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The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula

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ABSTRACT. The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula is revealed through field survey and meteorological data analyses. The regions of general flowering coincide with those which experienced a low night-time temperature (LNT) *c*. 2 mo before flowering. This supports the hypothesis that low air temperature induces the development of floral buds of dipterocarps. LNT was found to be caused by radiative cooling during dry spells in winter when the northern subtropical ridge (STR) occasionally migrates southwards with a dry air mass into the equatorial region. LNT events usually occur in La Niña episodes, not in El Niño episodes as believed previously. This is because the southward migration of the STR is associated with the intensification of local meridional Hadley Circulation in the western Pacific, which is strengthened in a La Niña episode. Results suggest that El Niño-like climate change in increased atmospheric carbon dioxide concentrations may be critical for the tropical rain forest biome in south-east Asia.

KEY WORDS: Dipterocarpaceae, El Niño Southern Oscillation, general flowering, La Niña-STR hypothesis, low night-time temperature, Malaysia, reproductive ecology

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INTRODUCTION

A general flowering event occurred in the Malay Peninsula in 1996 after a seven-year interval. This supra-annual cycle of plant reproduction takes place at irregular intervals of 2–10 years (Appanah 1985, Burgess 1972, Medway 1972, Ng 1977). Considering their short flowering periods (Chan & Appanah 1980) and high outcrossing rates (Kitamura *et al.* 1994, Murawski *et al.* 1994), dipterocarps are expected to have a mechanism to initiate the floral buds simultaneously within a local population by use of a shared external stimulus (Whitmore 1984, 1990). Several environmental factors have been suggested as the floral triggers for general flowering in dipterocarps, including prolonged drought (Appanah 1985, Burgess 1972, Medway 1972, Whitmore 1984), increase of insolation (Ng 1977, Wycherley 1973), increase or decrease of mean air temperature (Appanah 1985, Wycherley 1973), and a drop of minimum air temperature at night associated with the cloudless weather (Ashton *et al.* 1988).

Among these hypotheses, Ashton's hypothesis (Ashton *et al.* 1988) has been widely referred to recently (Appanah 1993, MacKinnon *et al.* 1996). Ashton *et al.* (1988) found that 5–8 nights with low night-time temperature (LNT) occur *c.* 2 mo before general flowering events in the Malay Peninsula. They deduced that this chilling causes young undifferentiated buds to form inflorescence primordia. They also suggested that the LNT events are caused by radiative cooling at night during a continuous dry period in the El Niño episode. Here we designate their two criteria as the 'LNT hypothesis' and the 'El Niño hypothesis', respectively.

The sifting of currents and fluctuation of the sea surface temperature off Peru known as El Niño Southern Oscillation (ENSO) have important effects on the climate in the western Pacific (Philander 1990). The positive anomalies of the sea surface temperature of the eastern Pacific in the El Niño episode causes greater atmospheric convection there and induces an anomalous easterly flow of air from the western Pacific. This tends to cut the trade winds that are a major source of orographic rainfall on the eastern slopes of Borneo, Sumatra, and the Malay Peninsula and causes severe droughts in the region. On the other hand, the positive anomalies of the sea surface temperature of the western Pacific in the La Niña episode causes great atmospheric convection in the western Pacific and induces heavy rains in south-east Asia. This supra-annual cycle of climate generated by ENSO may have strong influence on the phenology of tropical forests in south-east Asia (Appanah 1993, Ashton *et al.* 1988).

The aim of this paper is to evaluate Ashton's hypotheses through field survey and meteorological data analyses to reveal the mechanism of general flowering in Dipterocarpaceae. The relationship between the general flowering and ENSO is also discussed.

STUDY SITE AND METHODS

Fruiting survey

A fruiting survey of dipterocarps was carried out in June–July 1996 when young fruits, just after flowering, were growing on parent trees. Since dipterocarp species have a short flowering period (*c*. 2 wk) and do not flower simultaneously with one another in a local species assemblage (Chan & Appanah 1980, LaFrankie & Chan 1991), the survey to evaluate the status of general flowering in a large extent needs to be carried out in that period. Forest reserves, protected forests, and old secondary forests from lowland to hill accessible by vehicles were surveyed (62 locations in total). Observations were made from a distance with binoculars and a telescope. A fixed size observation area (*c*. 5 ha) was established in a forest and the density of fruiting dipterocarps was estimated. Each forest site was scored for fruiting: score 0 – no fruiting trees are found; score 1 – up to 25% of large dipterocarps bearing fruits; score 2 – 25–50% of large dipterocarps bearing fruits; score 3 – 50% or more of large dipterocarps bearing fruits.

