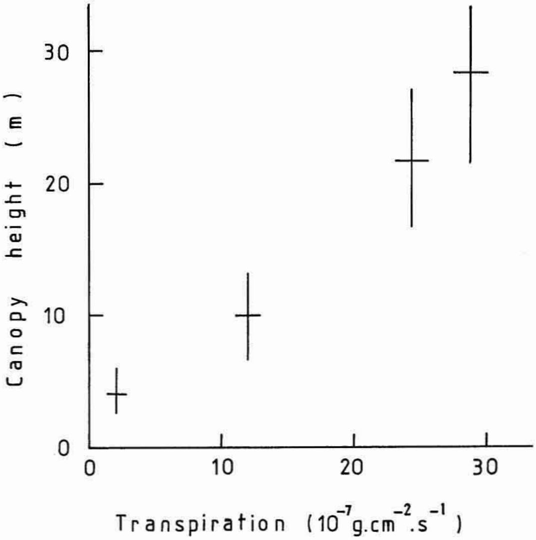

FIGURE 4. Scatter diagram showing canopy height and estimated rates of transpiration at four altitudes on Mt. Koroturanga, Taveuni. See text and Table 2 for further details.

DISCUSSION

The results of this study suggest that transpiration rates could be a major factor limiting the canopy heights of humid tropical forests, and that the stunted cloud-forests represent the most extreme situation. The transpiration rates estimated for the Taveuni cloud-forest are intermediate between those estimated by Gates (1969) and those measured for lower canopy leaves by Weaver et al (1973) at similar latitudes and altitudes in the neotropics.

Transpiration rates are not the only factor which can limit growth and Grubb (1977) is probably correct in suggesting that nutrient deficiency is the direct cause of much stunting. His dismissal, however, of low transpiration rates as a causal factor is based on evidence which is as indirect as the evidence he presents in favor of a limiting rate of nutrient mobilization in the soil. The effect of low light intensity, typically 20–40% daylight under cloudy conditions, must also contribute to reduced production, but it appears to be less significant than the reduced rate of transpiration. The potential importance of sunny periods for both transpiration and photosynthesis (Roth and de Bifano 1980) may be substantially reduced by the closure of stomata (Jane and Green 1985). Experimental studies and long-term monitoring evidently are required to determine the causes of stunting and the more general limits to tree height.

Lawton's (1982) observation that stunted ridge-top trees show a greater reduction in the length of trunk and branches than in their diameter is supported by the observations in this paper, both within and between species (Figure 2), but it is not obvious that this is the result of a thigmomorphogenetic response (i.e. shaking). Coastal trees and palms, e.g. *Cocos nucifera* L., are not obviously stunted when contrasted with trees further inland, where the coastal habitat is subject to much greater wind velocities and neither habitat is subject to the confounding effect of enveloping clouds. At high relative humidity and low light intensity, changes in wind velocity (e.g. 10–400 cm s^{-1}) have a relatively minor effect on leaf temperatures or transpiration rates (Gates and Papain 1971), and the association of wind velocity with the stunting of ridge-top cloud-forest appears to be indirect.

Gusts of 30–35 m s^{-1} are experienced during cyclones with a recurrence interval of about 4.5 years but there was little sign of uprooting or broken branches, and though less frequent severe cyclone gusts of 40–55 m s^{-1} may occur, the stem diameter-canopy height relationship (Figure 2) indicates that the ridge-top forests are stunted rather than an early stage of regrowth on a devastated site. The infrequent impact of devastating cyclones should not, however, be overlooked.

Kirkpatrick and Hassall (1985) considered wind to be a major determinant of the stunting of forest (8–12 m high) on Mt. Korobaba. On the basis of climatic records from the environs of Suva, the average mid-day rate of transpiration was estimated as 13×10^{-7} g cm^{-2} s^{-1} which is only slightly greater than the estimates from Taveuni for a forest of this height (Wind $\simeq 1$ m s^{-1}; light transmitted $\simeq 100\%$ for 15% year, 50% for 75% year, 20% for 10% year; relative humidity $\simeq 75$–95%; air temperature 21–27°C; leaf size and resistance as in Taveuni calculations). It appears that cloud cover, even though it is rarely at ground level, may be of more significance than wind velocity, though at times the winds may have a desiccating effect. Similar stunted forest occurs on most prominent ridges from about 350 to 900 m altitude, above which stunted cloud-forest becomes predominant. The frequency of enveloping cloud is indicated by the increasing abundance of epiphytic bryophytes.

The extent of cloud-forest in Fiji is very limited, occupying only the ridges on the highest peaks. In Taveuni cloud-forest occurs along about 10 km of the main range and in the other islands it is restricted to 1–2 km of ridges around isolated peaks which are separated by distances of 30–100 km. Although some species occur in most of the cloud-forests, others are apparently restricted to a few peaks: *Medinilla spectabilis* A. C. Sm. occurs only in Taveuni, *M. Waterhousei* occurs only in Taveuni and on Mt. Seatura in Vanua Levu, *Paphia vitiensis* Seem. is known only from peaks above 870 m altitude in Viti Levu, and *Ascarina swamyana* occurs only in Taveuni and on Mt. Voma in Viti Levu. As yet many of these cloud-forest localities have not been thoroughly investigated by botanists and the distribution of most cloud-forest species is inadequately known.

There is considerable similarity in the generic composition of the Fijian cloud-forest and those in Samoa (Banks 1982) and the Cook islands (Merlin 1985). Further taxonomic studies may reveal close affinity between these isolated populations, and whether they represent widely dispersed cloud-forest taxa or local evolution from lower altitude forest species to cope with the singular cloud-forest environment.

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