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Impacts of irrigation on the deciduous period of teak (Tectona grandis) in a monsoonal climate

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Complete List of Authors:	Tanaka, Katsunori; Japan Agency for Marine-Earth Science and Technology, Department of Environmental Geochemical Cycle Research Tanaka, Nobuaki; The University of Tokyo Matsuo, Naoko; Mie Daigaku, Graduate School of Bioresources Tantasirin, Chatchai; Kasetsart University, Faculty of Forestry Suzuki, Masakazu; The University of Tokyo, Graduate School of Agricultural and Life Sciences
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1 **Title: Impacts of irrigation on the deciduous period of teak (*Tectona grandis*) in a**
2 **monsoonal climate**

4 **Authors' names:**

5 Katsunori Tanaka¹, Nobuaki Tanaka², Naoko Matsuo³, Chatchai Tantasirin⁴, Masakazu
6 Suzuki⁵

8 **Addresses:**

9 ¹ Department of Environmental Geochemical Cycle Research, Japan Agency for
10 Marine-Earth Science and Technology, 3173-25 Showamachi, Kanazawa-ku, Yokohama,
11 Kanagawa 236-0001, Japan
12 katunori2005@gmail.com

13 ³Ecohydrology Research Institute, The University of Tokyo Forests, Graduate School of
14 Agricultural and Life Sciences, The University of Tokyo, Seto, Aichi 489-0031, Japan
15 tanaka@uf.a.u-tokyo.ac.jp

16 ⁴Graduate School of Bioresources, Mie University, 1577, Kurima-machiya-cho, Tsu
17 514-8507, Japan
18 naoko@bio.mie-u.ac.jp

19 ⁵Faculty of Forestry, Kasetsart University, 50 Ngam Wongwan Road, Chatuchuk,
20 Bangkok 10903, Thailand
21 fforcet@ku.ac.th

22 ⁶Graduate School of Agricultural and Life Sciences, The University of Tokyo,
23 Bunkyo-ku, Tokyo 113-0023, Japan
24 suzuki@fr.a.u-tokyo.ac.jp

25

26 **The current mailing address, e-mail address, telephone and fax numbers of the**
27 **corresponding author**

28 Communicated by Katsunori Tanaka

29 Graduate School of Agriculture, Kyoto University,

30 Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan

31 Email: katsunori2005@gamil.com; Tel: +81-75-753-6089; Fax: +81-75-753-6088

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Draft

41 **Abstract**

42 Leaf phenology in tropical deciduous forests significantly influences water and carbon
43 exchanges between vegetation and the atmosphere. Thus, a comprehensive
44 understanding of the effects of hydrometeorological variables on the growing period is
45 essential for predicting plant water use following climate change. We investigated
46 whether leaf phenology, bud break, and leaf abscission in mature deciduous teak trees
47 (*Tectona grandis*) were induced by the root zone soil moisture content. Using heat pulse
48 velocity and photographic imagery, we compared the deciduous periods (DPs) of two
49 teak trees under natural conditions and two under irrigated conditions. DPs ranged from
50 47 to 84 days under natural conditions, whereas irrigation shortened the DP by
51 approximately 2 weeks and promoted high levels of water use for 10 months. Thus, the
52 annual water use of irrigated trees far exceeded that of control trees. Under irrigated
53 conditions, leaf abscission and reduced water use were accelerated when the daily mean
54 vapor pressure deficit exceeded 14 hPa following a period of gradual senescence. This
55 study presents preliminary results regarding the impact of irrigation on the teak tree DP.
56 However, uncertainty remains due to insufficient replication; thus, further tests are
57 needed. Nonetheless, our results may predict leaf phenology after short dry periods.

58

59 **Keywords:** deciduous period, heat pulse velocity, irrigation, relative soil moisture, teak
60 (*Tectona grandis*)

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65 1. Introduction

66 Events related to leaf phenology in tropical deciduous forests, including bud break, leaf
67 growth, and leaf abscission, significantly influence water and carbon exchanges
68 between vegetation and the atmosphere. The annual canopy duration period (CDP) in
69 temperate forests fluctuates over a period of weeks (Wilson and Baldocchi 2000), but
70 the CDP of deciduous forests in dry tropical zones fluctuates over a period of months
71 (Do et al. 2005). Because of the high temperature and intense solar radiation in the
72 tropics, the impacts of interannual CDP fluctuations on annual carbon and water
73 exchanges tend to be larger here than elsewhere. A comprehensive understanding of the
74 effects of hydrometeorological variables on growing season length is a critical element
75 in predicting the extent to which climate change will affect carbon gains and water use;
76 thus, this is what we investigated in this study. We performed controlled watering
77 experiments to test our hypothesis that leaf phenology, bud break, and leaf abscission in
78 deciduous teak trees (*Tectona grandis* L. f.) are regulated by soil moisture in the root
79 zone.

