Developmental trajectories and Ecology of Monocarpic Trees: Insights from the genus Cerberiopsis (Apocynaceae).

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Developmental trajectories and Ecology of Monocarpic Trees: Insights from the genus *Cerberiopsis* (Apocynaceae).

Présentée par Camille SALMON
Le 27 mars 2023

Sous la direction de Patrick HEURET et Sandrine ISNARD

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Developmental trajectories and Ecology of Monocarpic Trees: Insights from the genus *Cerberiopsis* (Apocynaceae).

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Locations:

Montpellier (France), Nouméa (New Caledonia)

Time Frame:

2019 – 2023

Abstract

Semelparity is the ability of an organism to reproduce once and then die. In plants, this life history strategy is also named monocarpy. After a unique flowering event, the whole plant dies. This strategy inherently characterizes annual and biennial herbaceous, and frequently occurs in bamboo and palms, but remains extremely rare in woody branched plants such as shrubs and trees. Branched plants are long-lived organisms and present multiple meristems (growing points) that are as many opportunities to flower at different times. Therefore, the persistence of the monocarpic strategy in such plants is questionable since a premature death of the individual in the decades before the flowering will prevent any descendants. About twenty-nine monocarpic canopy tree species are recorded worldwide all included in two tropical and subtropical genera: *Tachigali* (Fabaceae) and *Cerberiopsis* (Apocynaceae). This latter is endemic to New Caledonia and consists of three species with different habits. While *C. neriifolia* and *C. obtusifolia* are respectively a polycarpic (multi-flowering) treelet and shrub, *C. candelabra* is a large monocarpic rainforest tree. In this thesis, we investigate the morpho-anatomical bases of monocarpy, its underlying ecological implications, and functional adaptations. (**1**) Through a comparative analysis, we highlight that the variation of only a few architectural traits has led to the emergence of this strategy within the genus *Cerberiopsis,* and flowering in *C. candelabra* is independent of tree age, size, or senescence. (**2**) Based on growth monitoring, we show that *C. candelabra* exhibits high survival and growth rates at the juvenile stage, and forms monodominant regenerations. These two studies pave the way to (**3**) an integrative retrospective analysis: we reconstruct the developmental trajectories of the *Cerberiopsis* species and demonstrate that their growth phenology is sensitive to climate seasonality. *C. candelabra* exhibits strong structural and temporal regularities, as well as a high degree of synchronization between all developmental processes. These particularities might have been preconditions for the evolution of its monocarpic strategy. Finally, my work introduces (**4**) a new type of annual growth ring that results from the production of circular tension wood, a potential adaptive feature related to the cyclonic season of New Caledonia. The processes underlying monocarpic flowering and its triggers are discussed throughout the different chapters of this thesis. We suggest that flowering depends on endogenous preconditions and is triggered in *C. candelabra* by large-scale disturbances such as fires and tropical cyclones.

Résumé

La sémelparité définit un organisme qui se reproduit une unique fois avant de mourir. Cette histoire de vie est également nommée monocarpie chez les végétaux. La plante meurt après un unique épisode de floraison. Cette stratégie est inhérente chez les herbacées annuelles et bisannuelles, et se rencontre fréquemment chez les bambous et les palmiers. Elle reste toutefois extrêmement rare chez les plantes ligneuses ramifiées comme les buissons et les arbres. Les plantes ramifiées sont des organismes à longue durée de vie et présentent de multiples méristèmes (points de croissance) qui sont autant d'opportunités de fleurir à différents moments. La persistance de la stratégie monocarpique chez ces plantes est ainsi questionnable car une mort prématurée de l’individu dans les décennies précédant la floraison effacera toute descendance. Environ vingt-neuf espèces d'arbres de canopée monocarpiques sont connues à l’échelle mondiale appartenant à deux genres tropicaux et subtropicaux : *Tachigali* (Fabaceae) et *Cerberiopsis* (Apocynaceae). Ce dernier est endémique de Nouvelle-Calédonie et comprends trois espèces aux biologies différentes. Tandis que *C. neriifolia* et *C. obtusifolia* sont respectivement un arbuste et un buisson polycarpique (à floraison multiple), *C. candelabra* est un arbre monocarpique. Dans cette thèse, nous explorons les fondements morpho-anatomiques de la monocarpie, ses implications écologiques et ses adaptations fonctionnelles sous-jacentes. (**1**) Nous mettons en évidence à travers une analyse comparative que la variation de seulement quelques traits architecturaux a conduit à l'émergence de cette stratégie au sein du genre *Cerberiopsis*, et que la floraison chez *C. candelabra* est indépendante de l'âge, de la taille ou de la sénescence de l'arbre. (**2**) Nous montrons sur la base d’un suivi de croissance que *C. candelabra* présente des taux de survie et de croissance élevés au stade juvénile, et forme des régénérations mono-dominantes. Ces deux études ouvrent la voie à (**3**) une analyse rétrospective intégrative : nous reconstruisons les trajectoires de développement des espèces du genre et démontrons que leur phénologie de croissance est sensible à la saisonnalité du climat. *C. candelabra* présente de fortes régularités structurelles et temporelles, ainsi qu'un haut degré de synchronisation entre l’ensemble des processus de développement. Ces particularités sont proposées être des conditions préalables à l'évolution de sa stratégie monocarpique. Enfin, mon travail introduit (**4**) un nouveau type de cerne de croissance annuel qui résulte de la production de bois de tension circulaire, un potentiel trait adaptatif à la saison cyclonique de Nouvelle-Calédonie. Les processus sous-jacents à la floraison monocarpique et ses déclencheurs sont discutés tout au long des différents chapitres. Nous suggérons que la floraison dépend de conditions préalables endogènes et est déclenchée chez *C. candelabra* par des perturbations à large échelle telles que les incendies et les cyclones tropicaux.

Foreword

This Ph.D. thesis is the achievement of a three-and-a-half-year work (October 2019 – March 2023) I carried out at the **AMAP** Lab (botany and modeling of plant architecture and vegetation; CIRAD (UR 51), CNRS (UMR 5120), INRAE (UMR 931), IRD (UMR 123), UM) of Montpellier (France) and Nouméa (New Caledonia). This thesis was funded by a grant from the doctoral school **GAIA** (ED 584) of the University of Montpellier. The operational budget (field missions, transports, equipment, and analyses) and the costs related to the thesis communication (participation in national and international conferences) were financed by the French National Research Institute for Sustainable Development (**IRD**), the National Research Institute for Agriculture, Food and Environment (**INRAE**), and the University of Montpellier (**UM**).

The dataset presented in this study is the result of 18-month fieldwork I conducted in New Caledonia in 2020 (8 months) and 2021 (10 months) under the widely restrictive conditions imposed by the covid pandemic. The data related to the morphology and functional traits of the species were acquired at the UMR AMAP in Montpellier. The acquisition of the species micro-anatomy data was carried out at the **SILVATECH** platform of the INRAE Grand-Est Nancy research center in the form of service provision.

I conducted this study with the support of Jennifer Read (School of Biological Sciences, Monash University, Australia) who, besides bringing the intriguing biology of *Cerberiopsis candelabra* to the interest of the scientific community, has shared with me the GPS localizations of all reported populations of the species in New Caledonia.

This thesis includes 7 Chapters following an article-based format.

Avant-propos

Cette thèse de doctorat est l'aboutissement de de trois années et demie de travail (octobre 2019 – mars 2023) que j'ai mené à l'unité mixte de recherche **AMAP** (botanique et modélisation de l'architecture des plantes et des végétations ; CIRAD (UR 51), CNRS (UMR 5120), INRAE (UMR 931), IRD (UMR 123), UM) entre les sites de Montpellier (CIRAD, France) et de Nouméa (IRD, Nouvelle Calédonie). Cette thèse a été financée par une bourse de l'école doctoral **GAIA** (ED 584) de l'Université de Montpellier. Le budget opérationnel (missions de terrain, transports, matériels et analyses) et les dépenses relatives à la diffusion de la thèse (participations à des colloques nationaux et internationaux) ont été financés par l'Institut de Recherche pour le Développement (**IRD**), l'Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement (**INRAE**) ainsi que l'Université de Montpellier (**UM**).

Le jeu de données présenté dans cette étude est le résultat de 18 mois de travail de terrain que j'ai réalisé en Nouvelle-Calédonie en 2020 (8 mois) et 2021 (10 mois), et sous les conditions largement contraignantes imposées par la pandémie de covid. Les données relatives à la morphologie et aux traits fonctionnels des espèces ont été acquises à l'UMR AMAP de Montpellier. L'acquisition des données relatives à la micro-anatomie des espèces a été réalisée à la plateforme **SILVATECH** du centre de recherche INRAE Grand-Est Nancy sous forme de prestation de service.

J'ai réalisé cette étude avec le soutien de Jennifer Read (École des sciences biologiques, Université de Monash, Australie) qui, en plus d'avoir porté à l'attention de la communauté scientifique l'intrigante biologie de *Cerberiopsis candelabra*, m'a partagé les localisations GPS de l'ensemble des populations connues de l'espèce en Nouvelle Calédonie.

Cette thèse se décompose en 7 chapitres suivant un format article.

Scientific contributions

Original research articles

Salmon C, Isnard S, Caraglio Y, Heuret P. 2023. Architectural traits underlie growth form diversity, and polycarpic versus monocarpic life histories in the genus *Cerberiopsis* (Apocynaceae). *Botanical Journal of the Linnaean Society*. Accepted for publication.

Salmon C, Heuret P, Hequet V, Isnard S. Seedling survival and growth phenology of a monocarpic tree, *Cerberiopsis candelabra* Vieill. *Journal of Tropical Ecology*. Accepted for publication.

Salmon C, Fambart J, Ruelle J, Isnard S, Heuret P. Circular tension wood: A new type of annual growth ring. In preparation.

Salmon C, Isnard S, Fambart J, Guichard C, Heuret P. An integrative dendrochronological approach to reconstruct developmental trajectories in the subtropical genus *Cerberiopsis* (Apocynaceae). In preparation.

Salmon C, Isnard S, Heuret P. Some evolutionary consequences of being a monocarpic perennials. In preparation.

Teaching

Two-year teaching assignments (135 hours) at the Biology, Ecology & Evolution (BEE) department of the University of Montpellier. 2019-2021. France: Montpellier.

National conference talk

Salmon C*, Isnard S, Heuret P. 17/12/2020. "Is *Cerberiopsis candelabra* Vieill. a suicidal tree?". *In* Models in Ecology and Evolution (MEE). Online conference.

International conference talks

Salmon C*, Isnard S, Caraglio Y, Heuret P. 07/06/2022. "Comparative architectural study of the genus *Cerberiopsis* (Apocynaceae): What distinguishes a monocarpic tree?". *In* European Conference of Tropical Ecology (GTOE). France: Montpellier.

Salmon C*, Isnard S, Fambart J, Guichard C, Heuret P. 14/07/2022. "Phenology and developmental rhythmicity of the *Cerberiopsis* species (Apocynaceae): The developmental trajectories of a monocarpic canopy tree". In 58th annual meeting of the Association for Tropical Biology and Conservation (ATBC). Colombia: Cartagena.

Citizen science

Involvement in the documentary "De NOU à vous". *In edition*. Jean Michel Bore - IRD IMAGES. Nouméa: New Caledonia.

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À l'ensemble des membres du laboratoire AMAP de Montpellier et de Nouméa. La thèse est une aventure professionnelle mais aussi humaine. AMAP est un lieu où l'amitié et l'entraide font partie prenante du quotidien de ceux qui y travaillent et, j'en suis intimement convaincue, un des moteurs principaux de la réussite de cette unité.

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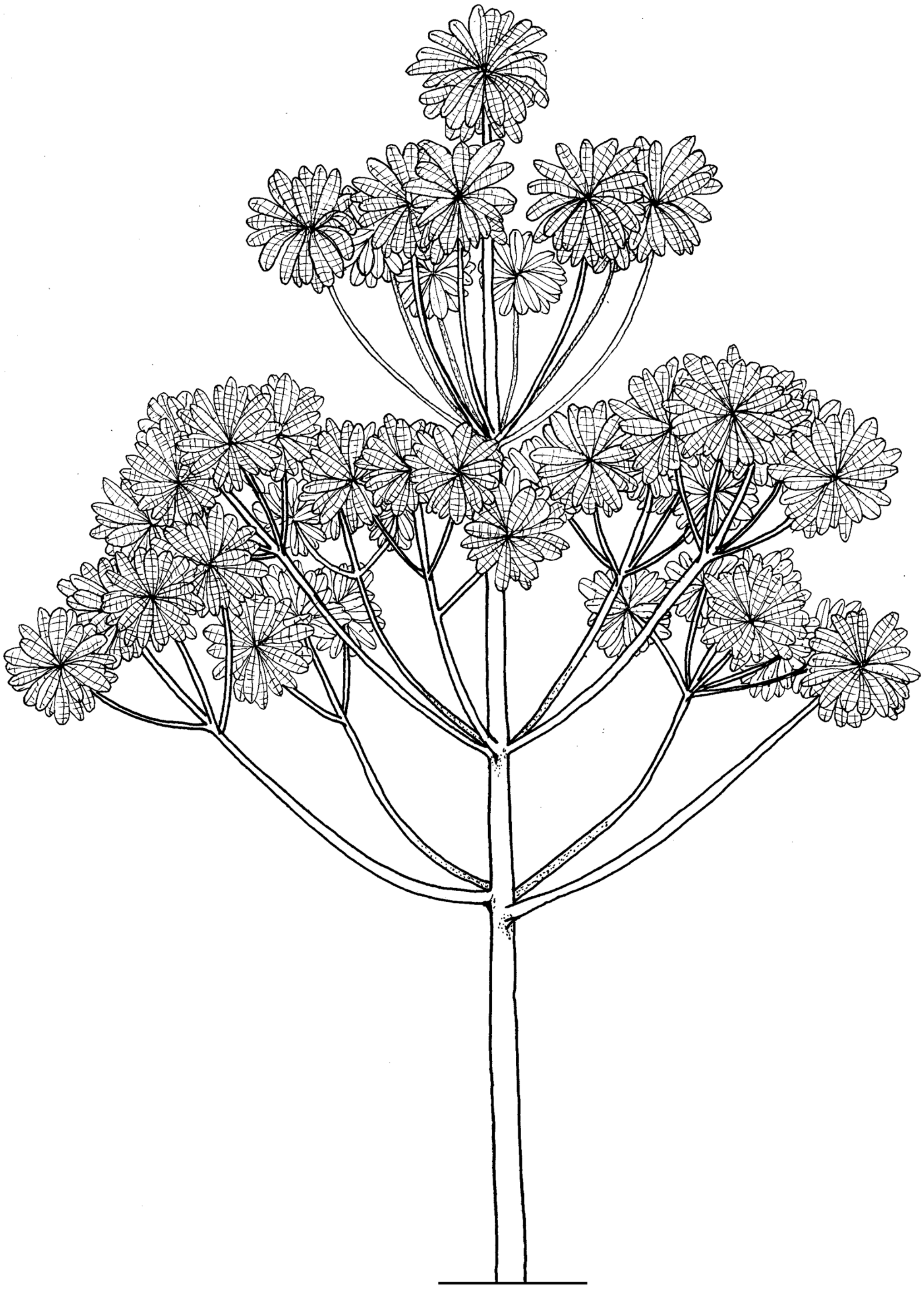

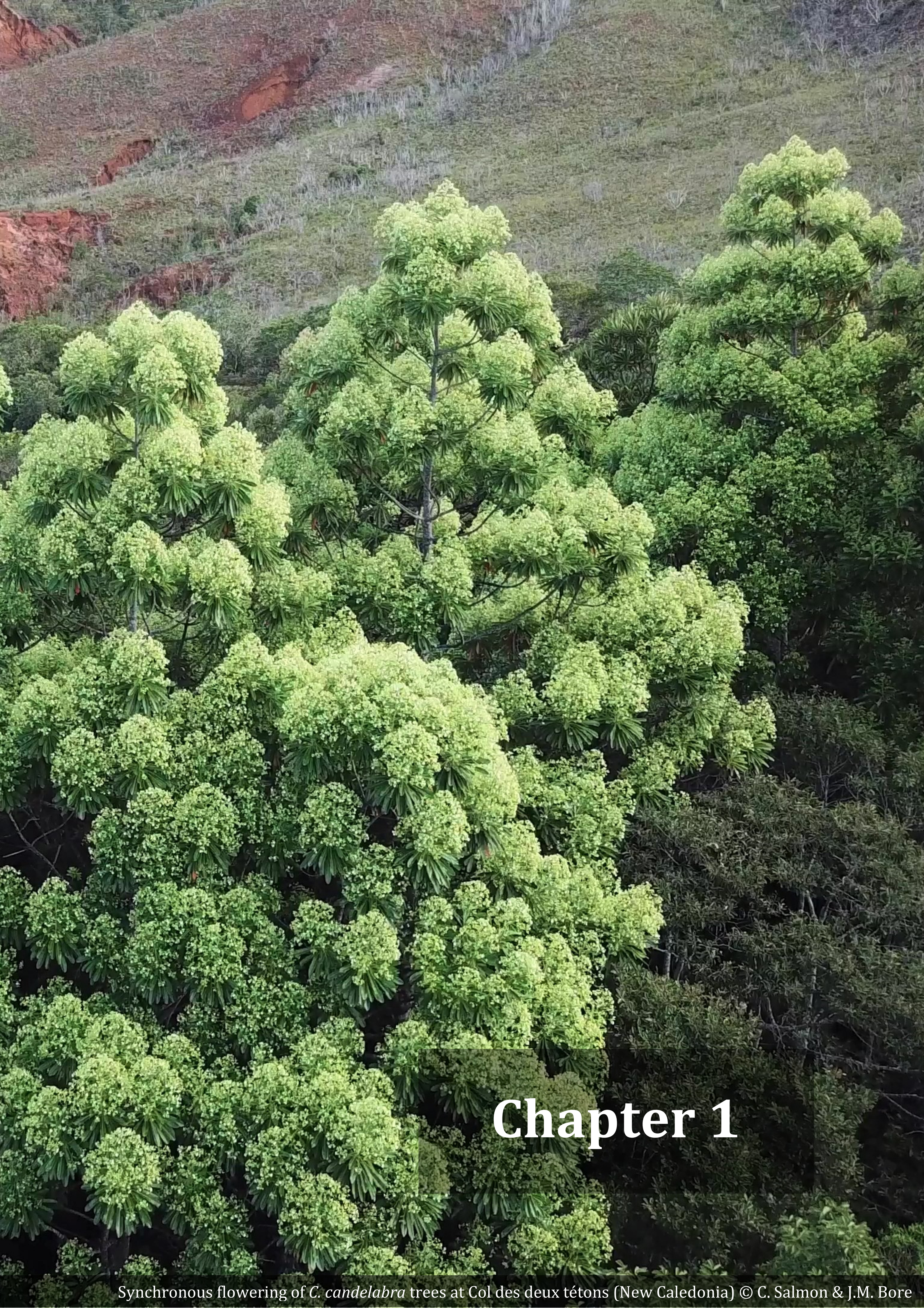

Chapter 1

Synchronous flowering of *C. candelabra* trees at Col des deux tétons (New Caledonia) © C. Salmon & J.M. Bore

Chapter 1 presents the general framework of this study. From the evolution of the tree growth form to the expression of the monocarpic strategy in canopy trees such as *Cerberiopsis candelabra* (Apocynaceae), we give a state-of-the-art on monocarpy in long-lived i.e. perennials plants. We provide a comprehensive overview of what we know about this intriguing life history, its underlying ecological implications, and functional adaptations. This chapter will be the starting point of a review article on monocarpy in perennial plants.

General introduction

Flowering plants (Angiosperms) show an outstanding taxonomical diversity. This diversity results from long-term speciations and extinctions (Crane et al., 1995; Barraclough & Savolainen, 2001; Friis et al., 2011) and is reflected in the vast morpho-anatomical, functional, and ecological diversification of plants (Magallón & Castillo, 2009). In tropical and subtropical regions, Angiosperm diversity is even higher as taxa have radiated under less constraining climatic conditions (Whitmore, 1998; Willig et al., 2003; Brown, 2014). Driven by evolutionary and ecological factors, they have spread rapidly and through a wide range of growth forms and life histories. This diversity of plant forms and strategies is considered one of the multiple mechanisms maintaining high species coexistence (McArthur and Levins, 1967; Chesson, 2000; Wright, 2002; Zhu et al., 2018).

The evolution of growth forms within Angiosperms is a complex history. Herbs, shrubs, lianas, and trees are distinguished by the functional organization of their stems, leaves, roots, and reproductive organs, as well as their diverging mechanical attributes (Rowe & Speck, 2005). These divergences largely arise from the extensive variations in secondary vascular growth (Rowe & Speck, 2004, 2005; Spicer & Groover, 2010; Carlquist, 2012). However, while the discrimination of plant growth forms is intuitive, there is little consensus on their convergent evolution and how they develop or adapt to varying environments. This observation paves the way to our very first question: What makes a tree a tree?

1. The tree growth form

Since the early 19th century, botanists have made great efforts to characterize and classify plant forms and functions (for a detailed history, see: Schulze, 1982; Millan, 2016; Sirvent, 2020). The first definitions were physiognomic. Trees were described according to their morphology as tall branched plants with large stems, leaves, and seeds (Humbolt, 1806; Drude, 1928; Du Rietz, 1931). More functional definitions were likewise proposed, and they were described with regard to their longevity and habitat as long-lived i.e. perennial plants experiencing contrasting light regimes throughout their lives (De Candolle, 1818; Warming, 1884; Raunkier, 1904). In 1934, the innovation of Raunkiaer's life form system was the consideration of apical meristem localization to define plant forms and functions. Trees (macro-phanerophytes) were defined as plants whose vegetative buds are located at the end of the stems, far from the ground, and able to live several years (Raunkiaer, 1934; Cain, 1950; Braun-Blanquet, 1951).

As our definition of trees has expanded, our understanding of their evolution has been refined. The tree growth form has evolved independently and convergently in nine distinct taxa of plants (Donoghue, 2005; Stein et al., 2007; McGhee, 2011) and predates the divergence of Angiosperms and Gymnosperms (Gifford & Foster, 1989; Niklas, 1997; Meyer-Berthaud et al., 2010). Several studies highlighted that plants with a tree habit evolve quickly from non-tree habit ancestors and exhibit higher rates of local adaptation than other growth forms (Böhle et al., 1996; Groover, 2005; Petit & Hampe, 2006). This adaptive ability largely stems from their woody and self-supporting characteristic (Van Valen, 1975; Barkman, 1988; Niklas, 1993; Thomas, 2000). The organization and dimensions of the tree body reflect converging allometries and strategies to (1) compete for resources, (2) overcome disturbances, and (3) reproduce (Küppers, 1989; Niklas, 1992; West et al., 1999; Enquist et al., 1999; Enquist, 2002).

