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The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact

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Climatic records for Danum for 1985–1998, elsewhere in Sabah since 1879, and long monthly rainfall series from other rainforest locations are used to place the climate, and particularly the dry period climatology, of Danum into a world rainforest context. The magnitude frequency and seasonality of dry periods are shown to vary greatly within the world's rainforest zone. The climate of Danum, which is aseasonal but subject, as in 1997–1998, to occasional drought, is intermediate between less drought-prone north-western Borneo and the more drought-prone east coast. Changes through time in drought magnitude frequency in Sabah and rainforest locations elsewhere in South-East Asia and in the Neotropics are compared. The 1997–1998 ENSO-related drought event in Sabah is placed into a historical context. The effects of drought on tree growth and mortality in the tropics are assessed and a model relating intensity and frequency of drought disturbance to forest structure and composition is discussed.

Keywords: tropical rainforest; drought magnitude frequency; tree–water relationships; El Niño Southern Oscillation (ENSO); climatic change; Borneo

1. INTRODUCTION

With growing evidence of recent changes in the frequency of extreme events, such as droughts and tropical cyclones in parts of the ever-wet tropics (e.g. Stoddart & Walsh 1992; Condit *et al.* 1996; Walsh 1996*a*, 1998), predictions of further change from climatic models (e.g. IPCC 1996; Hulme & Viner 1998) and continuing concern over rainforest deforestation and fragmentation, increased attention has recently been given to the possible impacts that different scenarios of climatic change might have on the remaining rainforests. Concern has focused mainly on changes in drought frequency and intensity, though mainly in the context of somewhat seasonal environments (e.g. Condit *et al.* 1996; Condit 1998, Borchert 1998). Comparatively little attention has been given to the possible impacts of increased drought frequency in wetter aseasonal environments of Malesia (e.g. Corlett & Lafrankie 1998; Whitmore 1998) and our understanding of forest–climate relationships in such areas remains poor. The Danum Valley Conservation Area in central-eastern Sabah lies in a key position close to the normally wet, but drought-prone eastern coastlands of Borneo. A major question concerning the forests of the region has been the extent to which they are affected by, and bear the imprint of, a history of drought events. Prior to the establishment of the climatic station at the Danum Valley Field Centre in 1985, climatic data for the Sabah interior have been very few and mostly unreliable. The climatic station records, together with ecological data from the long-term plots also established in 1985, now permit some provisional assessments of both the climate and forest dynamics (Newbery *et al.*, this issue) to be made, particularly as the records now encompass three warm-phase El Niño Southern Oscillation (ENSO) events (1986–1987, 1991–1994 and 1997–1998).

This paper has four aims: (i) to place the climate (and especially the dry period climatology) of Danum into both Sabah and international rainforest climatic contexts; (ii) to assess and place into a longer-term context the recent 1997–1998 ENSO event at Danum and in Sabah as a whole; (iii) to update the drought history of Sabah explored in a previous paper (Walsh 1996*a*) and explore its relationship to changes in ENSO magnitude frequency; and (iv) to consider forest-drought mechanisms and possible drought-related features of the forests at Danum and use them to reconsider and re-evaluate some of the ideas put forward in a tentative model relating drought magnitude frequency to forest characteristics in Sabah (Walsh 1996*a*, fig. 6).

As the paper makes considerable reference to ENSO events, a brief description of the phenomenon is given here. Of great significance in accounting for occasional extreme drought conditions in eastern Borneo is the

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atmospheric and oceanic anomaly, the ENSO phenomenon. This complex phenomenon, which is responsible for worldwide climatic anomalies, has been comprehensively reviewed elsewhere (Diaz & Markgraf 1992). A distinction should be drawn between the oceanic phenomenon of El Niño (EN) and the atmospheric phenomenon, termed the Southern Oscillation (SO), with which it is associated (Diaz & Pulwarty 1992; Enfield 1992). The SO refers to the interannual changes, normally over a cycle of three to four years, in pressure distribution and atmospheric circulation over the South Pacific region.

The most commonly used measure of this atmospheric component of ENSO events is the Southern Oscillation Index (SOI), which is the Tahiti minus Darwin sea level pressure anomaly (Ropelewski & Halpert 1987; Davey & Anderson 1998; Wolter & Timlin 1998). In normal and particularly cold-phase (La Niña) years the index is strongly positive, with high pressure over the central South Pacific (represented by Tahiti) and low pressure over Indonesia and northern Australia (represented by Darwin). Strong south-easterly trade winds in the eastern and central Pacific lead to upwelling of cold water off the South American coast and an area of cold water, stable atmosphere and low rainfall extending westward to the dateline in the Central Pacific. In contrast, rainfall is very high in the unstable low-pressure zone over Indonesia, New Guinea and Malaysia (including Borneo).

In ENSO years, however, the South Pacific high pressure weakens and the difference in pressure between Tahiti and Darwin is much lower than normal, leading to negative values of the SOI. The trade winds over the Pacific slacken and the cold current and upwelling off the South American coast is replaced by the El Niño warm current, and there is a dramatic rise in sea surface temperature and rainfall in the eastern and central Pacific. In contrast, the anomalously high pressure over the Indonesian region leads to more stable air conditions and a marked reduction of rainfall. The typical El Niño or warm-phase event lasts from about March in year 1 to May in year 2, but events vary greatly in strength, duration and spatial character, and only the stronger events tend to lead to significant drought in the Indonesian region. Rainfall tends to be lower than normal over the whole of an event, but the timing of intense drought varies within the Indonesian region with differences in rainfall regime related to the position of localities relative to the equator, coastlines and mountain ranges. In Sabah, the most intense drought conditions tend to occur in February to May in year 2.

Whereas events of at least weak intensity occur every three to four years, the strong events seldom occur less than six to seven years apart and, prior to the 1997–1998 event, only eight very strong events (the last being 1982–1983) had occurred in nearly five centuries (Enfield 1992). Many indices apart from the SOI have been devised to assess local, regional and large-scale oceanic and atmospheric aspects of the phenomenon (see Diaz & Kiladis 1992; Quinn 1992; Davey & Anderson 1998; Wolter & Timlin 1998). Thus Quinn (1992) produced two historical series extending back to 1500: a 'regional El Niño' series, which comprises a list of the years of occurrence and strength of the El Niño warm current off the South American coast; and a 'large-scale ENSO series', which is based on worldwide climatic and oceanic anomalies associated with the ENSO phenomenon. Time-series of such indices can differ somewhat from each other.

2. DATA SOURCES

The main climatic data sources used in this paper are: the daily records from 1985 to 1998 of the climatic station at Danum Valley Field Centre; archival records of rainfall held by the Malaysian Meteorological Service at Kota Kinabalu; published early accounts of the climate of British North Borneo (Scott 1889; Brooks 1921); published data in World Weather Records (Clayton 1927, 1944; Clayton & Clayton 1947) and on the World Climate Disc (Chadwyck-Healey Ltd 1992); and climatic data on the World Wide Web for the long-term research stations at Barro Colorado Island (Panama), La Selva (Costa Rica) and El Verde (Puerto Rico). The paper also draws upon the long-term forest plot data at Danum (Newbery *et al.*, this issue).

3. THE CLIMATE OF DANUM

Temperatures and relative humidity at Danum are typical of equatorial rainforest locations (table 1). Thus monthly mean temperatures range only 1.9 °C around the annual mean of 26.7 °C and the mean daily range, which also varies little through the year, is 8.4 °C. Temperatures exceed 34 °C only rarely, usually during prolonged dry spells, and the highest temperature of 36.3 °C was recorded in April 1998 during the 1997–1998 ENSO event (q.v.). As at most rainforest locations, relative humidities are close to saturation at 08.00. Relative humidity reaches a minimum in the early afternoon, averaging 72% at 14.00 compared with 81% at the wetter Mulu station (Walsh 1982).