80 Teak is one of the most valuable timber species in the world (Gajaseni and
81 Jordan 1990). This deciduous species occurs naturally in tropical Asia, mainly between
82 12° and 25° N and 75° and 104° E, in India, Myanmar, Laos, and Thailand (Kaosa-ard
83 1977), and these areas are subject to rainy as well as dry seasons (Nobuchi et al. 2005)
84 with trees becoming leafless during the latter. In northern Thailand, the climate is
85 largely governed by the Asian Monsoon with the wet season occurring from roughly
86 May to October and the dry season spanning from approximately November to April
87 (Tanaka et al. 2015a). Observations from a seasonal tropical forest in western Thailand
88 (Williams et al. 2008) have indicated that deciduousness is associated with a change in

89 photoperiod in some species (Rivera et al. 2002) and by the timing of rainfall (Borchert
90 1994a) or soil moisture content in the root zone (Tanaka et al. 2011) in others. However,
91 in more than a third of the species, the relationships among deciduous leaf phenology,
92 photoperiod, and soil moisture are unclear (Williams et al. 2008).

93 Williams et al. (2008) noted that further progress in resolving the underlying
94 internal and external mechanisms that control leaf gas exchange would require the
95 selection of specific taxa for detailed physiological and microclimatic studies. We
96 believe that studies on tree leaf phenology should focus not only on natural vegetation
97 but also on commercially valuable species grown on plantations to enhance water use
98 management and production yield.

99 Wright and Cornejo (1990) supplied water to targeted deciduous and evergreen
100 tree species to test the hypothesis that water stress is the proximal cue for leaf fall, and
101 they found that irrigation delayed leaf fall in two of nine tree species for which
102 quantitative data were available suggesting that plant water stress was a minor cue for
103 leaf fall in the forest as a whole. Borchert (1994a) irrigated deciduous trees in a tropical
104 dry forest to investigate the effects of irrigation on bud break and subsequent leaf
105 expansion. The buds began to expand 5–7 days after irrigation, and leaves were fully
106 expanded 2 weeks later. Rather than making observations under natural, unaltered
107 conditions, Wright and Cornejo (1990) and Borchert (1994a) performed controlled
108 watering experiments to determine whether water stress drove leaf abscission and bud
109 break across a selection of tree species. Myers et al. (1998) watered two deciduous tree
110 species and two evergreens in a tropical savannah region of northern Australia to
111 explore the effects of irrigation on leaf phenology; only one species was influenced by
112 irrigation. Leaf flushing was significantly accelerated, but canopy decline and leaf fall

113 occurred significantly later in watered than in non-irrigated trees. Based on monthly
114 observations, Priya and Bhat (1999) reported that mature teak trees lost their leaves
115 completely in plantations that were continually irrigated.

116 Using radiative transmittance and sap flux time series data, Yoshifuji et al.
117 (2006) found that variation in canopy duration and transpiration period at a teak
118 plantation in northern Thailand, from 2001 to 2004, spanned about 40 and 60 days,
119 respectively. They also found that soil moisture conditions are a major determinant of
120 large interannual variation in the growing season. The slight increase in leaf area index,
121 which had been estimated based on the radiative transmittance time series data, was
122 unclear for detecting the timing of leaf flush following an increase in soil moisture
123 before the spring equinox due to a slower response under the shorter (<12 hours)
124 photoperiod. Tanaka et al. (2011) discussed other factors such as the possibility that
125 photoperiod may trigger leaf flush. Based on photographic evidence from 2010 and
126 2012, Tanaka et al. (2015b) found that increases in root zone soil moisture before the
127 spring equinox may have resulted in early teak flushing and subsequent leaf growth and
128 expansion. However, the signal for leaf flush in the radiative transmittance time series
129 data is unclear. Nonetheless, the trigger for teak leaf flush has generally been
130 determined to be soil moisture, while the timing of it and the subsequent leaf growth
131 rate that follow heavy rains before the spring equinox has been observed to be different
132 among trees, which may be caused by heterogeneity in soil hydraulic characteristics. On
133 the other hand, a decline in transpiration and leaf abscission also appear to be strongly
134 controlled by low soil moisture as has been noted by Yoshifuji et al. (2006) and
135 Yoshifuji et al. (2011).

