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Vegetation and climate of the summit zone of Mount Kinabalu in relation to the Walker circulation

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Abstract

Mountains of the tropical Pacific are influenced by synoptic-scale air subsidence, which causes a temperature inversion and a distinct dry meteorological condition above the inversion. The inversion appears at a lower altitude in the eastern Pacific where descending air of the Walker circulation prevails. On the other hand, if or how the alpine ecosystem of the tropical mountains of the western Pacific is influenced by dry synoptic-scale air subsidence is not well documented. We studied the vegetation and climate of the summit zone of Mount Kinabalu (4095 m) of Borneo. The leaf-size spectrum and physiognomy of forest community changed abruptly along the slope approximately at 3200 m from microphyll to leptophyll, suggesting that dry climatological conditions influence the vegetation above that altitude. Mean daily vapor pressure deficits (VPDs), estimated daily potential evapotranspiration (ET_0), and the ratio of 30-day total ET_0 to 30-day total rainfall increased drastically during El Niño and the magnitude of the increase was greater in the summit zone than in the montane zones. Increased VPDs during El Niño were linked with katabatic winds in the summit zone. We suggest that such irregular dry spells caused by synoptic-scale air subsidence in El Niño years can be a major factor for the formation of xeromorphic vegetation of the summit zone of Mount Kinabalu.

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Introduction

Mountains of the tropical Pacific are influenced by synoptic-scale air subsidence, which causes the trade-wind inversion; a distinct dry meteorological condition prevails above the inversion (Nullet and Juvik, 1994). The inversion appears at a lower altitude in the eastern Pacific where descending air of the Walker circulation prevails, and at progressively higher altitudes toward the west; at approximately 900 m a.s.l. on Galapagos mountains and at 1900 m a.s.l. on Hawaiian mountains. The alpine ecosystems of Hawai‘i, demarcated by the inversion, are characterized by chronically dry air and soil and their vegetation is distinctively xeric (Leuschner and Schulte, 1991; Kitayama and Mueller-Dombois, 1994a, 1994b; Nullet and Juvik, 1994). The high-altitude ecosystem of Galapagos above the inversion is also dry (Trueman and d’Ozouville, 2011). On the other hand, if or how the alpine ecosystems of the tropical mountains of the western Pacific are influenced by dry synoptic-scale air subsidence is not well documented.

The patterns of altitudinal vegetation zones are described on tropical mountains in the western Pacific region (Indo-Malay, the Philippines, and New Guinea) (Whitmore, 1975; van Steenis, 1984; Ohsawa et al., 1985; Kitayama, 1992). Because the climate of the western Pacific region is humid without a marked arid zone, the physical factors forming altitudinal zones have been believed to be related to temperature (or warmth index as the sum of mean monthly temperatures that exceed 5 °C) (Ohsawa et al., 1985; Ohsawa, 1990; Kitayama, 1992). Ohsawa (1990) concluded that the forest limit on high mountains in the Far East across latitudes from the equator to the north coincides with the warmth index of 15 °C • months. There is so far no systematic discussion as to whether the alpine ecosystems on tropical mountains in the western Pacific are influenced by aridity except for Kitayama (1996), who indicated the occurrence of air subsidence and extensive aridity associated with El Niño in the alpine zone of Mount Kinabalu. Moreover, Smith (1980) and Kudo and Kitayama (1999) suggest that trees are killed by occasional droughts in the alpine zone of Kinabalu. These earlier studies point to the possibility of extensive aridity to control the alpine zone of Kinabalu. Leuschner (2000) suggested that high elevations of tropical mountains are more arid than temperate mountains due to high diffusion coefficients and a high radiation load.

Mount Kinabalu (the summit height 4095 m) is the best model site to study altitudinal vegetation zones and climatology of the alpine zone in the western Pacific because of its height and continuous occurrence of unbroken forest canopies from the mountain foot to the forest limit (Kitayama, 1992). Kitayama (1987) suggested that an evergreen mixed broad-leaved coniferous forest can occur up to 3700 m, and an alpine ericaceous scrub occurs up to the summit at 4095 m; accordingly, the altitude of 3700 m demarcates the climatic forest limit of Mount Kinabalu. The evergreen forest or the ericaceous scrub is actually restricted to patches of rock/sand deposits, and the other parts of this zone are dominated by exposed granitic rocks (Kitayama, 1987). The exposed granitic rocks occur widely above 3200 m. By contrast, Smith (1980) points out that the entire summit zone (even including the peak) lies within the climatic forest limit, and the entire mountain can potentially support forests; he further suggests that depth of soils determines the current distribution of the summit vegetation.

Although the altitude of the forest limit differs between Smith (1980) and Kitayama (1987), both suggested that the impoverished vegetation of the summit zone reflects slow vegetation development on the denuded rock surfaces that were formed during the last deglaciation. The summit zone is defined by the zone dominated by exposed rocks above 3200 m (following Smith, 1980). Smith (1980) suggested that the absence of soils and resulting impoverishment of vegetation are explained by high intensity of rainfall. On the other hand, Kitayama (1996) reported an extensive aridity in the summit zone. High rainfall and occasional droughts may therefore characterize the summit zone and explain the impover-

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ishment of vegetation. However, long-term weather patterns have not been elucidated for Mount Kinabalu. If droughts are a selective force, vegetation of the summit zone should demonstrate the traits that are related to drought tolerance. Moreover, these traits can be different from those of the humid forest communities just below the summit zone. The purpose of our paper is to characterize bioclimatic conditions of the summit zone of Mount Kinabalu using vegetation attributes and long-term weather data.

Materials and Methods

STUDY SITES

Mount Kinabalu (4095 m, 6°5′N, 116°33′E) is the highest mountain in SE Asia between the Himalayas and New Guinea. The mountain is non-volcanic and consists of sedimentary rocks below 3000 m and granitic rocks above 3000 m (Jacobson, 1970). Granitic rocks are intruded through sedimentary rocks and are still being uplifted. During the last glacial period, an ice cap was present above 3750 m, which became the source of glaciers flowing downslope. As has been stated earlier, summit granites are still exposed, reflecting the last deglaciation events, and give a rugged impression of the mountain. The summit zone consists of two exposed plateaus, where cirques and surface scratches are found as evidence of past glaciation. Moraines are now found as low as 3000 m.