Table 2 gives details of monthly rainfall recorded at Danum Valley Field Centre. Over the period 1985–1998, annual rainfall averaged 2669 mm, ranging from 3294 mm in 1995 to only 1918 mm (460 mm below that of any previous year on record) in the ENSO year of 1997. Monthly means range from 119.5 mm in April to 302 mm in January and October. The monthly regime reflects the northerly interior position of Danum within Borneo in relation to seasonal changes in the Indo-Australian monsoon system. In common with other stations in the interior, rainfall tends to be high during the transition months following the equinoxes (May–June and October–November) and is also high during the northerly monsoon months of December–January (figure 1). Rainfall is least in March–April, which are the months most prone to low rainfall in ENSO atmospheric conditions, and also in August–September when the south-westerly monsoon, which has travelled across the Bornean landmass, is at its height. Danum is thus intermediate in wetness between the drier east coast of Borneo and the wetter regions of south-western Sabah, Sarawak, and western and central Kalimantan. Rain falls on average on 218 days per year, compared with 186 days at Table Estate (near Tawau) in south-eastern Sabah but 247 days at Kuching (annual rainfall 4036 mm) and 275 days at Mulu (annual rainfall 5087 mm) in Sarawak (Walsh 1982).

The degree of continuity of wetness of a rainfall regime can be assessed using the perhumidity index (Walsh 1992,

Table 1. *Climatic data for Danum Valley Field Centre compared with Barro Colorado, La Selva, Manaus and Mulu*

(Sources: Danum, authors; Mulu, Walsh 1982; Manaus, Walsh 1996*b*; Barro Colorado and La Selva, World Wide Web pages. Dashes indicate no data available.)

climatic variable	Danum	Mulu	Manaus	Barro Colorado	La Selva
mean annual temperature (°C)	26.7	27.1	26.9	25.7	26.1
annual range (°C)	1.9	1.6	1.7	2.1	2.3
mean maximum (°C)	30.9	31.9	30.9	30.1	30.8
mean minimum (°C)	22.5	22.2	22.8	21.4	21.5
mean diurnal range (°C)	8.4	9.7	8.1	8.7	9.3
relative humidity 08.00 (%)	94	97	—	—	—
relative humidity 14.00 (%)	72	81	66	—	—
absolute maximum temperature (°C)	36.3	35.0	38.6	—	—
absolute minimum temperature (°C)	19.2	19.9	17.6	—	—
rain days per annum	218	275	—	—	—

Table 2. *Monthly rainfall (mm) at Danum Valley Field Centre 1985–1998*

(Dry months (< 100 mm) are in bold type. DM, dry months.)

year	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sep	Oct	Nov	Dec	annual
1985	—	—	—	—	—	—	159.1	214.2	265.1	351.6	195.4	267.1	—
1986	674.9	187.5	261.9	**68.5**	**74.4**	149.1	222.8	**77.2**	191.1	247.9	255.3	176.4	2586.6
1987	269.5	238.8	135.0	**49.7**	**74.1**	209.3	127.9	297.8	158.8	213.3	346.8	257.7	2378.2
1988	354.1	217.4	427.5	129.8	247.8	242.7	265.2	**71.3**	124.1	183.2	255.7	418.7	2937.5
1989	290.1	276.7	242.2	201.8	259.1	348.5	336.9	206.9	113.9	463.1	325.5	140.0	3204.7
1990	357.8	122.6	170.3	**37.4**	602.7	258.1	109.0	180.9	330.6	115.3	178.1	266.2	2729.0
1991	235.3	251.1	**24.4**	133.6	310.4	131.7	131.5	248.6	115.7	371.1	466.2	189.1	2608.7
1992	**95.9**	**86.4**	**66.3**	**28.0**	188.4	319.9	218.2	164.7	296.7	428.1	257.5	216.3	2366.4
1993	242.8	268.1	261.3	138.0	111.2	138.7	188.3	220.3	153.3	301.2	199.0	278.4	2500.6
1994	231.5	171.6	416.6	312.4	172.9	306.3	140.9	216.6	156.7	185.7	303.2	362.2	2976.6
1995	236.5	210.0	261.4	**96.8**	439.1	190.2	135.5	329.7	338.2	537.2	220.6	298.9	3294.1
1996	590.0	423.8	**42.9**	245.0	273.8	162.2	153.1	165.6	179.9	390.1	137.7	224.6	2988.7
1997	194.6	365.8	**87.8**	101.5	117.1	**52.5**	247.9	170.3	**64.9**	216.2	150.6	149.2	1918.4
1998	147.1	123.4	**86.9**	**11.3**	173.7	156.8	217.0	219.0	313.0	220.4	206.3	264.4	2139.3
mean	301.5	226.4	191.1	119.5	234.2	205.1	189.5	198.8	200.1	301.7	249.9	250.7	2668.5
n	13	13	13	13	13	13	14	14	14	14	14	14	13.5
DM	1	1	5	6	2	1	0	2	1	0	0	0	19

1996*b*), in which months averaging 100 mm or greater are ascribed positive scores and 'dry months' with less than 100 mm given negative scores. Rainforest locations have scores ranging from + 4.5 to + 24 (the maximum). By world rainforest standards, Danum, with a perhumidity index of 20, is marginal between the 'wet' (perhumidity index values of 10–19.5) and 'superwet' (20–24) classes of the system based on the index (Walsh 1996*b*). Perhumidity index values over most of Borneo are 20–24, but some east-coast stations have values less than 15 (figure 1). Such values, however, because they are based on rainfall averages, tend to understate the frequency of dry periods and give no indication of extreme dry periods.

4. DRY PERIOD MAGNITUDE FREQUENCY AT DANUM AND IN SABAH COMPARED WITH OTHER RAINFOREST REGIONS

(a) *Dry periods: the procedure adopted to analyse monthly rainfall series*

There is no satisfactory way of defining what constitutes an ecological drought in tropical rainforest, as (i) forests differ in their character, experience of and susceptibility to drought (Brünig 1971); (ii) the speed with which water shortages develop will vary regionally and locally with soil characteristics, slope angle and topographic position; and (iii) different components (and species within the components) of the forest ecosystem will experience water shortage at different points as droughts develop, with epiphytes and ground herbs, for example, being much more susceptible than trees (Becker *et al.* 1991; Benzing 1998). There is considerable evidence, however, that monthly potential transpiration of lowland rainforest on terrain not short of water is of the order of 100 mm (for a review, see Walsh 1996*a*) and that figure to define 'wet' and 'dry' months is used as the basis of most analysis in this paper. Calendar month data are used, despite the arbitrary divisions and underrecording of shorter dry periods that are entailed (Brünig 1969; Becker 1992), to facilitate comparisons with stations for which daily data are unavailable and to enable long-term chronologies of droughts to be constructed.

The procedure used in analysing the Danum monthly rainfall series and those of other stations in Sabah and

