

1 **Interannual variation in leaf expansion and outbreak of teak defoliator at a teak stand in**
2 **northern Thailand**

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4 Katsunori Tanaka^{1,*}, Chatchai Tantasirin², Masakazu Suzuki³

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6 *¹Research Institute for Global Change, Japan Agency for Marine-Earth Science and*
7 *Technology, 3173-25 Showamachi, Kanazawa-ku, Yokohama, Kanagawa 236-0001, Japan*

8 *²Faculty of Forestry, Kasetsart University, 50 Phahonyothin Road, Chatuchuk, Bangkok*
9 *10903, Thailand*

10 *³Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi,*
11 *Bunkyo-ku, Tokyo 113-8657, Japan*

12

13 *Author for correspondence:

14 Tel: +81-45-778-5547; Fax: +81-45-778-5706

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1 **Abstract**

2 The leaf area index (LAI) is a key factor affecting tree growth in forests. Following the
3 outbreak of a defoliator, the LAI declines, serving as a useful indicator in forest management.
4 In this study, daily radiative transmittance from above the canopy, which decreases
5 exponentially with increasing LAI, was measured in a teak plantation (*Tectona grandis* L. f.) in
6 northern Thailand from March-July in 2001-2008. Volumetric soil moisture was also measured
7 at depths of 0.1, 0.2, 0.4, and 0.6 m. The negative logarithmic value of the ratio of daily
8 downward solar radiation on the forest floor to that above the canopy (NLR), $[-\ln(S_b\downarrow/S\downarrow)]$, was
9 calculated as an indicator of leaf flush and subsequent leaf expansion. The NLR data indicated
10 that leaf expansion began in late March and continued to the beginning of May during all eight
11 years (with the day the leaves began to expand defined as D_B). In addition, the peak in NLR
12 values (NLR_p), corresponding to the lowest value of a 99% confidence interval, occurred in
13 July. The day when NLR first reached NLR_p was defined as D_p , which always occurred in June,
14 31-85 days after D_B . The NLR indicated an increase in the population of *Hyblaea puera* (a teak
15 defoliator) that leaf areas greatly decreased during the two growth periods (D_B to D_p): from the
16 earliest D_B to D_p in 2001 and from the second earliest D_B to D_p in 2008. In almost all cases, soil
17 moisture data indicated that leaf expansion occurred after increases in soil moisture at depths of
18 0.1-0.4 m even without increases at 0.6 m; in contrast, increases in shallow soil moisture
19 (0.1-0.2 m) were insufficient to trigger leaf expansion at the stand level. Periods of soil drought

1 at 0.1-0.4-m soil depths inhibited leaf expansion, resulting in prolongation of the interval
2 between D_B and D_P during those years in which the D_{BS} occurred chronologically close to one
3 another. Moreover, when drought did not limit leaf expansion, the D_B - D_P growth periods
4 characterized by earlier D_{BS} tended to be longer than those with later D_{BS} .

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7 *Key words: dry tropical region, LAI, leaf expansion, soil drought, teak plantation, teak*
8 *defoliator.*

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Introduction

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2 The Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change
3 (IPCC 2007) stated that warming of the climate system is unequivocal. The authors concluded
4 that most of the observed increase in global average temperatures since the mid-twentieth
5 century has very likely been due to the increase in anthropogenic greenhouse gas
6 concentrations. Atmospheric CO₂, one of the main greenhouse gases, has increased as a result
7 of human activities since 1750. Recently, in the 10 years from 1995 to 2005, atmospheric CO₂
8 increased by about 19 ppm (IPCC 2007); the highest average growth rate recorded for any
9 decade since direct atmospheric CO₂ measurements began in the 1950s (Keeling et al. 1995).
10 The Kyoto Protocol specifically notes that achieving mitigation objectives for climate change
11 should be accomplished while taking into account “relevant international environmental
12 agreements; promotion of sustainable forest management practices” and promotion of
13 sustainable development (Marland et al. 2003). Reforestation and afforestation are considered
14 a mitigation option for reducing increases in both atmospheric CO₂ and predicted climate
15 change (e.g., Kraenzel et al. 2003), in particular in the tropics, where the climate supports rapid
16 vegetation growth rates and a decrease in atmospheric CO₂.

17 Absorption of atmospheric CO₂ in a forest relies on green-leaf area and photosynthetic
18 capacity. In deciduous forests, in particular, the initiation of green leaf development, its
19 expansion, and its duration are key factors controlling absorption, in conjunction with

1 hydro-meteorological variables. The interannual fluctuation in the canopy duration period
2 (CDP) in deciduous trees in dry tropical regions, i.e., up to a few months (Do et al. 2005;
3 Yoshifuji et al. 2006), is greater than that in temperate regions, where it is up to a few weeks
4 (Wilson and Baldocchi 2000; Barr et al. 2004). The impact of fluctuation in CDP on
5 interannual carbon gain seems greater in dry tropical regions than in temperate regions or at
6 higher latitudes, due to the higher temperature and more intensive downward radiation. Thus,
7 information regarding how leaf flush, its expansion, and its duration are sensitive to
8 hydro-meteorological variables is important for forest management and to assess the changes
9 in carbon gain in response to climate changes in dry tropical regions.