Tropical lowland or montane rain forests, which are evergreen, occur continuously from 300 m to approximately 3100 m (Kitayama, 1992). The structure, species composition, and function of the rain forests are described by Aiba and Kitayama (1999) and by Kitayama and Aiba (2002). The family Dipterocarpaceae dominates the lowland tropical rain forest below 1200 m, while the families Myrtaceae and Podocarpaceae dominate the montane tropical rain forest at higher altitudes. The vegetation of the exposed summit zone is described by Smith (1970, 1980). Briefly, in the summit zone, forests can develop on major depressions where deeper soils accumulate and scrubs are found on sandy depressions. Herbaceous communities and crevice communities are found on more exposed rocks. The most widespread species in the summit zone is *Leptospermum recurvum* (Myrtaceae, Fig. 1), which is extremely plastic in life form, demonstrating a tree form in a forest to a dwarf shrub (<10 cm height) in rock crevices.

The climate is humid tropical with weak influences of the Asian monsoon. Mean annual air temperature is 24.3 °C at 550 m a.s.l. and decreases linearly with increasing altitude with a mean lapse rate of 0.0055 °C m^{-1}. Month-to-month temperature variation is generally <2 °C. Mean annual rainfall during 1996–2000 ranges from 1900 to 2700 mm at 550 m a.s.l.

VEGETATION ATTRIBUTES

In order to bioclimatically characterize the summit zone, we investigated the leaf-size spectrum of tree species in forest communities at 3300 m and 3500 m a.s.l. We placed a 20 × 20 m quadrat in the most developed forest stand at each altitude and inventoried all tree species greater than 5 cm diameter at breast height. We collected several sunlit leaves from each species at each quadrat and brought them back to the laboratory. We scanned sampled leaves by species and determined the mean leaf size of each species (mean pinnae in case of compound-leaved species). Leaf-size spectrum of each forest was constructed as the distribution of mean leaf sizes. We compared leaf-size spectra of forest communities across altitudes from the lowland to the summit zone. For the leaf-size spectra of the forests below 3100 m, we cited data from Aiba and Kitayama (1999), who placed quadrats (of varying sizes) at 700, 1700, 2700, and 3100 m. We omitted gymnosperms to construct leaf-size spectra to exclude confounding effects of coniferous leaves.

WEATHER MONITORING

Four automated weather stations were established on the south slope (only the Poring station is on the east slope) of Mount Kinabalu in 1995 (Table 1) and maintained thereafter. The four stations are located at Poring (550 m), the Park Headquarters (hereafter PHQ, 1560 m), Carson Camp (2650 m), and Laban Rata (3270 m); they represent a lowland, lower montane, upper montane (cloud) forest, and the summit zone, respectively. Each site is open with-

FIGURE 1. Xeromorphic scrub vegetation at 3300 m on Mount Kinabalu. The scrub is dominated by species with leptophyll leaves consisting of Leptspermum recurvum, Rhododendron ericoides, Styphelia suaveolens, and others.

TABLE 1

Altitude, psychrometric constant, and mean daily maximum and minimum air temperatures of each weather station on Mount Kinabalu.

Altitude (m)	Air pressure (kPa)	Γ (psychrometric constant) (kPa C°$^{-1}$)	Mean daily air T (C°) Max.	Min.
550	94.96539	0.063152	31.27	20.47
1560	84.16898	0.055972	23.81	15.4
2650	73.65538	0.048981	17.12	9.56
3270	68.16722	0.045331	13.75	6.69

out obstacles at least within a 10 m radius. Each station consists of climate sensors connected to a CR10x data logger (Campbell Scientific, Logan, Utah, U.S.A.). The sensors of each station consist of a Vaisala HMP35C probe for air temperature and relative humidity, a 107B probe for soil temperature, a 257 Watermark Soil Moisture Block for soil moisture, a LI-COR 190SB quantum sensor for photosynthetically active radiation (PAR) (wavelength 400–700 nm), a LI200X pyranometer (400–1000 nm) for global radiation, a TE525MM tipping bucket rain gauge for rainfall, and an RM Young 03001 Wind Sentry for wind speed and direction. Vaisala HMP35C probes were used for the first 5 years, and later changed to Vaisala HMP45AC. LI-COR 190SB quantum sensors were annually renewed to prevent data drifting, which can occur due to sensor deterioration; however, we did not calibrate within-year drifts. Soil temperature and moisture were measured at 10 cm depth under short grass cover. All readings were taken at 10 s intervals, except for rainfall and wind speed values, which were taken instantaneously as pulse counts. Readings were reduced to 30 min means and/or totals and electronically stored in CR10s. We regularly visited each station and retrieved data from CR10x. There were occasional periods when data were missing due to sensor failure or vandalism. The entire system at 550 m failed in 2006 and was abandoned thereafter.

ESTIMATION OF AIR ARIDITY

Vapor pressure deficit (VPD) (i.e., drying power of the air) was calculated from air temperature and relative humidity (RH). First, the saturation vapor pressure was estimated as a function of air temperature (calculated using the function provided in CR10X), and VPD was obtained at every 30 min as VPD = saturation vapor pressure * (1 – RH 100^{-1}). Daily mean VPD values were calculated, and then 30-day running means were obtained based on daily values to smooth the changing patterns over the entire period.

In order to estimate the evaporative demands of the air, we estimated daily potential evapotranspiration (ET_0) at each station following the Penman-Monteith equation (FAO-56 Method; Allen et al., 1998):

$$ET_o = \frac{0.408\Delta(R_n - G) + \gamma \dfrac{900}{T+273} u_2 (e_s - e_a)}{\Delta + \gamma(1 + 0.34 u_2)} \qquad (1)$$

where

Rn = net radiation (MJ m^{-2} d^{-1}),
G = soil heat flux density (MJ m^{-2} d^{-1}),
T = mean daily air temperature at 2 m height (°C),
u_2 = wind speed at 2 m height (m s^{-1}),
es = saturation vapor pressure (kPa),
ea = actual vapor pressure (kPa),
Δ = slope of the vapor pressure curve (kPa °C^{-1}),
γ = psychrometric constant (kPa °C^{-1}), and
$es – ea$ corresponds to VPD.