136 Our study preliminarily aims to improve our ability to predict how tropical

deciduous trees in monsoonal climates will respond to increased precipitation, which will enable better management of valuable deciduous tree species. Climate models suggest that anthropogenic forcing has probably caused a small increase in global mean precipitation, a latitudinal redistribution of precipitation (increased precipitation at high latitudes, decreased precipitation at subtropical latitudes), and a shift in the position of the Intertropical Convergence Zone, which in turn, may have changed the distribution of precipitation within the tropics (Zhang et al. 2007). Much attention has been focused on the effects of climate change-associated decreases in water availability, including drought (Neelin et al. 2006), on components of plant phenology such as tree mortality (Breshears et al. 2013, Eamus et al. 2013, Luo and Chen 2015). However, few studies have explored the ways in which trees are likely to respond to climate change-associated increases in water availability. Irrigation treatments implemented in widely dispersed locations (e.g. Wright and Cornejo 1990) are unlikely to supply water homogeneously, and thus some trees receive inadequate water supplies in this arrangement. We therefore constructed an irrigation system specifically designed to supply water to the root zone of mature teak trees. We performed controlled watering experiments on mature teaks to answer the following questions: 1) Does irrigation delay the timing of mature teak leaf abscission? 2) When trees are irrigated, do new leaves flush while leaves from the previous generation remain attached? 3) Does irrigation after the completion of leaf abscission accelerate bud break? To answer these questions, we measured the heat pulse velocity (HPV, corresponding to sap flow) of subject teak trees under both natural and irrigated conditions to determine individual plant water use (or transpiration) and estimated seasonal changes in the plant area index (PAI) or leaf area at the stand level based on radiative transmittance through the canopy. Additionally,

we demonstrated the effects of ample soil watering on leaf phenology and transpiration rates of tropical tree species in monsoonal climates. We made comparative observations between trees in natural, unmanipulated areas and irrigated areas. The study was performed during a period of declining transpiration as leaves were shed. Our HPV measurements were corroborated by time-lapse photographic images of subject trees and estimated PAI at the stand level. Thus, we examined the differences in tree response under natural and irrigated conditions.

2. Material and methods

2.1. Site description

The experiment was performed in an even-aged teak plantation located in the Mae Mo District of Lampang Province in northern Thailand (18°25'N, 99°43'E; 380 m above mean sea level). Teak saplings were planted in 1969 by the Thai Forest Industry Organisation to produce a stand density of 440 trees ha⁻¹ as of November 2005, and mean ($\pm$ SD) stem diameter at breast height (DBH) and tree height were 22.4 $\pm$ 7.3 cm and 19.9 $\pm$ 3.5 m (n = 308), respectively, also as of November 2005 (Tanaka et al. 2015a). Climate at the site is largely influenced by the Asian Monsoon. As noted, the wet season extends from around May to October, and the dry season from about November to the April. Mean annual rainfall was 1361 mm for 2001–2012 with most rain falling in the wet season (Tanaka et al. 2015a). The trees become leafless in the late dry season, while teak foliage peaks in July (Tanka et al. 2011). Annual mean temperature for 2000–2012 was 25.4 °C with a minimum monthly mean of 21.7 °C in December and a maximum monthly mean of 29.1 °C in April (Tanaka et al. 2015a).

Within the plantation, the soil was a Loamy Paleustults (Thai classification) or

185 Ultisol (US Department of Agriculture, soil taxonomic classification) with a carbon
186 content of 1.5–3.5%, nitrogen content of 0.15–0.30%, and total porosity of 35–40%
187 (Kume et al. 2013). The soil depth was about 0.8–1 m, and both fine and coarse roots
188 were found in the top 0.4 m (Kume et al. 2013). The undergrowth consisted of shrubs,
189 such as *Lagerstroemia calyculata*, bamboos, and grasses, such as *Chromolaena odorata*,
190 and these were generally sparse at the plantation, particularly around the focal trees.

191 We established a control plot containing a 40-m high tower constructed in July
192 2005 to measure meteorological variables—such as radiation, temperature, humidity,
193 and eddy flux—and an experimental plot (containing a 25-m high tower) that had been
194 irrigated from March 2013 to May 2015. Downward solar radiation has been measured
195 since 2000 on the forest floor ~100 m from the 40-m tower to obtain radiative
196 transmittance through the canopy and to estimate seasonal changes in leaf amount
197 (Yoshifuji et al., 2006; Yoshifuji et al. 2011). We selected four focal teak trees (C1 and
198 C2 in the control plot and W1 and W2 in the irrigated plot). Height (m) and DBH (cm)
199 of C1, C2, W1, and W2 were 24.1 m and 33.7 cm, 26.6 m and 28.8 cm, 22.5 m and 34
200 cm, and 21.6 m and 22.4 cm, respectively. These specimens were larger-than-average
201 trees. Examination of the root distribution indicated that the roots of the trees in the
202 irrigated plots did not penetrate to soil depths below 75 cm. Roots disappeared when
203 soil penetration resistance exceeded ~3 MPa. Maximum root penetration depths for C1
204 and C2 were 72 cm and 65 cm, respectively.