Meteorological observations

Meteorological observations were made just above the forest canopy at the top level of an observation tower in the Pasoh Forest Reserve (2° 59′ N, 102° 19′ E), using a temperature and relative humidity meter (Vaisala HMP 35C), a rain gauge (Yokogawa Weathac Corporation B-011-00), and a net radiometer (Eko Instruments Trading Co. Ltd. MF-40) previously calibrated. They are installed 52.6 m above the ground (190 m asl), *c*. 3 m above the highest tree canopy near the tower.

In this paper, night-time refers to the period of 19h30–08h00 local time (UTC 11h30–00h00), i.e. from sunset to sunrise at the Pasoh forest, and one observation day refers to 24 h starting at 08h00 local time (UTC 00h00). The seasons refer to those in the Northern hemisphere.

Meteorological data sources

Daily and monthly minimum air temperature, monthly rainfall, and daily insolation observed at various meteorological stations in Malaysia were provided by the Malaysian Meteorological Service (MMS). A part of these data were published in MMS (1997). The upper air conditions over Singapore were provided by the Meteorological Service Singapore (MSS 1997). The relative humidity of the upper air was computed from the air temperature (T_{air}) and the dew point temperature (T_{dew}) at 850 hPa over Singapore at 08h00 by use of the Goff–Gratch formulation (Goff & Gratch 1946, List 1951). Satellite imagery of GMS-5 (Japan Meteorological Agency, JMA) were provided by Dr T. Kikuchi in Kochi University, Japan. Southern Oscillation Index (SOI), which refers to the normalised value of the surface air pressure difference between Darwin and Tahiti, was provided by JMA.

Criteria of LNT

Three criteria of LNT were employed in this paper, considering the difference of meteorological properties of the stations. The first criterion was $T_{air} <$ 20.0 °C, which has been proposed in Ashton *et al.* (1988). This criterion appears rather high in temperature, probably because the urbanisation surrounding the meteorological station to which they referred (Kepong in the north of Kuala Lumpur; 3° 14′ N, 101° 38′ E, 97.0 m asl). This criterion was applied to the LNT conditions at the ground stations in low altitude in Peninsular Malaysia, because some of them were located in urban areas. Some meteorological stations in strongly urbanised areas (e.g. Kuala Lumpur or Singapore) were eliminated from the analysis. Since the monthly minimum air temperature in Pasoh Dua (2° 44′ N, 102° 15′ E, 106.7 m asl), the nearest meteorological station from the Pasoh Forest Reserve, was *c.* 1.0 °C lower than that in Kepong, the second criterion ($T_{air} <$ 19.0 °C) was applied to the Pasoh Dua station. This criterion was equivalent to the lower 10% limit of the monthly minimum air temperature in the station during the period of 1980–1996. Lastly, the third criterion ($T_{air} <$ 21.0 °C) was applied to the forest canopy station in the Pasoh Forest Reserve, because the canopy station generally showed a higher minimum air temperature (*c.* +2.0 °C) than the nearest ground station in Pasoh Dua.

RESULTS

Distribution of general flowering and LNT events

In 1996, the forests with good fruiting were distributed widely in the Malay Peninsula except in the central west coast (Figure 1). In most parts of the Malay Peninsula, three LNT events occurred during the winter 1995/1996; 3–5 January, 16–19 January, and 29 February–6 March 1996. These all had T_{air} < 20.0 °C at a ground station (Figure 1). The intensity of LNT varied among events and regions. The first LNT event was weaker in southern regions, while the second and the third events were markedly strong enough to cover most parts of Peninsular Malaysia.

Each of the forest sites was assigned to its nearest meteorological station and the regions were classified into two categories according to the intensity of LNT during the winter: (1) those areas having a relatively high ($T_{air} \geqslant$ 20.0 °C) minimum air temperature (i.e. the central west coast, $n_1 = 18$) and (2) those which experienced strong LNT events ($T_{air} <$ 20.0 °C, i.e. other regions, $n_2 = 44$). The areas which experienced strong LNT events had significantly higher fruiting scores than those not having strong LNT events (Mann–Whitney's U-test, $P < 0.001$).