Net radiation R_n was estimated using a hypothetical albedo of 0.23 as follows:

$$R_n = \text{global radiation} * (1–0.23) – R_{nl} \qquad (2)$$

where

R_{nl} = net outgoing longwave radiation (MJ m^{-2} d^{-1}), which is obtained as:

$$R_{nl} = \sigma\left[\frac{(T_{max}+273.16)^4 + (T_{min}+273.16)^4}{2}\right]\left(0.34 - 0.14\sqrt{e_a}\right)\left[1.35\frac{R_s}{R_{so}} - 0.35\right] \qquad (3)$$

where

σ = Stefan-Boltzmann constant (4.903 × 10^{-9} MJ K^{-4} m^{-2} d^{-1}),
T_{max} = daily maximum air temperature (°C),
T_{min} = daily minimum air temperature (°C),
R_s = global radiation (MJ m^{-2} d^{-1}), and
R_{so} = clear sky solar radiation (MJ m^{-2} d^{-1}).

Some of the global radiation sensors failed after 1 year and could not be maintained thereafter. We therefore converted photosynthetically active radiation (PAR) to R_s using a site-specific linear regression, which was empirically obtained using PAR (μmol m^{-2} s^{-1}) and global radiation values at 30 min intervals in January–June 1996:

$$R_s = 0.2905 * \text{PAR} + 0.322\ (r^2 = 0.9967, \text{at 1560 m}), \qquad (4)$$

$$R_s = 0.2623 * \text{PAR} – 1.1279\ (r^2 = 0.9979, \text{at 2650 m}), \text{and} \qquad (5)$$

$$R_s = 0.3011 * \text{PAR} – 0.4089\ (r^2 = 0.9983, \text{at 3270 m}). \qquad (6)$$

In calculating R_{nl}, fixed T_{max} and T_{min} values were used at each station because month-to-month variations of air temperature were negligible on Mount Kinabalu, which are indicated in Table 1. The albedo of 0.23 was derived from the hypothetical reference crop of Allen et al. (1998) and assumed to be the same across all altitudes; our purpose was to compare the strength of evaporative demand across altitudes using a standard equation (see below).

Because water stress to plants develops with declining daily rainfall (or increasing daily ET_0) over time, we calculated 30-day running totals of daily rainfall and daily ET_0 at each station. Subsequently, we calculated the ratio of 30-day running total ET_0 to 30-day running total rainfall as an index of plant water status. Our intention of using Penman-Monteith equation here is to elucidate the temporal patterns of the evaporative demands of the air at a given station and spatial patterns among the four stations using a single standard equation, but not to construct the water budget per se.

In order to relate the spatiotemporal weather patterns of Mount Kinabalu with El Niño Southern Oscillation (ENSO), we used the monthly southern oscillation index (SOI) from Bureau of Meteorology, Australian Government (2012). The period 1997–1998 corresponded with one of the severest El Niño events in the past few decades, and we particularly focused on the among-site differences of weather data of this period. The lowest station (Poring at 550 m) was excluded from the among-site comparisons of air aridity because of too many missing data for that station.

We anticipate that strong katabatic winds dominate the western Pacific during El Niño, where Mount Kinabalu is located. Katabatic winds translate to north winds, while anabatic winds translate to south winds at 3270 m on the south face of Mount Kinabalu. We examined the relationships of daily mean VPDs and daily mean wind direction at 3270 m for the period 1996–2011. We also examined the relationships of daily mean VPDs at 3270 m with daily southern oscillation index (SOI) for the same period. Daily SOI values with the 1887–1989 base period were obtained from the Queensland Government (https://data.qld.gov.au/dataset/the-southern-oscillation-index-soi-daily/resource/bdbfafb4-4e6a-

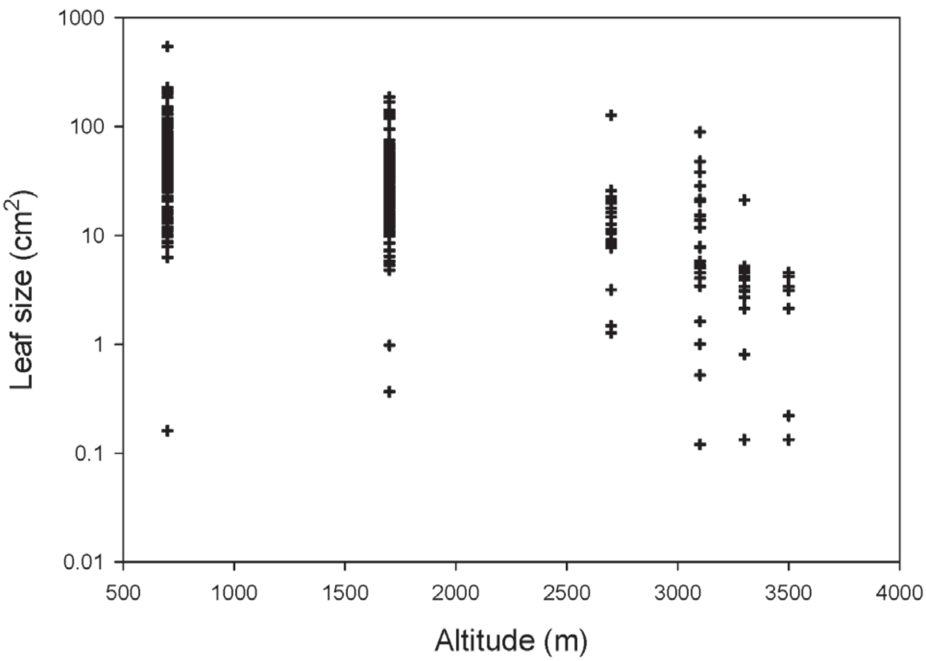

FIGURE 2. Altitudinal change in the leaf-size spectrum of forest communities on the south slope of Mount Kinabalu (4095 m).