205

206 **2.2. Irrigation system**

207 Irrigation began on March 5, 2013 for W1 after leaf flush on February 28, 2013 and on

208 March 3, 2014 for W2 after complete leaf abscission on March 2, 2014. Figure 1 shows
209 the plot and the watering system used. Watering area one (WA1) was a rectangular plot
210 (5×9.5 m) containing tree W1. In October 2010, a dye perfusion experiment was
211 conducted in this plot showing that water transport in teak sapwood is vertical (Sato et
212 al. 2015) and indicating that lateral projection of the foliage probably corresponds to
213 that of the root system. Thereafter, on October 19, 2012, a 10-cm-wide trench was
214 excavated to a soil depth of 40 cm around a frame constructed to fit the outline of the
215 crown projection of W1. The trench was filled with reinforced concrete to prevent
216 lateral movement of water through the soil out of the watered area, and a 10-cm high
217 waterproof dam was set above the trench to prevent overflows. On November 16, 2013,
218 trenches were cut along the longer sides of the rectangular plot perimeter. One root with
219 a diameter of 1 cm (probably from an adjacent tree) was found at a depth of 10 cm
220 below the concrete wall; the root had penetrated beneath the 40 cm deep trench into
221 WA1. We therefore excised the root and then dug the trenches deeper down to bedrock,
222 which occurred at depths of 74–94 cm, where we found no roots. The deeper trench was
223 filled with reinforced concrete. A second watering plot (3.8×5.8 m; WA2) was
224 established on November 17, 2013, and we subsequently measured root distribution and
225 performed penetration tests in September 2014. A 10-cm-wide trench was cut down to
226 bedrock (74–100 cm deep), filled with reinforced concrete, and topped with a 10-cm
227 high waterproof dam.

228 Three 1000-L tanks on 10 cm thick bases were used to store irrigation water
229 provided to WA1 and WA2. One side of each tank was slightly elevated so that water
230 flowed out of the tanks. Reservoir water was pumped from a pond located ~500 m from
231 WA1 and WA2 and collected in 200-L tanks, carried to the watering areas by car,

transferred from the 200-L tanks into the 1000-L tanks with a pump, and distributed to the shorter sides of the plots through rigid plastic pipes perforated with 2-mm diameter holes drilled at 50-cm intervals. Eight valves were installed in the watering system so that the supply could be directed to each plot separately; the valves also enabled equal distribution of water to the experimental areas. We measured the HPV of W1 under natural conditions during the dry season (from November 2012 to February 2013) and found marked declines as volumetric soil moisture (VSM) fell to values <0.145 ; thus, WA1 and WA2 were irrigated to achieve VSM values of 0.17 and 0.23 at 40 cm depth, respectively. To do this, we supplied ~ 3000 L to WA1 (47.5 m^2) and ~ 1500 L to WA2 (22 m^2), which corresponded to rainfall precipitations of ~ 63 – 68 mm, in addition to the rain that fell on the plots. The irrigation treatments began in the morning at 10:00 and were discontinued at 13:00 and 14:00 in WA2 and WA1, respectively.

2.3. Estimation of the deciduous period and HPV measurements

We estimated the deciduous period (DP, here defined as the period consisting of the end of transpiration in one season to the start of transpiration in the next) using HPV measurements of focal trees, and *in situ* observations of leaf abscission and leaf flush were made using time-lapse photographs. Focal trees were not able to transpire or absorb much CO_2 during the DPs. We determined the duration of complete leaf abscission (PCLA) by direct *in situ* observation and indirect examination of photographic images. Time-lapse cameras were pointed towards the foliage or crown of the control trees at a height of 24 m and at 25 m for the irrigated trees. Using photographs, we estimated the degree of openness (OD) of the foliage or crowns of the subject trees (equivalent to the degree of defoliation) to examine the relationship

256 between HPV and leafiness during the dry season. We classified OD into six categories
257 every two weeks spanning the range from leafy (0%) to leafless (100%): 0%, 20%, 40%,
258 60%, 80%, and 100%. Foliage estimations were made fortnightly from November 11,
259 2013 to March 17, 2014 and from October 13, 2014 to March 16, 2015. Soil moisture
260 content was measured in the root zones of the control and irrigated plots; data for the
261 period August 2013 to May 2015 are shown in Figure 2.

262 Air temperature and water vapor content were measured at a height of 39 m on
263 the tower in the control plot using a ventilated psychrometer (MS020S; Eko, Tokyo,
264 Japan), and we used the data to calculate vapor pressure deficits (VPDs). Calculated
265 average accumulated distributions of root dry matter indicated that up to 92% of the
266 roots were concentrated in the first 0.45 m of soil, and most roots were between 0.15 m
267 and 0.25 m deep. Accordingly, we measured volumetric soil moisture (θ) at depths of
268 0.2 and 0.4 m within the projected canopy areas of the subject trees using eight
269 time-domain reflectometers (TDR; CS-616; Campbell Scientific, Logan, UT, USA), and
270 this value was used to calculate minimum and maximum temporal volumetric soil
271 moisture ($\theta_{\min}$ and $\theta_{\max}$) and relative soil moisture ($\text{RSM} = (\theta - \theta_{\min})/(\theta_{\max} - \theta_{\min})$)
272 (Tanaka et al. 2009). Observations of leaf condition for all four focal trees, such as leaf
273 flush and abscission, were made with time-lapse cameras (GardenWatchCam; Brinno,
274 Taipei, Taiwan) mounted at heights of 24 m on the 40-m tower and 25 m on the 25-m
275 tower.