10 Teak (*Tectona grandis* L. f.) is one of the most valuable timber species in the world
11 (Gajaseneni and Jordan 1990). This deciduous species occurs naturally in tropical Asia, mainly
12 between 12° and 25° N and 75° and 104° E, in India, Myanmar, Laos, and Thailand (Kaosa-ard
13 1977); these areas are subject to rainy as well as dry seasons (Nobuchi et al. 2005), with the
14 trees becoming leafless during the latter. Teak is readily established in plantations, making it
15 one of the most promising plantation species in the tropics (Keogh 1996). Indeed, plantations
16 now constitute about 8% of the total plantation area in countries with climates suitable for teak
17 growth (Pandey and Brown, 2000). Teak has also been successfully grown as an exotic species
18 in areas outside its natural distribution, such as in Asia, Africa, and Central and South America
19 (White 1991, Katwal 2003). Thus, this species is of interest in most in reforestation and

1 afforestation efforts, and at the same time provides an option for commercially obtaining
2 timber while reducing atmospheric CO₂ in carbon emission trading.

3 In the natural forest, heavy defoliation by pests attacking isolated individual teak trees
4 and small groups has been recorded. Nair et al. (1985) found four pest species, with negligible
5 damage by all species except *Hyblaea puera*. Pure teak plantations are generally more
6 susceptible than mixed plantations of teak and other species in terms of pest vulnerability
7 (Pandey and Brown 2000). Disease outbreaks in a teak forest can lead to a decline in green-leaf
8 area, resulting in a decrease in carbon gain and in tree growth (Nair et al. 1996), in addition to
9 economic damage and the disturbance of sustainable forest management. Accordingly,
10 information on the risk of severe disease outbreak is needed for effective pest control in forest
11 management. To date, however, predictions of the potential damage to leaf area and the impact
12 of defoliation on forest carbon gain have received little consideration.

13 The present study documents interannual variation in the length of the period from the
14 beginning to the peak of leaf expansion at the stand level under natural conditions. Leaf growth
15 periods have not been investigated at the stand level, although previous studies have examined
16 annual variation in canopy duration in a teak plantation (Yoshifuji et al. 2006, Tanaka et al.
17 2009). Radiative transmittance was measured from March-July in 2001-2008, and seasonal
18 changes in leaf area were qualitatively estimated, based on this time series. Soil moisture and
19 its effect on leaf growth were also determined. Additionally, the effects of a heavy outbreak of

1 the defoliator *H. puera* during the leaf growth period on the timing of leaf initiation and
2 subsequent leaf growth are described.

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Materials and Methods

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Site description and measurements

6 The study was conducted at a teak (*T. grandis*) plantation in the Mae Moh plantation,
7 Lampang Province, northern Thailand (18°25' N, 99°43' E; 380 m above mean sea level;
8 Yoshifuji et al. 2006). Trees in the plantation had a mean canopy height of 17.2 m and an
9 average stem diameter of 0.195 m at breast height in 2000. Due to substantial decreases in
10 forested areas until the 1980s, forest rehabilitation and plantations have been promoted
11 throughout Thailand, resulting in the establishment of teak plantations by the Forest Industry
12 Organization (FIO), primarily in northern regions. The Mae Moh plantation was established by
13 the FIO around 1968. This even-aged teak stand was planted on an area of flat land, where the
14 stand structure is almost homogenous, and has a density of 360 trees ha⁻¹. Younger and shorter
15 trees, which grew from seeds of the originally planted trees, were interspersed among the older
16 and taller trees. The plant area index (PAI) was measured in July 2006 using a plant canopy
17 analyzer (LI-2000, Li-Cor, Lincoln, NE, USA) at the same site used to measure radiative
18 transmittance. Average PAI was 2.93. Teak trees were leafless during severely dry soil
19 conditions in the dry season. Leaves were also heavily damaged by increases in the population

1 of a teak pest (*Hyblaea puera*), particularly in 2001 and 2008.

2 The soil at the Mae Moh plantation is classified as Loamy Paleustults (Thai
3 classification). A penetration test indicated that soil strength gradually increased to a depth of
4 0.8 m and was much harder at a depth of 0.9 m (Tanaka et al. 2009). Measurements of roots at
5 six points near the measurements of downward short-wave radiation below the canopy ($S_b\downarrow$) in
6 July 2008 indicated that teak roots rarely occurred below ~0.4 m in depth (data not shown) due
7 to the presence of rock or hard soil.

8 Downward short-wave radiation above the canopy ($S\downarrow$) was measured using one
9 pyranometer (LI200X, Li-Cor) at a height of 22 m and another (CM21, Kipp and Zonen) at a
10 height of 41 m in 2001-2005 and 2006-2008, respectively. $S_b\downarrow$ was measured at 0.5 m above
11 the forest floor using two different pyranometers (MS-801, Eko; CM21, Kipp and Zonen) in
12 2001-2006 and 2007-2008, respectively. Volumetric soil moisture (θ) was measured at depths
13 of 0.1, 0.2, 0.4, and 0.6 m using time-domain reflectometers (TDR; CS-615, Campbell
14 Scientific). Rainfall was measured using a tipping bucket (No. 34T, Ohta Keiki) and a
15 storage-type rain gauge at an open site about 500 m away from the measurements of $S_b\downarrow$. Air
16 temperature and water vapor above the canopy were measured at a height of 26 m using an
17 aspirated psychrometer (HMP45D, Vaisala) and at a height of 39 m using a ventilated
18 psychrometer (MS020S, Eko) in 2001-2005 and 2006-2008, respectively.

