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Short Communication

Interrelationship between tree-ring width and supra-annual reproductive behaviour of *Cedrela odorata*: an alert for dendrochronological research

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Abstract

Allocating resources for reproduction involves ecological and evolutionary factors and can reduce vegetative growth in plants. This interrelationship is not easily observed in nature, as there are many parameters that can limit the production of reproductive structures or the addition of biomass. We related tree-ring width to supra-annual reproductive behaviour of *Cedrela odorata* L. (Meliaceae) in the Atlantic Forest of Rio de Janeiro State. In general, the development of reproductive structures occurred in wet years, without water deficit at the beginning of the growth season. However, in these years, tree-ring width was smaller. These results may be associated with the lack of correlation between tree-ring width and local climate. In this way, we highlight the importance of incorporating reproductive data in radial growth studies to expand the understanding of growth variability in tropical forests.

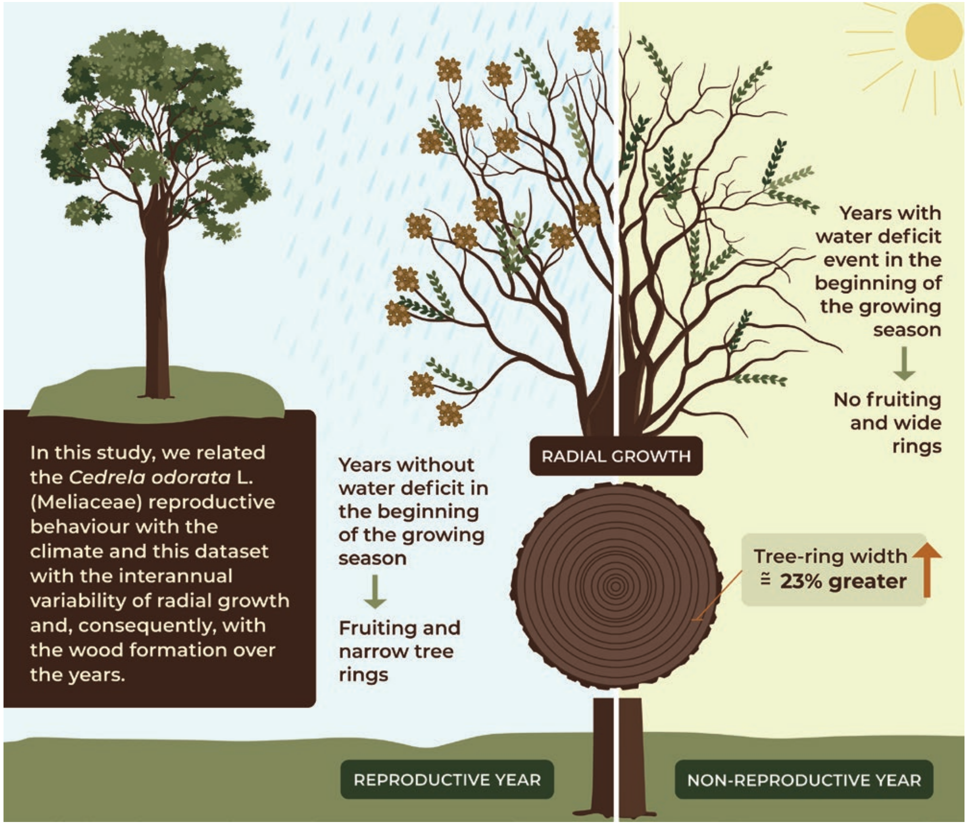
Keywords: plant growth strategy, dendrochronology, dendroecology, trade-off in reproduction

香椿的树木年轮宽度与超年生殖行为的相互关系：对树轮学研究的警示

摘要：资源分配到生殖过程涉及到生态和进化因素，可能会减少植物的营养生长。这种相互关系在自然界中不容易观察到，因为有许多参数可以限制生殖结构的产生或生物量的增加。我们将香椿(*Cedrela odorata* L.，楝科)在里约热内卢州大西洋森林中的树木年轮宽度与超年生殖行为相关联。总体而言，生殖结构的发育发生在湿润的年份，在生长季初期没有出现水分亏缺。然而，在这些年份，树木年轮宽度较小。这些结果可能与树木年轮宽度与当地气候之间缺乏相关性有关。因此，我们强调在径向生长研究中纳入生殖数据的重要性，以扩大对热带森林生长变异性的理解。