LNT events observed at the forest canopy

Three LNT events were also observed just above the forest canopy in the Pasoh Forest Reserve (Figure 2a, LNT criterion $T_{air} <$ 21.0 °C): on the 4 January, 14–19 January, and 29 February–6 March 1996 (Figure 2a, c). The lowest

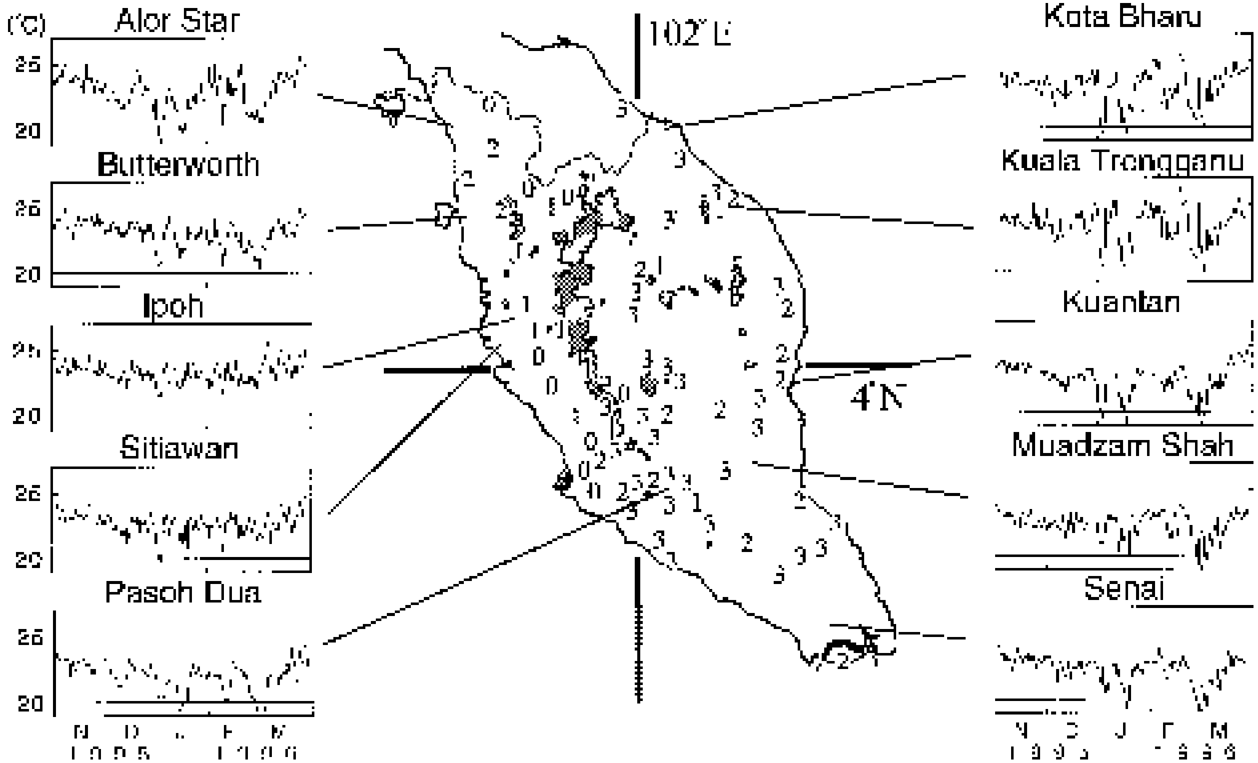

Figure [illegible] Fruiting status of forests and daily minimum air temperatures of several weather stations in the Malay Peninsula in winter 1995–1996. Each forest site was scored for fruiting: score 0 = no fruiting trees found; score 1 = up to 25% of large dipterocarps bearing fruits; score 2 = 25–50% of large dipterocarps bearing fruits; and score 3 = 50% or more of large dipterocarps bearing fruits. [illegible] (1996).