2. Our conceptual framework

This thesis investigates the intriguing relationship between the tree growth form and the monocarpic life history. Therefore, throughout the different chapters, we use a developmental (i.e. ontogenic) definition of the tree. We consider the plant a dynamic and multidimensional system characterized by temporal, geometrical, topological, and functional attributes (Tomlinson, 1978; Hallé, 2005, 2008; Petit & Hampe, 2006; Gschwantner et al., 2009). A tree is a long-lived photosynthetic and woody plant organized around one acrotonic and self-supporting main axis. At maturity, trees are tall branched systems whose different parts show functional differentiation. As articulated by Arber (1928), the definition of a tree is fundamentally a matter of scale. Here, we consider the tree as a growth form (individual scale) and not the trees as interacting organisms (population and community scales). Therefore, we assume that this definition excludes palm-like and monocaulous, i.e. unbranched, trees (Corner, 1949; Hallé & Mabberley, 1976; Hallé et al., 1978; Bruy et al., 2018).

3. Linking tree growth form and life histories

Plant life histories are investigated along phenological spectra. Phenology is the study of the timing of major biological events in the plant's life, such as leaf flushing, flowering, fruiting, or germination (Lieth, 1974; Rathcke & Lacey 1985; Fenner, 1998; Chapman et al., 1999; Borchert et al., 2015). In terms of reproduction, flowering patterns illustrate a continuum from polycarpic species that flower multiple times a year (e.g. rubber tree, *Hevea brasiliensis*, Euphorbiaceae), to monocarpic species that flower once in a whole lifetime (e.g. candelabra tree, *Cerberiopsis candelabra*, Apocynaceae) (Gentry, 1974; Newstrom et al., 1994a, b; Sakai, 2001). The number of times an organism reproduces and the temporality of these events are fundamental life history traits (Janzen, 1978; Stearns, 1992; Hughes, 2017), and flowering phenologies have evolved highly diverse within and among forests, especially in tropical and subtropical regions (Sarmiento & Monasterio, 1983; van Schaik et al., 1993; Reich, 1995; Sakai & Kitajima, 2019). Therefore, what makes a tree express a given life history while others do not?

Studying plant growth form as a function of their ontogeny and environment is of great importance in investigating the evolution of life histories (Zimmermann & Brown, 1971; Grime, 1977; Chapin, 1993; Craine, 2005, Hinckley et al., 2011; Díaz et al., 2016). Recent studies have demonstrated that only a few variations in the plant body organization can lead to a wide diversity of life histories (Isnard et al., 2012; Granados-Mendoza et al., 2014; Trueba et al., 2018; Anest et al., 2021), and that branching patterns have a substantial importance in determining these strategies (Charles-Dominique et al., 2012; Chomicki et al., 2017; Bruy et al., 2018). Nevertheless, although comparative morphology and functional ecology have gained considerable momentum, little is known about how tree growth forms and their underlying life histories are related and what were the drivers of their coevolution.

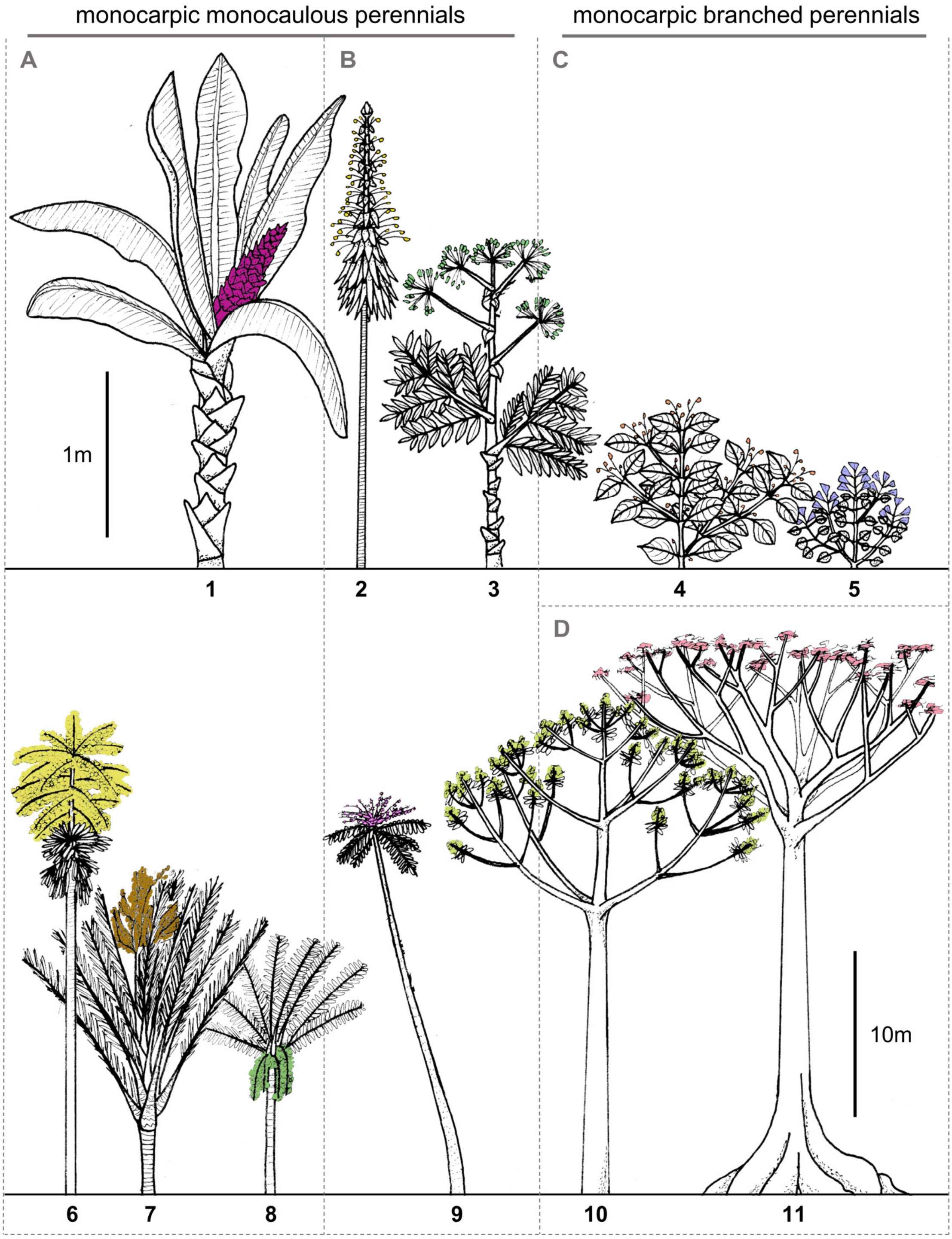

Figure 1. Diversity of monocarpic perennials. (**A**) Monocarpy is widespread in monocaulous monocots (1: *Ensete ventricosum* (Musaceae), 6: *Corypha umbraculifera* (Aracaceae), 7: *Metroxylon salomonense* (Arecaceae), 8: *Aranga pinnata* (Arecaceae)). (**B**) Monocarpy occurs in monocaulous eudicots with a palm-like tree habit (2: *Wilkesia gymnoxiphium* (Asteraceae), 3: *Angelica lignescens* (Apiaceae), 9: *Spathelia ulei* (Rutaceae)). (**C**) Monocarpy is unusual in branched eudicots with a shrub habit (4: *Strobilanthes cernua* (Acanthaceae), 5: *Mimulopsis solmsii* (Acanthaceae)). (**D**) Monocarpy is worldwide rare in branched eudicots with a tree habit (10: *Cerberiopsis candelabra* (Apocynaceae), 11: *Tachigali versicolor* (Fabaceae)).

4. The monocarpic life history

Monocarpy (/Monos/: one; /Karpos/: fruiting) refers to plants that reproduce only once in their lifetime (i.e. semelparous organisms), as opposed to polycarpic plants that reproduce multiple times (i.e. iteroparous organisms) (Gadgil & Bossert, 1970; Harper, 1977; Charlesworth, 1980; Amasino, 2009). This strategy has evolved several times and independently in diverse Angiosperm taxa but, surprisingly, has not been reported in Gymnosperms. 'Monocarpy' (De Candolle, 1818) or 'Hapaxanty' (Warming, 1884) were original designations used in Angiosperm classifications to distinguish annual and biennial herbs that flower and die following one or two growing seasons. Since these classifications, monocarpy has often been mistakenly used as an antonym for perennial. However, monocarpy also concerns some perennial plants living longer than two years, and occurs in a wide range of species, from annual herbs to long-lived trees (**Figure 1**) (Richard, 1996; Whitmore, 1989; Turner, 2001; Thomas, 2011).

As no exhaustive list of monocarpic perennials has been published since Hallé & Oldeman (1970), we attempt hereafter to provide an updated overview of monocarpy in long-lived Angiosperms to fill this gap (**Figure 2**) (for a complete list of the 214 monocarpic perennials recorded see **Appendix 1**). Monocarpy is a widespread strategy in palms (Arecaceae), with well-known representatives such as the talipot palm (*Corypha umbraculifera*), the giant fishtail palm (*Caryota obtusa*), the sugar palm (*Arenga pinnata*), and the rattan palm (*Plectocomia elongata*). A few dicotyledon palm-like trees are also renowned for showing a monocarpic strategy, such as the spathe tree (*Spathelia ulei*, Rutaceae), the maypole tree (*Sohnreyia excelsa*, Rutaceae), the pinnate tree (*Dendroseris pinnata*, Asteraceae), and the makua tree (*Harmsiopanax ingens*, Araliaceae). All these species share a body construction consistent with Holttum's architectural model (Hallé & Oldeman, 1970). They are structurally monocarpic as individuals (1) grow through a unique apical meristem (i.e. monocaulous), (2) flower terminally, and (3) die due to the absence of functional lateral meristems (**Figure 1A, B**) (Simmonds 1980; Davies & Gan, 2012; Hallé & Keller, 2019).

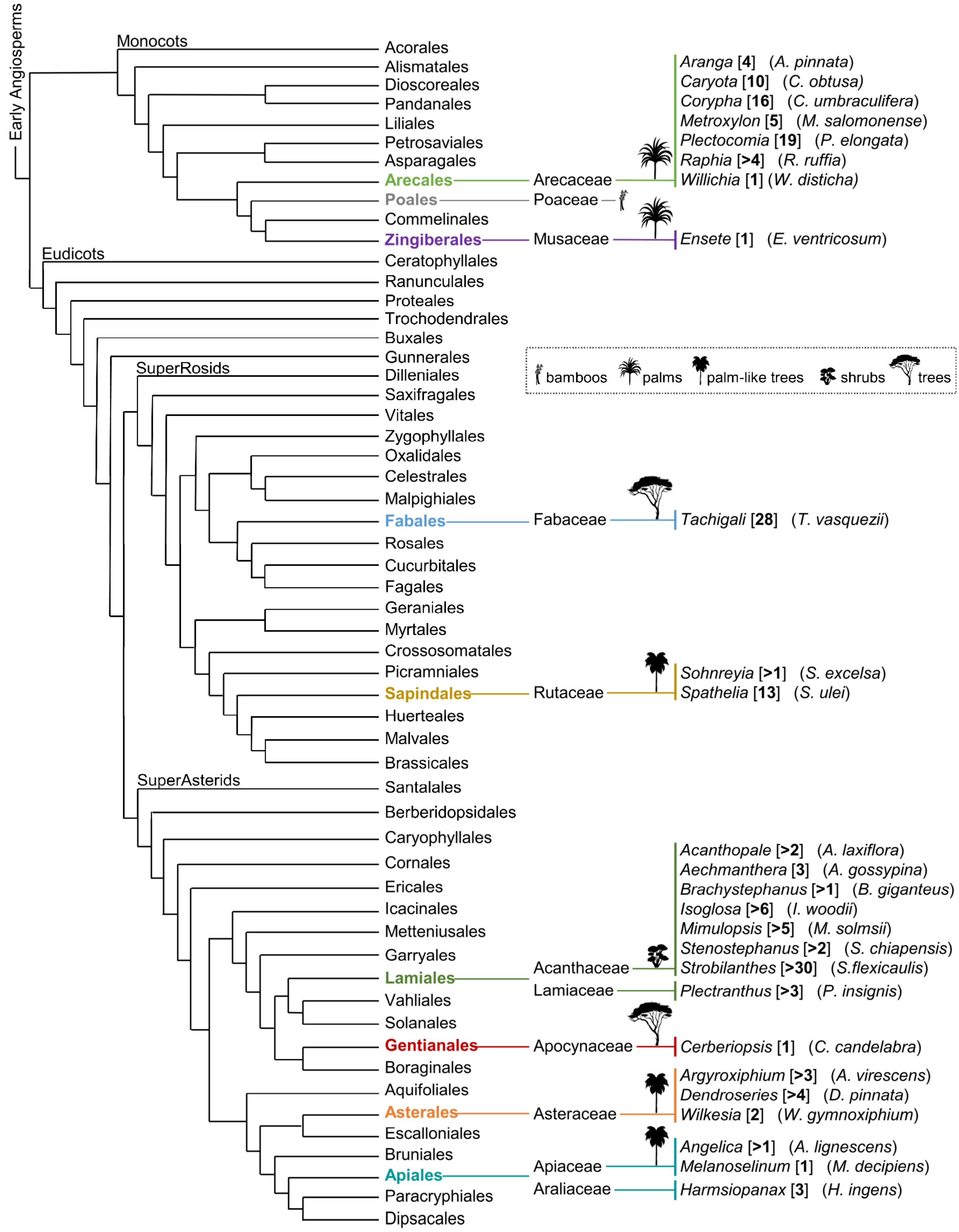

Figure 2. Updated review of monocarpic perennials. The number of monocarpic species recorded within each genus is shown in square brackets and a representative is indicated. Monocarpy occurs in perennial bamboos, palms, palm-like trees, shrubs, and trees. At least 214 species are recorded, including 126 branched perennials of which 29 species are rainforest canopy trees. For a complete overview of monocarpy in bamboos (17 genera, more than 45 species) see Janzen et al. (1976).

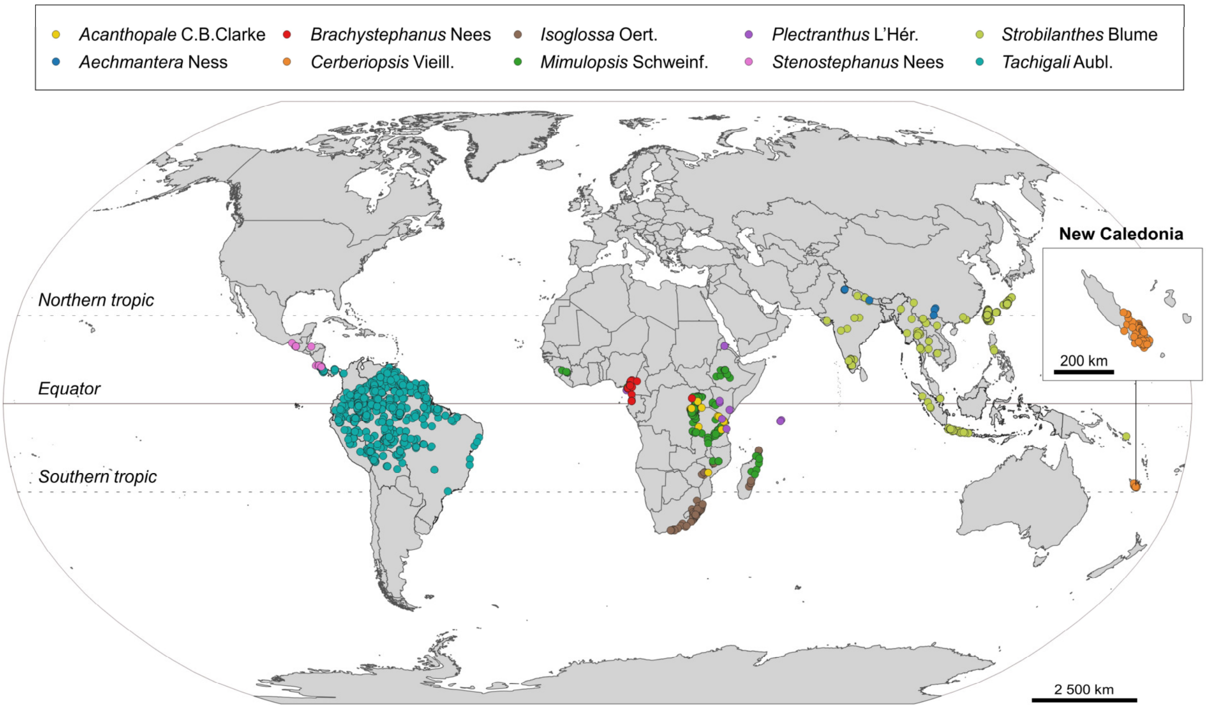

Figure 3. Worldwide distribution of monocarpic branched perennials from GBIF occurrence data (doi:10.15468/dl.8fmxev). All species belong to ten tropical or subtropical genera of which eight genera include monocarpic shrubs and two genera, *Cerberiopsis* (Apocynaceae) and *Tachigali* (Fabaceae), include monocarpic canopy trees. Monocarpic bamboos (e.g. *Chusquea*, *Phyllostachys*, and *Sasa* sp.) are not indicated for legibility concerns.

Since the monocaulous habit is structurally related to the monocarpic strategy in perennials species, some rosette plants have been erroneously characterized as monocarpic (e.g. *Agave americana*, *Echium wildpretii*, *Fourcroya gigantea*, *Lobelia deckenii*, *Puya raimondii*, *Yucca whipplei*). However, these species are not monocarpic per se since they exhibit both sexual and clonal reproduction. The flowering event may synchronously involve one or few ramets without concerning the whole plant (Sgorbati et al., 2004; Munné-Bosch et al., 2016; Simcha, 2017; Hughes, 2017).

Much rarer, a few studies have reported the occurrence of the monocarpic strategy in branched perennial species (**Figure 3**). These latter plants have multiple functional meristems that are as many opportunities to flower at different times (**Figure 1C, D**). They are not structurally monocarpic and lead to a new perception of monocarpy decoupled from the monocaulous habit (Simmonds, 1980; Davies & Gan, 2012; Thomas, 2011). To the best of our knowledge, these plants are included in seventeen bamboo taxa, such as the genera *Chusquea*, *Phyllostachys*, and *Sasa* (Poaceae) (Janzen, 1976; Keeley & Bond, 1999; Miyazaki et al., 2009; Abe & Shibata, 2012). They also occur in seven Acanthaceae genera of tropical shrubs (*Acanthopale*, *Aechmanthera*, *Brachystephanus*, *Isoglossa*, *Mimulopsis*, *Stenostephanus*, *Strobilanthes*) (Tweedie, 1965; van Steenis, 1978; Wood, 1994; Carine & Scotland, 2000; Daniel, 2006; Kakishima et al., 2019). Finally, they are included in two taxa of tropical and subtropical canopy trees, the genera *Tachigali* and *Cerberiopsis* (Veillon, 1971; Foster, 1977; Poorter et al., 2005; Read et al., 2006).

5. Monocarpy in trees: a worldwide rare strategy

Monocarpy in trees is worldwide rare. After a careful screening of the literature, we recorded 29 monocarpic canopy trees belonging to the tropical and subtropical genera *Tachigali* Aubl. (Fabaceae) and *Cerberiopsis* Vieill. (Apocynaceae) (**Table 1**). On the one hand, the genus *Tachigali* comprises 70 species of which 28 are monocarpic trees (Gentry, 1993; Van Der Werff, 2008; Van Der Werff & Zamora, 2010). Since the earliest report of a monocarpic *Tachigali* (Foster, 1977), *T. versicolor* and *T. vasquezii* have received the most attention (Kitajima & Augspurger, 1989; Loveless et al., 1998; Forget et al., 1999; Poorter et al., 2005). Both are pioneer trees reaching 35m in height and occurring in disturbed rainforests from Costa Rica to Colombia (*T. versicolor*) and Ecuador to northern Bolivia (*T. vasquezii*). On the other hand, the genus *Cerberiopsis* includes 3 species of which only one, *C. candelabra*, is a monocarpic tree reaching 30m in height and growing exclusively in the ultramafic rainforests and disturbed areas of New Caledonia (**Figure 1D**) (Veillon, 1971; Read et al., 2006, 2008).

Inheriting the work of E.J.H. Corner, such as 'The Durian theory' that characterized monocarpy and monocauly as relics of the regular features of early Angiosperms (Corner, 1949, 1953), several authors have defined these monocarpic tree lineages as archaic (Veillon, 1971), suicidal (Foster, 1977), or even as an evolutionary bottleneck (Poorter et al., 2005). However, while the monocarpic strategy in trees is extremely rare, *T. versicolor*, *T. vasquezii*, and *C. candelabra* are highly abundant in their native areas (Kitajima & Augspurger, 1989; Poorter et al., 2005; Read et al., 2006). Thus, what do we know about the ecology of these species?

Table 1. Exhaustive list of the 29 monocarpic canopy trees worldwide belonging in the two tropical and subtropical genera *Tachigali* Aubl. (Fabaceae) and *Cerberiopsis* Vieill. (Apocynaceae).