关键词：植物生长策略，树木年轮学，树木生态学，生殖权衡

Graphical Abstract



Cedrela odorata L., known as Spanish-cedar, has great commercial importance and a wide geographical distribution. It has high representation in tropical forests and is planted in numerous areas. Individuals are long lived (approximately 150 years) and have deciduous behaviour and excellent tree-ring distinctiveness (e.g. Botosso *et al.* 2000; Tomazello-Filho *et al.* 2000; Venegas-Gonzalez *et al.* 2018; Worbes 1999). These features, also found in *C. odorata* of the Atlantic Forest of the state of Rio de Janeiro (Costa *et al.* 2013), indicate the species as strategic for the establishment of dendrochronological networks. However, understanding the radial growth pattern of the species remains a challenge given the wide variation in correlation rates among trees in dendrochronological studies (e.g. Baker *et al.* 2017; Brienen and Zuidema 2005; 2006, Costa *et al.* 2013; Köhl *et al.* 2022).

Although the relationship between reproduction and radial growth has been scarcely studied, reproductive effort is known to have a decisive effect on forest ecosystem dynamics over time (Breda *et al.* 2006; Hacket-Pain *et al.* 2019; Thomas 2011). Plant resources are usually limited, being divided among the functions of survival, growth, and reproduction (Oborny 2019; Stearns 1989, 1992; Williams 1966). Resource consumption for reproduction has been related to decreases in resource allocation to other functions, such as vegetative growth and the future reproduction cycle itself (e.g. Bell 1980; de Jong and Klinkhamer 2005; Hacket-Pain *et al.* 2019; Iwasa and Cohen 1989; Oborny 2019; Sardans and Peñuelas 2013; Stearns 1989, 1992; Willson 1983). These trade-off relationships are not easily investigated in nature, as there are numerous biotic and abiotic factors that can influence an organism's life history (Guijarro 2002; Guillemot *et al.* 2017). Based on previous studies of dendrochronology and cambial activity (Arêdes-dos-Reis *et al.* 2016, 2019; Costa 2011; Costa *et al.* 2013), we analysed the relationship between supra-annual reproductive behaviour and growth rates and number of cambial cells of *C. odorata* L. (Meliaceae).

This Short Communication analyses the 6-year period of *C. odorata* radial growth, based on the methodology and data from previous studies on dendrochronology (64 rays from 16 trees), cambial activity (10 trees), and reproductive phenology (10 trees) for the species growing in a well-preserved remnant of the Atlantic Forest in Rio de Janeiro State, Brazil (Costa 2011; Costa *et al.* 2013).

The wet season at the study site occurs from September to April and the dry season from May to August, with June to July being the driest period. Minimum and maximum average temperatures varied between 18°C and 24°C during the evaluated period, while average annual precipitation was 1240 mm (Costa 2011; Costa *et al.* 2013; Vasconcellos *et al.* 2016). Climate diagrams for the studied period were built using the Climatol package working in the RStudio environment (Guijarro 2002) and showed episodes of water deficit typically at the end of the growing season (Fig. 1). However, water deficit events were also observed at the beginning of the growing season in the years 2004–2005 and 2007–2008 (September for both periods).

Cedrela odorata showed supra-annual reproductive behaviour in the study area, with the beginning of fruit formation at the end of the wet season, in March of years 2003–2004, 2005–2006, and 2008–2009 (Fig. 1). These fruits were observed in the treetops until July, with the release of winged seeds during the dry season. The lack of reproduction in 2004–2005 and 2007–2008 can be associated with a water deficit event during the beginning of each respective growth season (September). An exception to the reproductive pattern in response to climate occurred in the year 2006–2007, when no fruits were formed, despite the lack of water deficit at the beginning of the growth season (Fig. 1).