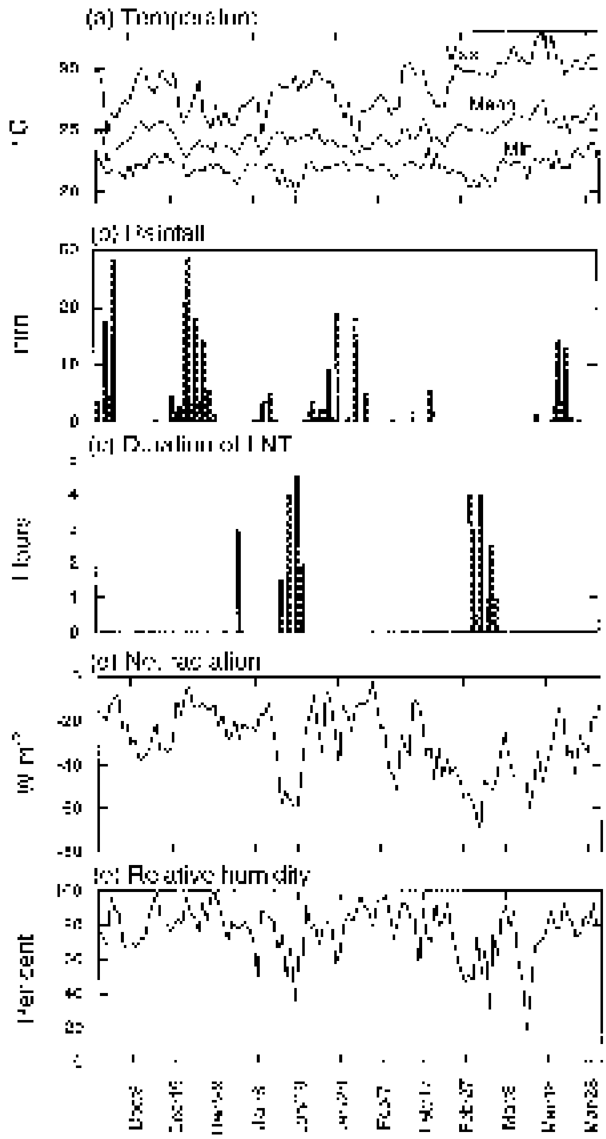

Figure 2. Meteorological conditions just above the forest canopy in the Pasoh Forest Reserve, and upper air conditions over Singapore in winter 1995/1996. (a) air temperature, (b) daily rainfall, (c) duration of LNT (T_{air} < 21.0 °C), and (d) mean night-time net radiation, observed at the top level of an observation tower in the Pasoh Forest Reserve; (e) relative humidity of upper air at 850 hPa over Singapore. The minus sign of net radiation indicates the out-going radiation.

minimum was 19.9 °C at dawn on 18 January. The LNT conditions lasted for 1–4.5 h in a night and were repeated 1–6 nights within a week (Figure 2c).

The second and the third LNT events showed similar meteorological conditions (Figure 2). These LNT events occurred after a few days of little rain (Figure 2b). Air temperatures were lower for the daily minimum and higher for the daily maximum (Figure 2a), and the mean night-time outgoing radiation was higher than other days (Figure 2d). Immediately before these two LNT events occurred, a remarkable dry condition (RH < 50%) prevailed in the lower troposphere (Figure 2e).

Satellite imagery at LNT events

The visible GMS-5 satellite imagery over the Malay Peninsula in the morning of the LNT events is shown in Figure 3. In the first LNT event, a clear sky area was observed from northern to north-eastern parts of the Malay Peninsula and thin clouds covered the western to south-western parts. In the second and the third LNT events, a clear sky area was observed from southern Indochina to the whole Malay Peninsula and part of Sumatra. At that time, convective cloud bands normally covering over the region in winter shifted southward temporarily.

General flowering and ENSO in the past

Figure 4 shows the relationship between LNT events in the Malay Peninsula and SOI. The plus and minus signs of SOI indicate La Niña and El Niño conditions, respectively. The first four LNT events in the figure were given in Ashton *et al*. (1988), and the others were identified by applying a criterion (T_{air} < 19.0 °C) to the monthly minimum air temperature observed at Pasoh Dua. No LNT events in the past appeared in El Niño phases, but all in the normal to La Niña phases. All LNT events were followed by general flowering (Ashton *et al*. 1988, LaFrankie & Chan 1991, Toy 1991, and the present study).