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Estimation of seasonal changes and peak leaf area

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2 To examine interannual variation in the canopy duration period, Yoshifuji et al. (2006)
3 measured daily radiative transmittance, which decreased exponentially with increasing LAI or
4 PAI from the top of the canopy (Monsi and Saeki 1953). In this study, the negative logarithmic
5 values of the ratio $[-\ln(S_b\downarrow/S\downarrow)]$ (NLR), which is approximately proportional to LAI/PAI, were
6 used as an indicator of leaf flush and the subsequent relative growth of trees and leaves (Tanaka
7 et al. 2009). Daily values of both $S_b\downarrow$ and $S\downarrow$ were used in this estimation. To minimize the
8 effect of small fluctuations in NLR on any given day, values were averaged with those from the
9 day before and the day after. Although the NLR data for March 2001 to February 2003 were
10 provided in Tanaka et al. (2009), we also present these data here.

11 A previous study of seasonal changes in NLR indicated that the growth rate decreased
12 upon reaching the peak, and peak values of leaf growth occurred before July (Tanaka et al.
13 2009). The day on which leaf area peaks is difficult to determine due to the gradual rise near the
14 peak and fluctuations in NLR. The peak value of NLR (NLR_p), therefore, was calculated as the
15 lowest value of a 99% confidence interval (CI) in July, when leaves appeared completely open.
16 Here, the D_p is defined as the day when the NLR value first exceeded the NLR_p during the
17 period beginning with the day on which leaf expansion first began to occur (D_B). The
18 determination of D_B in 2001-2008 is presented in the results.

19 Volumetric soil moisture (θ) data are presented as the relative soil moisture (RSM), which

1 was calculated as follows:

2

$$3 \quad RSM = \frac{\theta - \theta_{\min}}{\theta_{\max} - \theta_{\min}}, \quad (2)$$

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5 where θ_{\min} and θ_{\max} are the minimum and maximum volumetric soil moisture values,
6 respectively, at each depth over the 8-year study period. RSM was calculated at depths of 0.1,
7 0.2, 0.4, and 0.6 m. In this way, differences in both saturated and residential volumetric soil
8 moisture (θ_s and θ_r , respectively) among depths are cancelled out, enabling comparisons on the
9 same scale. Additionally, RSM at a 0.1–0.4-m soil depth ($RSM_{0.1-0.4\text{ m}}$), where the distribution
10 of roots appeared most concentrated, was defined as follows:

$$11 \quad RSM_{0.1-0.4\text{ m}} = \left(\frac{RSM_{0.1\text{ m}} + RSM_{0.2\text{ m}}}{2} \cdot 0.1 + \frac{RSM_{0.2\text{ m}} + RSM_{0.4\text{ m}}}{2} \cdot 0.2 \right) / 0.3 \quad (3).$$

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Results

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Climate conditions

15 In 2001–2008, the annual amount of rainfall was 1361 ± 243 mm (mean \pm SD), and the
16 annual mean temperature was $25.4 \pm 0.3^\circ\text{C}$ (mean \pm SD). Figure 1a presents monthly rainfall and
17 monthly and daily air temperatures. The beginning of the rainy season occurred from April,
18 during which the mean amount of rainfall during the 8-year period ($100 \text{ mm month}^{-1}$) was
19 almost the same as the standard deviation, to May, and the end occurred in October or

1 November (Fig. 1a). The monthly temperature was highest (~29°C) in April, decreased slowly
2 from May to October, and rapidly declined from November to December; the lowest value of
3 ~21°C occurred in December. Thus, seasonal changes in rainfall and air temperature delineated
4 three seasons: a rainy season, an early or (cool) dry season, and a late (or hot) dry season. Solar
5 radiation increased with solar elevation at noon from January to April (Fig. 1b) and then
6 gradually decreased and became more variable (gray area in Fig. 1b), due to cloud cover during
7 the rainy season, although solar elevation remained high. Air temperature exhibited a similar
8 pattern, but fluctuations in solar radiation were lower during the dry season, particularly in
9 April, than in the rainy season, whereas fluctuations in air temperature were lower during the
10 rainy season. The vapor pressure deficit (VPD) remained high from February to April (Fig. 1c),
11 indicating that atmospheric conditions were dry, and the atmospheric evaporative demand was
12 stronger during this period; the highest demand occurred in conjunction with the highest solar
13 radiation in April (Fig. 1b, c).

14

15 *Beginning of leaf expansion at the stand level*

16 Figures 2a-h present NLR values, which correspond to PAI, for March–July in
17 2001–2008. NLR values began to increase around late March in 2001, early April in 2008, mid
18 April in both 2005 and 2006, late April in 2007, and early May in 2002, 2003, and 2004. These
19 periods indicate the dates at which leaf flush occurred in each year.

1 Figures 2i–p present rainfall events and RSM time series at depths of 0.1, 0.2, 0.4, and 0.6
2 m during the same periods as in Figures 2a–h. Rainfall events (indicated by “×” in Fig. 2)
3 increased soil moisture at 0.1 m, and occasionally at 0.2 m, before the beginning of May in
4 2003 and 2004, mid April in 2005 and 2006, and early April in 2008. However, these rainfall
5 events did not increase soil moisture at 0.4 or 0.6 m, probably due to evaporation of surface soil
6 water under strong evaporative demand (Fig. 1). Hollow circles (○) indicate rainfall events
7 during which soil moisture increased from depths of 0.1 m to at least 0.4 m, although the rate of
8 increase at 0.4-m soil depth was slight in 2003. NLR values increased in association with
9 increases in deep soil moisture, although the rate was slower in 2005, 2006, and particularly in
10 2007. In contrast, shallow soil moisture increases (×) in 2003, 2004, 2005, 2006, and 2008 did
11 not result in continuous increases in NLR; the slight fluctuations after (×) in 2006 and 2008
12 were likely due to a decrease in $S_b\downarrow$ as a result of the moistening of branches and stems during
13 rainfall events. Nonetheless, shorter trees, which had grown from seeds of originally planted
14 trees and likely had shallower roots, often opened their leaves in response to increases in soil
15 moisture at shallow depths, although the opening of leaves did not increase NLR, due to both
16 the lower numbers and shorter heights of these younger trees. Rainfall events in early March
17 2001 adequately moistened the soil at depths of 0.1–0.6 m, but NLR values did not increase (▼
18 in Fig. 2a). Instead, the NLR began to increase after the spring equinox (△ in Fig. 2a). On a day
19 in early May 2002 when rainfall reached over 50 mm month⁻¹, NLR appeared to increase (◎ in