The presence of distinct tree rings in *C. odorata* allowed the ages of the studied trees to be determined, which varied from 39 to 137 years (Costa 2011). However, the master series was built using 13 radial samples from five different trees (Fig. 2). Although tree-ring boundaries were clearly distinct, intercorrelations among trees averaged 34% (Table 1). Rainfall and temperature had no influence on tree-ring growth pattern, with correlation tests between tree rings and these climatic factors being not significant ($P < 0.05$, Costa 2011).

Over the six analysed years, tree-ring width in non-reproductive years was on average 23% greater

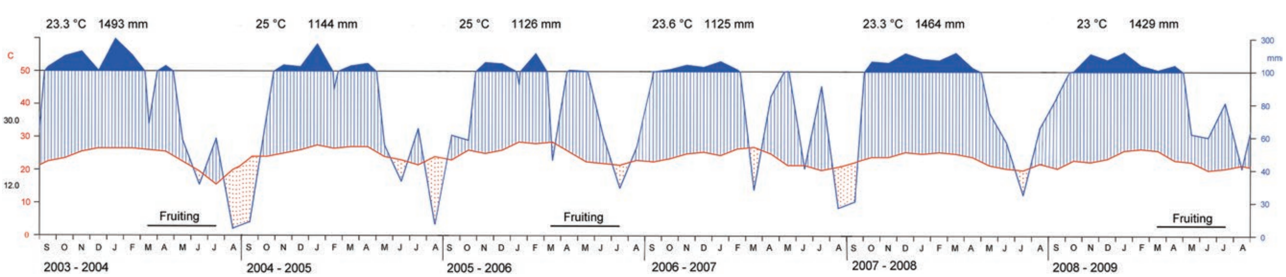


Figure 1. Walter and Lieth climate diagram for temperature (red line) and precipitation (blue line) series for Nova Iguaçu, state of Rio de Janeiro, Brazil. On the left axis, the values in black represent the absolute maximum and minimum temperature over the entire period. In the upper right corner, the values in black represent the average value of the average temperature and annual precipitation over the entire period. The presence of fruiting is indicated in the graphs.

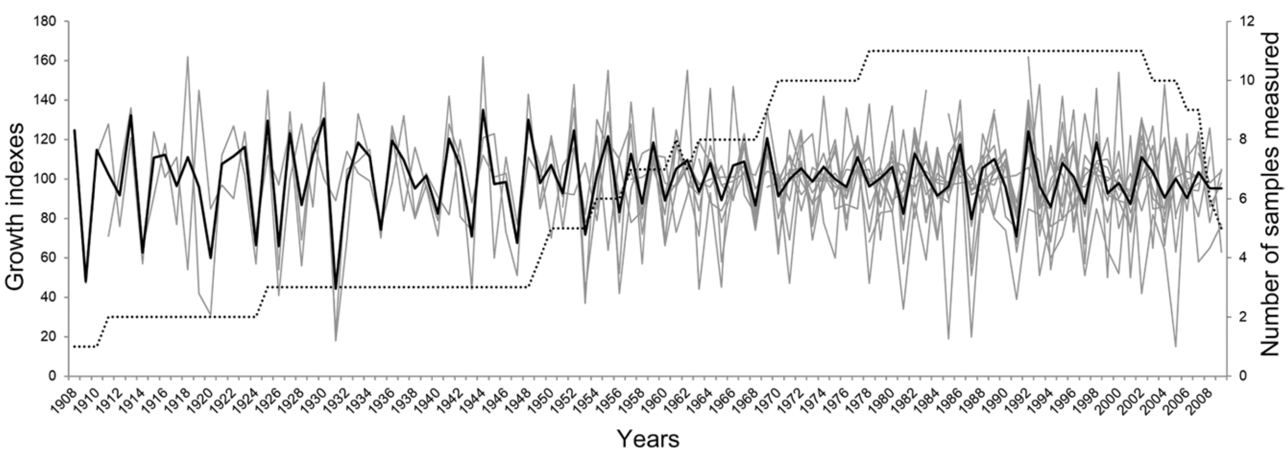


Figure 2. Standard chronology of the growth rings of five individuals of *Cedrela odorata*. The dotted line indicates the number of rays used in the chronology.