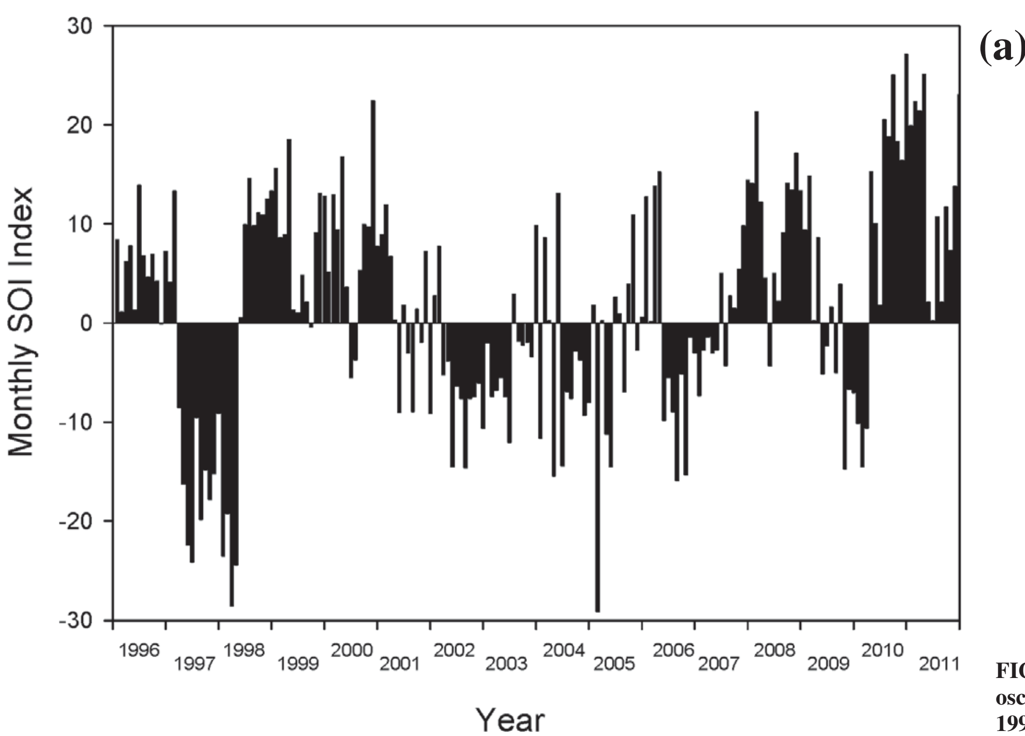

FIGURE 3. (a) Monthly southern oscillation index (SOI) between 1996 and 2011.

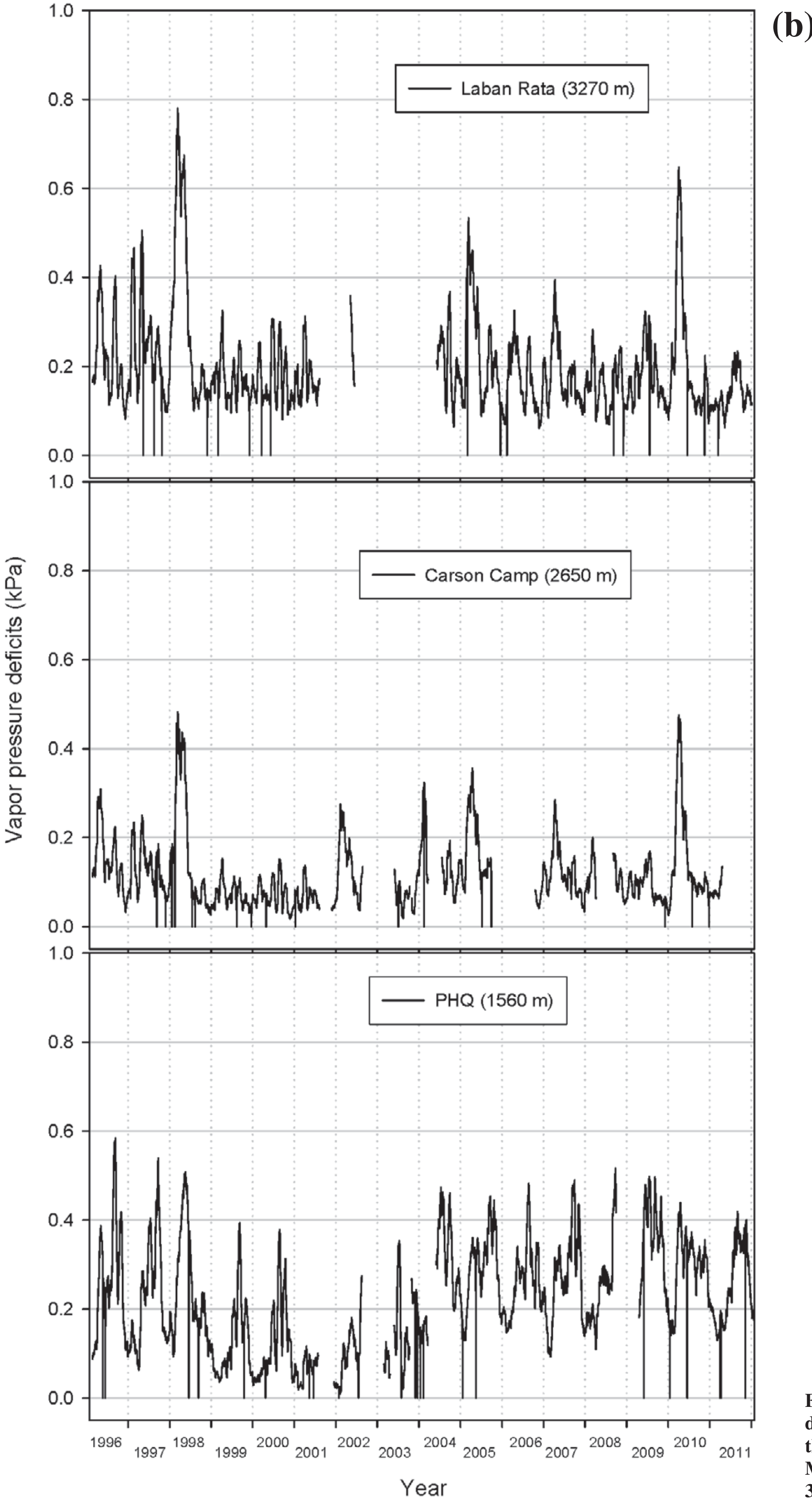

FIGURE 3 (continued). (b) Mean daily vapor pressure deficits (VPDs) at three altitudes between 1996 and 2011. Mean daily VPDs are demonstrated as 30-day running means.

