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Original paper

Duration of cambial activity is determined by water availability while cambial stimulus is day-length dependent in a Neotropical evergreen species

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ABSTRACT

Experimental manipulations are essential for understanding the causal factors of plant growth and cambial activity. Here, we studied the potential effect of water availability and natural variation of day length and temperature on cambial activity in *Cordiera concolor* (Cham.) Kuntze, an evergreen tropical species. Experiments were conducted in a greenhouse using ninety one-year-old plants divided into two groups. Each group was observed for five weeks during two different times of the year (early spring and late summer). Plants were subjected to three distinct water regimes (waterlogging, field capacity and water deficit). Temperature and day length were recorded daily and stem samples were taken weekly during both sampling intervals. Anatomical procedures were used to describe the cambial activity per stem. Our results suggest that soil water content and its influence on cambial activity depend on the time of year, while cambial stimulus was positively related to day length, independent of the time of year. In early spring, cambial activity was stimulated by an increase of day length, regardless of water supply. In contrast, in late summer, cambial dormancy was delayed in waterlogged plants and advanced in plants subjected to a water deficit, followed by decreasing day length. Analyses of the wood anatomy showed that the marginal bands of axial parenchyma were initial. Our study highlights a more complex scenario of plant functioning and its causal factors in tropical systems.

1. Introduction

Cambial activity in woody plants is influenced by extrinsic factors such as precipitation, day length and temperature (Borchert, 1999) and by intrinsic factors such as plant hormones (Little and Savidge, 1987). The variation of these factors throughout the year may lead to cambial seasonality, which depends on the environment in which the tree grows. Among the extrinsic factors influencing cambial activity, temperature has been considered the most important in cold temperate environments (Begum et al., 2013; Rossi et al., 2013). In tropical environments, cambial activity has been attributed mainly to precipitation, as reported previously for several tropical species by Worbes (1995) and more recently for five tropical species of Thailand (Pumijumnong and Buajan, 2012). For Brazilian species, the active period coincides with the wet season and the dormant period with the dry season (Marcati et al., 2006, 2008).

Most studies on cambial activity in tropical species were conducted on plants from the field, providing information about the temporal patterns of cambial activity throughout the year (see Aljaro et al., 1972; Avila et al., 1975; Dave and Rao, 1982; Worbes, 1995; Rao and Rajput, 1999; Rajput and Rao, 2000, 2001, 2002; Dié et al., 2012; Pumijumnong and Buajan, 2012; Trouet et al., 2012). For example, rainfall and cambial activity were not correlated in Chilean and Californian evergreen shrubs species, and in two of these species the cambial activity was observed in early spring while cambial dormancy in late summer (Avila et al., 1975). Maximum temperature and day length were the most important factors explaining cambial activity in Mexican evergreen species (Yañez-Espinosa et al., 2006). Recently, for Brazilian evergreen species of the Cerrado, a savanna-like ecosystem, day length (de Lara and Marcati, 2016) and temperature (Marcati et al., 2016) were important signals of cambial activity. For a better understanding of the relationship between abiotic factors (water, day length and temperature) and cambial activity, manipulative studies are required that experimentally modify some of these factors.

Experimental research on cambial activity has been limited to temperate species, either investigating the effects of temperature and/

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or day length (Wareing and Roberts, 1956; Waisel and Fahn, 1965; Mellerowicz et al., 1992a, 1992b; Oribe and Kubo, 1997; Oribe et al., 2001), or the effects of water availability (Rossi et al., 2009; de Luis et al., 2011; Balducci et al., 2013) on cambial activity. Under limited water availability, cell divisions and expansion of newly produced cells can decrease or even cease (Abe and Nakai, 1999; Abe et al., 2003). Long dry periods during summer may affect cambial activity in three-year-old seedlings (de Luis et al., 2011); two different water regimes, following a severe drought affect the resumption of cambial activity in four-year-old saplings (Balducci et al., 2013). Thus, recent studies showed the relevance of water availability for cambial activity in temperate species (Rossi et al., 2009; de Luis et al., 2011; Balducci et al., 2013). For tropical species, experimental studies providing a comprehensive view of cambial activity are currently unavailable.

Taking into account that for tropical species: (i) precipitation has been considered the main extrinsic factor related to cambial activity and may limit its activity; (ii) day length and temperature seem to be general signals to cambial activity and (iii) there is a lack of experimental studies on the subject, we investigated the causes of cambial activity variation in *Cordiera concolor* (Cham.) Kuntze (Rubiaceae), an evergreen shrub that occurs in the Brazilian central plateau (Zappi, 2015). Cambial activity of this species is seasonal (de Lara and Marcati, 2016) with growth markers in its wood (marginal bands of axial parenchyma) (see Sonsin et al., 2014), making it ideal to experimentally investigate growth patterns and their causal factors.