Table 1. *Cedrela odorata* increment data and tree-ring analysis statistics.

Number of trees analysed	Mean annual increment	Number of trees in the master series	Number of series in the master series	Series intercorrelation	Spline length (years)	Average mean sensitivity
12	0.29 (±0.10)	5	13	0.34	5	0.40

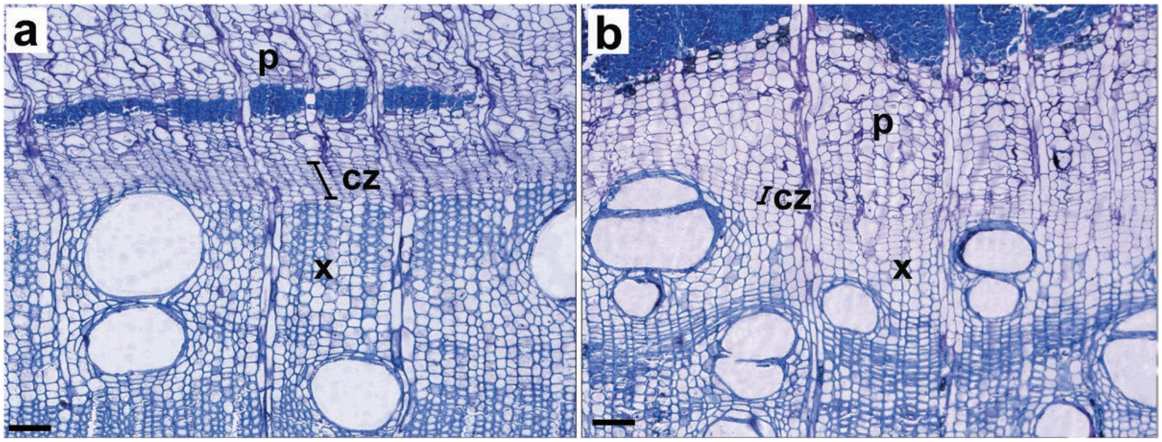


Figure 3. Cross sections of *Cedrela odorata* L. (Meliaceae) during the period of cambial activity in a non-reproductive year (a) and in a reproductive year (b). Cambial zone (cz) and adjacent newly formed xylem (x) and phloem (p). Scale bar: 50 µm.

than that in reproductive years (non-reproductive years mean = 3.24 ± 1.04 cm reproductive years mean = 2.62 ± 0.43 cm). This result was also corroborated by the analysis of the number of cell layers in the cambial zone of the trees in the non-reproductive year (10.2 ± 1.18 layers; Fig. 3a). These trees had on average a 7.5% larger cambial zone than trees in reproductive years (9.5 ± 1.9 layers; Fig. 3b).

The low intercorrelation values among tree-ring series at the study site can be associated with variation in radial growth, which also leads to the formation of false or absent rings. These conditions are related to the complex radial growth responses of *C. odorata* trees to environmental factors, which were also observed in other studies with the species growing in different locations (e.g. Baker *et al.* 2017; Brienen and Zuidema 2005; 2006, Costa *et al.* 2013).

A high frequency of false or absent rings is a common issue in the development of dendrochronological studies in tropical areas, and has been attributed mainly to climatic variation in these environments and/or to the particular life history of the individuals of a population (e.g. Blagitz *et al.* 2019; Palakit *et al.* 2015; Priya and Bhat 1998). The existence of possible endogenous control of radial growth periodicity has been indicated for *C. odorata* in the tropics (Baker *et al.* 2017; Brienen and Zuidema 2005, 2006, Costa *et al.* 2013). The differences in radial growth found between reproductive and non-reproductive years by the present study suggest that this endogenous control may be related to the reproductive behaviour of *C. odorata*.