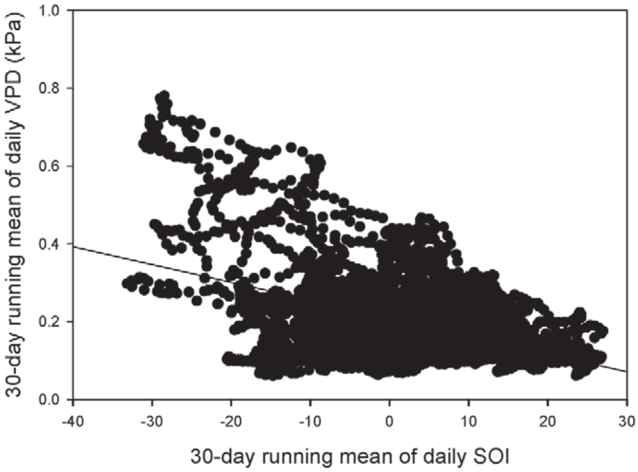

FIGURE 4. Relationships between daily southern oscillation indexes (SOIs) and daily vapor pressure deficits (VPDs) at 3270 m during 1996–2011 ($R^2 = 0.221$, $P < 0.001$, linear regression). Both daily SOIs and daily VPDs are demonstrated as 30-day running means.

TABLE 2

Yearly rainfall (mm), yearly potential evapotranspiration (ET0, mm), the ratio of yearly rainfall to yearly ET0, and yearly mean daily global radiation (Rs, MJ m^{-2} d^{-1}) of three weather stations on Mount Kinabalu.

	1996	1997	1998	1999	2000
PHQ (1560 m)					
Rainfall	3080.2	1685	1739.3	3314.6	2944.8
ET0	560.8	547.6	585.5	476.1	479.3
ET0/Rainfall	0.18	0.32	0.34	0.14	0.16
Rs	7.14	7.10	7.44	6.08	6.05
Carson Camp (2650 m)					
Rainfall	2541.3	1964.3	2008.4	3334.8	2635
ET0	439.4	419.9	444.1	376.3	375.5
ET0/Rainfall	0.17	0.21	0.22	0.11	0.14
Rs	5.53	5.47	5.19	5.08	5.00
Laban Rata (3270 m)					
Rainfall	3695.7	1980.3	2110.3	3653.8	3345.7
ET0	564.3	583.2	645.96	501.5	507.2
ET0/Rainfall	0.15	0.29	0.31	0.14	0.15
Rs	7.73	8.13	8.29	6.84	7.06

4f9d-8cdc-a6896dc85195?inner_span=True; as of March 3, 2014). To smooth variations, 30-day running means were calculated for both daily VPD and SOI before applying a regression analysis.

Results

The leaf-size spectrum changed abruptly above 3100 m a.s.l. Leaf-size spectrum of forest communities changed gradually with

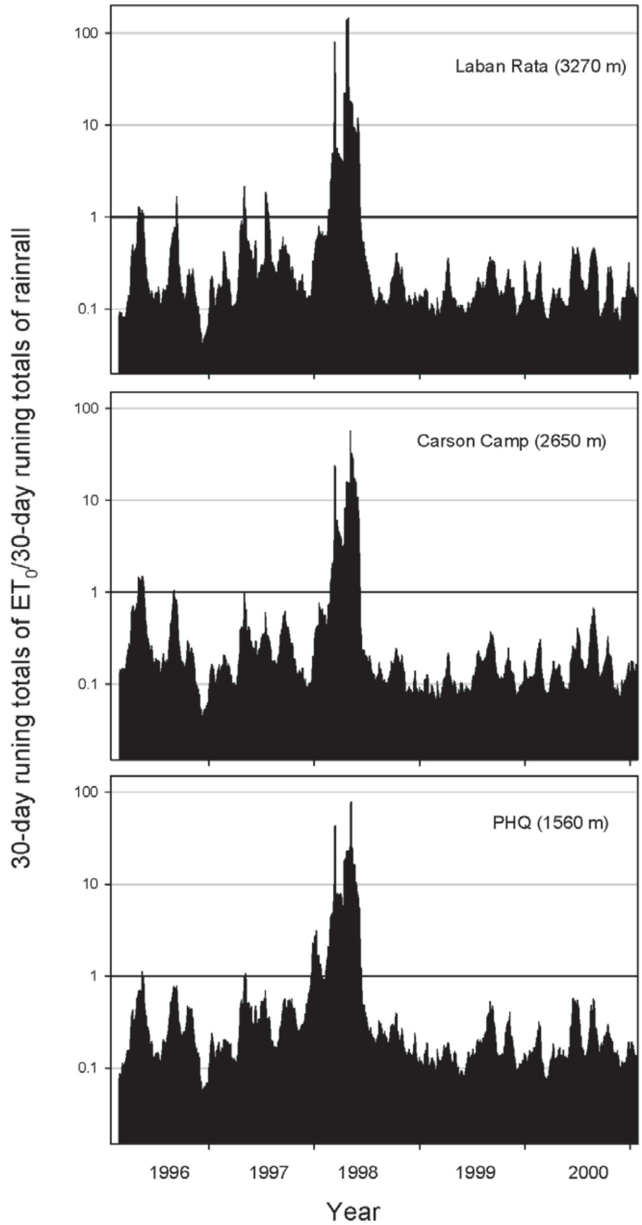

FIGURE 5. Spatio-temporal changes of the ratio of 30-day running total potential evapotranspiration (ET_0) to 30-day running total rainfall across three altitudes during 1996–2000.

increasing altitude from 700 m to 3100 m, and then abruptly above 3100 m (Fig. 2). The lack of larger leaf sizes (macrophyll and mesophyll) was the most prominent characteristic in the forests at 3300 and 3500 m (see Fig. 1).