Species	**Family**	**Native area**	**References**
Cerberiopsis candelabra Vieill.	Apocynaceae	New Caledonia	Veillon, 1971; Read et al., 2006, 2008
Tachigali alba Ducke	Fabaceae	Northern Brazil North, Guyana	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali amplifolia Ducke	Fabaceae	Northern Brazil, French Guiana, Suriname	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali argyrophylla Ducke	Fabaceae	Northern Brazil, Peru	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali barnebyi V.D.Werff	Fabaceae	Northern Brazil	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali candelabrum V.D.Werff	Fabaceae	Northern Brazil	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali catingae Ducke	Fabaceae	Northern Brazil	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali cenepensis V.D.Werff	Fabaceae	Peru	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali dwyeri R.S.Cowan	Fabaceae	Venezuela	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali eriopetala Ducke	Fabaceae	Northern Brazil	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali ferruginea V.D.Werff	Fabaceae	Ecuador	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali formicarum Harms	Fabaceae	Northern Brazil, Colombia, Ecuador, Peru	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali goeldiana Huber	Fabaceae	Northern Brazil	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali grandistipulata Harms	Fabaceae	Northern Brazil	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali guianensis Benth.	Fabaceae	Northeast South America	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali longiflora Ducke	Fabaceae	Northern Brazil, Peru	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali micrantha L.O.Williams	Fabaceae	Peru	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali odoratissima Spruce	Fabaceae	Northern Brazil, Colombia, Venezuela	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali pimichinensis R.S.Cowan	Fabaceae	Venezuela	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali plumbea Ducke	Fabaceae	Northern Brazil, Colombia, Venezuela	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali poeppigiana Tul.	Fabaceae	Bolivia, Northern Brazil, Colombia, Peru	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali prancei H.S.Irwin	Fabaceae	Northern Brazil, Brazil West-Central	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali ptychophysca Spruce	Fabaceae	Northern Brazil, Colombia	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali pubiflora Benth.	Fabaceae	Guyana, Venezuela	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali richardiana Tul.	Fabaceae	Northern Brazil, French Guiana	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali rigida Ducke	Fabaceae	Northern Brazil, Colombia, Venezuela	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali vasquezii Pipoly	Fabaceae	Bolivia, Brazil, Ecuador, Peru	Turner, 2001; Poorter et al., 2005
Tachigali vaupesiana V.D.Werff	Fabaceae	Northern Brazil, Colombia	V.D.Werff, 2008; V.D.Werff & Zamora, 2010
Tachigali versicolor L.O.Williams	Fabaceae	Northern Colombia, Costa Rica, Panamá	Foster, 1977; Kitajima & Augspurger, 1989

6. What do we know about monocarpic trees?

The ecology of monocarpic branched perennial species has long been of interest to evolutionary biologists. Indeed, the persistence of the monocarpic strategy in such plants is questionable since a premature death of the individual in the decades before the flowering will prevent any descendants. Since Cole (1954), several models have been performed to understand the preconditions for monocarpic life histories persistence in trees (Metcalf et al., 2003; Ress & Rose, 2002; Kuss et al., 2008, Vaupel et al., 2013). From these predictions, three main hypotheses have been proposed considering (1) tree size at maturity, (2) stand regeneration, and (3) population monodominance and masting.

Tree size at maturity – As the timing of flowering and cost of reproduction are key determinants of plant fitness, monocarpic trees should flower at a size that maximizes their reproductive output and offsets the lack of successive flowering (Young, 1990; Youngs & Augspurger, 1991; Shaffer & Rosenzweig, 1977; Metcalf et al., 2003). Therefore, monocarpy could be of selective advantage if delayed flowering reduces the cost of reproduction by increasing tree size-related fecundity (Cole, 1954; Schaffer, 1974a, b; Bell, 1976, 1980). Read et al. (2006) demonstrated in *Cerberiopsis candelabra* that flowering occurs over a wide range of tree sizes, with an almost complete overlap between flowering and nonflowering trees. This result emphasizes that age at flowering is not the result of a strict age-size threshold but is intimately related to the tree's developmental trajectory (Burd et al., 2006; Read et al., 2006, 2008).

Stand regeneration – The second hypothesis suggests that monocarpy is of selective advantage if trees are more competitive than polycarpic ones during stand regeneration. Since Cole (1954), it has been proposed that the fitness benefit gained by polycarpic over monocarpic strategy is very slight. Monocarpy is advantageous if the survival rate of monocarpic juveniles is higher than those of conspecific adults and other polycarpic juveniles (Bryant, 1971; Charnov & Schaffer, 1973; Stearns, 1976; Vaupel et al., 2013). As expected, monocarpic *Tachigali* species show higher seedling survival rates than other polycarpic trees, but these rates don't maintain beyond the sapling stage (Kitajima & Augspurger, 1989; Poorter et al., 2005). Therefore, high growth rates as well as high survival rates could offset the negative demographic effect of monocarpic reproduction. Trees with high growth rates reach sexual maturity quickly and reduce their probability of pre-flowering mortality (Foster, 1977; Poorter et al., 2005).

Population monodominance and masting – The third hypothesis suggests that monocarpy would drastically optimize individual fitness if combined with gregariousness (monodominance) and synchronous flowering (masting) at the population level (Simmonds, 1980; Augspurger, 1981; Young & Augspurger, 1991; Che-Castaldo & Inouye, 2011). Masting or big-bang reproduction (Humphries & Stevens, 2001) higher the reproductive success of populations by increasing (1) cross-pollination and (2) seed survival thanks to predator satiation (Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002; Schauber et al., 2002). Subsequently, the synchronous death of parental trees in monodominant populations facilitates seedling recruitment by opening large canopy gaps (Janzen, 1976; Struhsaker, 1997; Tsvuura et al., 2011). Monodominance and masting syndromes have been reported in several monocarpic branched species, such as *Strobilanthes flexicaulis* (Kakishima et al., 2011, 2019), *Tachigali versicolor* (Foster, 1977; Kitajima & Augspurger, 1989), and *Cerberiopsis candelabra* (Read et al., 2006, 2008, 2021).

7. Value of retrospective approaches

All studies exploring monocarpy in trees have focused on the population and community levels. They reveal key preconditions for the evolution and persistence of monocarpic life histories in branched perennial plants. However, the developmental trajectories of the species remain unknown. This remaining issue is of particular interest to this thesis.

Trees are immobile organisms whose bodies continuously reflect the fate of meristems, determined both by an endogenous species-specific program and by the exogenous conditions imposed by the environment (Hallé et al., 1978; Barthélémy et al., 1989; Barthélémy & Caraglio, 2007). Retrospective approaches lie in the study of morpho-anatomical traits, such as growth rings, leaf and inflorescence scars, or pith size, which retrospectively reflect past meristem functioning. These traits are used to define structural regularities all along the axis constituting the plant body. Plant structural regularities, such as variations in growth ring number or phytomer length (the stem portion separating a leaf from another), reflect the relative temporality of plant development (Passo et al., 2002; Heuret et al., 2006; Nicolini et al., 2012; Noyer et al., 2019). Growth ring and phytomer analyses have conceptual proximity. They both consider growth increments to reconstruct plausible chronosequences of tree development. (De Reffye, 1991; Heuret et al., 2000; Passo et al., 2002; Taugourdeau et al., 2012; Mangenet, 2013). While the study of growth rings investigates the dynamics of the vascular cambium (i.e. the plant's secondary growth or enlargement) (Killman & Thong, 1995; Rozendaal & Zuidema, 2011; Schweingruber, 2012; De Micco et al., 2019), the study of phytomers explores the dynamics of the primary meristems (i.e. the plant's primary growth or elongation) (Heuret et al., 2002; Grosfeld &

Barthélémy, 2004; Zalamea et al., 2008; Nicolini et al., 2012).

Retrospective approaches analyze the fundamental relationship between 'structure', 'function', and 'time'. This latter observation could explain why they have long been unused in tropical and subtropical regions. For a long time, it was accepted that tropical and subtropical trees did not experience sufficiently severe seasonality to show distinct structural regularities. However, phenological patterns of growth, branching, and flowering are expressed according to seasons and on an annual temporality in several tropical trees (van Schaik et al., 1993; Reich, 1995; Sakai, 2001; Zalamea et al., 2012; Sakai & Kitajima, 2019). In addition, various tropical species have been reported with distinct and annual growth rings (Worbes, 2002; Brienen et al., 2016; Schöngart et al., 2017; Rodriguez et al., 2022).

Retrospective approaches have long lagged behind prospective ones based essentially on growth monitoring. Nevertheless, they are well suited to studying the developmental patterns of trees whose size and lifetime exceed the human scale and involve strong methodological constraints (Condit, 1995; Sheil, 1995; Worbes, 1995; Mangenet, 2013). In this thesis, we conjointly used two retrospective approaches, one qualitative (i.e. architectural analysis) and one quantitative (i.e. dendrochronological analysis), to reconstruct the developmental trajectories of the monocarpic canopy tree *Cerberiopsis candelabra* (**Figure 4**).

8. Problematic and objectives

At the individual scale, the monocarpic life history could impact long-term persistence in trees since it carries two substantial risks. (1) The plant is putting its whole reproductive effort into a unique flowering event at a time that may not be favorable for seedling recruitment (Kitajima & Augspurger, 1989; Read et al., 2008, 2021), and (2) the plant fitness depends on a probability of pre-flowering mortality that should be close to zero to guaranty the transmission of the individual's genetic heritage (Poorter et al., 2005; Burd et al., 2006).

According to the so-called 'resource allocation principle' (Levins, 1968; Bazzaz et al., 2000; Reekie & Bazzaz, 2005), trees that do not invest large amounts of carbon and nutrients into flowering each year are supposed to reallocate these resources in the other two fundamental dimensions of plant demography: growth and survival (Harper & White, 1974; Stearns, 1989; Obeso, 2002; Thomas, 2011; Weiner, 2012). In this thesis, we investigate the developmental patterns of a monocarpic tree. We aim to explore the morpho-anatomical bases of monocarpy, its underlying ecological implications, and functional adaptations. The species of our particular interest is *Cerberiopsis candelabra* Vieill., a monocarpic canopy tree endemic from New Caledonia.

- What developmental patterns distinguish *C. candelabra* from its two sister species belonging to the genus *Cerberiopsis*?
  - Can we highlight architectural traits that lead to monocarpy?
  - What is the developmental phenology of growth, branching, and flowering processes?
  - How are these processes coordinated within the plant body?
  - How does New Caledonia seasonality influence these processes?
- What is the ecology of *C. candelabra* seedlings?
  - Do the seedlings show high survival and growth rates as expected for a monocarpic tree?
  - What is their developmental phenology under full light conditions?
- Are functional adaptations required to sustain the monocarpic strategy at the individual scale?
  - Can we identify functional traits that enhance *C. candelabra's* performances on highly-constrained ultramafic soils?
  - Do trees exhibit biomechanical adaptations to improve their probability of survival?

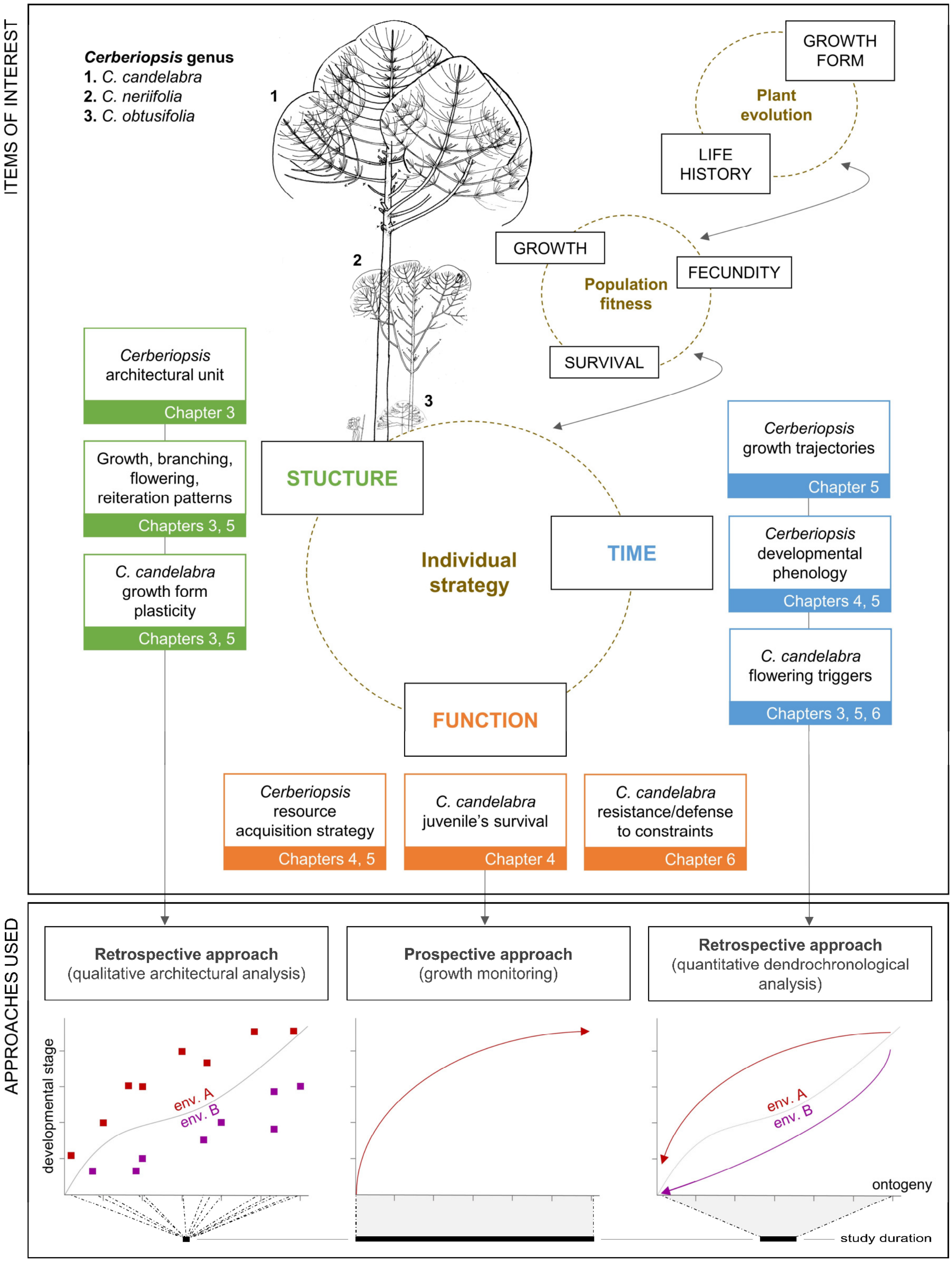

Figure 4. Thesis heuristic map. We investigate the developmental patterns of the monocarpic tree *Cerberiopsis candelabra*. with considerations of its sister species (*C. neriifolia* and *C. obtusifolia*) and its environment. Three approaches are conjointly used: a qualitative architectural analysis and a quantitative dendrochronology analysis (retrospective approaches), and a growth monitoring (prospective approach). Bottom figures: arrows in red and purple indicate the temporal direction of the study along the ontogenic chrono-sequence.

9. Thesis outline

Combining an architectural analysis, an integrative dendrochronological analysis, and a growth monitoring, we aim to improve our understanding of the structure-function-time relationships that underlie the developmental trajectories of *C. candelabra* (**Figure 4**). The relationship between a growth form and a life history is dynamic, multidimensional, and the result of a complex evolutionary history. Therefore, we examine the ontogeny of *C. candelabra* with considerations to (1) the ontogeny of its two polycarpic sister species and (2) the seasonality and abiotic constraints of its environment.

Chapter 2 is a general methodology chapter presenting the main feature of New Caledonia, the *Cerberiopsis* species, the sites studied, and the sampling carried out.

Chapter 3 analyzes the architecture of the three species belonging to the genus *Cerberiopsis* and underlines the architectural traits that sustain the monocarpy of *C. candelabra.*

Chapter 4 presents the survival and growth rates of 134 *C. candelabra* seedlings established under natural conditions that we monitored for 20 months.

Chapter 5 quantitatively analyzes the growth, branching, and flowering patterns of the three *Cerberiopsis* species and highlights the high developmental synchronism of *C. candelabra*.

Chapter 6 presents a new type of annual growth ring due to circular tension wood in *C. candelabra*, a potential functional requirement to sustain its monocarpic life history.

Chapter 7 is a general discussion summarizing the developmental patterns of *C. candelabra* and discussing the contributions of this study to our understanding of the ecology of monocarpic trees.

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Appendix 1. Updated review of monocarpic perennials based on current scientific literature. At least 214 species are recorded, including 126 branched perennials of which 29 species are rainforest canopy trees. For a complete overview of monocarpic bamboos see [8]. Rosette plants exhibiting both sexual and clonal reproduction are excluded (e.g. *Agave americana*, *Echium wildpretii*, *Fourcroya gigantea*, *Lobelia deckenii*, *Puya raimondii*, *Yucca whipplei*).

	Familly	**Genus**	**Species**	**Representative**	**Type**	**Refs**
monocotyledon	Arecaceae	*Arenga*	4	*A. pinnata*	palm tree	[1, 2]
		Caryota	10	*C. obtusa*	palm tree	[3, 4]
		Corypha	16	*C. umbraculifera*	palm tree	[1, 5]
		Metroxylon	5	*M. salomonense*	palm tree	[1, 3]
		Plectocomia	19	*P. elongata*	palm tree	[5, 7]
		Raphia	> 4	*R. ruffia*	palm tree	[1, 6]
		Wallichia	1	*W. disticha*	palm tree	[2, 7]
	Musaceae	*Ensete*	1	*E. ventricosum*	banana tree	[1, 5]
	Poaceae	17	> 45	*Sasa veitchii*	bamboo	[8, 9]
dicotyledon	Acanthaceae	*Acanthopale*	> 2	*A. laxiflora*	small shrub	[10, 11]
		Aechmanthera	3	*A. gossypina*	small shrub	[12, 13]
		Brachystephanus	> 1	*B. giganteus*	small shrub	[2, 14]
		Isoglossa	> 6	*I. woodii*	small shrub	[15, 16]
		Mimulopsis	> 5	*M. solmsii*	large shrub	[10, 17]
		Stenostephanus	> 2	*S. chiapensis*	small shrub	[10, 18]
		Strobilanthes	> 30	*S. flexicaulis*	large shrub	[5, 19, 20]
	Apicaeae	*Angelica*	> 1	*A. lignescens*	palm-like tree	[1, 21]
		Melanoselinum	1	*M. decipiens*	palm-like tree	[1, 21]
	Apocynaceae	*Cerberiopsis*	1	*C. candelabra*	canopy tree	[22, 23, 24]
	Araliaceae	*Harmsiopanax*	3	*H. ingens*	palm-like tree	[25, 26]
	Asteraceae	*Argyroxiphium*	> 3	*A. virescens*	palm-like tree	[26, 27]
		Dendroseris	> 4	*D. pinnata*	palm-like tree	[26, 28]
		Wilkesia	2	*W. gymnoxiphium*	palm-like tree	[26, 29]
	Fabaceae	*Tachigali*	28	*T. vasquezii*	canopy tree	[30, 31, 32]
	Lamiaceae	*Plectrantus*	> 3	*P. insignis*	small srub	[2, 5]
	Rutaceae	*Sohnreyia*	> 1	*S. excelsa*	palm-like tree	[1, 33]
		Spathelia	13	*S. ulei*	palm-like tree	[1, 5, 33]

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Chapter 2

Gregarious *C. candelabra* trees flowering in a rainforest patch at Mont-Dore (New Caledonia) © C. Salmon & J.M. Bore

Chapter 2 provides an overview of the particularities of New Caledonia. It introduces the main features of the three species belonging to the genus *Cerberiopsis*, the sites studied, and the sampling carried out. Although the specific methodology of each study is presented in detail in its dedicated chapter, we felt it advisable to add a general methodology chapter, to include elements that the article format of the following chapters did not allow us to address.

General methodology

1. New Caledonia: location, orography, and climate

New Caledonia is a South-West Pacific archipelago located 130km north of the Tropic of Capricorn, about 1400km east of Australia, and 2000km north of New Zealand (**Figure 1A**). It includes a main island, *Grand Terre*, and other smallest islands such as the Loyalty Islands (Ouvéa, Lifou, Maré), the Belep islands, and the Ile des Pins. The Grande Terre is a thin land strip about 400km long and 50-70km large, covering a total area of 16,460km^2. Standing on the Norfolk continental ridge, this territory presents a contrasting relief characterized by a long mountain range whose highest peaks, Mt. Panié and Mt. Humbolt, culminate respectively at 1,628 and 1,618m altitudes (**Figure 1B**). This orography results in distinct regimes on both coastal plains of the island, in terms of mean annual precipitation ($\overline{map}$), rainy day ($\overline{mar}$), and wind speed ($\overline{maw}$) (**Figure 1D, E**). On the northeastern coast, upwind, the climate is more humid and windy ($\overline{map}$ = 4000mm.y^{-1}; $\overline{mar}$ = 134 days.y^{-1}; $\overline{maw}$ =19 knots), then on the southwestern coast, downwind, less exposed ($\overline{map}$ = 800 mm.y^{-1}; $\overline{mar}$ = 86 days.y^{-1}; $\overline{maw}$ = 12 knots) (MétéoFrance, 2008a; Maitrepierre, 2012). More broadly, New Caledonia's climate is subtropical and characterized by a cool-dry season from June to September and a warm-wet season from December to March, interspersed by transitional periods. Like many archipelagos located in the intertropical region, New Caledonia is exposed to the trade winds (south-east winds > 19km.h^{-1}) for about 157 days per year. From November to April, under the influence of the Southern Pacific climate oscillation (El Niño / La Niña), these winds can strengthen and give rise to tropical cyclones and storms (MétéoFrance, 2008b; Ibanez et al., 2019b). These extreme events are nearly annual and an integral part of New Caledonia's climate.

2. A subtropical biodiversity hotspot

New Caledonia is renowned as one of the world's most significant and smallest biodiversity hotspots for conservation priorities (Myers, 1988; Myers et al., 2000). It hosts more than 3400 vascular species of which about 75% are endemic (Morat et al., 2012; Munzinger et al.,

2022) and widely threatened due to 80% loss of natural vegetation (Sloan et al., 2014; Ibanez et al., 2019a).