1 Fig. 2b); however, soil moisture data are lacking for this period. Thus, these three particular
2 types of days (indicated by \circ , \triangle , and \odot) corresponded to the beginning of leaf expansion
3 (D_B).

4

5 *Growth of leaves at the stand level and heavy outbreak of teak defoliator*

6 The NLR always appeared to fully peak in July over the 8 years of the study. Solid
7 circles (\bullet) in Figure 2 indicate the points at which NLR reached NLR_p , which corresponds to
8 the lowest value of the 99% CI in NLR values for July. The mean values of NLR (99% CI) in
9 July in 2001–2008 were 1.41 ± 0.08 , 1.56 ± 0.09 , 1.61 ± 0.17 , 1.57 ± 0.11 , 1.53 ± 0.09 , 1.69 ± 0.09 ,
10 1.65 ± 0.12 , and 1.34 ± 0.06 , respectively. The overall mean value of 1.69 was equivalent to the
11 PAI of 2.93 measured in 2006 (see Materials and Methods). The D_p occurred in June
12 (Fig. 2a-h), and the interannual difference in D_p was smaller than that in D_B .

13 The solid green bars in Figure 2 indicate the growth period between D_B (\circ , \triangle , and \odot)
14 and D_p (\bullet). The length of this period differed greatly among years, ranging from 31 days in
15 2002 to 85 days in 2001, indicating that leaf expansion occurred at different rates after each
16 annual D_B (Fig. 2a–h). Differences in the rate of leaf expansion were likely due to the variable
17 occurrence of soil drought (i.e., periods during which $RSM_{0.1-0.4\text{ m}}$ dropped below 0.2). These
18 events, indicated by vertical red bars in Figure 2, occurred twice during the 2001 growth period
19 and once each in 2003, 2004, 2005, and 2008. The longest drought duration was 34 days in

1 2005, whereas the shortest was 5 days in 2003. During these periods of soil drought, the NLR
2 only slightly increased compared with periods of wetter soil conditions. As the NLR values
3 clearly declined in mid-May during D_B – D_P in both 2001 and 2008, the population of *Hyblaea*
4 *puera*, a teak defoliator and the most serious teak pest (Nair 2001), appeared to increase, and
5 leaf areas decreased. The smaller decline in NLR in mid June in 2001 and 2008 also suggests
6 that the pest population probably increased again, and leaf areas declined. During D_B – D_P in
7 other years, decreases in leaf area may have been caused by *H. puera*, but the scale of these
8 declines was relatively small.

9 Figure 3a illustrates the relationship between D_B and the D_B – D_P growth period, which is
10 classified by values of $RSM_{0.1-0.4\text{ m}}$. When D_B occurred in early May, the growth period was
11 longer in 2004 than in 2003 due to the longer duration of drought conditions ($RSM_{0.1-0.4\text{ m}} <$
12 0.2) in 2004. The relationship was similar for the growth periods beginning in mid April in
13 2005 and 2006. For cases when D_P occurred at the beginning of June in 2006 and 2007,
14 $RSM_{0.1-0.4\text{ m}}$ values did not fall below 0.2 during D_B – D_P (Fig. 2). Although values of
15 $RSM_{0.1-0.4\text{ m}}$ did not fall below 0.2 in 2006 and 2007, the growth period (D_B – D_P) was longer due
16 to the earlier D_B in 2007 than in 2006. The driest period of $RSM_{0.1-0.4\text{ m}} < 0.2$ in 2005 was longer
17 than that in either 2001 or 2008; the growth period was nearly the same as in 2008 and shorter
18 than in 2001. Overall, growth periods beginning on earlier D_B s appeared to be longer than
19 those beginning on later D_B s, even in years without drought. The difference between the mean

1 NLR for the 31 days in July and the NLR on D_B , when the NLR values only represent the
2 effects of branches and stems, roughly corresponded to the interannual variation in LAI peak
3 values (Fig. 3b). These values were lowest in 2001 and 2008 because of the dramatic increase
4 in the population of *H. puera* (Fig. 2a, h). Interestingly, the D_{BS} for these 2 years were the
5 earliest and the second earliest of the entire 8 years of the study. The value was highest in 2006,
6 but values for other years did not clearly differ from one another (Fig. 3b).