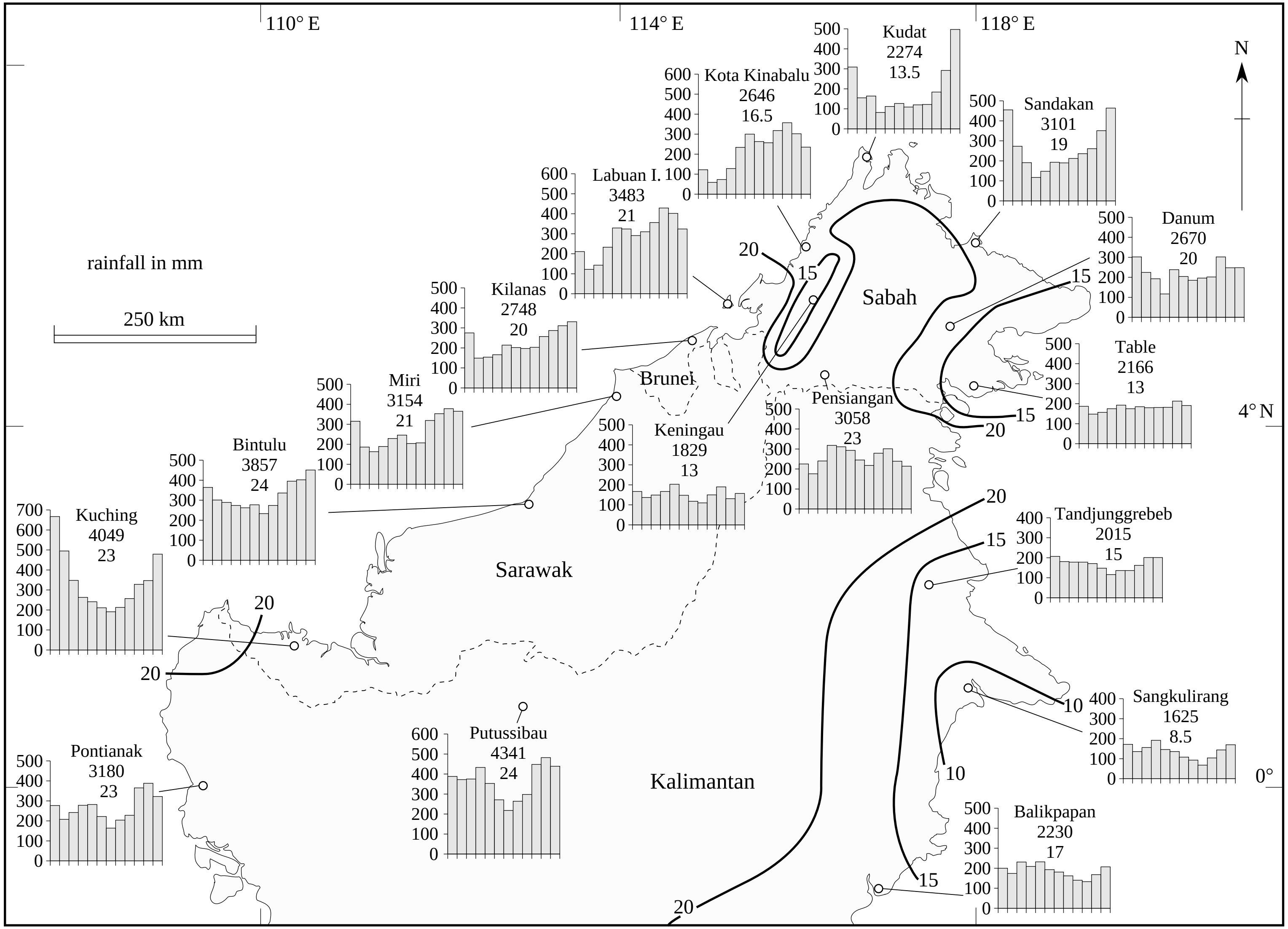

Figure 1. Northern Borneo: rainfall regimes and perhumidity index (Danum data revised; otherwise after Walsh (1996*a*)).

Table 3. *Notable rainless and near-rainless sequences at Danum 1985–1998*

(a) Rainless periods (periods greater than ten successive days with no rain or less than 1.0 mm)

year	period	length (days)
1986	Feb 17–26	10
	Apr 26–May 8	13
	May 19–Jun 2	15
	Aug 26–Sep 6	11
1987	Apr 6–24	13
1988	Apr 14–26	13
1991	Mar 1–14	14
	Jul 21–31	11
1992	Apr 18–27	10
1994	Feb 16–26	11
	Sep 1–10	10
1996	Mar 5–19	15
1997	Sep 23–Oct 4	12
1998	Jan 31–Feb 9	10
	Mar 13–23	11
	Apr 6–18	13

(b) Near-rainless periods (periods greater than 20 successive days each with less than 5.0 mm)

year	period	length (days)	total rain (mm)
1986	Apr 18–May 12	25	8.5
1987	Apr 6–26	21	4.8
1990	Mar 30–Apr 22	24	16.2
1992	Apr 2–May 1	30	8.6
1997	Mar 11–31	21	18.1
1998	Jan 3–25	23	19.8
	Feb 25–Mar 11	15	2.8
	Apr 1–May 4	34	11.3

the Neotropics has been described in a previous paper (Walsh 1996*a*). Using the definition of a 'dry month' as being one with less than 100 mm rain, all sequences of dry months in a monthly rainfall series were denoted. All dry periods (defined as periods with one or more consecutive dry months) were then categorized in two ways: in terms of their duration and intensity. 'Drought duration' is simply the number of consecutive dry months that a dry period lasted. 'Drought intensity' was assessed by calculating the 'cumulative rainfall deficit' (CRD) of a dry period by summing the amounts by which the rainfall of each month in a dry month sequence fell below 100 mm. By analysing the entire record, the mean frequencies of (i) droughts of different duration and (ii) droughts of different intensity for a station could be calculated.

(b) *The Danum record in a Sabah and international rainforest context*

Over the period of record to date covering August 1985 to December 1998, 19 dry months have been recorded (table 2), comprising one event of four months' duration, three of two months' duration and nine single dry months. The longest and most intense dry period was that of January–April 1992, with a CRD of 123.4 mm. This and the three two-month dry periods of April–May 1986, April–May 1987 and March–April 1998 were all linked to the three warm-phase ENSO events that have occurred since 1985: the moderate episode of 1986–1987; a moderate, but exceptionally long event from 1991–1994; and the very strong event of 1997–1998 (Wolter & Timlin 1998). Dry months have occurred in all months except October–December, but have been particularly frequent in March and April (table 2). In terms of daily sequences, table 3 gives details of notable rainless and near-rainless periods. The longest period without rain is only 15 days, but there have been 16 rainless periods of at least ten days' duration. Of the seven near-rainless periods with at least 20 successive days without a daily fall of at least 5.0 mm, two were associated with the recent 1997–1998 ENSO event.

The record to date at Danum indicates a climate with dry periods of intermediate magnitude frequency between the more drought-prone east coast and more reliably wet western Borneo. Figure 2 shows drought duration-frequency diagrams for Danum compared with (*a*) other stations in northern Borneo and also Jakarta in Java, and (*b*) selected locations in the Neotropics.

The contrasts in drought duration frequency between different rainforest areas are striking. The two western Borneo stations of Kuching (Sarawak) and Pontianak (Kalimantan) have never experienced dry-period sequences exceeding two and three months respectively, despite particularly long records stretching back to the 1870s; Iaourete in the western Amazonia, El Verde (Puerto Rico) and La Selva (Costa Rica) are likewise only prone to similarly short dry periods. Danum has a duration profile rather similar to Kilanas (Brunei), which experiences rather more frequent dry periods of sometimes three to four months' duration, but none longer than four months. In western Sabah (Kota Kinabalu) there is a rather more regular short dry season of two to four months (producing a mode at three months' duration in its graph) as well as occasional extreme droughts in some ENSO years. The rather seasonal locations of Manaus, Santarém-Taperinha (in central and eastern Amazonia) and Barro Colorado Island likewise have modes at four to five months' duration in their graphs. In contrast, the normally aseasonal eastern Sabah stations of Sandakan, Lahad Datu and Tawau are characterized by predominantly short dry periods of one to two months, but occasionally very long droughts of five to six months' duration. The record at Keningau, the only interior station in Sabah with long records, is interesting, as long droughts of five to eight months' duration have occurred on six occasions during the 76-year record, but its location in the low rainfall area to the lee of the Crocker Range mean that its drought pattern is unrepresentative.

Similar contrasts emerge from an analysis of drought intensity frequency based on CRD of the dry-month sequences (table 4). At the reliably wet locations of Kuching in Sarawak and Iaourete in western Amazonia, the highest recorded CRDs are less than 100 mm. Danum, with two CRDs exceeding 100 mm in a 13-year record and a maximum CRD of 123.4 mm, is a little more prone to drought than La Selva and El Verde, both of which also have maximum recorded CRDs only just in excess of