276 We measured the HPVs corresponding to the water use of the individual trees,
277 using the heat ratio method (HRM) (Burgess et al. 2001). The measurements were made
278 with a sap flow meter (SFM1; ICT International, Armidale, NSW, Australia) using the
279 methods described by Pfautsch et al. (2011). We installed one or two SFM1 devices on

each of the focal trees (1.0–1.5 m above ground level). The bark was 13–17 mm thick where the SFM1s were mounted, but we scraped it down to 4–8 mm to install the temperature sensors; the outer and inner temperature sensors were inserted within the sapwood. Sato et al. (2015) measured sap flux density near WA1 and WA2 using the thermal dissipation method; the Granier-type sensors (Granier 1987) faced the four cardinal directions. We found that the magnitude of sap flux density differed among sensors facing different directions. However, the diurnal patterns were similar to those reported by Sato et al. (2015), indicating that the similarity among cardinal directions that they found was largely the result of similarities in solar radiation on the four sides of the trees, which resulted from the high density of trees in the plantation they studied. We installed SFM1 devices facing the direction where the foliage of the focal trees was most dense.

We covered the scraped areas of bark with silicon wrap to prevent them from drying out and logged data at intervals of 20 min. Calibrations to zero HPV were performed under conditions of zero vapor pressure deficit (VPD) and wet soil (e.g., on rainy days at night), i.e., when there was likely no sap flow. Data were linearly transformed. Gaps in the data were probably caused by misalignment or incorrect placement of the probes (Burgess et al. 2001). The HPV time series for C2, W1, and W2 were based on measurements with two different sensors, which provided the longest HPV time series: the period August 2013 to May 2015. We logged simultaneous scale differences in HPV between pairs of sensors resulting from the different sensor locations within the sapwood.

302

2.4. Estimation of PAI at stand level

To compare leafing and abscission among the four focal teak trees and those at the stand level, the negative log of the ratio (NLR) of daily downward solar radiation ($S_{\downarrow}$) on the forest floor 100 m from the control area to that in the area above the canopy ($NLR = -\ln(S_{b\downarrow} / S_{\downarrow})$) was used as an indicator of canopy duration at stand level as proposed by Tanaka et al. (2009). PAI was obtained by converting from NLR following Tanaka et al. (2015b). Based on the radiative transmittance time series data among the five points—including a point near the watering area—from January to July 2012, it was confirmed that the fluctuations in PAI were similar to each other (Tanaka et al. 2015b).

3. Results

3.1. Meteorological and hydrological conditions

Seasonal changes in rainfall indicated that the dry seasons extended from approximately November 2013 to April 2014 and from October 2014 to April 2015 (Fig. 2a). Under controlled irrigation, the soil moisture content started to decrease at the end of October in 2013 and in mid-September in 2014 (Figs. 2b, c), and it decreased significantly faster in the second dry season. Under conditions of high VPD values and extended periods with no rainfall, soil moisture fell until December 2014 when intense rainfall saturated the soil into early January 2015. Based on a penetration test, soil moisture retention in the root zone was more prolonged for C1 than for C2.

Relative soil moisture at 0.4 m depth in WA1 remained above ~30% due to irrigation during August 2013–May 2015 (Figs. 2d). The first irrigation period in WA2 began on March 3, 2014 after leaf abscission had completed (on the previous day).

327 Thereafter, relative soil moisture in WA2 remained above ~50% at 0.4 m soil depth.

328 During the first dry season, air temperatures were lowest in December 2013
329 and peaked at ~32 °C in March and April 2014 (Fig. 2a). Daily mean temperatures
330 ranged from 15 to 33 °C, which differed from the range of temperatures (17–37 °C)
331 recorded in the plantation studied by Priya and Bhat (1999). The VPD also gradually
332 increased with air temperature during the dry season peaking at >25 hPa in March 2014.
333 During the second dry season, the air temperature was lowest in January due to intense
334 rainfall. VPD began increasing in October 2014 and peaked in April 2015.

335

336 **3.2. The deciduous period and water use of individual trees**

337 Start and end dates of both the DP and PCLA, which were obtained based on measured
338 HPV and time-lapse photography or *in situ* observation, respectively, are summarized in
339 Table 1. Under natural conditions before irrigation began for W1 in 2013, the start of the
340 DP occurred earlier than it did for C2 by ~2 weeks, while the start of the PCLA
341 occurred earlier for C2 than for C1. Under natural conditions before irrigation began for
342 W2 in 2014, DP and PCLA both started at almost the same time as for C2 and W1,
343 while they started a few weeks later for C1. Thus, the start dates of DP and PCLA
344 generally occurred in the order W1, W2, C2, and C1 under natural conditions. We
345 observed that C1 was one of the teak trees that lost all its leaves latest at the plantation.
346 On the other hand, the end dates of PCLA (or leaf flush) occurred in the order W1 and
347 W2, C1, and C2 in 2013 after 32 mm of rain fall on February 21 and 22, 2013.