VPDs as 30-day running means fluctuated greatly at all altitudes between 1996 and 2011 (Fig. 3, part b) and corresponded well with monthly southern oscillation indexes (SOI) (Fig. 3, part a). VPD values demonstrated strong intra-annual seasonal changes in the lower montane zone at 1560 m. At 3270 m, seasonality was less clear, but there were spikes of high VPD values clearly indicating air aridity associated with El Niño Southern Oscillation (ENSO). The greatest spike occurred in 1997–1998, followed by the one in 2010. There were spikes of VPD in the cloud zone at 2650 m; however, the magnitude of aridity was

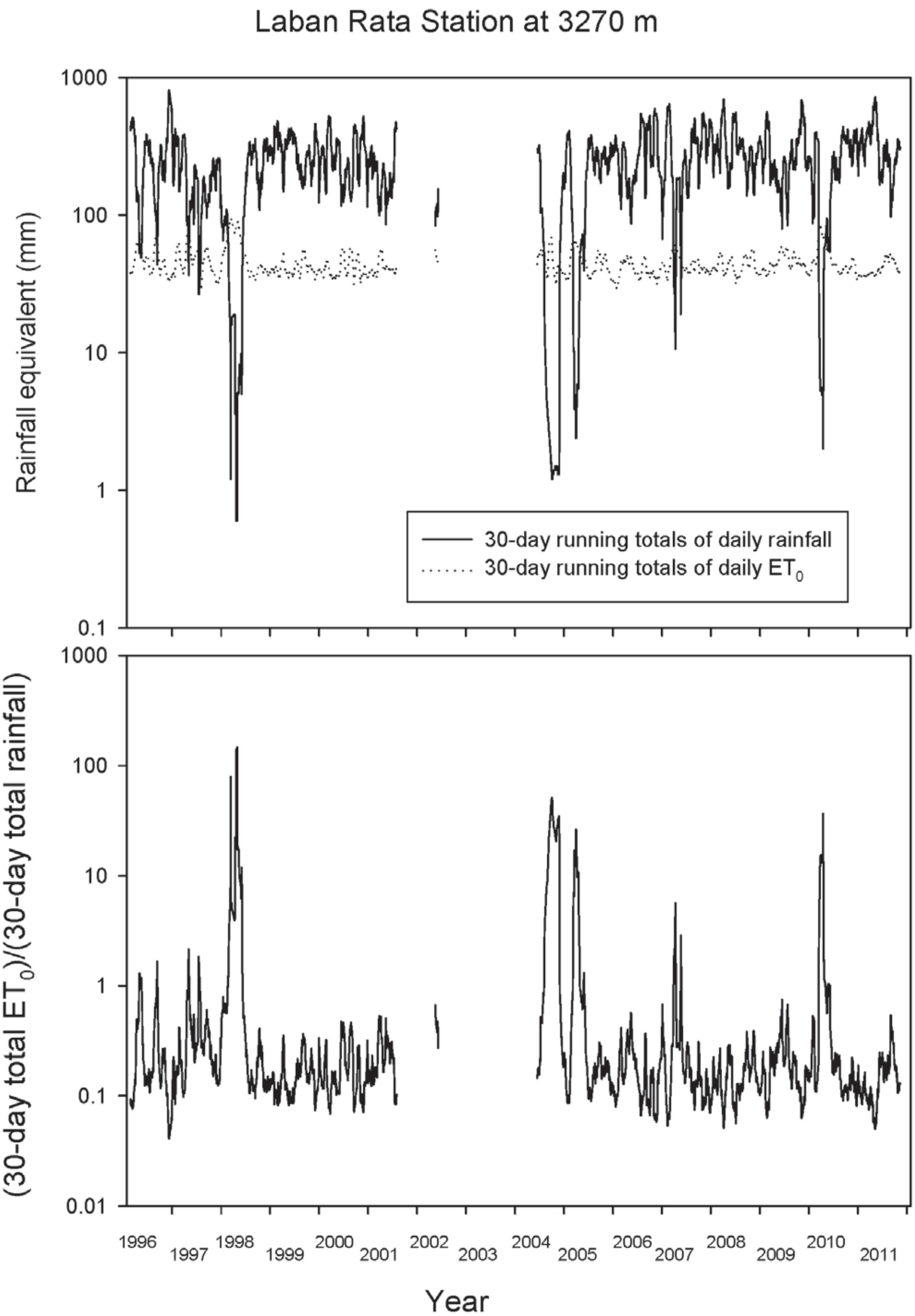

FIGURE 6. Changes of 30-day running total potential evapotranspiration (ET_0) and 30-day running total rainfall at Laban Rata (3270 m) during 1996–2011 (upper diagram) and the ratio of 30-day running total potential evapotranspiration (ET_0) to 30-day running total rainfall (lower diagram).

much less than at 3270 m. ENSO affected air aridity unequally across altitudes; the severest aridity occurred at 3270 m in spite of the coldest climate. Thirty day running means of daily VPDs at 3270 m are significantly correlated with 30-day running means of daily SOI values between 1996 and 2011 (Fig. 4; $R^2 = 0.221$, $P < 0.001$, linear regression). This result again suggests that VPD values at 3270 m are strongly linked to ENSO (represented by more negative SOI).