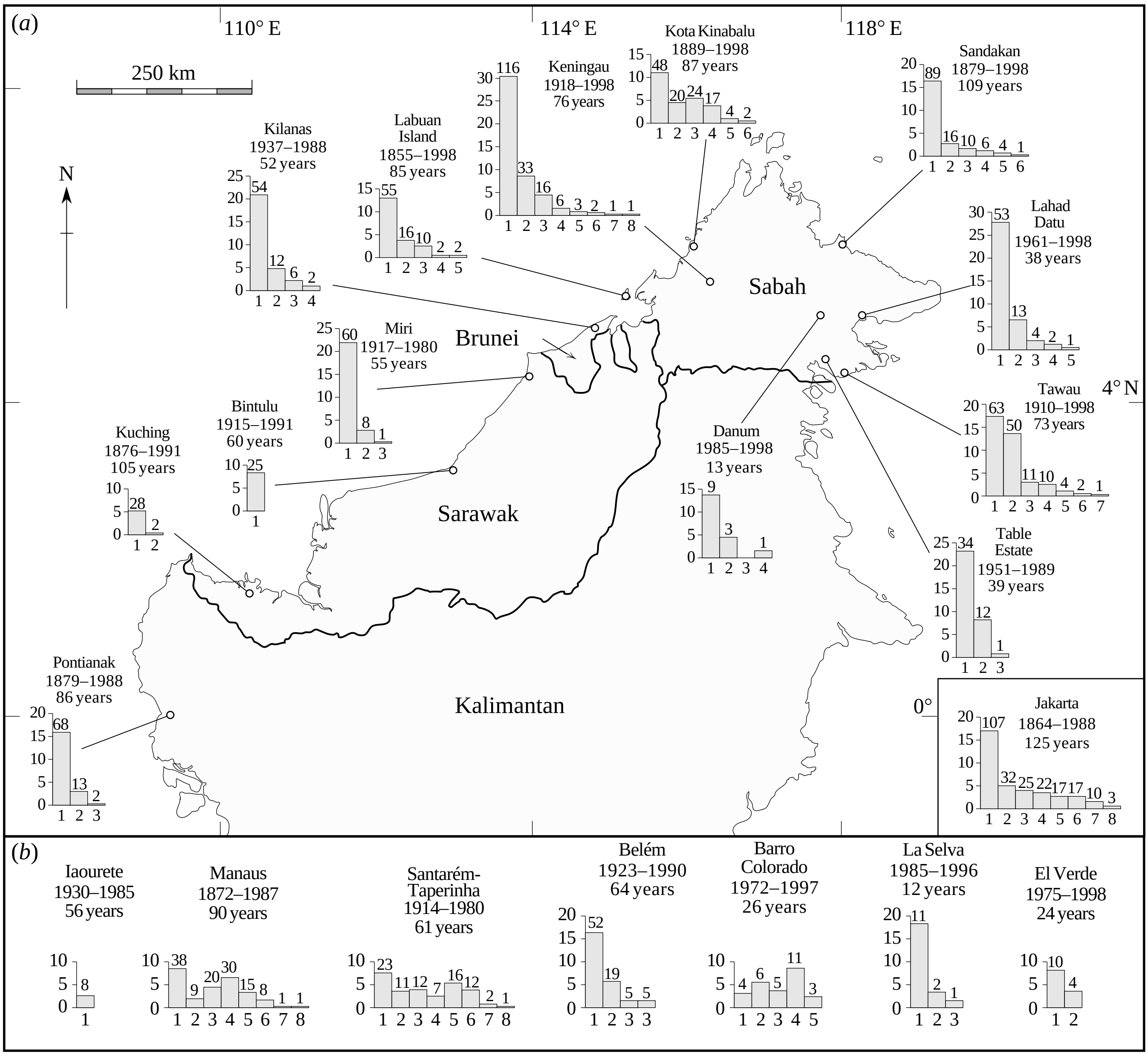

Figure 2. Drought duration magnitude-frequency in northern Borneo and at Neotropical locations in Amazonia (Iaourete, Manaus, Santarém-Taperinha and Belém), Panama (Barro Colorado Island), Costa Rica (La Selva) and Puerto Rico (El Verde). Vertical axis: frequency per 20 years; horizontal axis: drought duration (successive months with < 100 mm) in months. The numbers above each bar are the total number of droughts of that duration recorded in the entire record.

100 mm. Kilanas (maximum CRD 229.3 mm) and even more so Labuan Island (maximum CRD 341.1 mm) are occasionally subject to significantly greater CRDs than have to date occurred at Danum. The combination of frequent CRDs of 100–299 mm magnitude associated with its short dry season and occasional more extreme CRDs associated with ENSO events characterizes Kota Kinabalu, whereas droughts are less frequent but equally severe in intensity at the east coast stations of Tawau and Sandakan. Drought intensity frequency at the central and eastern Amazonian stations of Manaus and Santarém-Taperinha and at Barro Colorado are more akin to Kota Kinabalu (reflecting their strong seasonality by rainforest standards) and are in complete contrast to Danum, eastern and western Borneo. Thus Barro Colorado experiences a CRD of at least 150 mm in 84% of years and of 300 mm or greater in 30.8% of years. Comparative figures for Manaus are 62.3% and 7.8%. These compare with 46.6% and 8.2% at Kota Kinabalu, but only 14.6% and 3.6% at Sandakan, 26% and 4.1% at Tawau and near-zero or zero values at Danum and in western Borneo.

5. THE 1997–1998 EL NIÑO DROUGHT AND RECENT CHANGES IN DROUGHT FREQUENCY IN SABAH

(a) *The 1997–1998 ENSO event*

The 1997–1998 ENSO event has been assessed as the strongest on record in terms of some (particularly sea surface temperature) indices, though overall and in terms of the SOI it was easily outranked by the 1982–1983 event (Davey & Anderson 1998; Wolter & Timlin 1998). The evolution of the event has been documented by Slingo (1998) and McPhaden (1999). Following La Niña conditions as late as November 1996, El Niño-phase

Table 4. *Frequency of droughts of different intensity (as measured by cumulative rainfall deficits (CRDs)) for Danum, other stations in Borneo and selected locations in the Neotropics*

(For definition of cumulative rainfall deficit, see text. Dashes indicate no data present.)

		frequency per century of CRD (mm) of specified magnitude									
location	period of record and number of years	100–149	150–199	200–249	250–299	300–349	350–399	400–449	450–499	500–599	highest CRD (mm) and year
(a) Borneo											
Danum	1986–1998 (13)	15.4	—	—	—	—	—	—	—	—	123.4 1992
Sandakan	1879–1998 (109)	5.5	4.6	4.6	1.8	0.9	1.8	0.9	—	—	443.7 1903
Tawau	1910–1998 (73)	19.2	13.7	4.1	4.1	1.4	—	2.7	—	—	418.7 1968–1969
Kota Kinabalu	1889–1998 (86)	19.8	19.8	9.3	9.3	3.5	2.3	1.2	—	1.2	530.0 1997–1998
Labuan Island	1855–1998 (86)	11.8	4.7	3.5	3.5	1.2	—	—	—	—	341.1 1997–1998
Keningau	1918–1998 (76)	19.7	3.9	7.9	—	2.6	1.3	—	—	—	359.6 1997–1998
Kilanas	1937–1988 (52)	7.7	7.7	5.8	—	—	—	—	—	—	229.3 1987
Kuching	1876–1991 (106)	—	—	—	—	—	—	—	—	—	95.4 1914
Pontianak	1879–1988 (86)	4.7	3.5	—	—	—	—	—	—	—	168.0 1967
Tarakan	1911–1975 (59)	—	—	—	—	—	—	—	—	—	66.1 1959
(b) Neotropics											
Iaourete, Brazil	1930–1985 (56)	—	—	—	—	—	—	—	—	—	63.1 1970
Manaus, Brazil	1872–1987 (90)	21.1	26.7	17.8	10.0	5.6	—	2.2	—	—	443.2 1906
Santarém, Brazil	1914–1980 (62)	9.6	6.5	14.5	14.5	16.1	12.9	3.2	3.2	—	474.6 1958–1959
Belém, Brazil	1923–1990 (64)	9.4	3.1	—	—	—	—	—	—	—	169.3 1960
La Selva, Costa Rica	1985–1996 (12)	8.3	—	—	—	—	—	—	—	—	114.0 1987
El Verde, Puerto Rico	1975–1998 (24)	8.3	—	—	—	—	—	—	—	—	109.0 1984
Barro Colorado Island, Panama	1972–1997 (26)	7.7	19.2	19.2	15.4	23.1	7.7	—	—	—	383.0 1984–1985

conditions developed unusually rapidly in early 1997, such that each month from June to December 1997 record high monthly sea surface temperatures occurring in the eastern equatorial Pacific. Negative SOI values (as measured by the Tahiti–Darwin pressure anomaly) were recorded for each month from March 1997 to April 1998, with the greatest anomalies (−3.2 to −5.4 mb) in early 1998. Sea surface temperatures remained anomalously high until the event was brought to an abrupt end in mid-May 1998, when trade winds suddenly returned to normal strength and the SOI index became positive (McPhaden 1999).