7

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Discussion

9 The growth periods of teak from the beginning to the peak of leaf expansion (D_B – D_P) at
10 the stand level (based on the NLR values) broadly varied, from 31 to 85 days, over an 8-year
11 period. Moreover, the NLR values reflected the heavy defoliation during the D_B – D_P period in
12 2001 and 2008. This is the first reported study to demonstrate this pattern of growth, from D_B to
13 D_P , and damage by a defoliator at the stand level under natural conditions in a dry tropical
14 region in which teak grows naturally. Measures of seasonal variation in indicators of PAI
15 estimated using the transmittance of downward solar radiation though the canopy must take
16 into account the effect of differences in solar elevation. Nonetheless, the NLR served as a
17 sufficient indicator of PAI at the site because the effect of seasonal changes was less there,
18 particularly in March to July (Fig. 1b), than in areas of higher latitude.

19 During the 8-year study period, the D_B occurred during a span of 38 days from late

1 April to the beginning of May. The beginning of leaf expansion occurred in 2003-2008 when
2 soil moisture increased at 0.1-0.4-m soil depths (Fig. 2c-h). Although soil moisture changed
3 little at the 0.6 m depth on the D_B in both 2003 and 2004, the LAI began to increase because the
4 distribution of roots was likely concentrated between 0.1-0.4-m soil depths. In 2002, rainfall of
5 over 50 mm on the D_B appeared to sufficiently moisten the soil layers to a 0.4 m-depth,
6 although soil moisture data were lacking (Fig. 2b). These results were similar to those reported
7 for deciduous woody species in a north Australian tropical savanna (Williams et al. 1997).
8 Predictions of the beginning of leaf expansion should take into account the history of rainfall
9 interception by branches and stems and soil evaporation in soil-plant-atmosphere continuum
10 (SPAC) systems, as well as rainfall events prior to the onset of leaf expansion.

11 In contrast, in 2001, the increase in soil moisture at 0.1-0.6 m depth did not initiate leaf
12 expansion; instead, leaf expansion began around the time of the spring equinox under
13 well-watered soil conditions. This result raises the question of whether leaves were not ready to
14 expand in response to an earlier time of increased soil moisture. Leaf primordia may not always
15 be formed at the time of the first increase in soil moisture at 0.1-0.6 soil depths, or they may
16 not have reached the appropriate age or stage of development (e.g., Sinha 1999; Friml et al.
17 2003) to elongate themselves in response to a rise in water status. Because well-watered soil
18 conditions apparently rarely occurred before the spring equinox in the dry season (Fig. 1),
19 these issues should be examined by watering trees before and after the spring equinox and

1 evaluating when leaf primordia form and how they develop. The slower rate of leaf expansion
2 after earlier D_{BS} (Fig. 2e–h) might also be related to the age of leaf primordia. No relationship
3 was observed among the leaf expansion rate at the onset of expansion, solar radiation, air
4 temperature, and VPD for 5 days after D_B , including the cases of faster rates of leaf expansion
5 on D_B in 2002–2004.

6 We demonstrated that soil drought inhibited the leaf expansion rate of teak at the stand
7 level. A relationship between NLR values and air temperature (i.e., thermal time) was not
8 clear; instead, the relationship was similar to the time series of NLR (Fig. 2a–h) due to the
9 higher air temperature at our study site compared with areas where the relationship between
10 NLR and thermal time is stronger (e.g., Lizaso et al. 2003) and compared to the air conditions
11 in experimental systems (e.g., Granier and Tardieu 1998). Our results are consistent with
12 those from studies of corn, soybean, sunflowers, eucalypt, and teak (Boyer 1970, Metcalfe et
13 al. 1990, Saab et al. 1990, Rajendrudu and Naidu 1997). For example, Saab et al. (1990)
14 demonstrated that the rate of leaf expansion in maize seedlings decreased when soil water
15 potential was low, and Metcalfe et al. (1990) showed that drought treatment caused a
16 reduction in leaf expansion rate of *Eucalyptus globules*. Rajendrudu and Naidu (1997)
17 demonstrated that *T. grandis* was inhibited by declines in soil water content under drought
18 treatment. Such declines in the leaf growth rate of teak at the stand level should often be
19 observed during the transition period from the dry to the rainy season in nearly all dry tropical

1 areas in which teak occurs naturally. The length of the growth period ($D_B - D_P$) was longer
2 with longer durations of soil drought for years when the D_{BS} fell close together. Growth
3 periods beginning on earlier D_{BS} tended to be longer than those beginning on later D_{BS} , as was
4 the case when no soil droughts occurred in 2006, 2007, and possibly 2001 (although data were
5 missing for that year (Fig. 2j), numerically simulated soil moisture levels (Tanaka et al. 2009)
6 indicated well-watered conditions at 0.1-0.4 m soil depths during the growth period from
7 $D_B - D_P$). Longer growth periods with earlier D_{BS} may also be related to the age of leaf
8 primordia (Sinha 1999), because not all primordia may be fully developed and ready to
9 expand on early D_{BS} . On earlier D_{BS} , the developmental stage of leaf primordia may differ
10 greatly among nodes, and leaf expansion may exhibit more time lags in development among
11 nodes than on later D_{BS} . The leaf expansion rates during periods without soil drought
12 appeared to be minimally related to solar radiation, air temperature, and VPD (Fig. 1).

