Original Articles

Pattern and driving factor of intense defoliation of rubber plantations in SW China

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ABSTRACT

The pattern of intense defoliation of rubber trees (*Hevea brasiliensis*) in Southwest China is assumed to mainly be attributable to drought stress. However, this has never been proven, and the pattern remains unclear. Our objectives were to reveal the driving factor and pattern of intense defoliation, and to explore the characteristics of sap flow density (J_s) and relate them to climatic factors before, during and after the intense defoliation period. We continuously measured J_s and related climatic factors in a rubber plantation in Southwest China from 2013 to 2016 and found that (1) the cold stress (< 10 °C) was more relevant to intense defoliation than drought stress, and after encountering cold stress the rubber trees might enter dormancy for approximately 50 days during the *defoliation* period; (2) J_s showed a self-regulating ability to respond to high air temperature (T_a) and water vapor pressure deficit (*VPD*) with a time lag of approximately one hour during all periods except during the *defoliation* period; (3) the sensitivity of J_s to T_a weaken (*slope* = 0.14, *r* = 0.17, *P* > 0.05) during the *defoliation* period, but it rebounded back to a relative high level (*slope* = 1.44, *r* = 0.55, *P* < 0.01) during the *refoliation* period which was similar to that during the remaining periods; and (4) the relationship between J_s and T_a was generally positive, while both SWC_5 and SWC_{100} exerted inhibitory effects on J_s, and the interactive effects among T_a, SWC_5 and SWC_{100} on J_s were significant during the *refoliation* period (*P* < 0.01). Based on these findings, we evaluated J_s as a crucial physiological indicator of the processes underlying important phenological transition periods, and the cold stress rather than drought stress was likely the driving factor of the pattern of intense defoliation occurred in Southwest China rubber plantations.

1. Introduction

Phenology has been defined by the International Biological Program as "the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species" (Lieth, 1974). Plant phenology is generally highly sensitive to climate change (Richardson et al., 2013) and is an important indicator of how ecosystems and their constituent species function and respond to climate change (Badeck et al., 2004; Bradley et al., 1999; Chuine, 2010; Cleland et al., 2006; Parmesan, 2007; Peñuelas et al., 2002; Rosenzweig et al., 2008; Schwartz, 1998; Schwartz et al., 2006). In recent years, seasonal patterns and physiological changes in trees have been assessed both at the stand and leaf levels (Ensminger et al., 2004; Kelly and Goulden, 2016; Monson et al., 2005; Zarter et al., 2006). Taking tropical dry

forests as an example, the growth of many plants may coincide with and appear to be regulated by drought stress during the dry season (Reich, 1995; Richardson et al., 2013), or cold stress including chilling (< 20 °C) or freezing (< 0 °C) (Chinnusamy et al., 2007). Plants may exhibit similar responses to low temperature and unfavorable water status (Kramer, 1940), e.g., abscission of leaves (hereafter referred to as "defoliation"), which occurs in response to abiotic (e.g., drought and cold) stresses, through changes in the expression of thousands of genes operating at different scales. These responses affect plant growth and development and constrain the spatial distribution of plants and agricultural productivity (Chinnusamy et al., 2007). Severe defoliation can lead to a significant decrease in photosynthesis, thereby limiting the production and accumulation of carbohydrate reserves (Simbo et al., 2013).

Although canopy/hydraulic conductance is of great power to study

physiological regulation of water use (Jinagool et al., 2015; Kobayashi et al., 2014), however, year-round sap flow measurements can provide a promising and direct approach for monitoring tree physiology during certain important transitional periods (i.e., the period before or after defoliation) (Chan and Bowling, 2017; Sevanto et al., 2006; Vanhatalo et al., 2015). The Granier heat dissipation approach is widely used despite several interpretational difficulties (Chan and Bowling, 2017; Granier et al., 1996; Hölttä et al., 2015; Poyatos et al., 2016; Steppe et al., 2010; Vandegehuchte and Steppe, 2013) and remains a powerful means of addressing fundamental questions related to plant and eco-system physiology (Burgess and Dawson, 2004; Cochard et al., 1996; Goldstein et al., 1998; Hubbard et al., 1999; Poyatos et al., 2016), ecosystem functioning (Forrester et al., 2010), and silvicultural or agronomic practices (Aranda et al., 2012; Jones, 2004).

Intense defoliation of rubber trees in Southwest China has been mainly attributed to drought stress or the interactive effects between drought and cold stresses (Li et al., 2016; Liu et al., 2013; Priyadarshan, 2017), but many uncertainties remain, and more direct evidence is required. Furthermore, although the rubber plantations in China have been demonstrated to act as "water pumps" (Lin et al., 2016; Tan et al., 2011) and are blamed for water shortages (Qiu, 2009; 2010), it remains uncertain whether the rubber trees are water limited, especially during the dry-hot season. Although the sap flow density (J_s) of rubber trees has been studied in Asia and elsewhere (Isarangkool Na Ayutthaya et al., 2011; Kobayashi et al., 2014; Lin et al., 2016; Rao et al., 1990; Zhao et al., 2014), little is known about how J_s and the underlying physiology respond to cold and drought stresses (Cruiziat et al., 2002; Tyree and Ewers, 1991). In addition, there is limited information on the sensitivity and relation of J_s to climatic factors during different periods, especially before, during and after the *defoliation* period. Here, we tackle the following research questions: (i) What are the driving factors and characteristics of intense defoliation observed in rubber plantations in this region? (ii) What are the diurnal dynamics of J_s and how it in response to highly related climatic factors during different periods? (iii) How are the sensitivity and relation of J_s to climatic factors before, during and after the intense defoliation period? (iv) What are the re-lationships between J_s and air temperature or soil water content, and are there interactive effects between these variables? We address these questions using four years of continuous J_s measurements and me-teorological data collected at 30-minute intervals.