The intensity of the drought conditions that it caused in northern Borneo is shown in figure 3, which compares monthly rainfall during 1997–1998 with long-term averages and, where data are available, for the 1982–1983 ENSO event. Rainfall was particularly low at most stations in Sabah during the latter part of the March 1997 to May 1998 ENSO event. Droughts occurring during the event were the most severe ever recorded at the north-western Sabah stations of Kota Kinabalu, Labuan Island and Kudat. Record CRDs of 530.0 mm, 341.1 mm and 359.6 mm were recorded at Kota Kinabalu, Labuan and Keningau, respectively (table 4). At Sandakan, the drought of January–May 1998 (CRD of 390.2 mm), although more intense than in 1983 (CRD of 235.2 mm), was both shorter and less intense than the record six-month drought of 1903 (CRD of 443.7 mm). At Tawau and Lahad Datu in south-eastern Sabah, however, the 1997–1998 drought was rather less intense than those of 1982–1983 (figure 3) and also 1992. As annual rainfall at Danum has a much stronger correlation with stations in south-eastern Sabah ($r = +0.90$ for the relationship with annual rainfall at Tawau) than at Sandakan, this would suggest that droughts of considerably greater intensity could occur at Danum in the future. Also, although the CRD recorded at Danum itself was comparatively modest (just 101.8 mm), it probably understates the event, as a critical aspect at Danum was the very modest monthly rainfalls of 123.4–150.6 mm recorded in the normally very wet months of November 1997 to February 1998 prior to the dry months of March and April 1998. This would have meant that soil water reserves would have been much below their normal levels in early 1998. March 1998 was easily the driest month on record with only 11.3 mm and early 1998 was also characterized by three rainless periods of 10–13 days each and two long near-rainless periods (table 3).

(b) *Recent drought frequency changes in Sabah*

Rainfall records in Borneo are unusually long for a rainforest region, with records extending back to 1876 at Kuching, 1879 at Sandakan and at some stations in Kalimantan, and to 1855 (but unfortunately with large

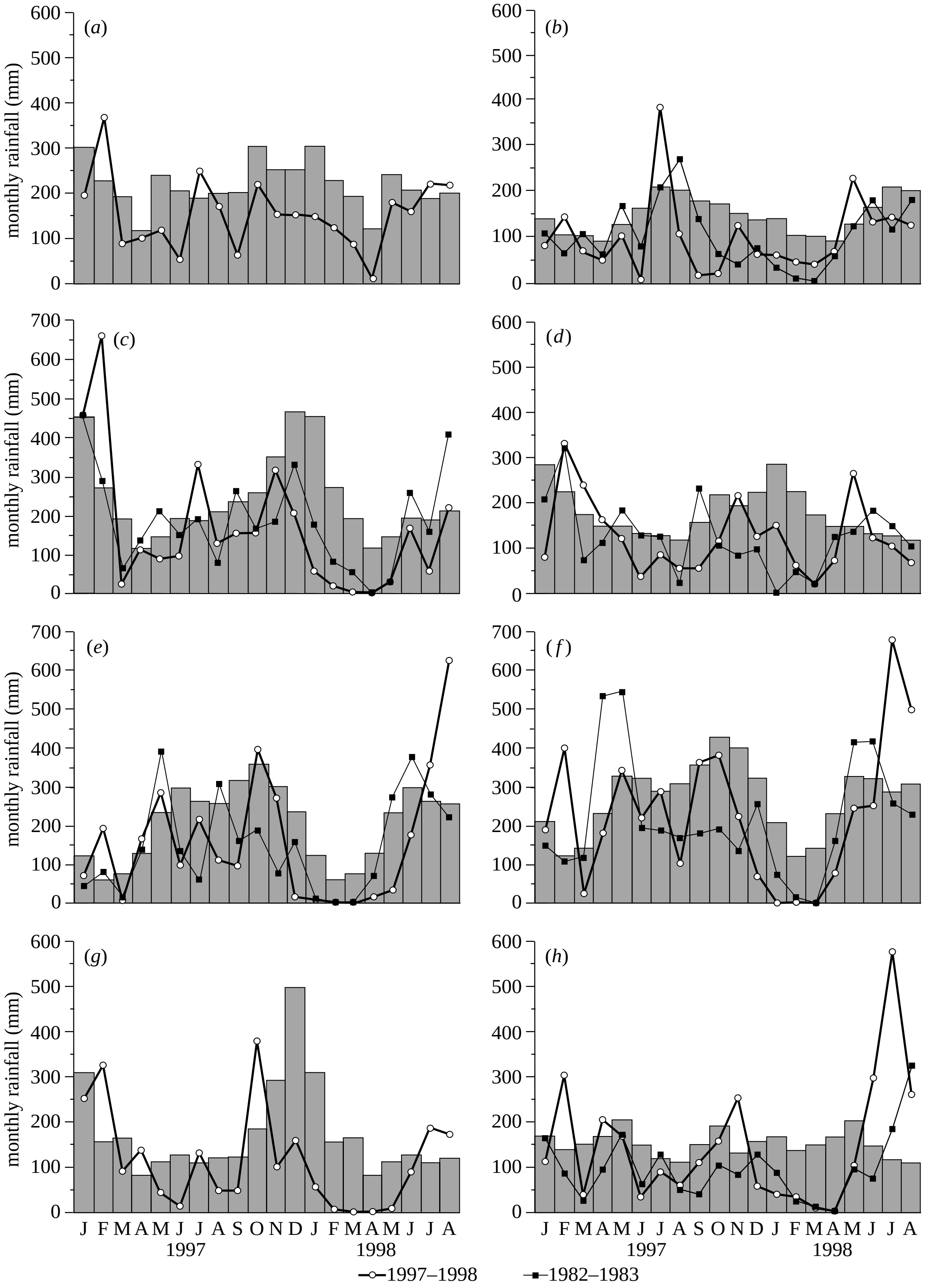

Figure 3. Rainfall during the 1997–1998 El Niño event in Sabah compared with long-term averages (the background histogram) and the 1982–1983 event. The warm phase of the 1997–1998 ENSO event lasted from March 1997 to mid-May 1998. (*a*) Danum, (*b*) Tawau, (*c*) Sandakan, (*d*) Lahad Datu airport, (*e*) Kota Kinabalu, (*f*) Labuan Island, (*g*) Kudat, (*h*) Keningau.

breaks in the record) at Labuan. The chronology of droughts up to 1992 in northern Borneo was covered in a previous paper (Walsh 1996*a*); the record for some stations is extended here to 1998 to include the recent ENSO drought. Figure 4 shows the temporal distribution of major droughts (defined as those with CRDs of at least 150 mm) at the east-coast stations of Sandakan and Tawau and the somewhat seasonal north-west coast location of Kota Kinabalu in Sabah. Of particular interest is the series for Sandakan, because of its unusually long

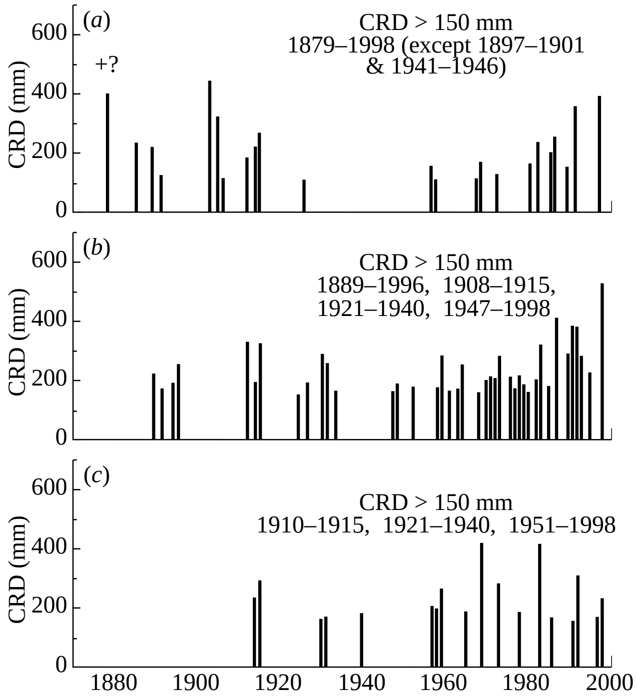

Figure 4. Chronology of major droughts above a 150 mm cumulative rainfall deficit (CRD) threshold at (*a*) Sandakan, (*b*) Kota Kinabalu and (*c*) Tawau.

(1879–1998) record, with only two short gaps in 1897–1901 and 1941–1946 (during the Japanese Occupation). The record at Sandakan suggests a period of higher drought frequency and intensity in the late 19th to early 20th century, a comparatively drought-free period from 1916 to the 1960s, and increasing frequency and intensity in recent decades. It is also interesting to note that the most severe drought, both in terms of duration (six consecutive dry months) and intensity (a CRD of 443.7 mm), occurred in 1903, rather than in the current drought-prone epoch, and contemporary descriptions suggest that the 1878 drought was at least as severe (Walsh 1996*a*). The less complete records at Tawau and Kota Kinabalu also indicate a recent increase in drought frequency and intensity (figure 4), with the increase in CRD intensity at Kota Kinabalu being particularly marked. At Kota Kinabalu, five out of the seven droughts with CRDs exceeding 300 mm have occurred in the last ten years (in 1983, 1987, 1991, 1992 and 1998), the other two occurring during the pre-1916 drought-prone period in 1911–1912 and 1915.