13 Exposure to water deficit conditions during leaf growth reduces the final leaf size
14 (Rawson et al. 1980; Takami et al. 1981; Mazzoleni and Dickmann 1988). The LAI in
15 *Eucalyptus* plantations declined with water stress (Battaglia et al. 1998). However, in this
16 study, the peak of leaf area in 2005, which experienced the longest drought, was comparable
17 to peaks in 2003 and 2004 with shorter droughts (Fig. 3b). Although the LAI peaks in 2006
18 and 2007 without droughts were somewhat higher than in other years, the peak in 2002,
19 during which a drought may not have occurred, was smaller; thus, the relationship between

1 soil drought and reductions in final leaf area was unclear. In a series of experiments on teak
2 leaf expansion under drought and re-watering treatments, final leaf length was comparable to
3 the length grown under nearly well-watered conditions when only a portion of the growth
4 period from the beginning to the peak experienced drought, whereas the final leaf length was
5 shorter when nearly the entire growth period was in drought (Rajendruru and Naidu 1998).
6 Thus, teak leaves are apparently relatively tolerant to drought, and the effect of drought on the
7 reduction in leaf area may not be obvious at the stand level. Alternatively, even if a reduction
8 in leaf area occurs, the position of leaves may be optimized with decreased leaf areas, such
9 that solar radiation can be intercepted more effectively and photosynthesis is more active
10 (Monsi and Saeki 1953).

11 The increase in the population of *H. puera* during D_B – D_P (from the earliest and second
12 earliest D_{BS}) clearly caused the most effective decreases in leaf area. Because *H. puera*
13 typically appears during the beginning of the growing season (Nair 2001), the two longest
14 D_B – D_P growth periods may have stimulated increases in the pest population with tender
15 immature leaves. Herbivorous insects are generally thought to exhibit enhanced performance
16 and outbreak dynamics on water-stressed host plants, due to induced changes in plant
17 physiology (Huberty and Denno 2004). However, the NLR values showed that *H. puera*
18 damage was only slight during the D_B – D_P growth periods experiencing drought. *H. puera* is
19 the most notable and economically threatening pest affecting teak in plantations in non-native

1 teak countries, such as Costa Rica and Brazil, where outbreaks appeared suddenly during
2 1995 and 1996, respectively, as well as in natural forests and native plantations in native teak
3 countries, such as India, Myanmar, and Thailand (Nair 2001; Gowda and Naik 2007).
4 Moreover, outbreaks appear to be imminent in Latin America and Africa (Nair 1988) and this
5 is likely to become a global problem.

6 Do earlier D_{BS} contribute to more absorption of carbon or tree growth? In most cases,
7 soil drought probably occurred during the D_B – D_P growth period from April to May and was
8 related to the duration of time experiencing no rainfall and stronger evaporative demand
9 (Fig. 1). Boyer (1970) indicated that photosynthesis and respiration were inhibited by drought
10 later and less severely than leaf expansion. However, during drought, net photosynthesis
11 appeared to decrease, due to stomatal closure caused by the dry conditions and the subsequent
12 rise in both leaf temperature and respiration. In particular, in 2005, the longest drought period,
13 over 1 month, likely severely limited net photosynthesis, with a rise in respiration induced by
14 higher temperatures (Fig. 1a). This resulted in the latest D_P over the 8-year study period, and
15 the advantage of the earlier appearance of leaves likely contributed little to carbon securement.
16 Numerical simulations of canopy net assimilation (A_n) taking into account seasonal LAI
17 using a SPAC-model indicated a reduction in net photosynthesis due to the smaller LAI and
18 soil dry conditions during the drought in 2001, whereas values of A_n simulated assuming peak
19 LAI values indicated a loss of carbon and that the drought was unlikely to maintain higher leaf

1 areas (Tanaka et al. 2009). Thus, the limitation of leaf expansion may subsequently avoid
2 carbon loss during drought. A later end to the growing season, which occurs somewhere
3 between the end of the rainy season and the onset of the dry season (Yoshifuji et al. 2006),
4 may contribute to more carbon gain.

5 For the cases of the earliest and second earliest D_{BS} (in 2001 and 2008, respectively),
6 the decrease in LAI due to teak defoliators likely reduced carbon gain during the entire
7 growing season as well as during the early growing season. Nair et al. (1996) reported that
8 defoliation resulted in a 44% loss of the potential volume increment in young plantations in
9 Nilambur, in southern India. Thus, pest control measures may be needed to avoid limiting tree
10 growth, especially for such cases when the D_B occurs from late March to early April.

11 Watering to obtain sufficiently wet soil down to a depth of 0.1-0.4 m likely accelerates the leaf
12 growth rate and reduces the population of teak defoliators, but this operation is problematic
13 with respect to water resource management in dry tropical regions. The use of rainfall
14 interception and/or transpiration by dead/living grasses and small trees in the understory of
15 plantations may reduce the amount of soil moisture and postpone leaf initiation, although,
16 typically, the dead grasses are burned during the plantation's dry season, before leaf initiation.
17 The loss of transpiration by actively cutting or burning the understory after flushing may
18 allow moisture to reach deeper portions of the soil and accelerate leaf growth, which could be
19 exploited as an effective strategy. The impact of the above-mentioned operations on the

1 hydrological processes and the subsequent influence on carbon gain may be worth examining
2 in further studies.

3

4

Conclusions

5 Monitoring of the NLR and soil moisture from March–July for 8 years indicated that
6 soil moisture at 0.1-0.4 m soil depths greatly affected leaf flushing and subsequent leaf
7 growth in a teak plantation in a dry tropical region. Additionally, the D_B – D_P growth periods
8 with earlier D_{BS} tended to be longer than those with later D_{BS} , without the limitation of
9 drought. The results of this study indicated that heavy outbreaks of *H. puera* during D_B – D_P in
10 2001 and 2008 clearly caused the most significant decreases in LAI, likely inducing the
11 decline in annual carbon gain. Moreover, the earliest and second earliest D_{BS} and the
12 subsequently slower leaf growth may stimulate a heavy outbreak of defoliator.