Yearly total rainfall and estimated yearly total potential evapotranspiration are demonstrated together with yearly means of daily global radiation (R_s) in Table 2 for each station (except for Poring at 550 m) for the period 1996–2000. After the year 2001, there were missing data and yearly values could not be calculated. Yearly rainfall was approximately 3000 mm at 1560, 2500–3000 mm at 2650 m, and 3300–3700 mm at 3270 m during non–El Niño years (1996, 1999, and 2000); yearly rainfall was greatest at 3270 m. Yearly rainfall decreased by 1500 mm at all altitudes during El Niño years (1997 and 1998). Estimated yearly potential evapotranspiration (ET_0) was generally low and ranged from 480 to 580 mm at 1560 m, from 370 to 440 mm at 2650 m, and from 500 to 640 mm at 3270 m. Generally low ET_0 values correspond to prevailing cloudy conditions on Mount Kinabalu. Indeed, daily global radiation (R_s) was consistently low across altitudes and years (generally below 8.0 MJ m^{-2} d^{-1}, Table 2). Estimated yearly ET_0 increased during El Niño years (1997 and 1998) and the magnitude of the increase was greatest at 3270 m. The summit zone at 3270 m was

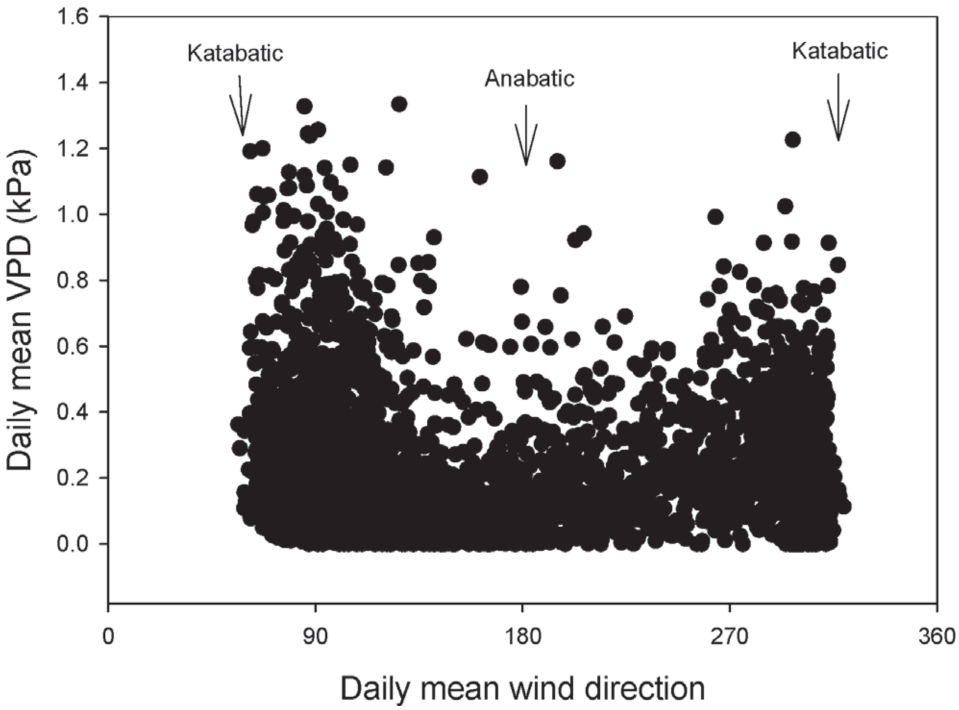

FIGURE 7. Relationships between mean daily wind direction and mean daily vapor pressure deficits (VPDs) at Laban Rata (3270 m) during 1996–2011.

therefore most wet in terms of rainfall, but most arid in terms of evaporative demands.

The ratio of 30-day total ET_0 to 30-day total rainfall (i.e., the magnitude of drought) changed considerably during 1996–2000 at all stations (Fig. 5). However, highest ratios occurred at 3270 m among the three stations, again suggesting that the severest drought occurred in the summit zone during El Niño.

Long-term year-to-year oscillations of rainfall and ET_0 at 3270 m during the time course from 1996 to 2011 are indicated in Figure 6 in terms of 30-day total values. Elevated evaporative demands (i.e., ET_0) and droughts as indexed by the ratio of 30-day total ET_0 to 30-day total rainfall occurred sporadically in 1998, 2004, 2007, and 2010; droughts are not a rare event.

During the strong ENSO conditions, katabatic winds prevailed in the summit zone of Mount Kinabalu. Greater VPD values were associated with katabatic (descending) winds, while smaller VPD values were associated with anabatic (ascending) winds (Fig. 7). During El Niño periods, katabatic winds probably caused droughty conditions in the summit zone.

Discussion

Measured VPDs, estimated potential evapotranspiration (ET_0), and ratios of 30-day total ET_0 to 30-day total rainfall during El Niño years were consistently greater at 3270 m than at 2650 m and 1560 m in spite of its cold temperature. On the other hand, the weather station at 3270 m demonstrated greatest yearly rainfall values during non–El Niño years among the three stations. Therefore, extreme year-to-year oscillations of aridity-wetness characterize the summit zone of Mount Kinabalu, which must have been working as a strong selective force for the vegetation. Indeed, droughts in the summit zone during El Niño years caused high tree mortality. Many *Leptospermum recurvum* trees and shrubs (the most widespread species in the summit zone) were killed by the 1983 El Niño drought (Kitayama, personal observation). Kudo and Kitayama (1999) reported high mortality of trees and shrubs in the ericaceous alpine scrub vegetation after the 1998 El Niño drought. *Leptospermum recurvum* has leptophyllous leaves and xeromorphic morphology. Such leptophyllous leaves and xeromorphism must be an adaptation primarily to droughts, although the other alpine conditions (i.e., high ultraviolet, coldness, and low nutrients) may be involved. However, mortality is still high, suggesting that selection is still operating on the alpine shrubs on Mount Kinabalu; this may be related to the geological youthfulness of the summit zone. Droughts and associated high mortality can be one reason why the development of vegetation is slow in the summit zone after deglaciation in spite of its seemingly wet environments.