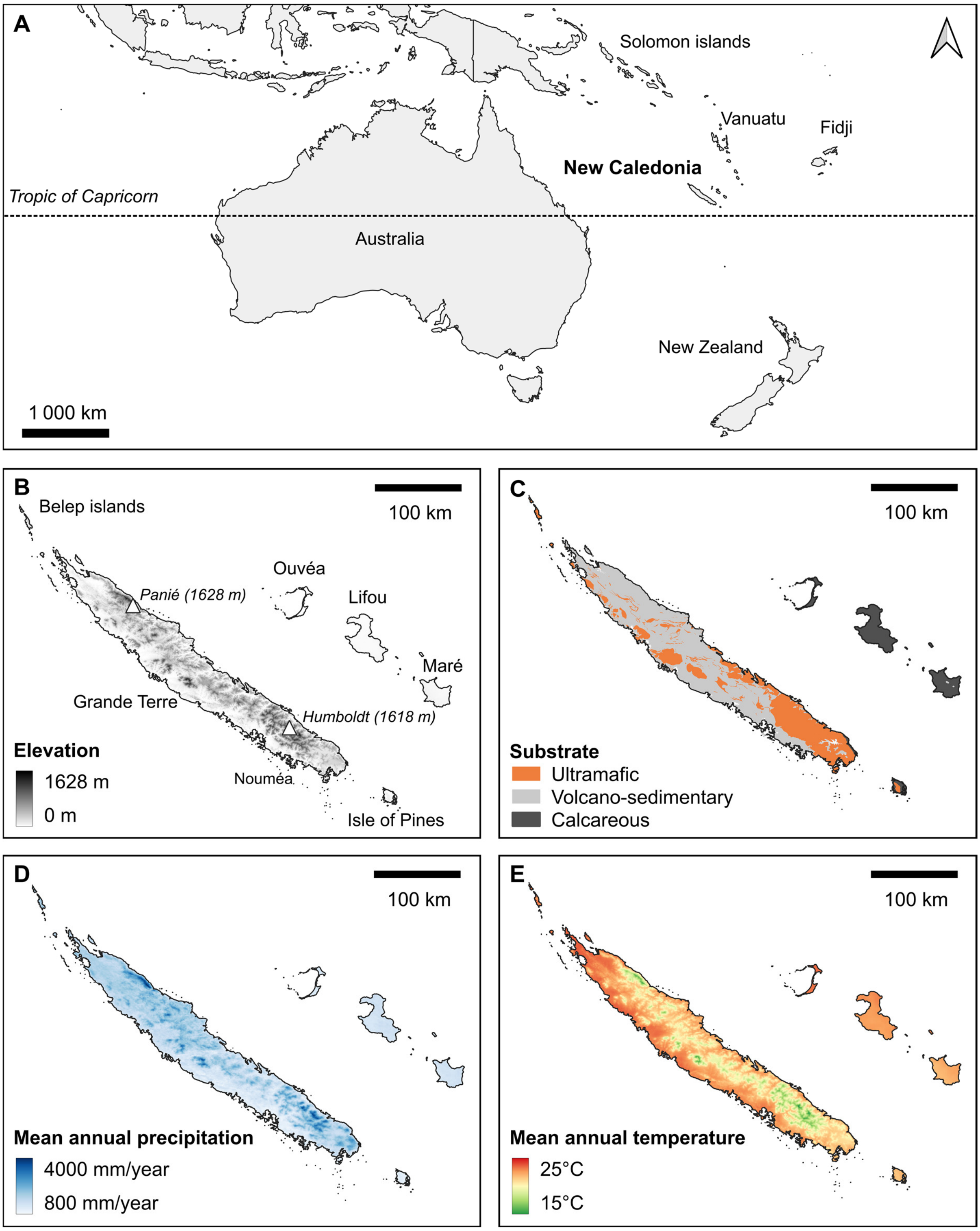

Figure 1. New Caledonia's main geographic and climatic characteristics. (**A**) New Caledonia location in the South-West Pacific Ocean; (**B**) Orography of the main island; (**C**) Distribution of the main substrates covering the archipelago; (**D - E**) Mean annual precipitation and temperature. Climat data are available at WordClim 2 (doi:10.1002/joc.5086).

The high taxonomic diversity and the strong endemism of the flora are largely due to the isolation, orography, and climate of the main island, but also to its geological history (Pillon, 2012; Pouteau et al., 2015; Isnard et al., 2016). From the Paleocene to the Eocene, New Caledonia was submerged and obducted under the Pacific plate at 34Ma, leading to its covering by an ultramafic substrate (Cluzel et al., 2012; Maurizot & Campbell, 2020). This substrate has led to a great diversity of soils resulting from the alteration of peridotites, poor in nutrients (P, K) and rich in metals and trace metals (Ni, Mn, Cr, Co, Fe) (Isnard et al., 2016; Jaffré, 2022). These soils covering 1/3 of the main island are mainly encountered in the south region (**Figure 1C**). They host megadiverse ecosystems, from the emblematic sclerophyll scrublands, the so-called 'maquis', to the rainforests.

3. An intriguing vascular flora

New Caledonia is a privileged place to investigate the evolution and adaptation of plants. The archipelago's isolation and ultramafic substrates have acted as drastic environmental filters on species radiation (Murienne et al., 2005; Grandcolas et al., 2008). Therefore, the flora of New Caledonia is considered disharmonic as some taxa are either over- or under-represented compared to continental flora (Jaffré, 1980; Pillon et al., 2010, 2019). Among the intriguing endemic species that grow on ultramafic substrates, we can mention *Araucaria columnaris* (Araucariaceae), a 60m tall pine with a columnar growth pattern (Veillon, 1980); *Parasitaxus usta* (Podocarpaceae), the only known parasitic gymnosperm (Jaffré, 1995); or *Pycnandra acuminata* (Sapotaceae), a nickel-hyperaccumulator tree with a neon blue latex (Isnard et al., 2020) (**Figure 2D, F, J**). Finally, we can mention the endemic taxon of our particular interest: the genus *Cerberiopsis* (Apocynaceae) which includes three species exclusively occurring on ultramafic substrates. *Cerberiopsis candelabra* (Vieill.) is the only canopy tree of the genus and is renowned for its monocarpic life history (Veillon, 1971). Although its flowering strategy is rare, the species is widely distributed in low- and mid-elevation rainforests where it forms gregarious and often monodominant populations (**Figure 2A, F, G**).


A
B
C
D
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Figure 2. Illustration of New Caledonia endemic flora diversity. (**A**) Inflorescences of the monocarpic tree *Cerberiopsis candelabra*, the main actor of this thesis; © P. Heuret. (**B**) Inflorescence of the polycarpic treelet *Cerberiopsis neriifolia*, the second species belonging to the genus *Cerberiopsis*; © C. Salmon. (**C**) Flower of the polycarpic shrub *C. obtusifolia*, the third species of the genus *Cerberiopsis*; © C. Salmon. (**D**) *Parasitaxus usta*, the only know parasitic gymnosperm worldwide; © M. Deus. (**E**) *C. neriifolia* reaching 15m tall in a riparian maquis; © V. Hequet. (**F**) *C. candelabra* (foreground) reaching 20m tall and *Araucaria columnaris* (background) reaching 50m tall; © J.M. Bore. (**G**) Gregarious *C. candelabra* growing in a rainforest around the trunk of an old dead conspecific; © C. Salmon. (**H**) An emblematic maquis vegetation (low sclerophyll scrubland) of New Caledonia's southern region; © C. Salmon. (**I**) C. obtusifolia reaching 2.5m tall in an open maquis; © C. Salmon. (**J**) The neon blue latex of *Pycnandra acuminata*, a nickel hyperaccumulator tree; © S. Isnard.

C. candelabra trees can reach up to 30m in height for a maximum observed diameter at a breast height of 79cm (Read et al., 2006, 2008). Some smaller individuals are also recorded in disturbed open areas along cleared roadsides and trails. In contrast, the two remaining species of the genus, *C. neriifolia* (S.Moore) and *C. obtusifolia* (Van Heurck & Müll.Arg.) are polycarpic (i.e. iteroparous) species growing exclusively in the maquis (**Figure 2H**). *C. neriifolia* is a treelet reaching a maximum height of 15m and micro-endemic of the Grande Terre's southeastern coastal plains (**Figure 2B, E**). *C. obtusifolia* is a shrub reaching a maximum height of 8m and is micro-endemic to the northwestern coastal plains (**Figure 2C, I**). Both species are classified as vulnerable as they show population decline (Endemia, 2022; IUCN, 2022). In New Caledonia, most species extinctions are due to habitat loss and fragmentation consequently to intensive nickel mining activities, past logging, and human-triggered bushfires that burned every year 2% of the main island (Curt et al., 2015; Gomez et al., 2015).

4. Study sites

All data used in this thesis have been collected in New Caledonia. With the support of the UMR AMAP of Nouméa, two field missions were realized from March to October 2020 (8 months) and from April 2021 to January 2022 (10 months). The samplings were conducted in 7 sites distributed throughout the main island (**Figure 3**).

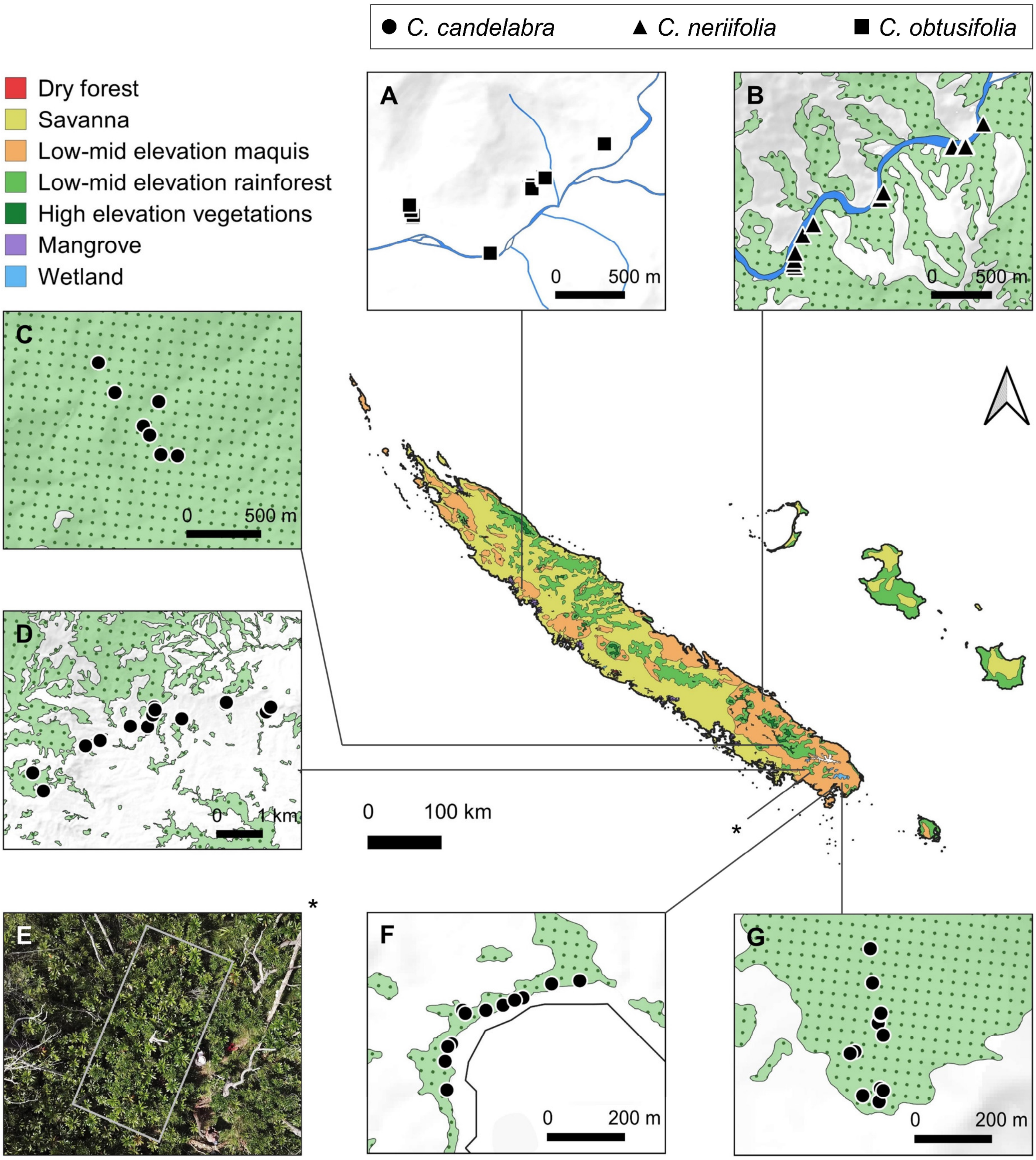

Figure 3. Study site locations. The descriptions and samplings conducted for the retrospective and comparative analyses have been performed on 20 individuals per species located at (**A**) Taléa (commune of Voh) for *C. obtusifolia* species; (**B**) Nékadé (commune of Thio) for *C. neriifolia* species; and (**C**) Rivière bleu (commune of Yaté) and (**D**) Mouirange (commune of Mont-Dore) for *C. candelabra* species. (**E**) An aerial view of the forestry plot located at Col des deux tétons (commune of Mont-Dore) where a 22-month growth monitoring have been conducted on 134 *C. candelabra* seedlings from May 2020 to January 2022. (**F** & **G**) Location of *C. candelabra* trees samples for further wood analysis at (F) Baie Nord (Commune of Mont-Dore) and (G) Pic du Grand Kaori (commune of Yaté). Vegetation data are available at doi:10.5281/zenodo.7376634.

The descriptions and samplings performed for the comparative (**Chapter 3**) and retrospective analyses (**Chapters 5, 6**) were realized on individuals located at Mouirange (commune of Mont-Dore: 22°12'34.54"S, 166°40'35.64"E) and Rivière bleue (commune of Yaté: 22°4'55.43"S, 166°37'46.42"E) for *C. candelabra* species, and Nékadé (commune of Thio: 21°42'2.70"S, 166°19'21.95"E) and Taléa (commune of Voh: 20°59'25.84"S, 164°44'30.17 "E) for *C. neriifolia* and *C. obtusifolia* species. The dataset used for the prospective analysis (**Chapter 4**) was obtained from a 20-months growth monitoring in a forest plot located at Col des deux tétons (commune of Mont-Dore: 22°12'23.72 "S, 166°42'13.91 "E). Wood samples from 60 *C. candelabra* individuals were collected at the previous study sites and two additional, at Baie Nord (commune of Mont-Dore: 22°19'17.38 "S, 166°51'33.66 "E) and Pic du Grand Kaori (commune of Yaté: 22°17'19.56 "S, 166°53'47.24 "E). Only the results of a limited number of these samples are presented (**Chapter 6**). The remaining ones are undergoing further analysis and are the subject of a forthcoming study.

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Chapter 3

Flowering *C. candelabra* trees in the rainforest patch of Mouirange (New Caledonia) © C. Salmon

Chapter 3 is an original research article analyzing the architecture of the three species belonging to the genus *Cerberiopsis*. Based on a punctual approach (i.e. a qualitative architectural analysis), we first explore the architectural similarities and dissimilarities between the *Cerberiopsis* species. We secondly underline *C. candelabra*'s growth form plasticity in habitats of differing openness and the architectural features that support its monocarpic life history.

Architectural traits underlie growth form diversity, and polycarpic versus monocarpic life histories in the genus *Cerberiopsis* (Apocynaceae)

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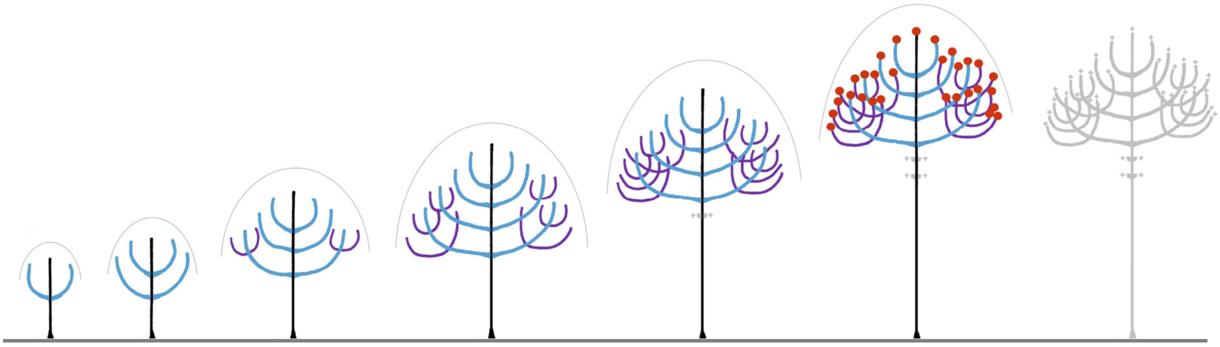
Running head

Salmon et al. — Architecture of the genus *Cerberiopsis*.



Abstract

Plant architecture strongly influences plant growth habits, as it determines the arrangement, function, and fate of meristems. How architecture could be involved in the monocarpic life history, i.e. dying after flowering, remains poorly investigated. Monocarpy is evident in some species since there are annual or because their single stem flower apically. But monocarpy in long-lived branched trees is rare and remains poorly understood. We aim to highlight the architectural features involved in the monocarpic strategy of *Cerberiopsis candelabra*, a rainforest tree endemic to New Caledonia. We conducted a comparative analysis of the genus, counting three species representing different growth habits. Twenty plants of each species are studied at different ontogenic stages. We compared their developmental sequence and analyzed their processes of growth, branching, flowering, and reiteration. We identified a combination of traits that distinguish the species, and we found a syndrome of two architectural features that support the monocarpic strategy in *C. candelabra*: the synchronous flowering of all terminal meristems and the absence of delayed branching. Flowering in *C. candelabra* preferentially occurs when the complete architectural sequence is developed but the plant never shows signs of senescence, suggesting that environmental stresses, such as wind disturbance, could be the main trigger for flowering. The architecture of *C. candelabra* is suggested to be the most derived within the genus.

Key Words

Cerberiopsis – ecological diversification – flowering synchronicity – growth pattern – monocarpy – New Caledonia – plant architecture – senescence – tropical rainforest.

1. Introduction

The diversity of plant growth forms and ecological strategies has long fascinated botanists, who have developed various approaches to describe and study plant forms. The earliest works were based on physiognomic descriptions (Humboldt, 1806; du Rietz, 1931) and since Raunkiaer's life form system (1934), several classifications have been proposed based on the functional characteristics of plants (Adamson, 1939; Aubréville, 1963; Lebrun, 1966; Galán de Mera et al., 1999). Plant architecture has long lagged behind other approaches, probably due to its more recent development and apparent complexity of implementation. Several recent studies have however taken on the discipline and show that architectural features occupy a central position in the phenotypic network (Charles-Dominique et al., 2017; Messier et al., 2017; Millan et al., 2019) and the evolutionary framework (Chomicki et al., 2017; Bruy et al., 2018; Anest et al., 2021).

Plant architecture offers a multilevel and dynamic approach to plant development, and underlines the construction of the plant body, composed of morphological elements differing in their structure and function (Hallé & Oldeman, 1970; Hallé et al., 1978; Barthélémy et al., 1989). A plant can be divided into various hierarchical levels of organization, composed of repetitive botanical entities (phytomer, morphogenetical unit, axis, etc.) that sustain multiple and specific biological functions (e.g. photosynthesis, exploration, reproduction). The architecture of a plant is thus defined according to the topological and geometrical arrangement of each of its parts in space and time (Edelin, 1984; Barthélémy & Caraglio, 2007).

Leaf and inflorescence scars, growth rings, and pith area variations reflect the functional history of plant meristems and transcribe the relative temporality of the plant's body construction (Hallé et al., 1978; Puntieri et al., 1999; Grosfeld & Barthélémy, 2004; Zalamea et al., 2008). The study of these morpho-anatomical markers allows the reconstruction of the plant's past development without long-term growth monitoring (de Reffye et al., 1991; Heuret et al., 2000, 2002, 2006; Passo et al., 2002; Nicolini et al., 2012; Noyer et al., 2019). Architectural analysis is therefore a retrospective approach and is not to be confused with form or physiognomy, as it studies the dynamics of plant growth. As such, it includes the identification of the plant's optimal developmental sequence. Each ontogenetic stage (seedling, sapling, adult tree) being defined by the expression of a precise syndrome of characters. This major aspect of plant architecture provides a formal basis for comparative studies at intra- and inter-specific scales. At the intraspecific scale, comparisons of ontogenic stages highlight the phenotypic plasticity that a species can express under different environmental conditions (Stecconi et al., 2010; Taugourdeau et al., 2012; Dang-Le et al., 2013; Trueba et al., 2016; Fortunel et al., 2020; Levionnois et al., 2020). At the interspecific scale, comparative studies of closely related species can further highlight divergences or timing shifts, known as heterochronies, in species developmental sequences (Smith, 2001; Olson & Rosell, 2006; Buendía-Monreal & Gillmor, 2018).

Recent studies have demonstrated that architectural traits are substantial determinants of plant life history and ecological diversification (Isnard et al., 2012; Granados-Mendoza et al., 2014; Chomicki et al., 2017; Bruy et al., 2018; Anest et al., 2021). In phylogenetic frameworks, converging growth forms and strategies are well reflected in architectural traits (Anest et al., 2021). However, few studies compare the developmental sequences of species to identify the traits involved in their divergence and the drivers behind them (Chomicki, 2021). Therefore, which architectural traits lead to the expression of a specific strategy, such as monocarpy in trees, remains unknown.

Islands are noted for hosting famous cases of radiation and original adaptive plant strategies. In New Caledonia, a South Pacific archipelago known for its remarkable endemic flora (Morat et al., 2012; Isnard et al., 2016), the genus *Cerberiopsis* has radiated into three species exhibiting different growth habits. While *Cerberiopsis neriifolia* (S.Moore) and *Cerberiopsis obtusifolia* (Van Heurck & Müll.Arg.) are multi-flowering (polycarpic) treelet and shrub, *Cerberiopsis candelabra* Vieill. (ex. Pancher & Sebert) exhibits a unique and fascinating strategy for a long-lived tree, as the species is monocarpic (Veillon, 1971; Read et al., 2006, 2008, 2021).

In plant biology, monocarpy refers to what is more generally known as semelparity, i.e. an organism that reproduces once and dies (Gadgil & Bossert, 1970). Therefore, monocarpic species are plants that die following a single and massive flowering event (Simmonds, 1980; Davies & Gan, 2012). This life history strategy has evolved many times and independently in many taxa. For instance, monocarpy is inherently found in annual and biennial plants, but also in some bamboo and palm species (Janzen, 1976; Abe & Shibata, 2012; Dayanandan et al., 2018). The latter plants are monocarpic as they grow from a unique apical meristem. However, monocarpy is rare among long-lived woody plants. Excluding unbranched "palm-like" trees and shrubs (e.g. *Spathelia*, *Strobilanthes*, *Mimulopsis*), this strategy is recorded in twenty-nine species of canopy trees worldwide, in only two tropical genera: *Tachigali* (Fabaceae) and *Cerberiopsis* (Apocynaceae) (Veillon, 1971; Foster, 1977; Poorter et al., 2005; Read et al., 2006, 2008; van der Werff, 2008).

Here, we conduct a comparative architectural analysis to dissect the morphological basis of monocarpy and discuss the evolutionary background that may have led to the evolution of this life history in the genus *Cerberiopsis*. Therefore, our study addresses two questions: (1) What architectural traits diverge among *Cerberiopsis* species, explaining their divergent growth habits? and (2) What traits are involved in the monocarpic strategy of *C. candelabra*?

2. Materials and methods

2.1. Species and study sites

The genus *Cerberiopsis* (Apocynaceae), endemic to New Caledonia, includes three long-lived woody species (Boiteau, 1981). All three species grow exclusively on the ultramafic substrate which covers one-third of the main island (Jaffré, 2022). While *C. neriifolia* and *C. obtusifolia* are polycarpic species, *C. candelabra* is a monocarpic plant (Veillon, 1971). *C. candelabra* is a large tree emblematic of low and medium-altitude forests in the main island's southern massif. It can reach up to 30 meters in height for a maximal observed diameter at breast height of 79 cm (Read et al., 2006). Based on the core's ring counts, the oldest tree's age has been estimated above a century (Read et al., 2021). This species also occurs sporadically in the open maquis. *C. neriifolia* is a microendemic treelet restricted to the southeast of the main island. It is mainly encountered in the bushy maquis to maquis passing forest but can also occur at forest edges where it can reach 15 meters in height. *C. obtusifolia* is a shrub occurring in riparian to tall maquis in the northeast of the main island. This species is not observed in forests and can reach a maximum height of 8 meters. *C. neriifolia* and *C. obtusifolia* are classified as vulnerable since they show population decline (IUCN, 2022).