13

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16 collected by the CREST/JST Program, led by M. Suzuki.

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10 northern Thailand. *Forest Ecology and Management* 229:333–339.
- 11

1 **Figure legends**

2 Figure 1. a) Seasonal changes in mean monthly rainfall (bars) and air temperature (red line) for
3 2001–2008. Error bars indicate means + 1 SD (for rainfall) and means \pm 1 SD (for air
4 temperature). The upper and lower boundaries of the red shaded area are the means \pm 1 SD of
5 daily air temperatures for the 8 study years. b) Seasonal changes in the mean monthly solar
6 radiation (black line) for the 8 study years (means \pm 1 SD) and solar elevation at noon (blue
7 line). The upper and lower boundaries of the gray shaded area are the means \pm 1 SD of daily
8 solar radiation for the 8 years. c) Seasonal changes in the mean monthly vapor pressure deficit
9 (VPD) for the 8 study years (means \pm 1 SD). The upper and lower boundaries of the gray
10 shaded area are the means \pm 1 SD of VPD for the 8 years.

11

12 Figure 2. Changes in (a–h) the negative logarithm of the ratio of daily downward solar
13 radiation on the forest floor to that above the canopy, $[-\ln(S_b\downarrow/S\downarrow)$; NLR], and (i–p) relative soil
14 moisture (RSM) at depths of 0.1, 0.2, 0.4, and 0.6 m and daily rainfall from March–July in
15 2001–2008. The \times symbols represent rainfall events during which RSM increased at a depth of
16 0.1 m and occasionally at 0.2 m. Hollow circles (\circ) indicate rainfall events during which RSM
17 increased at depths of 0.1 m to at least 0.4 m, followed by an increase in NLR. The solid
18 triangle (\blacktriangledown) indicates that the NLR did not increase, even though RSM increased at depths of
19 0.1 to 0.6 m; NLR instead began to increase starting at the point indicated by the hollow

1 triangle (Δ). The double circle (\odot) indicates an increase in NLR during the period for which
2 soil moisture data were missing. Black solid bars from June–July in a–h indicate the lowest
3 value of a 99% confidence interval in July (NLR_p) when values fully reached the peak. Solid
4 circles (\bullet) indicate the day when NLR values first reached NLR_p . Solid green bars indicate the
5 growth period beginning on Δ , \odot , or \circ until \bullet in each panel. Vertical red bars indicate
6 intervals during which $RSM_{0.1-0.4\text{ m}}$ dropped below 0.2 (soil drought) at depths of 0.1–0.4 m
7 from D_B – D_P . Upward vertical arrows indicate decreases in NLR, due to the appearance of the
8 teak defoliator in 2001 and 2008.

9
10 Figure 3. a) The relationship between the D_B – D_P growth period and D_B . b) The relationship
11 between D_B and the difference between NLR values (means \pm 1 SD) in July and NLR on D_B .

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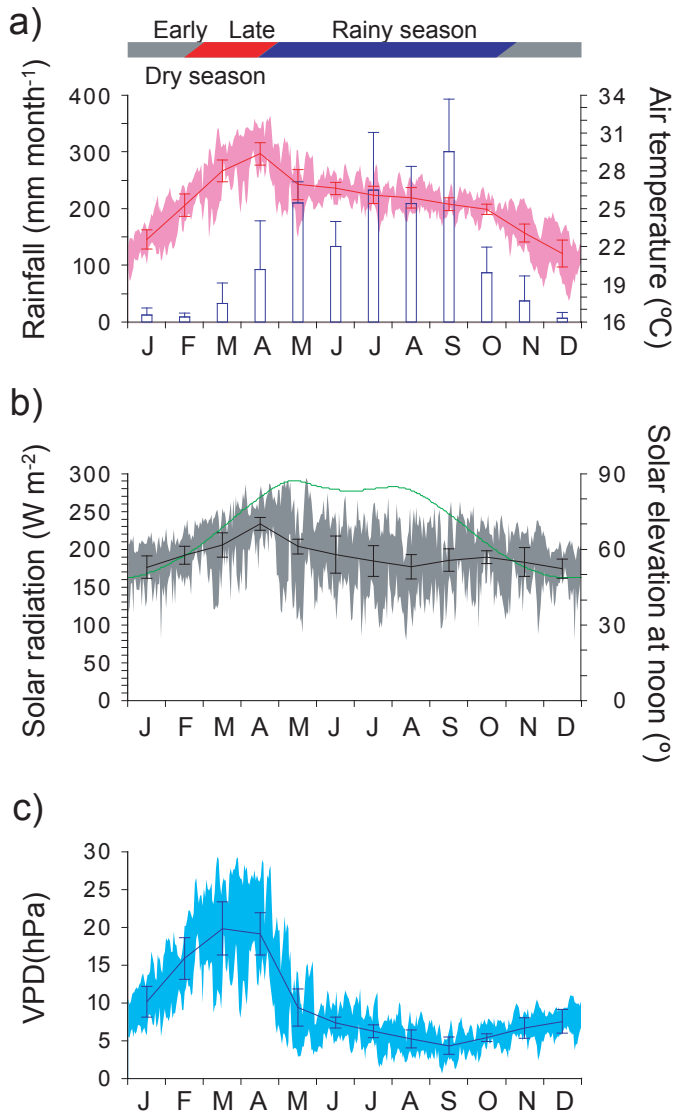