Other meteorological conditions in the winter 1995/1996

There were no prolonged droughts over the Malay Peninsula during the winter 1995/1996. The monthly rainfall was near to the long-term mean, though some meteorological stations showed either slightly positive or negative anomalies. The insolation in January 1996 in terms of the daily global radiation was near to the long-term mean over the Malay Peninsula and those in February and March increased slightly because of continuous fine weather from late February to early March 1996.

DISCUSSION

LNT event as floral trigger

The regions of good fruiting coincided with the areas experienced strong LNT events in the winter 1995/1996 (Figure 1). This provides supporting evidence for the LNT hypothesis. Since the fruiting survey was carried out on large forest remnants immediately after flowering, it is not likely that the bad fruiting in the central west coast was caused by the factors acting in post-induction, such as pollinator abundance, fruit development rates, or fruit abortion. Furthermore, the prolonged drought hypothesis (Appanah 1985, Burgess

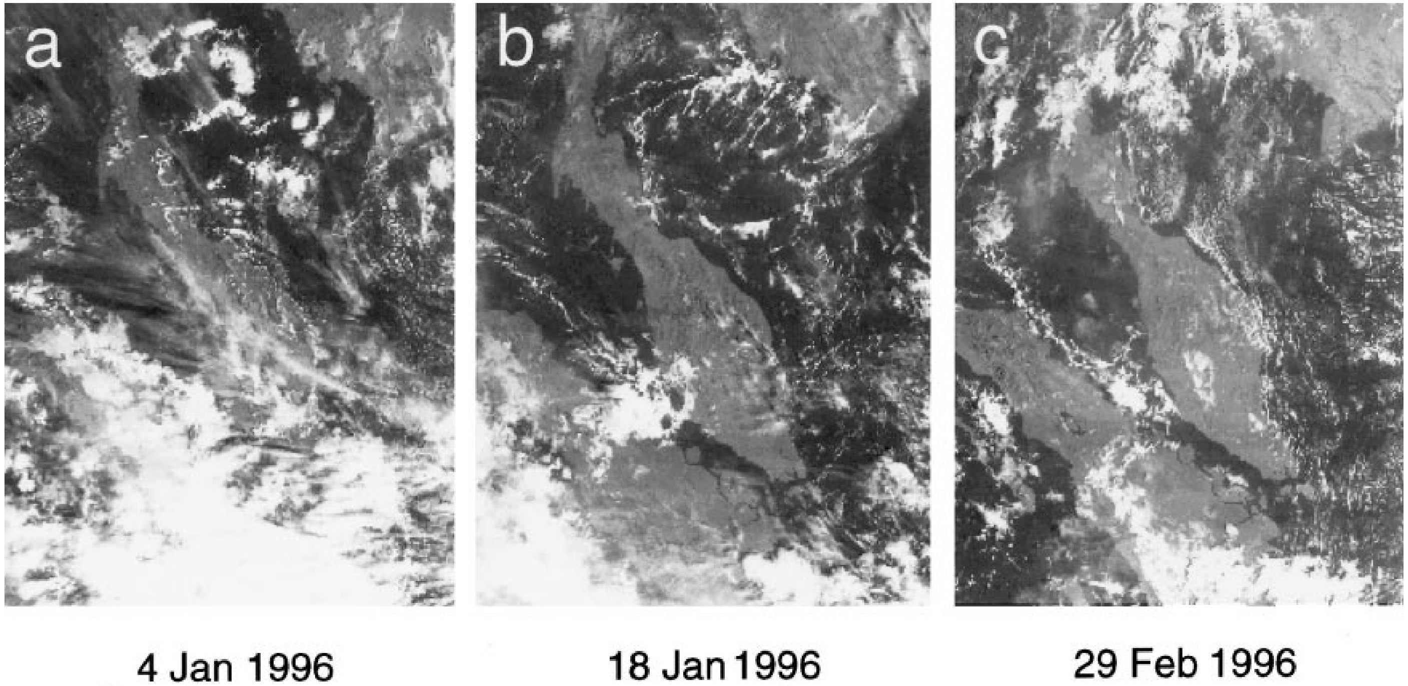

Figure 3. Visible GMS-5 satellite imagery over the Malay Peninsula at 09h00 at local time (01h00 UTC) in LNT events. On 18 January and 29 February 1996, clear sky area was observed from southern Indochina to the whole Malay Peninsula and to part of Sumatra. Convective cloud bands normally covering the region shifted southward during the LNT events.