C. candelabra trees were described in the communes of Yaté (22° 4'55.43 "S, 166°37'46.42 "E) and Mont-Dore (22°12'34.54"S, 166°40'35.64"E). The abundance and frequency of the species in these areas, allow the description of trees established in a wide range of environmental conditions. They were observed along a gradient from the open maquis to the dense rainforest. Plants of *C. neriifolia* and *C. obtusifolia* were described in their respective native habitat, around Thio (21°42'2.70"S, 166°19'21.95"E) and Voh (20°59'25.84"S, 164°44'30.17 "E). Both species have a restricted distribution and covered a narrower range of habitats compared to *C. candelabra*.

Mean annual temperatures ($\bar{T}$) between study sites are comparable ($\bar{T}_{\text{Yaté}}$ = 23.7°C; $\bar{T}_{\text{Mont-Dore}}$ = 24.2; $\bar{T}_{\text{Thio}}$ = 23.6°C; $\bar{T}_{\text{Voh}}$ = 23.0°C; Météo-France, 2022a). However, they stand out by their mean annual precipitation ($\bar{P}$) and annual amount of precipitation days ($\bar{p}$) (Yaté: $\bar{P}$ = 2684.4 mm, $\bar{p}$=169.3 days; Mont-Dore: $\bar{P}$ = 1405.6 mm, $\bar{p}$ = 116.4 days; Thio: $\bar{P}$ = 1742.8 mm, $\bar{p}$ = 104.9 days; Voh: $\bar{P}$ = 988.6 mm, $\bar{p}$ = 75.4 days; data collected from 1981-2010; Météo-France, 2022b).

2.2. Plant material and measurements

Twenty plants of each species were studied at different developmental times in their natural environments (**Table 1**). The study consists of a complete description of the aerial parts. As plant size and chronological age are not always reliable indicators of ontogenic stages, we use architectural analysis to define them (Roggy et al., 2005; Coste et al., 2009; Dang-Le et al., 2013). Once a plant is selected, we collected standard information used for its discrimination (GPS coordinates, main axis height (H), number of living branch tiers (Bt), height of the first living branch (H_{Bt}), base diameter (D), diameter at breast height (DBH), habitat type and soil thickness).

The plant is then analyzed according to the architectural method describes hereafter in detail. Plant architecture is summarized in schematic drawings that synthesize the plant's main characteristics, such as the relative arrangement of their axes and the position of flowering. For all three species, in addition to the twenty plants described, over a hundred supplementary individuals were observed in natural habitats distinct from study sites. These observations are done to confirm the developmental sequence of each species.

	Plant characteristics						
Species	DBH (cm)	Height (m)	First branch height (m)	Tier of branches	Fertile tree	Sterile tree	Voucher ID
C. candelabra	1 - 87	1.3 - 29.4	0.7 - 16.4	0 - 17	3	17	*Salmon 6* (NOU), NOU054460
C. neriifolia	2 - 24	1.1 - 14.6	1.3 - 6.9	0 - 12	16	4	*Salmon 4* (NOU), NOU054458
C. obtusifolia	1 - 8	1.1 - 5.1	0.4 - 1.9	0 - 13	17	3	*Salmon 5* (NOU), NOU054459

	Habitat characteristics			
Species	Type	Location	Topography	Soil thickness
C. candelabra	open maquis: 8	open: 8	rocky ground: 6	> 5cm: 7
	forest edge: 3	understory: 4	creek: 7	< 5cm: 5
	rainforest: 9	canopy: 5	talweg: 6	< 2cm: 2
		emergent: 3	swamp: 1	indurated ferralsol: 6
C. neriifolia	bushy maquis: 15	open: 15	rocky ground: 12	> 5cm: 4
	forest edge: 5	understory: 3	creek: 2	< 5cm: 6
		canopy: 2	talweg: 5	< 2cm: 6
				indurated ferralsol: 4
C. obtusifolia	bushy maquis: 20	open: 20	rocky ground: 7	< 5cm: 9
			creek 13	< 2cm: 5
				indurated ferralsol: 6

Table 1. Plant and habitat characteristics of the 60 individuals selected for the architectural analysis of the genus *Cerberiopsis* (n=20 per species). Top table: Range of values (min-max) is given for each variable studied; Bottom table: For each habitat, the number of established plants (out of 20) is indicated. Soil thickness is obtained by measuring the vertical thickness of the soil organic horizon (humus).

2.3. Architectural analysis

Architectural analysis is based on the observation of several plants (i) at different ontogenic stages and (ii) established in a wide range of environments in order to assert what, in the plant's developmental sequence, is the result of an endogenous program and not the influence of the environment.

During development, a plant establishes axes following a precise developmental sequence. These different axes can be grouped into branching orders (A1, A2, A3, *etc.*) and axis categories (C1, C2, C3, *etc.*) (**Figure 1**). Branching orders are logically defined following their rank of appearance. Hence, a stem carried by the main axis (A1) is an order-2 axis (A2) that, if it branches, carries an order-3 axis (A3), and so on. On the other hand, axis categories are defined by a combination of morphological, anatomical, and functional traits. They consist of axes that share the same structure and support the same functions. For instance, the Atlas cedar (*Cedrus atlantica*, Pinaceae) can be described with only five axis categories, even though it has almost unlimited branching orders (Sabatier & Barthélémy, 1999). Indeed, the number of axis categories constituting a plant's body is invariant, finite, and relatively small, regardless of the plant's complexity. The number of these categories, their characteristics, and their spatial arrangement constitute the architectural unit (AU) of the species. The AU is the species-specific expression of its developmental sequence and thus the expression of its ecological strategy (Edelin, 1977; Barthélémy et al., 1989). In many species, this AU is repeated, partially or totally, inside the plant's body. This developmental process is known as reiteration (see Barthélémy & Caraglio, 2007).

Several processes need to be studied to qualify the AU of a species, namely: (i) growth, (ii) branching, (iii) flowering, and (iv) reiteration of all axis within the plant's body. As these processes are dynamic while the study is punctual, we use morphological markers to qualify developmental sequences. Each axis is described using stem, leaf, and flower markers (internodes length, leaf size, axes diameter, inflorescence and branch scars, axes position and orientation, *etc.*). These markers result from the rhythmic functioning of primary meristems and persist for variable durations (Grosfeld et al., 1999; Heuret et al., 2002; Nicolini et al., 2012). They retrospectively transcribe the relative temporality of the plant's body development, and this, at all organization levels (**Figure 1**).

The plant's lowest level of organization is the phytomer. It refers to the botanical entity formed by (i) a node, a leaf and its related axillary bud, and (ii) the subtending internode (Barthélémy & Caraglio, 2007). Variations in internode length or leaf size of consecutive phytomers allow the definition of a higher level of organization: the morphogenetical unit (MU) (Prat, 1936). Here we define the MU as the stem portion between two zones of internode length shortening. Most often, these zones of short internodes indicate a growth stop when the growth is rhythmic. In this case, the MU corresponds to a growth unit (GU), i.e. the portion of stem established during an uninterrupted period of elongation. A higher level of organization, the module, has also been described, notably for the Apocynaceae family. Introduced by Prévost (1967), a module corresponds to the portion of an axis edified by a single terminal meristem and repeated indefinitely (**Figure 1**) (for an overview of plant body's organization see Hallé & Oldeman, 1970; Barthélémy et al., 1989; Barthélémy & Caraglio, 2007).

The architectural description of one plant requires 2 to 8 hours of work depending on the plant's size and accessibility. All individuals were used to characterize the developmental sequence from the sterile unbranched seedling to the fertile senescent tree. The process leading to the understanding of plant architecture is not linear. Each step of the diagnosis is based on the construction of hypotheses that, if refuted, force the analysis to be reset (Charles-Dominique et al., 2012).

2.4. Statistical analyses

We use the R-4.2.0 software (R Core Team, 2022) for sample statistical comparisons. As our quantitative data do not satisfy the applicability conditions of standard parametric tests (no normality and homogeneity of residuals), we use non-parametric statistics. Kruskall-Wallis ($_{KW}\chi^2$) and Wilcoxon-Man-Whitney (w) tests (Stats package; R Core Team, 2022) are performed for mean comparisons respectively when the samples are independent or paired (Hollander & Wolf, 1973). To explore the influence of the qualitative variable 'habitat' on the distribution of *C. candelabra* quantitative data, a Factor Analysis of Mixed Data (FAMD) is performed (FactoMineR package; Lê et al., 2008). This method is relevant since a small number of qualitative variables is considered (Pagès, 2014).

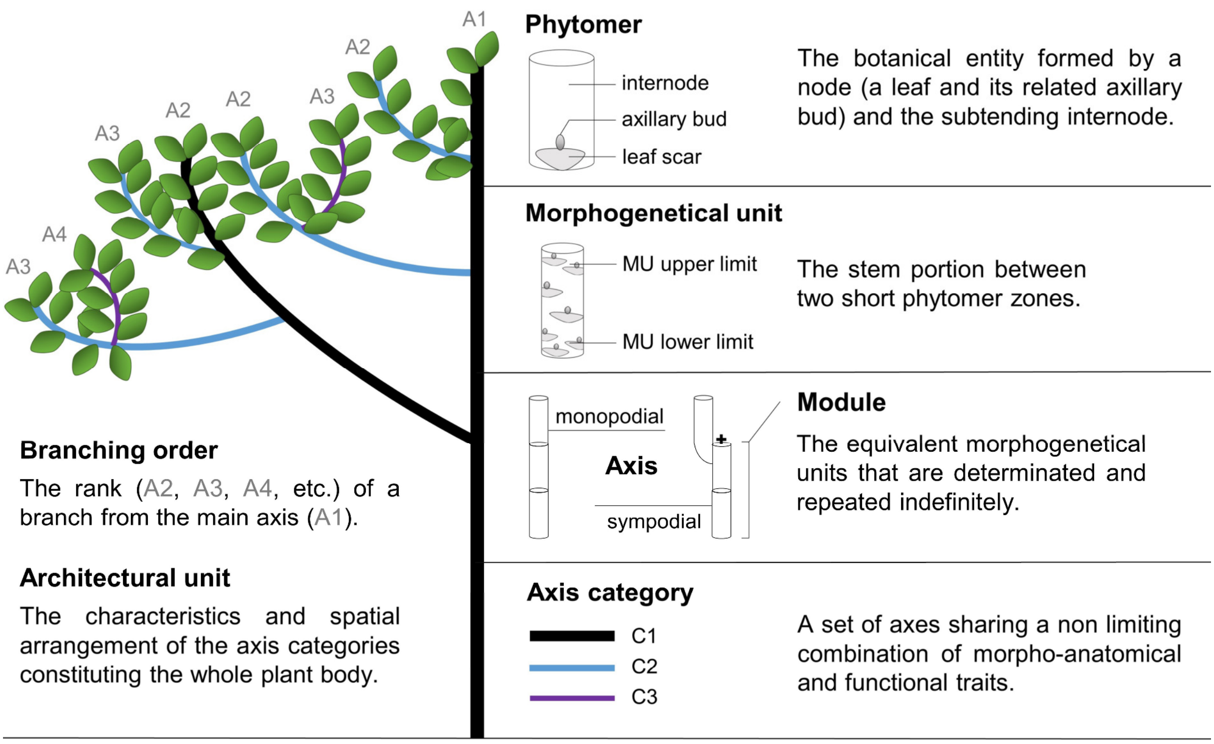


Figure 1. Definitions and concepts for plant architecture. Architectural analysis is based on the definition of branching orders and axis categories which is achieved by subdividing the plant into several levels of hierarchical organization such as the phytomer, the morphogenetical unit (MU), the module, and the axis. For each species, the analysis allows determining its architectural unit (AU) which is the specific expression of its axis categories, their characteristics, and their spatial arrangement inside the plant body.

3. Results

3.1. The seedling

The seedling stage is the first step of the plant's developmental sequence. The plant's body is reduced to a single unbranched, orthotropic main axis (A1). This axis consists of a succession of phytomers that show an alternation of long and short internode zones combined with a reduction in leaf areas. The main axis (A1) is thus a succession of MUs (**Figure 2B', B"**).

Figure 2. Habit of *Cerberiopsis candelabra* Vieill. (ex. Pancher & Sebert), a monocarpic tree endemic to New Caledonia. (**A**) sapling in the understory exhibiting a single tier of branches; (**B**) tree with successive tiers of branches - arrow in B' and B'' shows a short internode zone that marks the periodic growth of axes; (**C**) terminally flowered seedling; (**D**) adult tree with total and partial reiterations - arrow shows a third-order axis (C3) acquiring the characteristics of a second-order axis (C2); (**E**) tree growing in an open environment whose crown has been built by

traumatic total reiteration following the breakage of the main axis (in **E'**); (**F**) aerial view showing the synchronous flowering of several trees at Pic du Grand Kaori rainforest (Sept. 2021); (**G**) lateral aerial view of an adult tree where all axes flowered at the terminal position; (**H**) dead tree after a massive flowering that was expressed at the adult stage - this defoliated structure illustrates the rhythmic branching.

Figure 3. Habit of the polycarpic species of the genus *Cerberiopsis* (Apocynaceae) endemic to New Caledonia. A and B: illustrations of *C. neriifolia* (S.Moore) Boiteau. (**A**) tree consistent with its architectural unit exhibiting three axis categories arranged in successive tiers of branches and expressing flowering; (**B**) flowering of a basal branch and its twigs in an adult tree - arrows show the axis terminal flowering that will lead to the death of the whole branch as no delayed branching is observed. C to E: illustrations of *C. obtusifolia* (Van Heurck & Müll.Arg.) Boiteau. (**C**) senescent tree showing a self-pruning of the lowest branches and a dismantling of the crown linked to high branch mortality; (**D**) branches having a sympodial construction, each relay develops a module consisting of one or more morphogenetical units and bounded by the apical meristem death; (**E**) branch of an adult tree falling and leaning on the ground – arrow shows the terminal flowering of the apical meristem leading to the branch's sympodial construction.

3.2. The sapling

We define the transition from the seedling to the sapling stage as the moment when the branching process is expressed (**Figure 2A**). It occurs when plants exceed 1.5cm in DBH in *C. candelabra* ($\overline{DBH}$ = 1.82 ± 0.69cm; $\overline{H}$ = 1.92 ± 0.62m) and *C. neriifolia* ($\overline{DBH}$ = 1.71 ± 0.45cm; $\overline{H}$ = 1.64 ± 0.24m) and correspond, in both species, to the elongation of 5-10 MUs by the main axis. In *C. obtusifolia*, plants do not reach more than 1.3cm in basal diameter when branching for the first time, corresponding to the elongation of 1-3 MUs by the main axis ($\overline{H}$ = 0.80 ± 0.18m; $\overline{D}$ = 1.29 ± 0.57cm). All three species show a main axis growing through a unique apical meristem (monopodial construction).

Construction of branches — In all *Cerberiopsis* species, the branching is rhythmic with the establishment of successive tiers of branches (**Figures 2B, H** and **3A**). The main axis (A1) produces plagiotropic branches (A2) which, in *C. candelabra* and *C. neriifolia*, secondarily acquire an orthotropic orientation (**Figure 4**). The lack of proximal cataphylls and the presence of a relatively long proximal internode are indicative of an immediate branching. Branches developed in acrotonic position on MUs and have a growth marked by the alternation of long-short internode zones (**Figure 4A, B**). In *C. candelabra* and *C. neriifolia*, branches elongate from a unique apical meristem and have a monopodial construction (**Figure 4D, E**). However, in *C. obtusifolia*, the initial apical meristem has a determined growth. After its death, one or few new stems immediately produced by the last lateral meristems continue the branch development (sympodial construction) (**Figure 4F**). In *C. obtusifolia*, branches (A2) are therefore a succession of modules consisting of one or more MUs (**Figure 3D**).

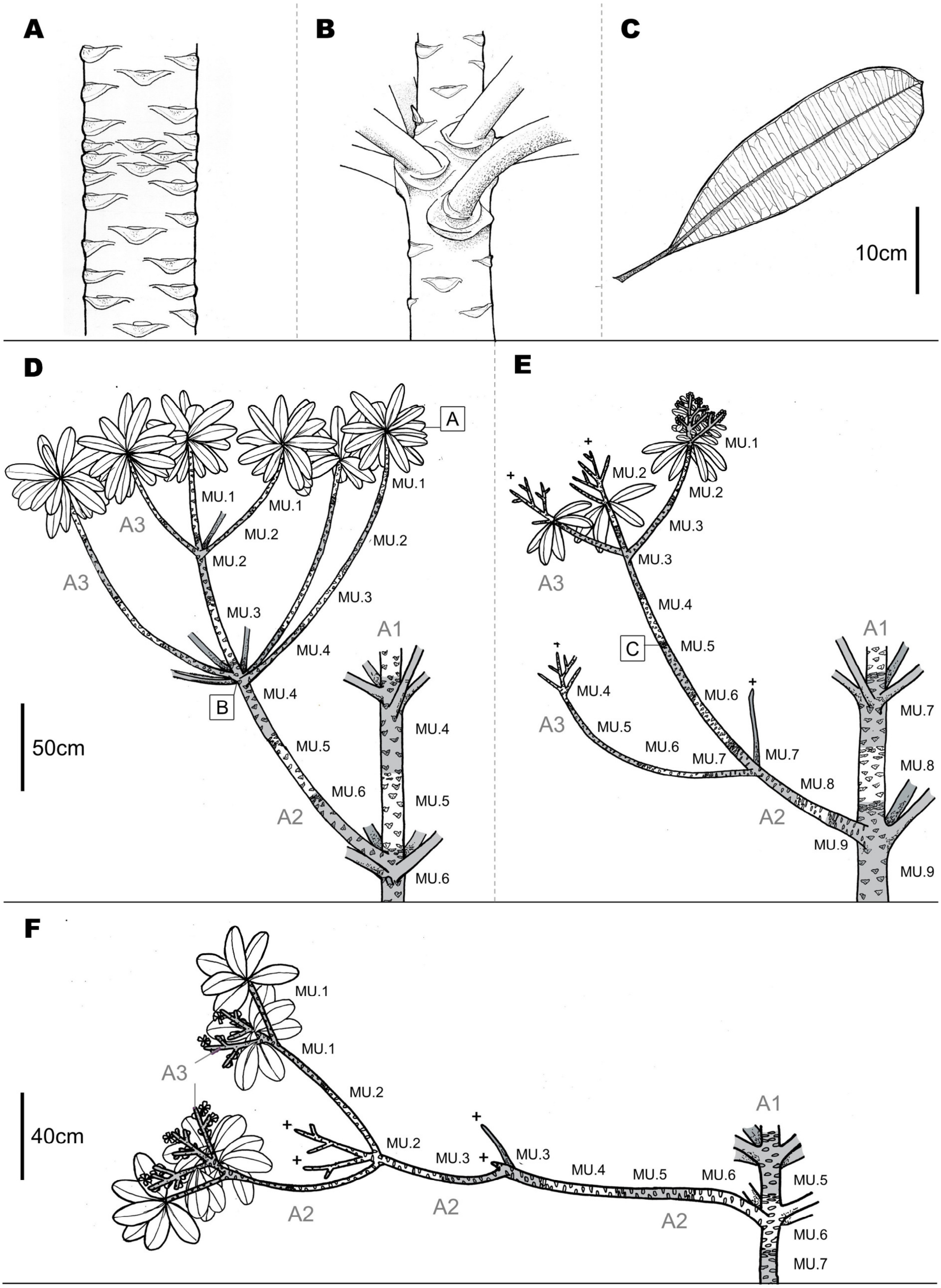


Figure 4. Details on *Cerberiopsis* species architecture. (**A**) Short phytomer zone, visible through a reduction in internode length, delineating a MU; (**B**) arrangement of a tier of branches produced by an immediate and rhythmic branching; (**C**) A leaf of *C. candelabra* tree; (**D**, **E**, **F**) The relative position of branching orders A2 and A3 along the main axis (A1) in *C. candelabra* (**D**), *C. neriifolia* (**E**), and *C. obtusifolia* (**F**). Shades of gray delineate successive morphogenetical units (MU) along the axes. **D** and **E**: branches (A2) have an orthotropic orientation, a monopodial construction, and they produce immediate tiers of twigs (A3); **F**: branches (A2) have a plagiotropic orientation, a sympodial construction, and they produce immediate twigs (A3).

MUs and length ratios — In each species, we found differences in developmental rhythms between the main axis (A1) and the branches (A2). We define MUs ratio as the mean ratio of the number of MUs constituting a branch to the number of MUs constituting the main axis above its insertion (MU_{A2}/MU_{A1}). In the same way, we define length ratio as the mean ratio of the total length of a branch to the length of the main axis section above its insertion (L_{A2}/L_{A1}). In all *Cerberiopsis* species, the same number of MUs is observed between the branch and the main axis ($MU_{A2}/MU_{A1} = 1$). However, in *C. obtusifolia*, branch MUs are longer than those of the main axis at the same rank ($L_{A2}/L_{A1} >> 1$). Hence, branches are significantly longer than the main axis above their insertion. This excessive lateral growth produces branches that frequently fall and lean on the ground (**Figure 3E**). Instead, in *C. candelabra* branches are slightly shorter than the main axis above their insertion ($L_{A2}/L_{A1} < 1$). *C. neriifolia* shows an intermediate behavior ($L_{A2}/L_{A1} \geq 1$).

3.3. The adult tree

In *Cerberiopsis* species, we define the adult stage as the establishment of the architectural unit (AU). In *C. neriifolia* and *C. obtusifolia*, this event is concomitant with the expression of flowering (**Figure 3A**).

The architectural unit — In all three species, AU construction is completed when twigs are produced. Twigs (A3) are initiated by lateral meristems in acrotonic positions on the MUs of branches (A2). Their branching is also rhythmic and immediate (**Figure 4D, E, F**). The twigs have a monopodial construction and show a growth marked by the alternation of long-short internode zones. They are short-lived axes composed of a small number of MUs (*C. candelabra*: 1-9MUs; *C.*

neriifolia: 1-4MUs; *C. obtusifolia*: 1-2MUs). The AU of the three *Cerberiopsis* species is thus based on three distinct axis categories: the main axis (C1), the branches (C2), and the twigs (C3) which correspond, at the beginning of the adult stage, to three branching orders (A1, A2, A3) (**Table 2**).