In terms of drought length, figure 5 updates to 1998 the analysis of changes in drought duration frequency (Walsh 1996*a*). At Sandakan droughts of at least four months' duration occurred five times in the period 1879–1915 (in 1885, 1903, 1905, 1906 and 1915) and again on six occasions in the recent period 1968–1992 (in 1969, 1983, 1986, 1987, 1992 and 1998), but in the intervening 52-year period none was recorded. Records at Tawau, Kota Kinabalu, Labuan Island and Kilanas (in neighbouring Brunei) are shorter and/or less complete, but all suggest a recent increase in drought frequency and severity, both in terms of duration and CRDs, compared with prior to the 1960s. At Tawau, six out of the seven droughts of more than four months' duration, including all three with CRDs exceeding 300 mm (in 1969, 1983 and 1992) have occurred in recent decades.

The pattern of relatively high drought magnitude frequency in the late 19th century, a period largely free of major droughts from the 1920s to the 1960s, and increasing drought magnitude frequency in recent decades (as indicated by the Sandakan and Kota Kinabalu series) is strikingly similar to the broad temporal pattern of ENSO magnitude frequency as indicated by sea surface temperature anomalies in the equatorial Pacific since 1860 (McPhaden 1999, fig. 4). The recent increase in drought magnitude frequency tallies also with an increase in the frequency and strength of ENSO warm-phase events as indicated by analyses of the SOI (Wang 1995; Nicholls *et al.* 1996) and the recent coral growth record (Tudhope *et al.* 1995). Nevertheless, although many of the droughts in Sabah are associated with ENSO events, there is no simple relationship between ENSO strength (as measured by the SOI or other indices) and drought intensity (Walsh 1996*a*). Thus the most intense drought at Sandakan in 1903 occurred in year 2 of a comparatively mild 1902–1903 event, rather than in 1983 or 1998.

Increased drought frequency and intensity has also been reported from parts of the Neotropics. At Barro Colorado (Panama), a sharp increase in the intensity of the dry season (from mid-December to mid-April) has occurred since 1966 (Condit *et al.* 1996; Condit 1998). Whereas prior to 1966 one year in six experienced less than 100 mm rain in the dry season, since 1966 the frequency of such intense dry seasons has doubled to one in three years. A sharp increase in the magnitude frequency of drought duration since 1959 at the marginal rainforest location of Roseau in the Eastern Caribbean island of Dominica has also been reported (Stoddart & Walsh 1992; Walsh 1998). Finally, the long-term record of CRDs up to 1991 at Manaus is shown in figure 6. It is interesting to note that, though the temporal pattern is very different from the stations in Borneo, six out of the seven CRDs exceeding 300 mm were registered in the period 1901–1923.

6. IMPLICATIONS FOR RAINFOREST DYNAMICS

(a) *The context for considering the role of drought*

The analysis presented above suggests that Danum is subject to droughts of significantly lower intensity than along parts of the east coast of Sabah and East Kalimantan (Leighton 1984), perhaps of similar intensity and frequency to Brunei, but of higher intensity than in superwet locations such as in much of western Borneo, western Amazonia, and at El Verde and La Selva. In addition, drought magnitude frequency is totally different to that found in the rather seasonal rainforest environments in much of central and eastern Amazonia and at Barro Colorado. The analysis also suggests that there has been a recent increase in drought intensity and frequency at the longer-term stations both on the west and east coasts of Sabah and that (given the reasonably strong correlations of annual rainfall with the south-eastern stations of Tawau and Table Estate) this may also be the case in relative terms at Danum. Of equal significance, however, is the evidence of droughts of equal or, in the

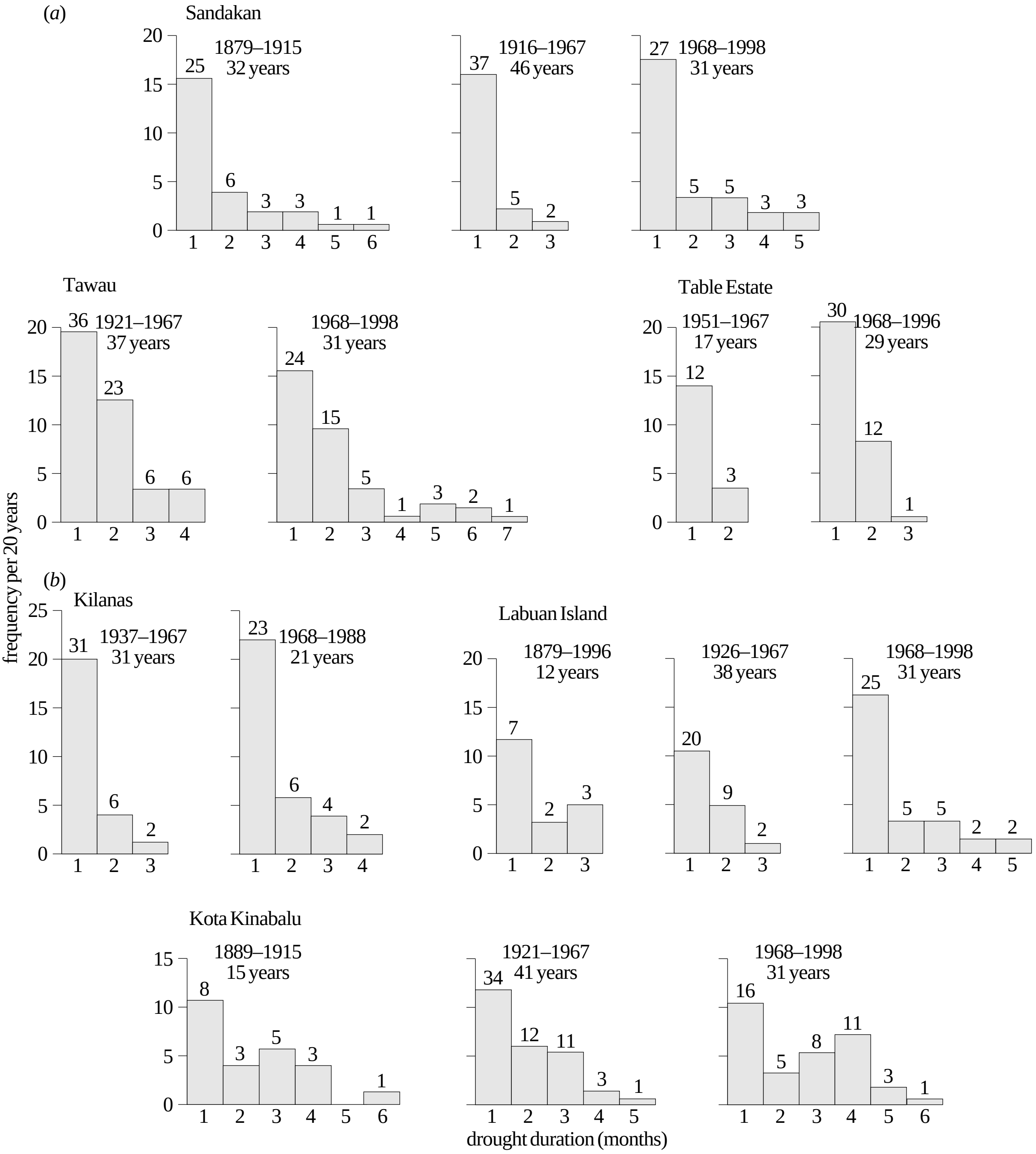

Figure 5. Changes in drought duration magnitude frequency at stations in northern Borneo. Vertical and horizontal axes are as in figure 2 (after Walsh (1996*a*), updated to 1998). (*a*) East coast, (*b*) west coast.

case of Sandakan, even greater intensity in the late 19th and early 20th century. There is also increasing evidence that ENSO-related droughts, although probably varying significantly in magnitude frequency, have occurred in Borneo throughout the Late Pleistocene and Holocene. Thus Goldammer & Seibert (1989, 1990) have found evidence of fire (and presumably drought also) in Borneo in the form of charcoal with radiocarbon dates ranging from *ca*. 18 million years before present (yr BP) to 350 yr BP. Shulmeister & Lees (1995) have presented pollen evidence from tropical Australia suggesting an onset of an ENSO-dominated climate around 4000 yr BP. Finally, analysis of a 15 000-year record of deposits in an alpine lake in south-western Ecuador derived from ENSO event-related debris slides indicates that the return period of warm-phase ENSO events shortened from around 15 years in 15 000–7000 yr BP to 2–8.5 years from 5000 yr BP to the present (Rodbell *et al*. 1999). This suggests that one may be dealing with a range of forests in Borneo that may be resilient to drought (but perhaps only to droughts of a particular magnitude-frequency range), where occasional drought and their associated drought impacts may be an integral part of the dynamic equilibrium of the forest. This formed the basis of a tentative model presented in a previous paper (Walsh 1996*a*, fig. 6), which proposed that some forest attributes in Bornean forests will vary and can be linked to differing magnitude frequencies of drought.