Figure 1

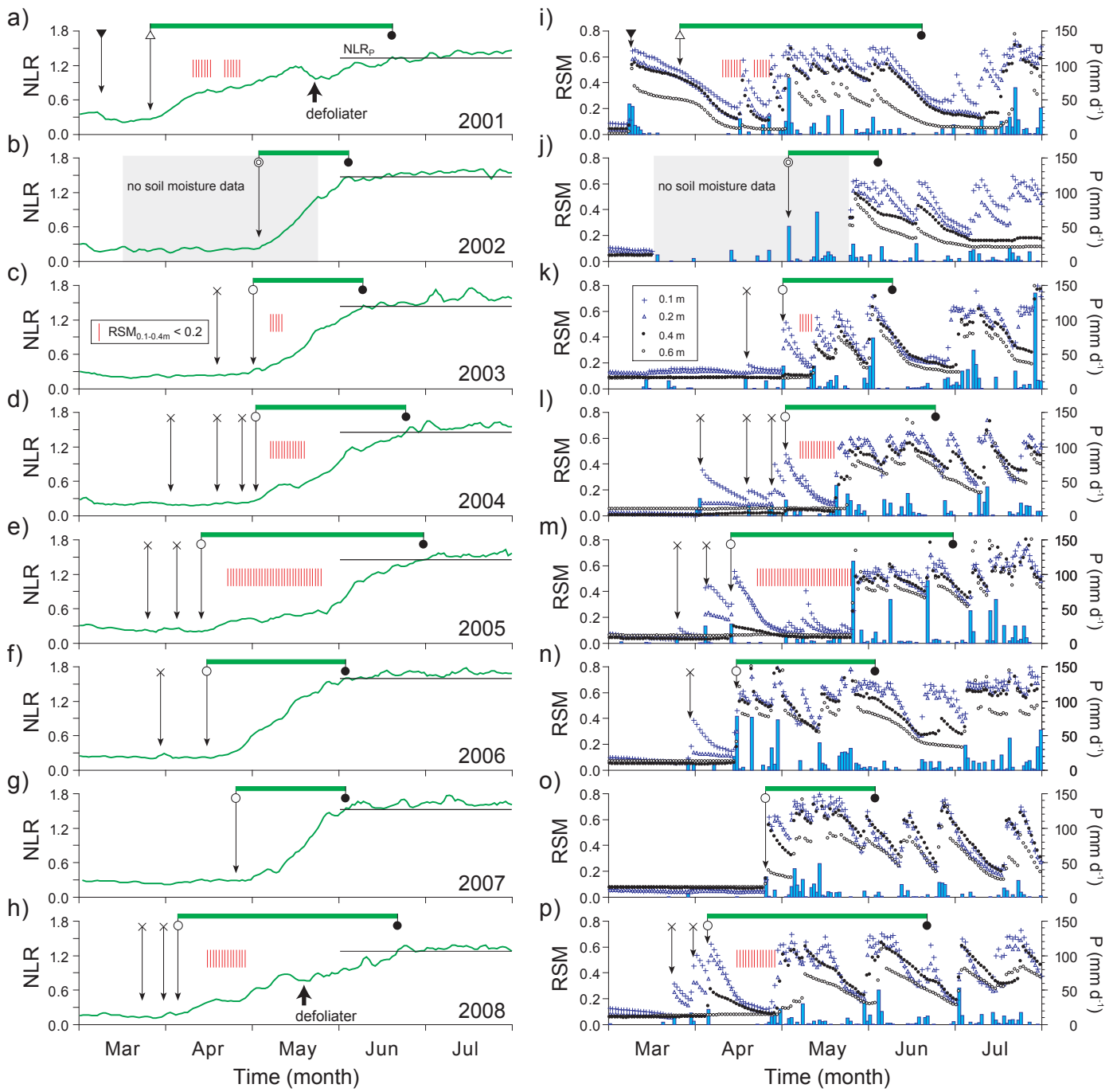


Figure 2

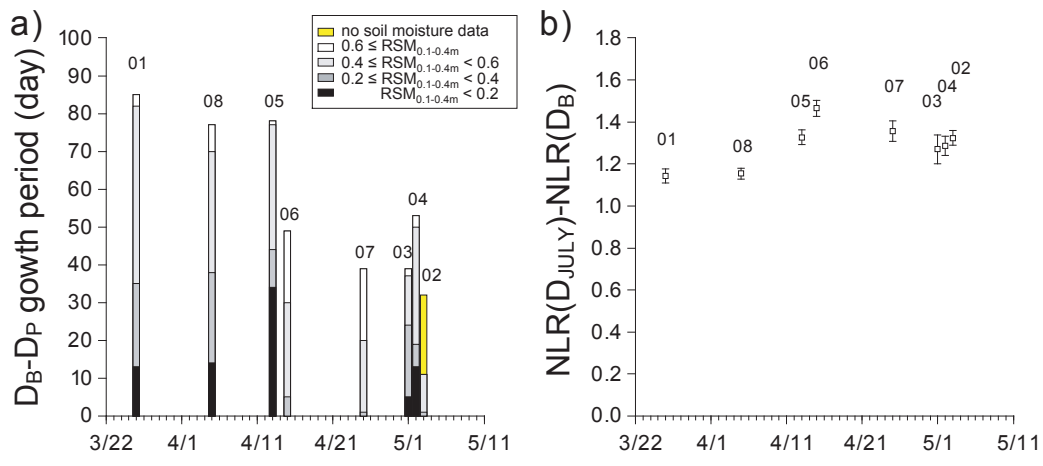


Figure 3