***Cerberiopsis* architectural features**				
Axis categories		**C1**	**C2**	**C3**
Construction		monopodial	***	monopodial
Phyllotaxis		spiral	spiral	spiral
Symmetry		radial	radial	radial
Growth I	Timing	periodic	periodic	periodic
	Orientation	orthotropic	plagiotropic	plagiotropic
	Lifespan	long term	***	short term
Growth II	Expression	strong	weak	weak
Morphogenetical Unit	Markers	reduction in internode length and leaf area		
	Number	unlimited	***	limted
Branching	Type	rhythmic	rhythmic	unbranched
	Timing	immediate	immediate	-
	Cladoptosis	-	long term	short term
Flowering	Position	terminal	terminal	terminal
	Temporality	***	***	***
Reiteration	Localisation	lateral	subterminal	-
	Timing	sequential	sequential	-
	Origin	growing axes	growing axes	-
Type		main axis	branch	twig

***	**Construction - C2**	**Lifespan - C2**	**MU number - C2**	**Flowering - C1, C2, C3**
C. candelabra (tree)	monopodial	long term	unlimited	*synchronized*
C. neriifolia (treelet)	monopodial	*mid term*	*limited*	desynchronized
C. obtusifolia (shrub)	*sympodial*	long term	unlimited	desynchronized

Table 2. Synthesis of the architectural analysis of the genus *Cerberiopsis*. For each species, the definition of the architectural unit is based on the identification of three axis categories (C1, C2, C3). In the sub-section *Branching*: (i) Type is a variable characterizing the development of branches/twigs, which can be rhythmic (in successive stages) or continuous; (ii) Timing is a variable characterizing the periodicity of axis development, branches/twigs can develop immediately or with a delay (through a dormant bud); (iii) Cladoptosis is a variable characterizing the capacity of axes to self-pruning after a short, medium or long time. Architectural differences between species are underlined by stars in the upper table and presented in the lower table.

Flowering process — In each *Cerberiopsis* species, all axis categories (C1, C2, C3) flower in terminal position. In *C. neriifolia* and *C. obtusifolia*, flowering is desynchronized at the plant level according to an acropetal gradient. Referring to the main axis, most basal branches and most proximal twigs express sexuality successively (**Figure 3B**). When a branch (C2) flowers, all its twigs (C3) flower synchronously (MU_n) or after one or two additional growth cycles (MU_{n+1} or MU_{n+2}). In *C. neriifolia*, the branch's life span is thus defined by reproduction. The terminal flowering of the branch precedes the death and the self-pruning (i.e. cladoptosis) of the whole branch-twigs complex in a short time (**Figure 4E**). However, in *C. obtusifolia*, the branch's life span is longer thanks to its sympodial construction. After terminal flowering, the branch continues to grow through a lateral axis (C2) that has not flowered (**Figure 4F**).

In the monocarpic *C. candelabra*, the adult stage is not bounded by a flowering event. Flowering can occur at any stage, from unbranched seedlings (though probably a rare event) to reiterated adult trees (**Figure 2C, G**). When the flowering is triggered, the whole set of apical meristems, of all axis categories (C1, C2, C3), flower synchronously (**Figure 2F, H**).

Architectural reiteration — In all three *Cerberiopsis* species, the reiteration process can be expressed at the adult stage. The plant crown becomes more complex by adding AU reiterates, increasing the number of branching orders (**Figure 5**). Throughout the developmental sequence, some lower branches (C2) straighten and duplicate the structure and functions of the main axis (C1). Since they establish new tiers of branches (C2) that bear tiers of twigs (C3), reiteration is total (**Figure 5A9, B9, C9**). In addition, the reiteration is sequential as it appears to be fully part of the plant's ontogeny. In all species, partial reiteration can also be observed. A distal twig (C3) may sporadically straighten and duplicate the structure and functions of its bearing branch (C2) (**Figure 2D**). In some instances, if the apical meristem of the main axis is damaged or broken, traumatic total reiteration can occur. One or more branches (C2) straighten up and assume the main axis functions (**Figure 2E, E'**).

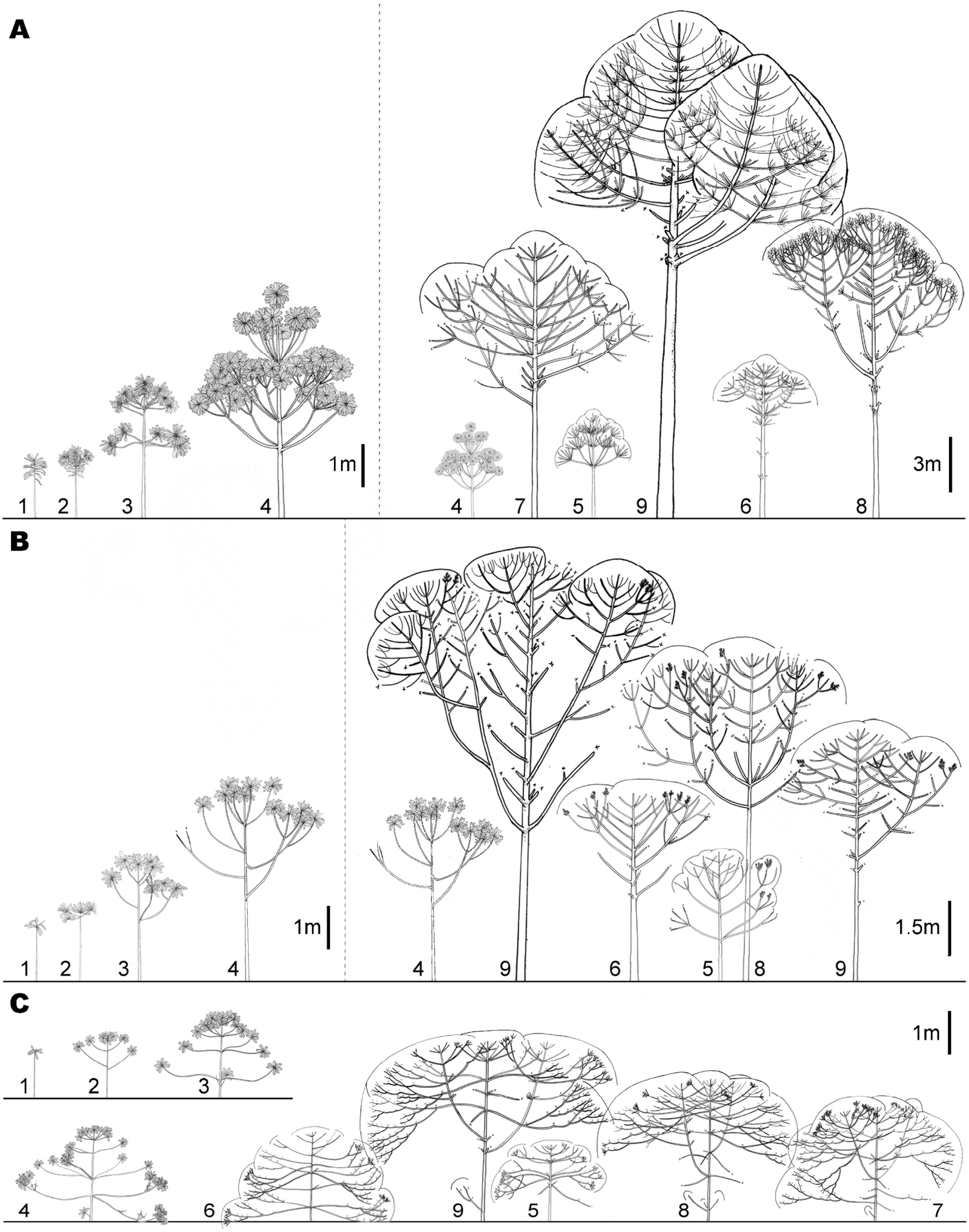


Figure 5. Developmental sequence of (**A**) *C. candelabra*, (**B**) *C. neriifolia* and (**C**) *C. obtusifolia*. Each sequence illustrates the successive ontogenic stages that punctuate the plant's life. **1**: seedling stage with architecture reduced to a single main axis; **2** and **3**: sapling stage with the expression of the branching process. In (**A**) *C. candelabra*, **4 to 9**: adult stages with the establishment of the architectural unit (three branching orders); **8** and **9**: trees expressing sequential total reiteration;

8: a flowering individual; No signs of senescence are observed in this species. In (**B**) *C. neriifolia*, and (**C**) *C. obtusifolia*, **4 to 7**: adult stages with the establishment of the architectural unit, which is concomitant with the expression of flowering; **8** and **9**: senescent stage characterized by the development of increasingly smaller morphogenetical units, an increase in branch mortality and a gradual dismantling of the crown; **7 to 9**: plants showing sequential total reiteration - in (**C**) *C. obtusifolia*, plants showing additional delay reiteration.

Size variations in adult trees — The main axis (C1) of *Cerberiopsis* species is a perennial stem whose life span is defined by the apical meristem flowering. In the adult stage, plants carry several tiers of branches (**Figure 5A7, B7, C7**), and *C. candelabra* reaches higher dimensions ($\overline{DBH}$, $\overline{H}$, $\overline{H}_{Bt}$, $\overline{Bt}$) than *C. neriifolia* and *C. obtusifolia* (all details are presented in **Appendix 1**). Therefore, plant-specific size and length ratio (see *MUs and length ratio*) distinguish the three species by their shape. While *C. candelabra* has a pyramidal tree-like habit, *C. neriifolia* and *C. obtusifolia* have respectively a funnel-shaped shrub-like habit and a shrub/leaning habit (**Figure 5A4, B4, C4**).

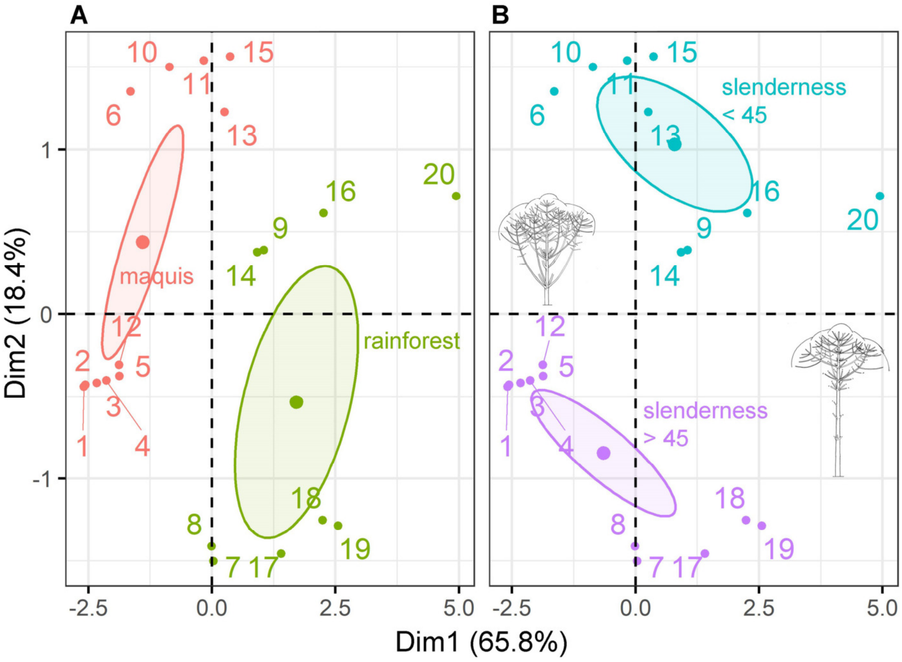


Figure 6. FAMD factor map of the 20 *C. candelabra* trees according to their (i) DBH, (ii) total height, (iii) first branch height (iv) self-pruning capacity (yes/no) (v) slenderness (< 45 / > 45), and (vi) habitat (maquis/rainforest). The quantitative variables 'DBH', 'total height', 'first branch height', and 'self-pruning' explain 81% of dimension 1 (Cos2 > 0.80). The quantitative variable 'slenderness' explains 71% of dimension 2 (Cos2 = 0.61). Dimensions 1 and 2 explain 84% of the

total eigenvalue variance. (**A**, **B**) Dots - 1 to 20 - show the relative distribution of trees; the closer dots are the most similar plants. (**A**) Confidence ellipses show that trees in the rainforest (green) have significantly larger dimensions than trees in the open maquis (red). (**B**) The average slenderness ($\overline{H/DBH}$) is 45; all adult trees (11-20) are highly stable ($\overline{H/DBH} < 50$); confidence ellipses show (i) there are no significant differences in slenderness between trees (ellipses overlap on Dim2) and (ii) trees that are more slender (blue) or less slender (purple) are not specifically occurring in the rainforest or in the open maquis.

While *C. neriifolia* and *C. obtusifolia* are almost exclusively distributed in the bushy maquis, *C. candelabra* grows in both open maquis and rainforests. Significant variations in size are observed between the trees from these two environments (**Figures 2E, F** and **6**). In forests, adult trees develop a main axis and a first living branch tier significantly higher ($\overline{H}_{forest}$ = 20.9m; $\overline{H}_{maquis}$ = 9.5m; w = 23; P < 0.05*). In addition, they undergo an intense self-pruning of the lowest branches (**Figure 6A**). In open maquis, this mechanism is less observed. However, slenderness factors (H/DBH) indicate that rainforest trees are not more slender, and mechanically more unstable than the trees in the open maquis ($\overline{H/DBH}_{forest}$ = 45.2 $\pm$ 14; $\overline{H/DBH}_{maquis}$ = 40.7 $\pm$ 20; w = 17; P > 0.05) (**Figure 6B**).

3.4. The senescent tree

We define the transition from the adult to the senescent stage as the moment when the main axis growth slows down by setting up increasingly smaller MUs. Branch mortality increases and the crown gradually dismantles (**Figure 3C**). In *C. neriifolia* and *C. obtusifolia*, branches (C2) and twigs (C3) flower successively from the base to the apex of one or more main axes (C1), depending on AU reiterates (**Figure 5B6, C6**). At the same time, these main axes continue to produce new branches and older ones are self-pruned. When the flowering reaches C2-C3 complexes at the top of the crown, the apical meristems of the main axes flower in their turn. In *C. neriifolia*, this leads to plant death as no new axis is produced by delayed branching (**Figure 7B**). In *C. obtusifolia*, trunk flowering precedes a cessation of branch (C2) development. No modules are produced to continue the branch sympodial construction, leading to plant death (**Figure 7C**).

In *C. candelabra*, the flowering event is unique and leads to tree death as (i) it concerns all apical meristems synchronously and (ii) no delayed branching is initiated after flowering (**Figure 7A**). Among the hundreds of trees studied, no *C. candelabra* was observed showing signs of senescence or dying without having massively flowered.

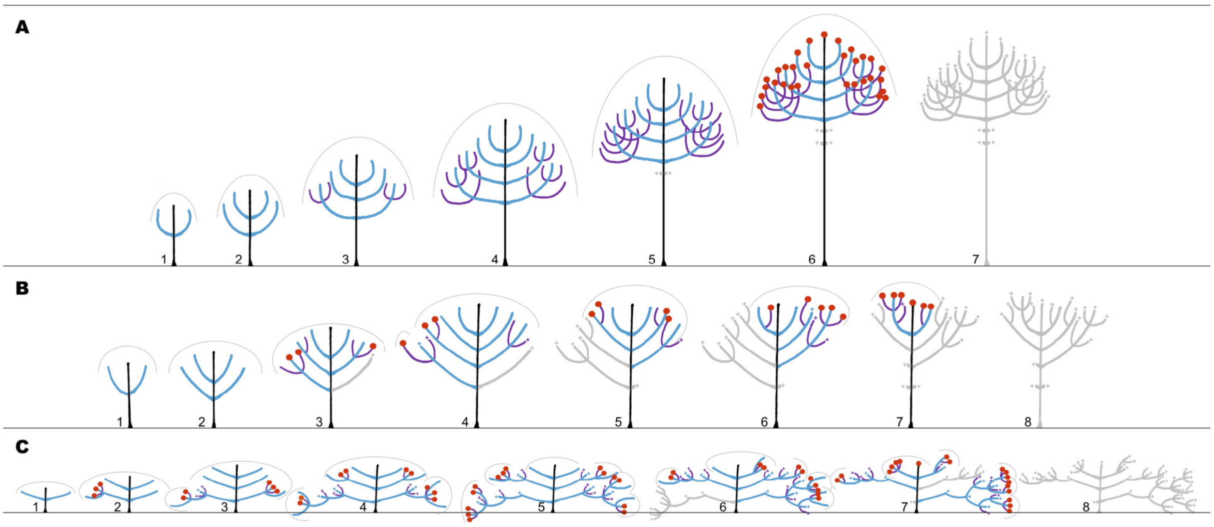


Figure 7. Theoretical developmental sequences of the *Cerberiopsis* species. For legibility, reiteration processes have not been represented. (**A**) *C. candelabra* trajectory: the architectural unit based on three axis categories (C1, C2, C3) is progressively established (**1-4**) and is followed by the lowest branches pruning (**5**). At a given time, a massive terminal flowering, which concerns all the apical meristems, is expressed (**6**) and leads to the death of the whole plant (**7**); (**B**) *C. neriifolia* trajectory: the architectural unit based on three axis categories (C1, C2, C3) is progressively established and completed with the expression of flowering (**1-3**). Branches and their twigs flower terminally following an acropetal gradient along the main axis (**4-6**). They die and are pruned in turn. Terminal flowering of the main axis leads to the death of the whole plant (**7-8**); (**C**) *C. obtusifolia* trajectory: the architectural unit based on three axis categories (C1, C2, C3) is progressively established and completed with the expression of flowering (**1-2**). Branches and their twigs flower terminally following an acropetal gradient along the main axis (**3-5**). The branch's vegetative growth continues through sympodial construction (**5-7**). Sympodial relays are progressively less numerous and finally cease, leading to the death and pruning of the branches. Terminal flowering of the main axis leads to the death of the whole plant (**8**).

4. Discussion

4.1. Few architectural variations induced a diversity of growth forms

The architectural unit of *Cerberiopsis* species has a rather similar nature and is organized according to the repetition of three axis categories: the main axis (C1), the branches (C2), and the twigs (C3). During ontogeny, sequential reiteration can be expressed, thus increasing the orders of branching. In all species, axes die following terminal flowering. While Veillon (1971) describes the branching in *C. candelabra* as sympodial for the higher order branches, our study rather shows that all axes remain monopodial.

We found that the main differences between species rely on the combination of three architectural traits: (i) the modalities of branch construction (sympodial or monopodial), that determine their ability to grow following the apical meristem flowering, (ii) the length ratios between the branches and the main axis, and (iii) the timing and the synchronicity of flowering of all axis categories. The species-specific expression of this trait syndrome explains their growth form divergences, from shrubby to tree-like habits. Our results are thus consistent with previous studies showing that closely related species tend to share the same architectural construction (Chadzon, 1991; León Enriquez et al., 2008). Therefore, divergences in growth form could be attributed to environmental filters such as resource availability (Bruy et al., 2018; Anest et al., 2021).

4.2. Two major traits lead to monocarpy

Two architectural traits explain the monocarpy, or “big-bang reproductive strategy” (Humphries & Stevens, 2001), in *C. candelabra*: (i) the synchronous flowering of all apical meristems and (ii) the absence of delay branching, preventing regrowth after this massive flowering. Thus, we demonstrate that the modalities of branching are intrinsically related to the occurrence of the monocarpic strategy in the genus *Cerberiopsis*. Monocarpy has been variously considered as a highly risky “suicidal” strategy or even as an evolutionary bottleneck for long-lived woody plants (Foster, 1977; Poorter et al., 2005; Read et al., 2006). The above combination of two architectural traits underlies why the monocarpic strategy is expressed only in *C.*

candelabra within the genus. However, the advantage of this trait syndrome is still unclear. Read et al. (2006, 2008, 2021) suggest that monocarpy may be advantageous if the death of the parental trees increases gap sizes and enhances seedlings recruitment, light availability being a critical resource for rainforest trees. In addition, they suggest that cyclones could be one of the triggers for *C. candelabra* mass-flowering. If cyclones are triggers for flowering, the tree's mechanical resistance to wind appears essential for monocarpy to be evolutionarily viable.

4.3. Is *C. candelabra* a highly disturbance resistant tree?

Wind regimes and cyclones are major determinants of the plant's structural allometries and the forest structuration (Valinger et al., 1993; James et al., 2006; Peltola et al., 2013; Thomas et al., 2015; Ibanez et al., 2018). Previous work showed that *C. candelabra* have a high resistance to wind damage, probably due to its wood composition and "candelabra" physiognomy (Read, et al 2011). The regular tiers of long and thin branches, the intense self-pruning, and the reduced branching order (not exceeding 3), might indeed also contribute to reducing the drag and mechanical damages caused by high winds. In addition, we found that the slenderness factor of the adult trees is in a high-stability range (H/DBH < 50) (Petty & Worrell, 1981; Petty & Swain, 1985; Wang et al., 1998; Kontogianni et al., 2011). Although trees in the rainforest are significantly taller than in the open maquis, the slenderness factor does not differ between these two environments. The H-D allometry of *C. candelabra* appears as an adjustable trait that allows trees to maintain their stability within a mechanical safety threshold regardless of the environment's openness.

4.4. *C. candelabra* does not senesce

According to Takeno (2016), stress-induced flowering, is the ultimate adaptation to stress, because plants can survive as a species if they flower and produce seeds even if they cannot survive as an individual (Wada & Takeno, 2010; Yaish et al., 2011; Riboni et al., 2014; Kazan & Lyons, 2016). Such a flowering strategy is therefore particularly adapted for a tree that only flowers once, endemic to a cyclone-prone area (Stevenson & Hope, 2005; Ibanez et al., 2018). The timing of flowering is indeed a critical trait for a long-lived monocarpic tree, as it ensures the survival of the species (Wada et Takeno, 2010; Blanvillain et al., 2011; Takeno, 2016; Ionescu et al., 2017). The best opportunity for flowering and fruiting is most probably when the plant's nonstructural carbon reserves are optimal, before trees begin to senesce (Hoch, 2015; Qiu et al., 2021).

Our results show that *C. neriifolia* and *C. obtusifolia* flower at determined ontogenic stages. First, concomitantly with the setting up of the architectural unit (production of twigs), and then repeatedly in the adult and senescent stages. This is in line with the fundamentals of plant architecture as the "automatic flowering" concept (Barthelemy, 1988; Blaise et al., 1998). According to this concept, flowering represents a step in the plant's developmental sequence, generally occurring when individuals acquire a certain threshold of complexity (Hallé et al., 1978; Barthélémy, 1989; Barthélémy & Caraglio, 2007). Flowering is thus autonomously regulated and modulated by well-known environmental factors such as photoperiod (Thomas & Vince-Prue, 1997; Bernier & Périlleux, 2005; Sung & Amasino, 2005; Romera-Branchat et al., 2014). However, our architectural study did not emphasize a "readiness" ontogenic stage or any trait syndrome that would trigger flowering in *C. candelabra*. Flowering occurs without trees showing signs of senescence and leads to plant death regardless of its ontogenic stage. This result suggests that external factors, such as physiological stresses experienced by trees during long dry seasons or tropical cyclones (Read et al., 2006, 2008), trigger monocarpic flowering.