348 After irrigation began for W1, the PCLAs for C1 and C2 occurred from March
349 19 to April 7 and from March 3 to April 9, respectively, in 2014 and from March 13 to
350 31, and January 14 to April 1, respectively, in 2015 (Table 1). The PCLA of W1 could

not be determined during either of the dry seasons (Table 1) because few buds broke and very few leaves from the previous generation survived (Fig. 3a). Complete leaf abscission occurred for W2 on March 2, 2014 under natural conditions, and bud break occurred on March 6, 2014 following the first irrigation on March 3, 2015 (Table 1). However, we were unable to determine the PCLAs of the irrigated trees in 2015 because of leaf flush making it difficult to see when complete abscission of the old leaves had occurred.

HPV measurements indicated that the DPs of C1 and C2 occurred from March 10 to May 1, 2014 and from February 23 to April 28, 2014, respectively, during the first dry season, and from March 8 to April 13, 2015 and from January 8 to April 1, 2015, respectively, during the second dry season (Figs. 2f, g). Thus, the DPs ranged from 47 to 84 days under natural conditions between the two dry seasons, and the DP of C2 was longer than that of C1, especially during the second dry season. The DP of C2 started before the period of intense rainfall in early January 2015, but the start of the C1 DP extended until March 2015. Under controlled irrigation, the 2014 and 2015 DPs of W1 occurred from March 10 to 25 and March 16 to 28, respectively, and for W2, they occurred from February 21 to March 11 in 2014 during the transition from natural conditions to irrigated conditions and March 7 to 18, in 2015 under controlled irrigation conditions. Interestingly, the start of the DP for W1 was close to that for C1, which had the latest occurring PCLA under natural conditions during the first dry season after irrigation and was postponed by a week during the second dry season (Figs. 2f, h and Table 1). Similarly, the start of the DP for W2 was close to that for C1 during the second dry season after the irrigation treatment was applied (Figs. 2f, i and Table 1). Thus, the DPs of the irrigated trees were much shorter than those of the control trees were. The

375 DPs of W1 occurred during the spring equinox periods in both dry seasons, whereas the
376 W2 DP occurred before the spring equinox in the second dry season. In general, the DPs
377 were longer than the PCLAs. *In situ* and photographic observations showed that outside
378 the time of the PCLAs (but during the DPs), leaves were either (i) large, brown, and old
379 or (ii) small, green, and new.

380 The HPVs of C1 and C2 gradually increased after their respective DPs in 2014,
381 peaking in September and July 2014, respectively, and decreasing in November 2014
382 during the second dry season. HPVs decreased with increasing foliage openness (or
383 OD) both after October 2014 and again from December 2013 to March 2014. The HPVs
384 of the trees in the controlled irrigation plots increased sharply following the 2014 and
385 2015 DPs and peaked approximately 2 weeks later. Figure 1 shows that the irrigated
386 trees were leafy on April 21, 2014, whereas the leaves of surrounding trees were much
387 smaller. Leaf growth of these trees occurred during rapid increases in HPV, and peak
388 HPV values were maintained over ~10 months. Both watered trees' HPVs decreased
389 with decreasing foliage openness. During the period March 24, 2014 to March 23, 2015,
390 the sum of annual rainfall (1056 mm) and irrigation water was 1875 mm for WA1 and
391 2348 mm for WA2.

392 C1 HPV and PAI at stand level, corresponding to leaf area, exhibited similar
393 initial increases from late April to early May 2014 and in April 2015. PAI peaked in July
394 2014, while HPV did in September 2014 (Fig. 2f), and suspension of HPV occurred
395 slightly later than for PAI. C2 HPV increased similarly to PAI until they peaked, while
396 suspension occurred earlier for HPV than for PAI, in particular in 2015 (Fig. 2g). On the
397 other hand, the increase in HPV for the irrigated trees clearly started earlier than it did
398 for PAI (Figs. 2h and i) as shown in Figure 1; although, suspension occurred at a similar

399 time.