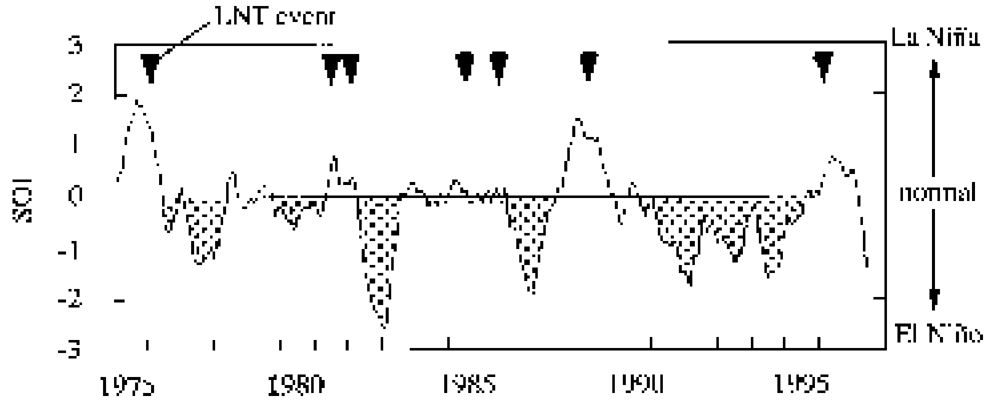

Figure 4. The relationship between LNT events in the Malay Peninsula and the Southern Oscillation Index (SOI). The first four LNT events are from Ashton *et al.* (1988) and the others were identified by applying a criterion (T_{air} < 19.0 °C) to monthly minimum air temperature in Pasoh Dua. Five-month moving averages of SOI are shown. The plus and minus signs of SOI indicate La Niña and El Niño conditions, respectively.

1972, Medway 1972, Whitmore 1984) and the increase of insolation hypothesis (Ng 1977, Wycherley 1973) were irrelevant to the general flowering in 1996, because neither prolonged droughts nor increase of insolation was observed over Peninsular Malaysia during the winter (MMS 1997).

There were three LNT events in most parts of Peninsular Malaysia (Figure 1). The first LNT event (3–5 January) was weaker in southern regions where most forests had good fruiting and was therefore not likely to have acted as the trigger on the Malay Peninsula scale. The third LNT event could not be the floral trigger, because the earliest flowering dipterocarp species *Shorea macroptera* Dyer., which takes *c.* 1 mo to develop inflorescences (Chan & Appanah 1980), flowered in the middle of March in the Pasoh Forest Reserve. Therefore, we concluded that the second LNT event (16–19 January) was the most important floral trigger to induce the general flowering over the Malay Peninsula in 1996, even though the first LNT event might have acted as a floral trigger in the limited areas of the northern regions.

To detect the LNT events as the floral trigger, the air temperature should be monitored just above the forest canopy. Although the data observed in meteorological stations can be used as a simple index, much attention should be paid to the properties of the station, e.g. urbanisation or altitude. For this purpose, the lower 10% limit of the monthly minimum air temperature can be recommended as an index.

ENSO and LNT events

No LNT events that have been considered to induce general flowering in the past appeared in El Niño phases, but in the normal to La Niña phases instead (Figure 4). Ashton *et al.* (1988) correlated fruiting of dipterocarps and El Niño based on the yearly data without considering the time lags of about 7–8 mo from floral trigger to fruit shedding. Ashton *et al.* (1988) said that the El Niño hypothesis seems to stand up in the eastern part of south-east Asia, especially in East Kalimantan. We concluded that the El Niño hypothesis does not apply in the Malay Peninsula. Since it is unlikely that Kalimantan dipterocarps have a different floral trigger, the mechanism of LNT events might be somewhat different among regions. Further studies are needed in various locations.

Mechanism of LNT events in the Malay Peninsula

There may be three different time-scales to explain how LNT events frequently occur in the Malay Peninsula under La Niña conditions: interannual, annual and intraseasonal variability of climate in the region.