4.5. Architectural divergences reflect a diversification of ecological strategies

It has been emphasized that variations of architectural traits can reflect a diversification of ecological strategies at different taxonomic scales (Isnard et al., 2012; Chomicki et al., 2017; Bruy et al., 2018; Anest et al., 2021). In the overall architecture of *C. neriifolia* and *C. obtusifolia*, the relatively small size of the main axis and the higher growth intensity of the branches explain their respectively shrub-like habits. Both species establish in the maquis of New Caledonia, known as a harsh environment (Morat, 1993; Isnard et al., 2016; Pillon et al., 2021). In this habitat, shrubby forms are dominant since they provide advantages against physical and physiological stresses (Wilson, 1995; Bond & van Wilgen, 1996; Scheffer et al., 2014; Jaffré, 2022). In *C.*

obtusifolia, the high degree of branching that results from the branch sympodial construction confers a competitive advantage in the maquis where plants are frequently exposed to drought, fire, and wind. This architecture increases the number of apical meristems and provides many opportunities for growth and flowering in case of plant damage (Rundel, 1991; Schenk et al., 2008; Charles-Dominique et al., 2012; Götmark et al., 2016).

In contrast, *C. candelabra* is the only *Cerberiopsis* species that occurs predominantly in rainforests. Tree forms provide a competitive advantage in high forest stands by favoring vertical exploration structures. They allow the colonization of the forest's highest strata and increase the light-capturing capability of plants (Givnish, 1988; Clark & Clark, 1992; Westoby et al., 2002; Poorter et al., 2006). Although *C. candelabra* in the rainforest and open maquis share the same architectural unit, our results show that tree height, diameter, and self-pruning intensity are significantly higher in the rainforest. It is widely known that trees growing in dense stands reach greater heights and diameters than in open areas due to the selective pressure for crown exposure to light (Horn, 1971; Iwasa et al., 1985; Franklin et al., 2012; Fransson et al., 2021). Plasticity in plant architecture allows species to cope with environmental heterogeneity and to specialize in a given ecological niche (Delagrange et al., 2004; Chambel et al., 2005; Valladares et al., 2006; Gratani, 2014).

4.6. Is monocarpy derived within the genus *Cerberiopsis* (Apocynaceae)?

Architectural analysis can make an important contribution to understanding plant ecological diversification (Bruy et al., 2018; Anest et al., 2021). Here, we can hypothesize about the evolution of architectures and strategies within the genus *Cerberiopsis*. This hypothesis can only be validated by integrating the genus into the existing phylogeny.

One of the outstanding architectural traits of the Apocynaceae is their construction by apposition of modules (module definition is given in the materials and methods section). This construction occurs in many plant families but was first defined for Apocynaceae since 64% of the species studied have a fully modular architecture (Prévost, 1967; Tomlinson & Zimmerman, 1978). Both *C. obtusifolia* and *Cerbera manghas* (Apocynaceae), the sister species of the

Cerberiopsis genus, conform to this construction (Alvarado-Cárdenas & Ochoterena, 2007; Endress et al., 2014). Instead, *C. neriifolia* and *C. candelabra* have a monopodial construction. In *C. neriifolia*, like in *C. obtusifolia*, the axis terminal flowering is desynchronized and leads to the death of the whole branch. In *C. candelabra* the terminal flowering of all axes is synchronized and leads to the death of the whole tree. Considering this deviation from the generic and subtribe architecture, *C. candelabra* seems to express the most derived growth form. Therefore, our study suggests that monocarpy is a derived life history strategy within the genus *Cerberiopsis*.

5. Conclusion

We found that *Cerberiopsis* species share a similar architectural construction. Around this generic construction, the variation of three architectural traits leads to the diversity of growth forms and associated diversification of ecological strategies within the genus. The monocarpic tree *C. candelabra* exhibits a specific combination of two architectural traits: (i) the complete synchronization of flowering at tree scale, with flowering extending to all apical meristems of all axis categories, and (ii) the inability of delayed branching, preventing regrowth after terminal flowering. Respectively, the polycarpic sister species share one of these architectural traits but never both. Finally, we found that flowering in *C. candelabra* is independent of the developmental sequence and that the trees don't show any signs of senescence. These results suggest that aging does not trigger flowering and that external factors, such as physiological stresses, are the main triggers of monocarpic flowering.

6. Additional information

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6.2. Author contributions

CReDIT authorship contribution statement - Conceptualization: *PH, SI, CS*; Funding acquisition: *SI, PH*; Data Curation: *CS*; Formal Analysis: *CS*; Investigation: *CS, PH, SI, YC*; Vizualization: *CS, PH*; Writing-original draft: *CS*; Writing, Review & Editing: *CS, PH, SI, YC*; Project administration & Supervision: *PH, SI*.

6.3. Data availability statement

The data that support the findings of this study are openly available in Zenodo (https://zenodo.org) at https://doi.org/10.5281/zenodo.6806161

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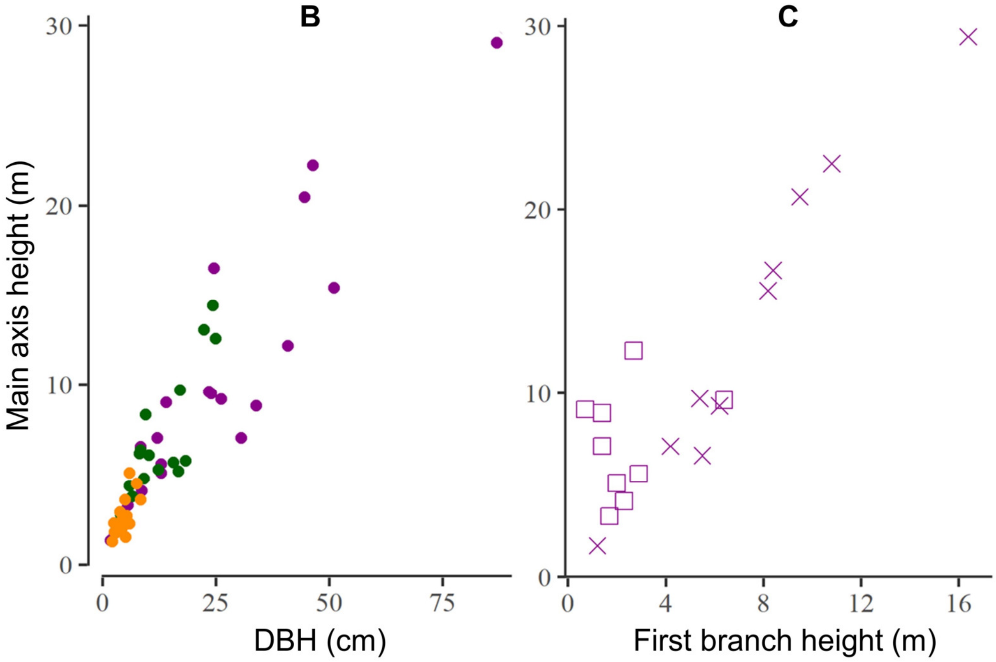
Appendix 1. (**A**) Dimensions of *Cerberiopsis* species at the adult stage; for each variable maximum value is indicated; statistics confirm the hypothesis (H0) that trees of *C. candelabra* are significantly different from *C. neriifolia* and *C. obtusifolia* plants. (**B**) Distribution of the 60 *Cerberiopsis* plants studied as a function of the main axis height and the DBH; orange: *C. obtusifolia*; green: *C. neriifolia*; purple: *C. candelabra*. (**C**) Distribution of the 20 *C. candelabra* trees as a function of the main axis height and the first living branch height; crosses indicate trees in the rainforest and squares indicate trees in the open maquis.

A

	C. candelabra	***C. neriifolia***	***C. obtusifolia***	*Stats*
DBH (cm)	38.3	12.8	3.9	KWχ2 = 30.1; P < 0.001***
DBH$_{\textbf{max}}$ (cm)	87.4	24.4	6.7	
H (m)	15.3	7.3	2.6	KWχ2 = 32.6; P < 0.001***
H$_{\textbf{max}}$ (m)	29.4	14.6	5.1	
Bt (no)	9	8	5	KWχ2 = 13.9; P < 0.001***
Bt$_{\textbf{max}}$ (no)	17	12	8	
H$_{\textbf{Bt}}$ (m)	7.0	2.9	0.8	KWχ2 = 26.2; P < 0.001***
H$_{\textbf{Bt.max}}$ (m)	16.4	6.9	1.8	



Chapter 4

The edge of Col des deux tétons' rainforest patch, four years after a bushfire © C. Salmon & J.M. Bore

Chapter 4 is an original research article focusing on the ecology of *C. candelabra* seedlings. It presents the results of a 20-months growth monitoring of 134 juveniles under natural conditions. We analyze the survival and growth rates of seedlings in relation to New Caledonian seasonality. Improving our understanding of the developmental phenology of *C. candelabra* juveniles is relevant since successful seedling recruitment is a critical issue for the persistence of monocarpic species.

Seedling survival and growth phenology of a monocarpic tree, *Cerberiopsis candelabra* Vieill. (Apocynaceae)

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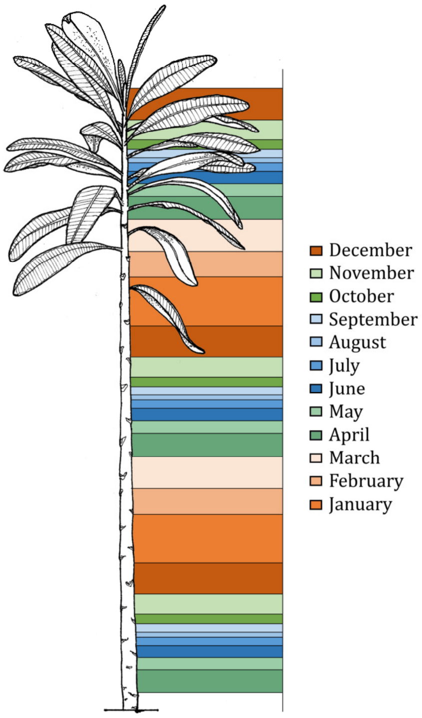
Salmon et al. — Seedling ecology of *Cerberiopsis candelabra*.



Abstract

We study two demographic aspects of a monocarpic tree, *Cerberiopsis candelabra*: (1) the juvenile survival rate and (2) the growth phenology, from germination to sapling. 134 juveniles in natural conditions have been described monthly from June 2020 to January 2022. Mortality rates and population density are recorded. The height growth rate, the number of phytomers produced, their elongation, and their corresponding leaf area are measured for each plant. In addition, three juveniles are described nodes by nodes to reconstruct their developmental trajectory since germination. Over 20 months, *C. candelabra* mortality rate was 32.92 %, with higher monthly mortality rates during the warm-dry transitional season. Juveniles show height growth rates up to 6.4 cm.mth^{-1} during the warm-wet season, corresponding to the production of a new phytomer every eight days. In juveniles fully described, we identify three morphogenetical units delimited by zones of internode length and leaf area reduction. Each one is associated with the formation of a growth ring during the cool-dry season. As expected for a subtropical monocarpic tree, *C. candelabra* shows high survival rates at the juvenile stage. While primary growth is continuous and sensitive to seasonality, secondary growth is annual.

Key Words

Cerberiopsis – demography – continuous growth – life history strategy – masting – mortality rate – New Caledonia – phyllochron – phenology

1. Introduction

In the tropics, tree species, and more broadly plants, show an outstanding diversity of life history strategy. A large number of studies indicate that this diversity is maintained by multiple mechanisms of coexistence (McArthur & Levins, 1967; Janzen, 1970; Clark & Clark; 1992; Wright 2002; Zhu et al., 2018), but many life history strategies remain poorly understood preventing a clear disentanglement of how so many species can coexist (Chesson, 2000).

The number of times an organism reproduces is a fundamental life history trait (Young, 1981; Stearns, 1992; Hughes, 2017). It spans a continuum in plant reproductive biology between two main life histories: the polycarpy (multiple reproductions) and the monocarpy (one-lifetime reproduction event) (Harper, 1977; Simmonds, 1980; Amasino, 2009). While polycarpic strategies are widespread in perennial woody species, monocarpic strategies are mainly encountered in annual and biennial species and are uncommon among long-lived plants. Although extremely rare, a few monocarpic canopy trees are recorded in different tropical rainforest communities (Whitmore, 1998; Turner, 2001; Thomas, 2011). About twenty-nine species are known worldwide (excluding unbranched palm-like trees and shrubs; e.g. *Spathelia*, *Strobilanthes*, *Mimulopsis*, *etc.*) and distributed in two tropical genera: *Tachigali* (Fabaceae) and *Cerberiopsis* (Apocynaceae). Compared to long-lived palms such as *Aranga* or *Corypha* species, which are structurally monocarpic (Hallé & Oldeman, 1970; Simmonds, 1980; Dayanandan et al., 2018), these two genera include branched species with several apical meristems that constitute as many possibilities of growth and reproduction (Salmon et al., 2023).

Monocarpy in trees is still poorly understood, especially the adaptive traits that support individual fitness. This unusual life history has been described as a suicidal strategy (Foster, 1977), a big-bang reproduction (Humpries & Stevens, 2001), or an evolutionary bottleneck (Poorter et al., 2005), and could impact long-term persistence in long-lived trees (Read et al., 2006; 2021). Indeed, this strategy seems risky as the reproductive value at the individual scale depends on a single reproductive event whose success must be guaranteed to ensure species persistence. Therefore, understanding the adaptive value of monocarpy in trees requires the investigation of its demographic advantages in terms of (1) survival, (2) growth, and (3) reproduction output (Harper & White, 1974; Schaffer, 1974; Roff, 1992; Metcalf et al., 2003).

Several studies have explored the adaptative advantages of the monocarpic life history in trees (*Tachigali* species have received the most attention), and several hypotheses have been proposed. Following the resource allocation principle (Levins, 1968; Bazzaz et al., 2000; Reekie & Bazzaz, 2005), some studies suggest that monocarpic trees have higher growth rates as they do not invest in reproduction each year. They reach their optimal reproductive size more quickly, thus reducing their pre-flowering mortality probability (Foster, 1977; Poorter et al., 2005; Burd et al., 2006). Since monocarpy is frequently associated with masting and gregarious behavior, it was suggested to reduce the selection pressure from predation (Janzen, 1970). The production of a substantial seed number in a short time interval would lead to predator satiation and ensure the germination of a significant portion of the seed bank (Forget et al., 1999). Additionally, masting behavior and flowering asynchrony within the cohort are proposed to promote long-distance pollen movement and genetic diversity (Loveless et al., 1997).

Nevertheless, a few studies have focused on the juvenile stage, suggesting that the maintenance of the monocarpic life history in trees relies on the successful recruitment of seedlings. They propose that the survival rate of monocarpic juveniles should be higher than polycarpic juveniles and monocarpic adults (Cole, 1954; Stearns, 1976; Cook, 1979) and that the parental tree promotes the establishment and survival of its offspring by opening a canopy light gap when it dies (Foster, 1977; Kitajima & Augspurger, 1989; Read et al., 2006). However, Read et al. (2008, 2021) emphasize that light gaps created by the death of parental trees are not always sufficient and hypothesize that environmental disturbances could also promote juvenile recruitment by opening larger canopy gaps. Therefore, monocarpic life history in trees may be advantageous in disturbance-prone environments (Salmon et al., 2023).

We study two fundamental demographic aspects of a monocarpic tree species: (1) juvenile survival and (2) the developmental phenology, from seed germination to the sapling stage, with consideration to seasonal climatic variations. Phenology is the study of the timing of recurring biological events that characterize the life of an organism (Sakai, 2001). Here we investigate the phenology of growth and branching processes (axes and leaves organogenesis) which are key components of a tree's developmental trajectory. Our research focuses on *Cerberiopsis candelabra* Vieill. (Veillon, 1971), the unique monocarpic tree of this genus and the only one known in the South Pacific (Boiteau, 1981). We hypothesize that for the monocarpic strategy to be sustainable in *C. candelabra*, the plants germinated in large, post-disturbance, open areas must achieve particularly high survival and growth rates. Only short developmental trajectories, from germination to the sapling stage, should ensure the new cohort establishment and population persistence.

2. Materials and methods

2.1. Species description

Cerberiopsis candelabra Vieill. (ex. Pancher & Sebert) is a monocarpic tree endemic to New Caledonia (Veillon, 1971). Populations are mainly distributed in low- and medium-altitude forest formations in the main island's southern ultramafic massif (Read et al., 2006; 2008). Although the species presents a gregarious behavior in the rainforest, some isolated plants are observed in open scrublands. At the adult stage, trees can exceed 30 m in height with a diameter at breast height (DBH) up to 79 cm (Read et al., 2011) and are distinguishable by their pyramidal shape. The flowering season extends from August to December, but trees have been reported flowering beyond this period (Veillon, 1971). The single flowering event is massive and inflorescences are produced by all apical meristem of the crown. While flowering can spread over several months (2-6 mths), fruit maturation and seed production are more rapid (2-3 mths). Under optimal temperature conditions (25-35°C), germination occurs three weeks after sowing (ORSTOM, 1986).

2.2. Study site

New Caledonia's climate is characterized by two main seasons, the cool-dry season from June to September and the warm-wet season from December to March. They are interspersed by short transitional seasons, a warm-dry period from October to November, and a cool-wet period from April to May (MétéoFrance, 2022a). A growth monitoring plot of 12 m^2 (2 x 6), including 134 *C. candelabra* juveniles growing in natural conditions, has been established in June 2020. The plot is located near the 'Col des Deux Tétons' in the commune of Mont-Dore, south of the main island (22°12'23.72 "S, 166°42'13.91 "E). In this region maximal and minimal monthly temperatures are respectively recorded in January ($\overline{T}_{01}$ = 26.8°C) and July ($\overline{T}_{07}$ = 20.7°C). In 2021, precipitations are reported for 117 $days.y^{-1}$. Monthly precipitation is maximal in January-February ($\bar{p}_{01\text{-}02}$ = 600 $mm.mth^{-1}$) and minimal in July-August ($\bar{p}_{07\text{-}08}$ = 50 $mm.mth^{-1}$) (MétéoFrance, 2022b).

The juveniles are established in an open environment at the edge of a rainforest patch and constitute a mono-dominant regeneration rarely observed, as mature trees may require more than a century to flower once (**Figure 1A**). They are growing in an area cleared by a fire that partially burned the forest from 28 December 2017 to 2 January 2018 (RESCCUE, 2018) (**Figure 1B, B'**). As seeds lose their germinative capacity above 35°C (ORSTOM, 1986), we estimate that parental flowering-death and seedling germination have occurred after this event.

2.3. Plant measurements

All 134 juveniles have been described monthly from June 2020 to January 2022. The mortality rate (m) was measured each month and used to calculate the population density (d) within the plot.

Growth monitoring – Seedlings correspond to juveniles whose architecture is reduced to a single unbranched stem with a spiral alternate phyllotaxis (**Figure 1C, D**). Saplings are the juveniles that express branching (**Figure 1E**; see Salmon et al. (2023) for more details on the architectural development sequence of the species). For each plant, we measured the trunk basal diameter at 2 cm (D), the trunk total height (H), the monthly height growth (i.e. the distance between the last leaf produced in $month_n$ and the last leaf produced at $month_{n+1}$) (G), the monthly leaf production (i.e. the number of leaves produced in one month) (L), and the leaf lifespan (i.e the time elapsed between the production of a leaf and its observed fall) (L_s - this value may be overestimated as the monitoring temporal resolution is one month). An internode is defined as the vertical distance between two successive leaf insertions. One internode and its subtending leaf, and the associated axillary production, constitute a phytomer, the plant's smallest botanical unit (Barthélémy & Caraglio, 2007). Firstly, from G/L, we calculate the monthly internode length i.e. the mean length of internodes developed between the last leaf produced in month_n and month_{n+1} (IN). Secondly, for one phytomer per plant, we measured the internode elongation time (IN_e). The same internode was measured each month since its phytomer initiation in June 2019, the measurement stops when the same length value is observed for two consecutive months.

In November 2020 and 2021 no surveys were conducted due to security restrictions during New Caledonian independence referendums. November values were extrapolated linearly from December measurements: $X_{nov.} = \frac{X_{dec.}}{(days_{nov.-dec.}/days_{nov.})}$

Plant retrospective reconstruction – In December 2021, 3 juveniles were sampled from the growth monitoring plot and measured nodes by nodes. This includes one seedling and two branched saplings in May 2021 (**Figure 1E**). For each individual, we measured at each successive internode constituting the main axis from the base to the apex: (1) the internode lengths (IN), (2) the number of growth rings (GR) visible on a cross-section, and (3) when a leaf was present, the leaf area (LA) and the leaf mass area (LMA). LMA was obtained by measuring LMA was obtained by measuring the mass of 3 cm^2 of leaf blade (excluding the main veins) dried at 70°C for a week. IN, GR and LA are morpho-anatomical traits that mark the phenology of a plant's development. They transcribe the primary meristem functioning (Heuret et al., 2002; Grosfeld & Barthélémy, 2004; Nicolini et al., 2012). The characterization of (1) their variations and (2) the timing of their variations (thanks to the overlap with the field data), allows us to associate an absolute temporality to the plant's developmental trajectory since its germination.

Figure 1. Juveniles of *C. candelabra* Vieill. (ex Pancher & Sebert), a monocarpic gregarious tree endemic to New Caledonia. (**A**) Plants growth in an open environment and constitute a mono-dominant regeneration; (**B**) Growth monitoring plot located at the edge of a rainforest patch partially burned in early 2018 – in **B'** authors collecting data in the plot after 18 months monitoring; (**C**) Plants show a spiral alternate phyllotaxy - arrow indicates a growth slowdown marked by a reduction in internode length and leaf area – in **C'** a juvenile infected by a fungi pathogen causing malformation in July 2021; (**D**) Drawing of a seedling whose architecture is limited to a single unbranched stem; (**E**) A sapling developing a first tier of branches on the trunk in May 2021.

2.4. Statistical analysis

All analyses were performed with the R-4.2.0 software (R Core Team, 2022). As our data do not satisfy the applicability conditions of standard parametric tests (no normality and homogeneity of residuals), we use non-parametric statistics for sample statistical comparisons. We performed Wilcoxon-Mann-Whitney (Wilcox.) and Kruskall-Wallis (${}_{KW}\chi^2$) tests (Stats package; R Core Team, 2022) for mean comparisons (Hollander & Wolf, 1973).