400

401 **3.3. Changes in relationships between HPV and VPD**

402 Figure 4 shows the relationship between HPV and VPD for C1, C2, and W1 from
403 August 2013 to March 2014 and for C1, C2, W1, and W2 from August 2014 to March
404 2015. HPV generally increased with increasing VPD. The HPV:VPD ratio is an
405 indicator of an individual tree's water use activity or conductivity (this relationship has
406 been demonstrated in many studies; e.g., Hogg and Hurdle 1997), and higher and lower
407 values indicate higher and lower water use, respectively, for a given VPD. The ratios
408 were highest in August in both 2013 and 2014 for W1 (Fig. 4c), and in 2014, the ratios
409 for all focal trees were highest in August (Figs. 4d-g). The ratios for C1 and C2
410 decreased sharply in October and December, respectively (Figs. 4a-e), while those for
411 W1 gradually decreased after January in both 2014 and 2015, and that for W2 gradually
412 decreased after January 2015 (Figs. 4c, f, g). The HPV:VPD relationships for W1 and
413 W2 were similar from August 2014 to March 2015, but in January 2015, the ratio for
414 W2 was lower. Daily mean VPD exceeded 14 hPa in February in both 2014 and 2015
415 under irrigated conditions, and HPV values fell sharply afterwards and were close to
416 zero in March of both 2014 and 2015.

417

418 **4. Discussion**

419 This study is the first to provide comparative heat pulse velocity (HPV) data for mature
420 teak trees, photographic documentation of teak foliage and crowns, and soil moisture
421 content in the root zones of natural and controlled irrigation plots over an extended
422 period of time. HPV data were also compared with plant area index (PAI) data at the

stand level. Irrigation treatments hastened the timing of leaf flush, accelerated subsequent leaf growth, and shortened the deciduous period (DP) by two weeks. Watered trees did not retain foliage throughout the year, even under irrigated conditions, and few new leaves opened. These findings are consistent with the observations of Priya and Bhat (1999) and imply that teak may be a semi-deciduous species although it is widely known as a deciduous species. Irrigation provided a constant source of water for transpiration for 10 months, and the first irrigation period induced bud break in one irrigated tree after complete leaf abscission had occurred under natural conditions. These observations are consistent with those of Borchert (1994a). Thus, the hypothesis that soil moisture exerts the greatest control over the leaf phenology of teak trees was confirmed. Although one control tree maintained its leaves longest, the results of the HPV and PAI analyses were unclear regarding whether there were discernible differences in leaf abscission between irrigated and control trees over the course of the study, and uncertainty remains due to insufficient replication. Thus, further tests will be needed, such as examining more focal trees, in particular, to confirm the hypothesis that irrigation postpones leaf abscission.

As Figure 4 shows, the HPV:VPD ratio, an indicator of an individual tree's water use activity or conductivity, was high for all trees in August each season; however, it tended to decline steeply for the control trees after this time, while declining more gradually for the irrigated trees. This decline in the ratio was largely the result of leaf abscission under natural conditions (Figs 2f, g: refer to foliage openness (or OD)), and the low soil moisture during the dry season significantly accelerated leaf abscission (Figs. 2b, c, f, g). On the other hand, trees were still leafy under irrigated conditions (Figs. 2h, 3b: refer to OD). Reduction in water use as well as leaf abscission is largely

the result of chlorophyll degradation, which is induced by decreases in the maximum rate of carboxylation during leaf senescence (Farquhar et al. 1980) and declines with stomatal conductance (Ball et al. 1987). The gradual increase in vapor pressure deficit (VPD) subsequently promoted high levels of water use in the irrigated trees during the dry seasons. In February, the HPV:VPD ratio drastically decreased when VPD values were >14 hPa (as the highest temperatures were reached) (Fig. 2a), and leaf color changed dramatically from green to brown at the same time. Thus, the HPV:VPD ratio captured the status of the foliage of irrigated trees (Fig. 4). Priya and Bhat (1999) reported that leaf shedding in mature plantation teak trees began in November and that the trees were bare by February, even when irrigated; leaf abscission occurred later at our study site. However, daily mean temperatures were higher in the plantation studied by Priya and Bhat (1999) than in our site. Tanaka et al. (2015b) reported reduced leaf growth under shorter photoperiods in the same plantation as the one used in the current study. Differences in the timing of leaf abscission of irrigated trees may be related to atmospheric factors—such as high temperature, low humidity, and a high evaporative demand (Reich and Borchert 1984, Write and Cornejo 1990)—rather than to differences in photoperiod (Rivera et al. 2002, Elliott et al. 2006).

Here, we classified deciduous trees into three categories: type I trees were associated with changes in photoperiod; type II trees were associated with changes in soil moisture; and type III trees could not be clearly classified into type I or type II. With their maximum root depths of 0.75 m, the irrigated trees were clearly unable to access deep soil water reserves (Borchert 1994b, Nepstad et al. 1994, Elliott et al. 2006) or the water table. Type II deciduous trees generally have shallow roots and are unable to obtain soil water throughout the year. The leaf phenology of types I and III deciduous

471 trees is not influenced by irrigation (Wright and Cornejo 1990, Myers et al.
472 1998)—these trees have deep roots that can access water reserves in deep soil—rather
473 they are controlled by photoperiod and other environmental factors unrelated to water
474 availability, whereas the leaf phenology of type II deciduous trees under controlled
475 irrigation like the ones we studied were more similar to that of type III trees. We found
476 that the effects of DP and transpiration decreased during senescence, an observation that
477 should be taken into account when considering interannual trends in the water and
478 carbon exchanges of mature teak trees subject to climate change-associated increases in
479 water availability. Teak phenology should be studied across a range of regions with
480 different climates and among trees with different functional structures using methods
481 similar to those that we employed in our study. This expanded approach will contribute
482 to a better understanding of the ways in which factors other than soil water in the root
483 zone influence leaf senescence and abscission.