2. Materials and methods

2.1. Study area

Our study site is located in the Xishuangbanna Tropical Botanical Garden (XTBG; 21°55′30″N, 101°15′59″E), Yunnan Province, Southwest China (Fig. 1). The original tropical forest of Xishuangbanna Prefecture is an extension of the tropical forest of Southeast Asia (Zhu and Yan, 2009) but has been replaced by rubber plantations across much of the region during the past 50 years. The rubber trees grown in this region are considered to be adapted to the local growing conditions as they are cold-resistant clones (PB86 and RRIM600). The climate is strongly seasonal, with two air masses alternating within a year (Zhang, 1963). During the rainy season from May to October, the tropical southern monsoon from the Indian Ocean delivers most of the region's annual rainfall, whereas the dry and cold air of the southern edges of the subtropical jet stream dominates the climate from November to April (Tan et al., 2011). The multi-year mean annual rainfall is 1490 mm, approximately 87% of which occurs during the rainy season. The mean monthly rainfall during the dry season, which is sometimes divided into the fog-cool (between November and February) and dry-hot seasons (March and April) (Zhang, 1963), is less than 40 mm. The mean annual temperature is 21.7 °C, with mean monthly values ranging from 15.9 to 25.7 °C (Tan et al., 2011). The general topography consists of hilly terrain with lateritic soil (pH 5.6) derived from siliceous rocks; the

physical and chemical characteristics of the soil are reported in a pre-vious study by our research team (Zhou et al., 2016).

The rubber plantation (plot area is 20 × 20 m^2) that we studied was planted in 1982 and exhibited a tree density of 346 trees per ha, a mean height of 22 m, and a mean diameter at breast height (*DBH*) of 31 cm (Lin et al., 2016, 2018; Zhao et al., 2014). The rubber trees were planted 2 m apart in rows with mixed spacing varying from 4 m to 12 m, and the main rubber-tapping period coincided with the rainy season and extended from May to November (Song et al., 2014). Fertilization with mineral fertilizer (containing 15% N as $(NH_2)_2CO$, 15% P as $NH_4H_2PO_4$, and 15% K as KCl) was performed in April and July of each year (Zhou et al., 2016), and understory weeds and seedlings were removed by hand or using herbicides. Plant phenology in these rubber plantations exhibits a clear physiological response to seasonal change, with an intense leaf-fall phenomenon occurring during the fog-cool season (Dou et al., 2007; Zhou et al., 2008). Rubber tree roots are mostly concentrated within the first 110 cm, while feeder roots are widely distributed on the surface of the soil to a depth of 15 cm (Devakumar et al., 1999; Guardiola-Claramonte et al., 2010).

2.2. Microclimatic observations

Climatic factors, including wind speed (W_s, m·s^{-1}), air temperature (T_a, °C), relative humidity (*RH*, %), water vapor (V_{apor}, hPa), water vapor pressure deficit (*VPD*, hPa), soil temperature (T_s, °C), soil water content (*SWC*, %), global radiation (R_g, MJ·m^{-2}), net radiation (R_n, MJ·m^{-2}), photosynthetically active radiation (*PAR*, mol·m^{-2}), and precipitation (P_{re}, mm), were measured by sensors mounted on a 55-m-tall micrometeorological tower installed in XTBG in 2009. The micro-climatic instruments used in this study included a rain gauge (Rain Gauge 52203, R. M. Young Co., USA) mounted at a height of 55 m, and radiation sensors for determining R_g (CMP11, Kipp & Zonen, Netherlands), R_n (NR01, Hukseflux, Netherlands) and *PAR* (LQS70-10, Apogee, USA) mounted at a height of 28.6 m. *VPD* and V_{apor} were di-rectly or indirectly calculated from T_a and *RH*, which were monitored using a hydrothermograph (HMP45C, Vaisala, Finland) mounted at a height of 28.9 m. W_s was monitored using a wind speed sensor (010C, MetOne, USA) mounted at a height of 28.9 m. *SWC* was monitored at depths of 5 cm (SWC_5) and 100 cm (SWC_{100}) using a reflectometer (CS616-L, Campbell Sci., USA), and T_s was monitored at a depth of 5 cm (109-L, Campbell Sci., USA). All meteorological data were collected every 30 min using a data logger (CR1000, Campbell Sci., USA).

2.3. Sap flow observations

We randomly selected six rubber trees in the plot and measured xylem J_s using heat dissipation sensors which were manufactured ac-cording to the original design specified by Granier (1985, 1987) (Fig. 2). Pairs of 20-mm-long and 2-mm-wide probes were inserted into the sapwood of each rubber tree at a height of 1.30 m above the stem base in the same direction after partially removing the bark from the areas where the probes were inserted, and the probes were shielded from solar radiation, thermal gradients and rainfall by reflective in-sulation. The upper probe was heated with a constant power of 0.2 W, and the lower probe was not heated and served as a reference for the upper probe, with a distance of approximately 10 cm between the two sensor probes to avoid thermal interference. The temperature difference between the two sensors was recorded using copper-constantan ther-mocouples placed at the center of the heating coil, and a data logger (CR10X, Campbell Sci., USA) was employed to collect the data (aver-aged and stored every 30 min). Then the temperature difference was used to calculate J_s (g·m^{-2}·s^{-1}) according to the empirical calibration equation specified by Granier (1985):

$$J_s = 119 \times [(\Delta T_m - \Delta T)/\Delta T]^{1.231} \tag{1}$$

where ΔT_m is the maximum temperature difference when the minimum