Firstly, the interannual and annual variabilities of air temperature are important. Night-time surface air temperature shows a clear seasonal pattern in the Malay Peninsula; high in May–June and low in January (Dale 1963). This annual temperature decline in winter is attributed to the Asian winter monsoon (Dale 1963, Webster 1987). The winter monsoon is intensified by the enhancement of local meridional Hadley Circulation, in which air rises near the equator and sinks in the subtropics, in the western Pacific under La Niña conditions, because positive anomalies of sea surface temperature in the region serve to strengthen the convective activity (Philander 1990). The intensification of the winter monsoon tends to transport a large amount of cold air, known as 'cold surges', from the Asian continent into deep equatorial south-east Asia (Cheang 1987). Additionally, as a consequence of the coupled atmosphere-ocean interactions, the air temperature of the tropical troposphere tends to decline in the La Niña phase (Pan & Oort 1983).

In the winter 1995/1996, when a weak La Niña condition persisted throughout the season (Cleland & Bate 1996, JMA 1996), the typical atmospheric conditions of La Niña were observed. The low-level northern subtropical ridge (STR), which corresponds to the sinking part of local meridional Hadley Circulation, was strengthened (Cleland & Bate 1996). The sea surface temperature of the southern South China Sea was 0.5–1.0 °C lower than the long-term mean (JMA 1996), which indicates the enhancement of cold surges (Tomita & Yasunari 1996). The seasonal average of the tropical troposphere temperature was *c.* 1.0 °C lower than the long-term mean (JMA 1996). These observations suggest that the interannual variability of climate amplified the annual decline of air temperature in the winter 1995/1996 in the western part of south-east Asia.

Lastly, the intraseasonal fluctuation of air temperature and the timing of the LNT events are relevant. There were three LNT events in the winter (Figures 1 and 2a). Although the third LNT event was not likely to be the floral trigger for this general flowering as described previously, the second and the third events showed similar meteorological conditions: consecutive rainless weather, lower daily minimum and higher daily maximum air temperature, and higher night-time outgoing radiation (Figure 2). These observations strongly suggest that the two LNT events resulted from radiative cooling under cloudless conditions.

The cloudless conditions may be caused by the migration of an upper dry air mass into the region, which is related with the atmospheric phenomena prevailing behind the tropical trough (Ramage 1955). It is known that, just behind the tropical trough in winter, the northern STR sometimes migrates deeply southward and brings an upper dry air mass to equatorial south-east Asia (Gan 1974). The higher dryness of the upper air (Figure 2e) and distribution of clouds (Figure 3) in those two LNT events support this hypothesis.

Cold surges are not the direct cause of LNT events, though the intensification of cold surges in La Niña episode may decrease the surface air temperature on a seasonal time-scale. A cold surge has been moistened over the long sea track from the Asian continent to the Malay Peninsula and brings heavy precipitation to the region (Cheang 1987), which is contradictory to the dry cloudless weather preceding the LNT events.

On the basis of this analysis the following conclusions have been drawn on the mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. In the winter of a La Niña episode, the air temperature of the tropical lower troposphere tends to be below normal as a consequence of the coupled atmosphere-ocean interactions. This may decrease the base line of surface air temperature on average on a seasonal time-scale. Additionally, the occasional southward migration of the northern STR brings an upper dry air mass that causes persistent dry cloudless weather in the region. Then, a strong radiative cooling generates LNT. In other words, strong LNT occurs when the air temperature fluctuations of the three different time-scales are in phase at their bottom. This hypothesis can be named the 'La Niña-STR hypothesis'.

Climate change and general flowering

The temperature change for the period 1990–2050 is estimated at an 0.5–1.0 °C increase for tropical regions, compared with a 1–3 °C increase for mid-high latitudes (IPCC 1996), and thus relatively less vegetation change has so far been predicted for tropical forests (Corlett & LaFrankie 1998, IPCC 1996). However, the increase of temperature for mid-high latitudes suggests that the source of the cold in winter is weakened. Furthermore, some recent studies using coupled ocean-atmosphere models showed that increased atmospheric carbon dioxide concentrations lead to El Niño-like climate changes (Meehl & Washington 1996, Tett 1995). This indicates loss of the mechanism for LNT events, since LNT events followed by general flowering hardly ever occur in El Niño phases in the Malay Peninsula (Figure 4). Therefore, numerous plant species depending on LNT as a floral trigger might be hindered in their population recruitment, which would be critical for the tropical rain forest biome in the region.

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