484

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616

617 **Figure legends**

618 Figure 1. Image of the irrigation system used to water teak trees (*Tectona grandis* L. f.)
619 (photo taken: April 21, 2014).

620

621 Figure 2. Time series of measured hydrometeorological parameters from August 2013 to
622 May 2015 in a teak plantation in northern Thailand. (a) Seasonal changes in daily
623 rainfall (blue), daily mean air temperature (T_a ; red), and daily mean vapor pressure
624 deficit (VPD; grey). (b-e) Relative soil moisture content (RSM%) at 20 (light blue) and
625 40 (blue) cm depth in the vicinity of (b) control tree C1, (c) control tree C2, (d) treated
626 (irrigated) tree W1, (e) and treated (irrigated) tree W2. Arrows in (d) and (e) indicate
627 dates of irrigation. (f-i) Daily heat pulse velocity (HPV) and degree of foliage openness
628 (OD) with plant area index (PAI, solid black line) for (f) C1, (g) C2, (h) W1, and (i) W2.
629 The top and bottom of the shaded light green and light blue areas indicate daily
630 maximum and minimum values of HPV, respectively. Solid green and blue lines in
631 panels (f-i) show mean values. Different colors in panels (g-i) refer to heat pulse
632 velocity (HPV) measurements made with different sensors; differences in scale between
633 HPVs depicted in blue and green were corrected with reference to the overlapping time
634 series of both HPVs. Black and grey bars in panels (b-i) refer to the complete leaf
635 abscission period (identified by time lapse photography) and deciduous period
636 (identified by HPV measurements), respectively. V_U and V_L (i.e., $-V_U/4$) are the upper
637 and lower values of HPV, respectively. Measured values of V_U were 32, 16, 14.4, and 32
638 cm h^{-1} for C1 (f), C2 (g), W1 (h), and W2 (i), respectively.

639

640 Figure 3. Leaf condition of irrigated tree W1 on (a) March 21, 2015 and (b) January 15,
641 2014 from time-lapse photographic images.

642

643 Figure 4. Relationship between the daily heat pulse velocity (HPV) and daily vapor
644 pressure deficit (VPD) of (a) control tree C1, (b) control tree C2, and (c) irrigated tree
645 W1 during the period August 2013 to March 2014 and (d) C1, (e) C2, (f) W1, and (g)
646 irrigated tree W2 during the period August 2014 to March 2015. To facilitate visual
647 interpretation, data for September and November in 2013 and 2014 have not been
648 included.

649

650

Table 1. Start and end dates for the deciduous period (DP) and the complete leaf abscission period (PCLA) for four teak trees (*Tectona grandis* L. f.) in northern Thailand. The period from the end of transpiration in one season to the start of transpiration in the next corresponds to DP as defined in this study. PCLA and DP were defined based on time-lapse photographic images or visual observation and measured heat pulse velocity (HPV), respectively. *: Irrigation treatment for W1 was started on March 5, 2013 after leaf flush. **: Irrigation treatment for W2 was started on March 3, 2014 after complete leaf abscission.

Year	Tree	Condition	Start of DP	Start of PCLA	End of PCLA	End of DP
2013	C1	Natural	NA	03 Mar 2013	04 Mar 2013	12 Mar 2013
	C2	Natural	14 Feb 2013	18 Feb 2013	07 Mar 2013	23 Apr 2013
	W1	Natural*	28 Jan 2013	NA	28 Feb 2013	06 Mar 2013*
	W2	Natural	NA	NA	28 Feb 2013	NA
2014	C1	Natural	10 Mar 2014	19 Mar 2014	07 Apr 2014	01 May 2014
	C2	Natural	23 Feb 2014	03 Mar 2014	09 Apr 2014	28 Apr 2014
	W1	Irrigated	10 Mar 2014	Unclear	Unclear	25 Mar 2014
	W2	Natural**	21 Feb 2014	02 Mar 2014	06 Mar 2014**	11 Mar 2014**
2015	C1	Natural	08 Mar 2015	13 Mar 2015	31 Mar 2015	13 Apr 2015
	C2	Natural	08 Jan 2015	14 Jan 2015	01 Apr 2015	01 Apr 2015
	W1	Irrigated	16 Mar 2015	Unclear	Unclear	28 Mar 2015
	W2	Irrigated	07 Mar 2015	Unclear	Unclear	18 Mar 2015

Figure 1

Figure 3

Figure 4