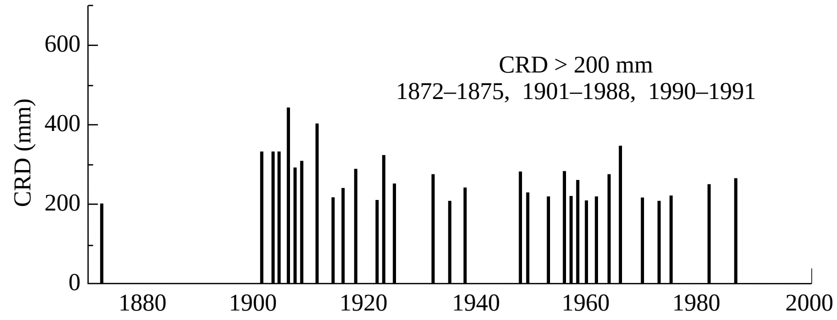

Figure 6. Chronology of major droughts above a 200 mm cumulative rainfall deficit (CRD) threshold at Manaus in Amazonia.

The following discussion, which focuses on drought–tree and drought–forest relationships in the 'normally superwet, but with occasional drought' environment of eastern Borneo, is used to re-evaluate and develop the ideas in that model. It does not seek to consider drought responses in more seasonal rainforest environments where the mechanisms may be rather different and have been explored to some extent elsewhere (e.g. Condit *et al.* 1996; Borchert 1998; Condit 1998; Jipp *et al.* 1998).

(b) *Water relationships and forest response to drought in the region*

The Borneo environment has been subject to major droughts at least back to *ca.* 18 000 yr BP and thus dipterocarps and other main canopy species have arguably evolved to deal with such events (Goldammer & Seibert 1990; Whitmore 1998); indeed it may be that dipterocarps have always lived in such disturbed environments. In east, north-east and north/north-west Borneo, drought has been more intense in the coastal regions and less severe at inland sites such as Danum. Very extreme drought followed by fire is indicated by dominance of *Eusideroxylon zwageri*, a fire-resistant species in East Kalimantan (Goldammer & Seibert 1990). Many dipterocarp species can thus arguably be viewed as being late successional tree species.

The degree of droughting experienced in East Kalimantan, Sandakan and north of the Crocker Range in 1982–1983 (Beaman *et al.* 1985; Leighton & Wirawan 1984; Woods 1989) was much more pronounced than at Danum judged by the intact state of the latter's forest in 1984–1985 (reconnaissance in 1984 by C. Marsh and D. M. Newbery; start of the first enumeration project in 1985, Newbery *et al.* (1992)). In Sarawak and Brunei, Brünig (1969, 1971) has suggested that frequent, short droughts, rendered effective by excessively permeable and hence drought-prone soils, are the cause of the heath forest formation. In contrast to other studies in Borneo, Becker & Wong (1993) found greatest mortality among the smaller trees after a 1992 drought in heath forest in Brunei. At Danum extensive tree defoliation was observed in April and May 1998 (R. P. D. Walsh and G. Reynolds, personal observation) but in December 1998 no substantial tree mortality was apparent, particularly on the ridges (D. M. Newbery, personal observation). A quantitative assessment is presently in progress for the two 4-ha plots of Newbery *et al.* (1992, 1996, this issue). Small branch litter was also abundant in December 1998, this probably being a lag effect of the drought. Possibly the only really major island-wide drought which significantly affected Danum was that of 1878 (Walsh 1996*a*). This might explain the present low basal area status of the forest and also its current aggradation despite probably several weak to moderate droughts (such as the 1997–1998 drought) in the 121 years since.

Droughts might be natural release periods for the onward growth of medium-sized dipterocarps on to the canopy and emergence, these pulses of growth further contributing to the unevenness of the canopy. Defoliation temporarily reduces the leaf area index and, with a lag, twigs and small branches are shed (on leaf flush), which allows more light further down the profile and thus a greater chance that dipterocarps will find improved conditions. The light red merantis (*Shorea* sp.) are expected to respond the fastest. Drought, however, also creates more drying in the understorey, temporarily reducing understorey–overstorey tree competition but then promoting more release when mesic conditions return. Other features that suggest the forest at Danum is in dynamic equilibrium and that maybe most species are well adapted to the disturbance are (i) the high frequency of lianas yet few pioneer trees; (ii) few small gaps at ground level yet a rough open canopy above; and (iii) a drought-tolerant guild on the ridges among the understorey yet elsewhere a strong dominance in the understorey (Newbery *et al.* 1992, 1996). Ashton & Hall (1995) have proposed that dipterocarp forests with rougher canopies and a tendency to have more distinct understories might be correlated with increasing frequency of occasional droughts in north-west Borneo.

If the tree species of the Danum forest are adapted then a mechanism is required to explain how the tree species in the different storeys are protected against high mortality. Several characteristics in tree anatomy, morphology and physiology are predictable from two main hypotheses currently advanced in the literature. Work in temperate forests, especially for oaks, has led to an advanced understanding of drought tolerance (Tyree & Ewers 1991; Tognetti *et al.* 1998). Reduced water deficits in leaves can, depending on the speed and effectiveness of stomatal control, lead to wilting and leaf loss, but also cavitation in the xylem, which leads to embolisms (air trapped in the vessels which substantially reduces hydraulic conductance). When drought is very severe a threshold is reached beyond which embolisms rapidly spread in a 'runaway' situation and complete irrecoverable loss of hydraulic conductance ensues (Tyree & Sperry 1988; Sperry 1995; Tyree & Ewers 1996).

Severe embolism is a major primary cause of death in droughted trees. Slight or partial cavitation is, nevertheless, a normal feature of the functioning tree (Zimmermann 1983), but after a few days of rainfall the water deficits are rapidly readjusted and the air is lost from the vascular system.

Mature trees, temperate and tropical, typically use 10–200 $\mathrm{kg\,d^{-1}}$ of water, these values being the 90% range from 52 whole-tree estimates reviewed by Wullschleger *et al.* (1998). Large tropical trees can use considerably more water, maximally to *ca.* 1000 $\mathrm{kg\,d^{-1}}$. Thus in typical sunny and mesic to saturated conditions in the rainforest, high evapotranspiration rates necessitate high hydraulic conductances. The selection for large vessel diameter to achieve this water flow, however, makes these trees very susceptible to cavitation and then embolism when they are droughted. Trees with smaller vessel diameters have much reduced maximal conductivities which means also potential limitations to growth rates under otherwise optimum conditions (Tyree & Ewers 1991; Sperry 1995). A simple trade-off in adaptive traits has been suggested (Zimmermann 1983; Baas 1986; Sperry 1995) such that drought tolerators have the cost of reduced conductances when adequately drought protected. Safety against embolism might also be achieved by narrower pores in pit membranes (Tyree & Ewers 1996); maximum conductance is reduced, but seeding of air bubbles is limited.