Reproduction is a key mechanism by which climate can influence radial growth and the consequent formation of wood in trees (Hacket-Pain *et al.* 2019). This circumstance may be relevant for *C. odorata* as its trees flower profusely, forming pendular inflorescences up to 30 cm long, with woody fruits that release about 30–40 winged seeds per unit (Carvalho 2003). The production of more than 1500 fruits and more than 60 000 fertile seeds per tree has already been reported for the genus (Carvalho 2003). Oborny (2019) observed that when a plant increases resource allocation for reproduction, the allocation to other functions can be reduced. Thus, it is believed that differences in reproductive allocation result in relative differences in other life history traits, reflecting a trade-off between fertility, vegetative growth, and survival probability (Breda *et al.* 2006; de Jong and Klinkhamer 2005; Hacket-Iwasa and Cohen 1989; Pain *et al.* 2019; Sletvold and Agren 2015). Our results indicate that climate induces supra-annual reproductive behaviour in *C. odorata* at the study site. However, they also suggest that reproduction may explain the weak correlations observed among trees and between chronology and the climate.

In this context, it is important to highlight the association between the absence of water deficit at the beginning of the growth season and *C. odorata* reproduction in the Atlantic Forest of the state of Rio de Janeiro. The species shows adaptations for drought conditions, with leaf abscission and cambial dormancy during the dry season, following the local seasonality of its growth sites (Costa *et al.* 2013). The resumption of cambial activity occurs in association with leaf flushing. However, radial growth is considered the last destination of nutritional resources in the modular plant growth hierarchy (e.g. Hacket-Pain *et al.* 2019; Kozlowski and Pallardy 1997; Sardans and Peñuelas 2013).

In *C. odorata* trees, carbohydrate reserves in stem parenchyma are only available for cambial activation after new leaves reach full development. Thus, there is a cycle in which nutritional reserves from the previous year are used for new leaf formation, and then, when their development is complete, they produce nutrients that will be used for cambial activation (Dünisch and Puls 2003). Changes in the amount nutritional reserves of *C. odorata* are also related to changes in water supply (Dünisch and Morais 2002; Dünisch and Puls 2003). Water loss through transpiration, and reduction in xylem flow in periods of low soil water potential and of high atmospheric vapour saturation deficits, have already been reported for this species (Dünisch and Morais 2002). Furthermore, water storage in xylem is insignificant in *C. odorata*, and water status depends directly on soil water content (Dünisch *et al.* 2002). The combination of the above features can be summarized as high drought sensitivity and a hierarchy for the use of energetic resources, where photoassimilates stored from the previous growth season are destined to new leaf formation (Dünisch and Puls 2003). Thus, vascular cambium and reproductive organs receive, predominantly, photoassimilates from the current growing season. Furthermore, sensitivity to water deficit also influences reproductive behaviour, and may even change the cyclic pattern of a plant in a particular region, as observed in the present study. In turn, alternations in the reproductive cycle are responsible for providing an additional component to the interannual variability of radial growth. This relationship becomes evident with the average increase of 23% in stem radial growth in years when there was no fruit production.

Besides the association of reproductive effort with low tree-ring series intercorrelation and with the correlation lags between climate and growth at our study site, it is important to highlight that there may be differences in responses between *C. odorata* tree populations at different locations, as observed in relation to radial growth (Baker *et al.* 2017; Costa *et al.* 2013), leaf phenological behaviour (Newton *et al.* 1998), and supra-annual reproduction (Cintrón 1990). It should also be noted that the intensity of reproductive investment can even compromise consecutive reproductive cycles (de Jong and Klinkhamer 2005). Thus, the lack of fruiting of *C. odorata* trees in 2006–7 may be a consequence of the costs of intense fruiting, characteristic of the taxon (Carvalho 2003), in the previous growing season (2005–6). These results corroborate the statement that the identification of the triggering factor for the growth rhythm in tropical trees is not always direct (Borchert *et al.* 2015).

This study is the first to report the effects of reproduction on radial growth of a tree species in South America and indicates that reproduction data must be incorporated into this type of study to broaden the understanding of growth variability in tropical forests.

In conclusion, the definition of multiple factors that influence plant growth is information of urgent need for the development of chronologies with tropical species. Our results also corroborate the premise established for temperate tree species (Hacket-Pain *et al.* 2019), that the future response of growth dynamics to climate change will be strongly influenced by the response of reproduction.

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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