Considering that there is an increase in the frequency and severity of droughts (IPCC, 2014) and that water is a limited resource, we tested the effect of water availability (including water deficit) on cambial activity in association with temperature and day length. We explored four main questions concerning the evergreen tropical species *Cordiera concolor*: (i) How does cambial activity changes over weeks? (ii) What is the effect of soil water availability on cambial activity? (iii) Is cambial activity related to natural variation of day length and temperature? (iv) Is the formation of axial parenchyma bands in wood initial, terminal or both?

2. Material and methods

2.1. Sources of plant material

We selected all individuals (n = 3) of *C. concolor* with mature fruits (n = 60) from a remnant of the cerrado *sensu stricto* in Rubião Jr., Botucatu, São Paulo, Brazil (S22°53′29,5″, W48°29′21″) for collecting seeds (n = 300) (Fig. 1A–D). The seeds were germinated in wet filter paper inside acrylic boxes under fluorescent lamps in a germination chamber at 25 °C ± 1 °C under alternating dark and light periods (12 h of dark and 12 h of light) (Bertani and dos Santos, 2013). After primary root protrusion, we replaced the wet filter paper by vermiculite, adding Hoagland and Arnon (1950) solution and transferred the plants to a greenhouse. Here, the term "plant" refers to the developmental stages beginning with the expansion of the first metaphyll pair (*sensu* Oliveira, 2001). We characterized metaphylls by analyzing leaf matrices.

2.2. Experimental design

Experiments were conducted in a greenhouse of 5 m width, 3 m height and 15 m length. The roof was covered with diffuse polyethylene film (150 μm) transparent to long-wave radiation to minimize radiative heating, and walls were covered with shading screen (Supplementary data, Fig. S1A). One-year-old plants were transplanted into plastic pots (volume of one liter) filled with soil collected from the cerrado *sensu stricto* where *C. concolor* occurs. We selected 90 plants of relatively uniform size (15.0 ± 0.6 cm of height and 2.3 ± 0.2 mm of diameter at the collar) for the manipulation of water availability. We conducted the experiment twice with plants of the same age: in early spring, from September 12th to October 17th (see Supplementary data, Table S1), and in late summer, from March 1st to April 5th (see Supplementary data, Table S2). Forty-five plants were used in each sampling interval. These two intervals had variation in day length and temperatures (Fig. 2). We chose these two intervals based on studies of woody species of the Brazilian Cerrado, according to which cambial activity occurs in early spring (Bosio et al., 2016; de Lara and Marcati, 2016; Marcati et al., 2006, 2008, 2016) and cambium dormancy in late summer (de Lara and Marcati, 2016; Marcati et al., 2006, 2016).

To determine the different experimental water treatments, we used a water retention curve according to Richards (1948) (Table 1). In addition, we performed physical and chemical analyses of the soil of the Cerrado area (Supplementary data, Table S3). We divided 45 plants at random into three treatments, 15 plants each, and transferred them to a greenhouse. The treatments were: (i) waterlogged with 21% humidity in the soil (T1) with plants placed in a tank (Supplementary data, Fig. S1B), where the water level was maintained at a level of 5 cm; (ii) close to field capacity with 8% humidity in the soil (T2); (iii) dry regime with plants kept at soil water content near wilting point (3% humidity in the

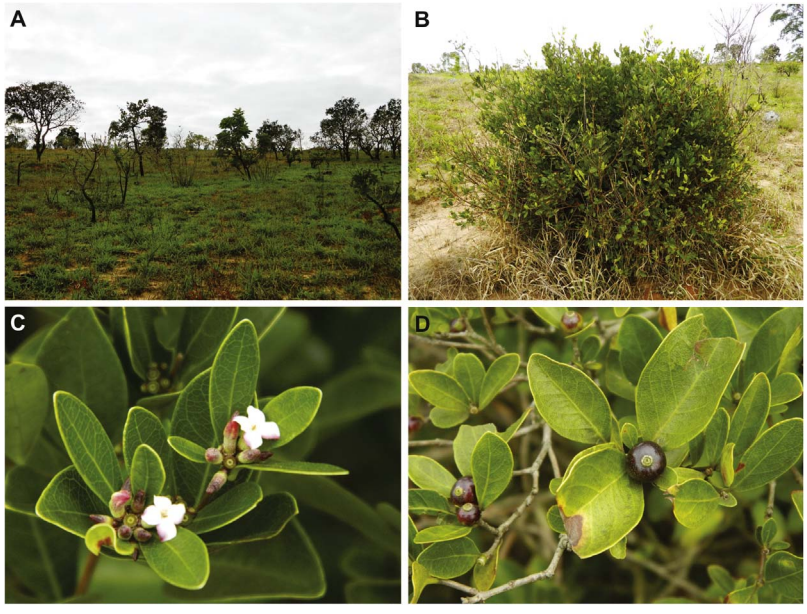

Fig. 1. *Cordiera concolor* (Cham.) Kuntze (Rubiaceae). **A** General view of cerrado *sensu* stricto. **B** A specimen of *C. concolor* growing in the area. **C** Flowers. **D** Mature fruit with violet pericarp (diameter approximately 1 cm). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)