Recent evidence suggests that the cost–benefits will depend not only on vessel size but on other connected mechanisms of avoiding serious drought effects. Machado & Tyree (1994) in Central American seasonal forest, and Sobrado (1997) in Venezuelan dry forest, compared evergreen and deciduous canopy species and found that both types of tree were equally highly susceptible to embolisms. Danum does not have a seasonal tropical environment so selection pressures may be different under its mostly mesic but occasionally drought-disturbed conditions: many aspects of the seasonal traits linked to phenology and regular stress would be lacking. Kursar (1998) concludes that rainforest trees are well adapted to extreme drought in seasonal sites due to strong selection in the past. The one further test to date in tropical 'aseasonal' forests is that of Tyree *et al.* (1998) in Brunei. Fourteen species from both heath forest (the forest type suggested by Brünig (1969) to be formed under frequent drought conditions on sandy soils) and dipterocarp forest (like Danum) were found to be also equally highly susceptible to water stress-induced embolisms, and more so than trees from seasonal tropical sites. (Practically all studies on vulnerability to embolism are made on excised twigs though, and not on the tree.) Other mechanisms must therefore be operating to protect the trees against the worst consequences of low water deficits.

Tyree & Sperry (1988) furthered the segmentation hypothesis of Zimmerman (1983) in which hydraulic architecture is dependent on tree form and detailed aspects of branch morphology and anatomy. Deficits and embolisms begin in the most apical regions (the branch tips) and work downwards with increasing water deficit. Many drought-adapted species seem to be able to contain the smaller embolisms in twigs and small terminal branches, this providing an overall means of protection to the tree. These small branches die, abscise and mostly stay on the tree until releafing leads to their fall. Stomatal closure and then leaf loss are the most immediate and effective means to reduce evapotranspiration under stress and thus lessen immediately the rate of decrease in the deficit in the branches (Sperry *et al.* 1993).

Drought-tolerant species, at least in temperate forests, appear to have wide error margins above the threshold so runaway embolism is avoided well in time (Tyree & Ewers 1991, 1996; Sperry 1995). The avoidance of severe drought effects by having small vessels and branch isolation is a well-established method for central European thermophilous oaks experiencing occasionally very dry summers (Tyree & Cochard 1996; Tognetti *et al.* 1998); a more recent finding is that there are xylem constrictions at the nodes of small branches (Lo Gullo & Salleo 1990). Locally narrowed vessels would allow embolisms to be contained in small terminal branches during the leaf wilting and loss phase. Baas (1986) also speculated on the presence of a bimodal distribution of vessel sizes in trees where protection was needed yet growth must not be limited under mesic conditions. Two other aspects remain unresolved: embolisms also forming in roots and how these are handled (Machado & Tyree 1994); and the role of water storage in tree stems (Holbrook 1995), which could alleviate cavitation effects during short droughts.

These ideas lead to some interesting questions for the forest at Danum regarding its reaction to occasional droughts. In the understorey, for true understorey species the trade-off in vessel size and conductance and/or embolism sensitivity might select for smaller vessel size (or smaller pores in pit membranes) because the evapotranspirational demands are probably not as high as for the canopy trees, and this might be specially developed among the suggested drought-adapted understorey guild on the ridges at Danum. However, for the overstorey species the hydraulic architecture hypothesis with segmentation and isolation of embolisms in terminal branches would be expected to operate because it would allow for the large vessels on which these trees doubtless normally rely, and it accords with our observations of leaf fall, limited mortality, small wood fall and opening of the canopy above the understorey in 1998 and inferred for 1983.

Anatomical traits could be searched for across a range of species and the branch shedding idea tested by carefully observing old branches for trauma at nodes combined with careful examination of vessel construction at the nodes of new twigs. Construction of embolism vulnerability curves for overstorey and understorey species (both drought adapted and apparently not so well adapted) would be instructive. Finally, the idea of architecture linked to tree hydraulics does beg a reinterpretation of the architectural models for tropical trees proposed by Hallé *et al.* (1978): different branching patterns and reiteration structures may well be adaptations to handling water stress problems in these trees, seasonal and aseasonal, with various severities and frequencies of occurrence. Some dipterocarps appear to be resistant to these moderate droughts. A search within the family for traits related to drought avoidance would be valuable when combined with a comparison between saplings and larger dipterocarp trees. Ontogenic change in vessel anatomy and branch architecture in relation to recruitment and onward growth within the forest stand is a possibility.

(c) *Re-evaluation of the Walsh (1996a) model*

It is becoming increasingly apparent that the (ground-level) gap-phase regeneration model is not the only way by which trees regenerate in forests, at least at Danum where gaps recently have been, and are expected to be in the future, relatively rare. A large amount of recruitment from the understorey to the canopy and onward growth is likely to be from existing saplings and pole-sized trees in the optimum mid-canopy light conditions. Drought effects may kill trees by first defoliation and then embolisms causing chronic disfunction, but the subsequent stages are likely to be a slow process of branch shedding and the eventual disintegration of the stem. A leafless, dead tree with reduced small-branch density offers reduced resistance to wind compared to a fully leafed and wetted one so large post-drought tree falls are not likely to be the main mechanism for opening the canopy.

Droughts where they are severe enough to kill trees will therefore leave them standing, and where milder droughts allow survival, the period of leaflessness also increases the radiation reaching the understorey. Thus occasional periodic droughts can thin the forest without large ground gaps occurring. The temporarily increased light and temperature with attendant evapotranspiration loads should lead to strong competition within the understorey, not only letting successful small canopy trees to grow but selecting for a more drought-tolerant understorey guild on the ridges in particular. This together enforces the rough canopy nature with sparse large trees yet also maximizes the density of the understorey. More light also permits more lianes to rapidly increase from within the understorey but it will select against pioneer species, which are unable to tolerate the shade of the understorey when they are small. The feedback in forming a stable understorey–overstorey ecosystem structure is explored in more detail in Newbery *et al.* (this issue). The model's indicated forest structure for 'interior Sabah, rare drought without fire' (Walsh 1996*a*, fig. 6) still stands, but in the light of recent research the dynamic mechanism involved requires revision.

7. CONCLUSIONS

Since climatic records commenced in 1985, Danum has been affected by relatively weak droughts compared with those farther east, but of higher intensity than in the largely drought-free very wet areas in parts of western Borneo.

The 1998 drought, which induced considerable canopy leaf loss, but little mortality, was comparatively mild on the coast at Tawau in south-eastern Borneo compared with locations farther north and west in Sabah, where it was the most intense recorded at several stations. At the station with the most complete record, Sandakan, however, it was not as intense as the 1903 drought and probably not as intense as the 1877–1878 drought. It is an open question as to how much more intense the drought at Danum would have been on those occasions and in 1914–1915.

Drought intensity and frequency is currently increasing at most stations in Sabah. This tallies with a recent increase in the frequency and magnitude of warm-phase ENSO events (Wang 1995; Nicholls *et al.* 1996). Furthermore some of the latest climatic model predictions (IPCC 1996; Hulme & Viner 1998) suggest that ENSO episodes may intensify further. This, coupled with the enhanced impact and increased risk of fire accompanying droughts that logged forests and their fragmentation tend to bring (Whitmore 1998), may mean that drought impacts are likely to increase significantly. In the absence of human impacts, however, the evidence of strong droughts in the 19th and early 20th century in Sabah, and of periods of equally high ENSO warm-phase magnitude frequency to current levels in parts of the period back to 5000 yr BP (Rodbell *et al.* 1999), suggests that it may be more appropriate to view occasional droughts as an integral part of the long-term climate–vegetation system to which the forest is atuned in a form of dynamic equilibrium.

The mechanisms by which drought influences rainforest may well vary between the very contrasting drought magnitude-frequency environments of the Bornean east coast (superwet with occasional severe droughts), the Danum area of interior Sabah (wet–superwet margin with moderate droughts), and the rather seasonal environments with occasional ENSO-related more severe dry seasons that characterize north-western Sabah, much of Eastern and central Amazonia and Barro Colorado.

It is suggested here that the Danum forest shows the influence not only of a past severe event (perhaps that of 1878) that induced significant tree mortality, but also of milder droughts that, because of the increased light that results from the combination of leaf loss and the embolism mechanism of branch loss, may also influence competition among the saplings and pole trees and canopy recruitment. Relative growth (and mortality) rates of understorey trees of different species in the long-term plots at Danum over the next five years may give a valuable insight into the impact of the 1998 moderate drought event.

The authors thank the Kota Kinabalu office of the Malaysian Meteorological Service for providing archival rainfall data for Sabah; NERC, EEC and the Royal Society for supporting field research in Sabah; Dr Tom Spencer for some very helpful comments on an earlier version of the paper; Mrs Nicola Jones for drawing the maps and diagrams; and Mrs Dunja Al-Jabaji for bibliographic assistance. This paper is publication no. A/282 of the Royal Society's South-East Asia Rain Forest Research Programme.

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