In terms of spatial pattern, the weather station at 3270 m is merely 2 km away from the station at 2650 m with a 600-m altitudinal difference. Therefore, weather conditions spatially change rather abruptly between 2650 m and 3270 m; the arid summit zone is demarcated from the lower forest zone at approximately 3100 m. Our leaf spectrum data also demonstrated a rather abrupt change between 3100 m and 3300 m. When one proceeds into the summit zone from the lower forest zone along the summit trail, an abrupt change in vegetation physiognomy is readily noticeable on Mount Kinabalu. However, the altitude of 3000 m demarcates also the lower limit of ice-abrading effects and soil removal by deglaciation. Therefore, the effects of the lack of soils on the formation of the sparse summit vegetation could not be separated from the effects of climatic conditions. We suggest that the extreme oscillation of wet-arid condition decisively influences the summit vegetation of Mount Kinabalu.

Why do the climatic conditions change rather abruptly at around 3100–3300m? It appears that sinking air (i.e., katabatic winds) prevails against convective uplifts of the wet air (i.e., anabatic winds) in the summit zone above 3100 m during El Niño, resulting in severe droughts; our suggestion is based on the prominent weather pattern that high VPDs during El Niño are linked with katabatic winds (Fig. 7). During non–El Niño years, anabatic winds as convective uplifts prevail in the summit zone resulting in wet conditions. Probably, the interface between sinking air and convective uplifts oscillates along the slope and shifts downslope during El Niño. However, its spatiotemporal patterns are not known from our data because of the coarse resolution of our data.

The interface between katabatic versus anabatic winds is more sharply formed as a trade wind inversion in the Hawaiian Islands (Nullet and Juvik, 1994; Kitayama and Mueller-Dombois, 1994a) and the Galapagos Islands (Trueman and d'Ozouville, 2011), which are under the persistent subsidence from the upper levels and the strong trade winds that bring strong orographic uplifts of the wet air on island mountain slopes. Consequently, the transition from the lower wet montane forest to the arid summit vegetation is more sharply demarcated on the high mountains of Hawai'i (Leuschner and Schulte, 1991; Kitayama and Mueller-Dombois, 1994b) and Galapagos (Kitayama, personal observation). The uplift of the wet air is predominantly convective on Mount Kinabalu and strong sinking air does not occur in non–El Niño years on Mount Kinabalu. This may be the reason why the demarcation of the xeromorphic summit zone is less obvious on Mount Kinabalu. This is, however, not meant to understate the importance of droughts as a selective force on the summit vegetation of Mount Kinabalu. If our hypotheses described here are correct, temperature warming per se will not have pronounced effects on the summit vegetation. Rather interactions of temperature and aridity need to be addressed in order to predict the effects of global change on the vegetation of Mount Kinabalu.

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References Cited

Aiba, S., and Kitayama, K., 1999: Species composition, structure and species diversity of rain forests in a matrix of altitudes and substrates on Mt. Kinabalu, Borneo. *Plant Ecology*, 140: 139–157.

Allen, R. G., Pereira, L. S., Raes, D., and Smith, M., 1998: *Crop Evaporation: Guidelines for Computing Crop Water Requirements.* Food and Agriculture Organization of the United Nations, Rome.

Bureau of Meteorology, Australian Government, 2012: Southern Oscillation Index (SOI), http://www.bom.gov.au/climate/current/soi2.shtml.

Jacobson, G., 1970: *Gunung Kinabalu Area, Sabah, Malaysia*. Geological Survey Malaysia, Report 8 (with a colored geological map on a scale of 1: 50,000). Kuching: Geological Survey Malaysia.

Kitayama, K., 1987: Vegetation of Mount Kinabalu (in Japanese). *Shin-rin Bunka Kenkyu*, 8: 103–113.

Kitayama, K., 1992: An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio*, 102: 149–171.

Kitayama, K., 1996: Climate of the summit region of Mount Kinabalu (Borneo) in 1992, an El Niño year. *Mountain Research and Development*, 16: 65–75.

Kitayama, K., and Aiba, S., 2002: Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil P pools on Mount Kinabalu, Borneo. *Journal of Ecology*, 90: 37–51.

Kitayama, K., and Mueller-Dombois, D., 1994a: An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian mountain: (1) climate and soils. *Phytocoenologia*, 24: 111–133.

Kitayama, K., and Mueller-Dombois, D., 1994b: An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian mountain: (2) Vegetation zonation. *Phytocoenologia*, 24: 135–154.

Kudo, G., and Kitayama, K., 1999: Drought effects on the summit vegetation on Mount Kinabalu by an El Niño event in 1998. *Sabah Parks Nature Journal*, 2: 101–110.

Leuschner, Ch., 2000: Are high elevations in tropical mountains arid environments for plants? *Ecology*, 81: 1425–1436.

Leuschner, Ch., and Schulte, M., 1991: Microclimatological investigations in the subtropical alpine scrub of Maui, Hawaii: evidence for a drought-induced alpine timberline. *Pacific Science*, 45: 152–168.

Nullet, D., and Juvik, J. O., 1994: Generalized mountain evaporation profiles for tropical and subtropical latitudes. *Singapore Journal of Tropical Geography*, 15: 17–24.

Ohsawa, M., 1990: An interpretation of latitudinal patterns of forest limits in south and east Asian mountains. *Journal of Ecology*, 78: 262–339.

Ohsawa, M., Nainggolan, P. H. J., Tanaka, N., and Anwar, C., 1985: Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. *Journal of Tropical Ecology*, 1: 193–216.

Smith, J. M. B., 1970: Herbaceous plant communities in the summit zone of Mount Kinabalu. *Malayan Nature Journal*, 24: 16–29.

Smith, J. M. B., 1980: The vegetation of the summit zone of Mount Kinabalu. *New Phytologists*, 84: 547–573.

Trueman, M., and d'Ozouville, N., 2011: Characterizing the Galapagos terrestrial climate in the face of global climate change. *Galapagos Research*, 67: 26–37.

Van Steenis, C. G. G. J., 1984: Floristic altitudinal zones in Malesia. *Botanical Journal of the Linnean Society*, 89: 289–292.

Whitmore, T. C., 1975: *Tropical Rain Forests of the Far East.* London: Oxford University Press, 282 pp.

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