3. Results

3.1. Juvenile mortality and density

From June 2020 to January 2022, *C. candelabra* mortality rate was 32.92 % (**Figure 2A**). Compared to other months, mortality rates are significantly higher from October to November ($\overline{m}_{10\text{-}11}$ = 2.67 %.mth^{-1}; Wilcox. = 15; P = 0.039*), corresponding to the warm-dry transitional season ($\overline{T}_{10\text{-}11}$ = 24.2°C.mth^{-1}; $\overline{p}_{10\text{-}11}$ = 175 mm.mth^{-1}). In August 2021, a high mortality rate is additionally recorded ($m_{08/21}$ = 4.31 %.mth^{-1}) (**Figure 2A**). It occurred after a prolific fungal pathogen infection in July 2021 (**Figure 1C'**). At the beginning of growth monitoring, the population density was greater than 10 plants per square meter (d = 11.17 ind.m^{-2}) (**Figure 2B**). Twenty months later, the population density was 7.8 ind.m^{-2} (**Figure 2C**).

3.2. Plant growth in the field

Juveniles have doubled in size over the 20 months of monitoring ($\overline{H}_{06/20}$ = 82.3 ± 17.2cm; $\overline{H}_{01/22}$ = 165.1 ± 32.2cm; $\overline{D}_{06/20}$ = 9.9 ± 2.1mm; $\overline{D}_{01/22}$ = 20.6 ± 6.4mm). In 2021, the mean annual height growth was 59.9 cm.y^{-1} and plants with the highest growth (the 90th percentile of height growth) showed a mean increase of 79.6 cm.y^{-1}. Compared to other months, we recorded a significantly higher growth rate from December to February ($\overline{G}_{12\text{-}02}$ = 6.4 cm.mth^{-1}; Wilcox. = 62; P = 0.033*), and a lower growth rate from June to September ($\overline{G}_{06\text{-}09}$ = 2.2 cm.mth^{-1}; Wilcox. = 14; P = 0.007**) (**Figure 3A**).

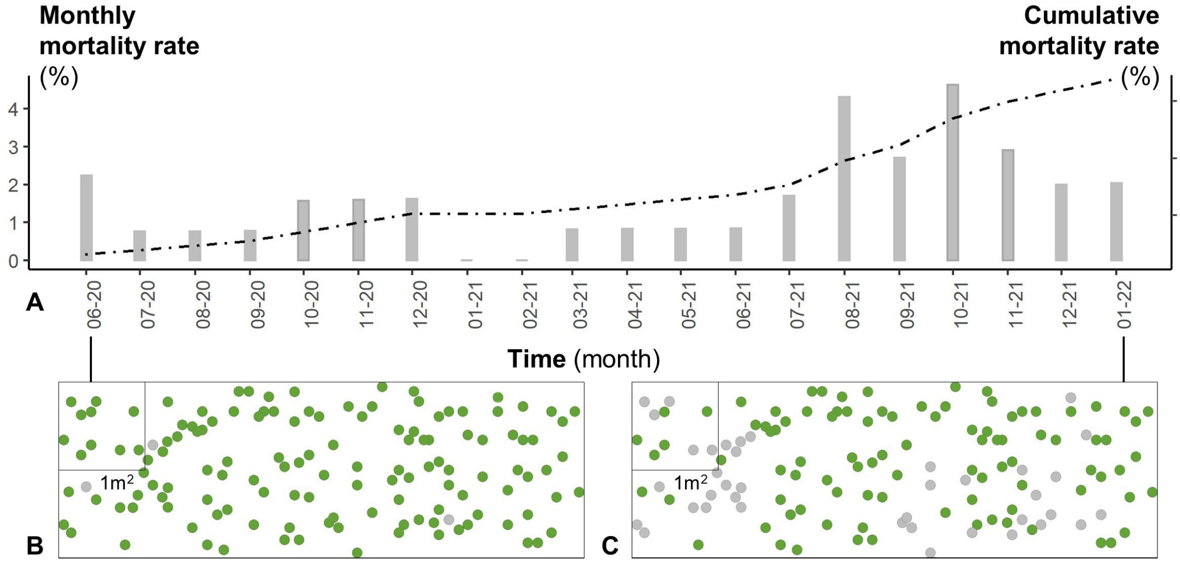


Figure 2. *C. candelabra* juvenile mortality and population density from June 2019 to January 2022. (**A**) Mortality rates recorded over 20 months within the monitoring plot, both monthly (gray histogram) and cumulative (black dashed line) rates are shown - annual mortality rate was 21.57% in 2021; (**B, C**) Scale displays of the growth monitoring plot - circles indicate the seedling localization with living plants in green and dead plants in grey; (**B**) In June 2019, population density is 11.17 ind.m^{-2}; (**C**) In January 2022, population density is 7.83 ind.m^{-2}.

Internode length variations – For phytomers initiated in June 2019, the mean elongation time of internodes was 14 weeks ($\overline{IN_e}$ = 98 ± 23 days), with 92% of the final internode length produced in the first month. Over the 20 months of monitoring, the mean internode length was 14.1 mm. We found significantly longer internode lengths for phytomers developed from December to February ($\overline{IN}_{12\text{-}02}$ = 16.8 mm; Wilcox. = 13; P = 0.033*) and significantly shorter internode lengths for phytomers developed from June to August ($\overline{IN}_{06\text{-}08}$ = 10.9 mm; Wilcox. = 77; P = 0.002**) (**Figure 3B**). These periods correspond respectively to New Caledonia's warm-wet season ($\bar{T}_{12\text{-}02}$ = 26.6°C.mth^{-1}; $\bar{p}_{12\text{-}02}$ = 540 mm.mth^{-1}) and cool-dry season ($\bar{T}_{06\text{-}08}$ = 21.1°C.mth^{-1}; $\bar{p}_{06\text{-}08}$ = 90 mm.mth^{-1}).

Leaf production rate – *C. candelabra* juveniles developed leaves that had an average lifespan of 8 months ($\overline{L_s}$ = 251 ± 45 days). The number of leaves produced is indicative of the species' phyllochrone (i.e. the number of days between the sequential emergence of successive phytomers). Over the 20 months of monitoring, the mean leaf production was 2.6 leaves.mth^{-1}. An average of 1 phytomer is thus produced every 12 days. Compared to other months, this rate is significantly higher from December to February, during the warm-wet season, when an average of 1 phytomer was produced every 8 days ($\bar{L}_{12\text{-}02}$ = 3.88 leaves.mth^{-1}; Wilcox. = 12; P = 0.025*) (**Figure 3C**). In contrast, no significant decrease in leaf production is recorded from June to August, during the cool-dry season ($\bar{L}_{06\text{-}08}$ = 1.92 leaves.mth^{-1}; Wilcox. = 57; P = 0.239).

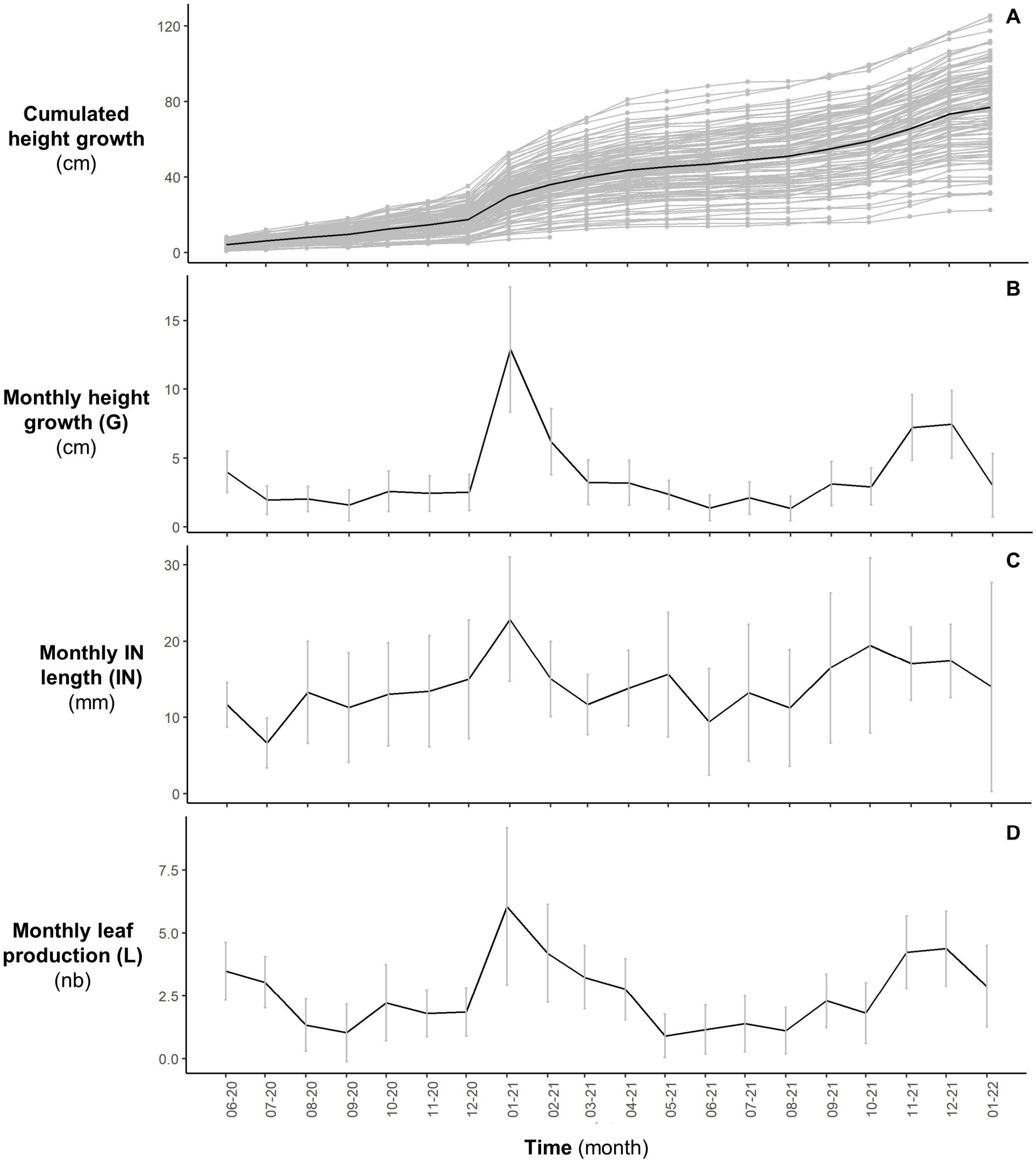


Figure 3. Growth of *C. candelabra* juveniles in natural conditions from June 2019 to January 2022. (**A**) Cumulated height growth - grey lines show the individual cumulated growth of each juvenile – the black line indicate the average growth; This growth pattern is explained by monthly variations of : (**B**) the height growth - with higher growth rate from December to February and lower growth rate from June to September; (**C**) the IN length - with longer IN length from December to February and shorter IN length from June to August; (**D**) the leaf production - with a higher leaf production rate from December to February.

3.3. Juvenile developmental trajectories

Since germination, the three fully described juveniles have respectively developed 117, 128, and 131 phytomers by the main axis. Each plant shows significant variation in internode length ($\overline{IN}_{\mathrm{min}} = 4.9 \pm 1.4$mm; $\overline{IN}_{\mathrm{max}} = 24.9 \pm 0.9$mm) and leaf area ($\overline{LA}_{\mathrm{min}} = 21.8 \pm 12.5\mathrm{cm}^2$; $\overline{LA}_{\mathrm{max}} = 179.4 \pm 16.7\mathrm{cm}^2$) along the trunk (**Figure 4**).

Patterns of internode length variations and leaf characteristics – *C. candelabra* plants have a primary growth marked by the alternation of long and short internode zones associated with a reduction in leaf area in the short zones (**Figures 1C** and **4A, B**). In all juveniles, axillary leaves in the short internode zones (considering the 3 leaves closest to the shortest internode) are significantly smaller than other leaves ($\overline{LA}_{\mathrm{zone-}} = 30.2\ \mathrm{cm}^2$; Wilcox. = 40; $P < 0.001$***) (**Figure 4B3, E3**). They are not significantly larger in the long internode zones ($\overline{LA}_{\mathrm{zone+}} = 117.1\ \mathrm{cm}^2$; Wilcox. = 39; $P = 0.173$) (**Figure 4B1, E1**). Two other zones of leaf area reduction, that are not correlated with a decrease in internode length, are additionally identified in all individuals (**Figure 4B2, B4**). Both reductions occur during the transitional seasons (**Figure 4C, D**). Regardless of the leaf area variations, leaf mass per unit area did not vary significantly and remains relatively constant with $\overline{LMA} = 170.4 \pm 20\ \mathrm{g.m}^{-2}$.

Expression of branching – Branching occurs in some plants in May 2021, during the cool-wet transitional season. It concerns 3.4 % of the juveniles (4/119). Branches developed from the last long internodes produced before the internode shortening zone. An average of 6 ± 1 branches is developed on successive nodes forming a compact tier of branches on the trunk (**Figure 1E**). From May 2021 to January 2022, these axes produced fewer leaves than the trunk above their insertion ($\overline{L}_{\text{trunk}}$ = 42 ± 3 leaves; $\overline{L}_{\text{branch}}$ = 21 ± 5 leaves) and significantly smaller leaves ($\overline{LA}_{\text{trunk}}$ = 89.8 cm^2; $\overline{LA}_{\text{branch}}$ = 62.1 cm^2; $_{KW}\chi^2$ = 4.6; P = 0.033*). As for the trunk, we found variations in internode length along the branches associated with a leaf area reduction in the short internode zones developed during the cool-dry season. Compared to the unbranched seedling, the two branched saplings were not larger in diameter ($_{KW}\chi^2$ = 0.8; P = 0.67) and did not develop longer internodes ($_{KW}\chi^2$ = 0.4; P = 0.83) or larger leaf areas ($_{KW}\chi^2$ = 5.8; P = 0.06).

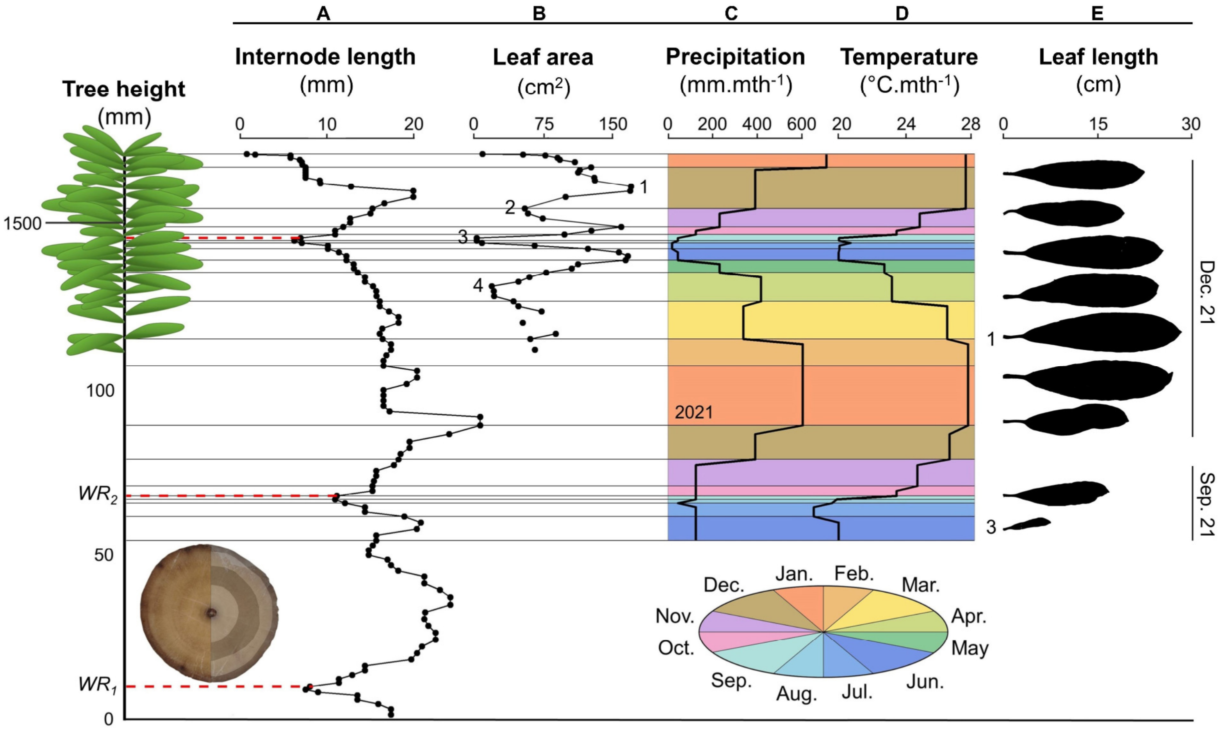


Figure 4. Retrospective reconstruction of a *C. candelabra* seedling's developmental trajectory from germination to three years old. (**A**) Length of each internode developed along the trunk - three morphological units are identified based on the alternation of long and short internode zones combined with the establishment of a growth ring in the short internode zones - red dashed lines indicate the setting location of the growth rings inside the trunk, WR$_1$ being the most basal; (**B**) Leaf area produced at each phytomer of the trunk - for one unit of internode length variation, three phases of leaf area variation are observed - in **3**: a zone of leaf area reduction associated with a short internode zone developed during the cool-dry season (Jun.-Sep.) - in **2**, **4**: zones of leaf area reduction set up during the transitional seasons (Apr.-May, Oct.-Nov.); (**C**, **D**) Monthly precipitation and temperature (from MétéoFrance, 2022a) - measurements are reported over a 20 month period as require overlap with the growth monitoring data (Jun.2019-Jan.2022); (**E**) Leaf size variability at the individual level - phyllochron is shorter during the warm-wet season (Dec.-Mar.) with a higher leaf production rate per month – **1**, **3** show leaves labeled in **B**.

Dating organogenesis – In all *C. candelabra* fully described, we identified 3 morphogenetical units (MUs) along the trunk, based on internode length variations (one unit being structurally defined by the succession of a long internode zone and a short internode zone). Each MU is associated with (1) 2 or 3 phases of leaf area variations and (2) the establishment of one macroscopically visible growth ring (**Figure 4**). Less significant fluctuations in internode length are observed within every MU but are not associated with the establishment of a growth ring (**Figure 4A**). In all juveniles, we count three distinct growth rings at the base of the trunk and a fourth in production. They are all initiated in the short internode zones when the height growth rate is lowest. By overlapping data from the retrospective reconstruction and the field, we assess the setting up of GR$_2$ and GR$_3$ respectively in September 2020 and 2021, at the end of the cool-dry season ($\bar{T}_{09}$ = 21.2°C.mth^{-1}; $\bar{p}_{09}$ = 113 mm.mth^{-1}) (**Figure 4C, D**). The juveniles described are therefore in their third year of growth.

4. Discussion

4.1. *C. candelabra* juvenile survival in full light conditions

The evolutionary success of the monocarpic life history strategy in trees is inherently linked to a low mortality probability of pre-flowering individuals (Burd et al., 2006; Read et al., 2006, 2008). Trees have only one chance to successfully reproduce and to transmit their genetic pool to the next generation and ensure species persistence (Foster, 1977; Poorter et al., 2005; Read et al., 2021). The juvenile stage is thus the most critical phase in the monocarpic life history. On the one hand, it corresponds to the establishment of the new generation, the only one to preserve the genetic heritage of the previous one. On the other hand, it's the stage with the highest probability of pre-flowering mortality (Kitajima & Augspurger, 1989; Forget et al., 1999; Read et al., 2006).

Kitajima & Augspurger (1989) and Poorter et al. (2005) reported that annual mortality rates of two monocarpic rainforest tree species, *Tachigali versicolor* and *Tachigali vasquezii*, were respectively 11 %.y^{-1} (for 1-2 year-old juveniles) and 34 %.y^{-1} (for 0-2 year-old juveniles). These mortality rates were lower than those recorded for other polycarpic species in the same community (see Poorter et al., 2005 - Appendix S1). As expected, we found similar high juvenile survival rates in *C. candelabra*. Considering plants in their 2nd year of life (from June 2020 to May 2021), the seedling mortality rate was 11.8 %.y^{-1}. Most remarkable is the population density at which *C. candelabra* achieves this survival rate.

Compared to *T. versicolor*, whose juvenile density at 2 years old in light gaps was 3.3 ind.m^{-2} for plants of 18 ± 4.6 cm height (Kitajima &Augspurger, 1989), *C. candelabra* achieves the same survival rate with a 9.9 ind.m^{-2} population density for plants of 131 ± 27.3 cm height. In our study, juvenile recruitment occurs in an open area at the edge of a rainforest and population regeneration is mono-dominant. In large canopy gaps, the population density of *C. candelabra* is reported to be equally high. Read et al (2008) record a population density of 7.5 ind.m^{-2}, 1 year after germination. Such tree densities are rarely observed, especially in tropical rainforests with high species richness (Gentry, 1992; Chesson, 2000; Wright, 2002). For instance, some large gap specialist trees in the Amazon rainforest, such as *Cecropia insignis* or *Cecropia obtusa* (Urticaceae), are known to show up to 0.45 ind.m^{-2} in gaps more than 50m^{2}, 1 year after germination and with individuals taller than 1m (Brokaw, 1986, 1987; Popma et al., 1988; Van der Meer et al., 1998). Like *C. insignis* and *C. obtusa*, *C. candelabra* is a light-demanding species and should be considered a large gap specialist.

4.2. Juvenile developmental phenology

Even in the tropics, plant growth phenology is influenced by seasonal rhythms (Newstrom et al., 1994; Sakai, 2001; Sakai & Kitajima, 2019). Many tropical and subtropical forests, such as those of New Caledonia, are characterized by a distinct annual dry season that affects the mechanisms regulating the development of trees (Reich, 1995; Sakai, 2001; Basio et al., 2016). In such forests, drought, rain, and insolation are likely to be the main factors explaining phenological patterns (van Schaik et al., 1993; Rivera & Borchert, 2001; Borchert et al., 2015).

An annual growth sensitive to seasonality – Our results suggest that *C. candelabra* developmental phenology is influenced by the seasonality of New Caledonia (**Figure 5**). During the cool-dry season, primary growth (stem elongation) is limited and shows a reduction in (1) height growth, (2) leaf production, and (3) leaf area in all juveniles. Subsequently, during the warm-dry transitional season, the highest mortality rates are recorded, suggesting that *C. candelabra* phenology is more sensitive to rainfall than temperature changes. Of the 134 juveniles studied, we recorded an average primary growth rate of 5.9 $cm.mth^{-1}$ at the warm-wet season, corresponding to the production of a new leaf every 8 days associated with a 1.6 cm long internode.

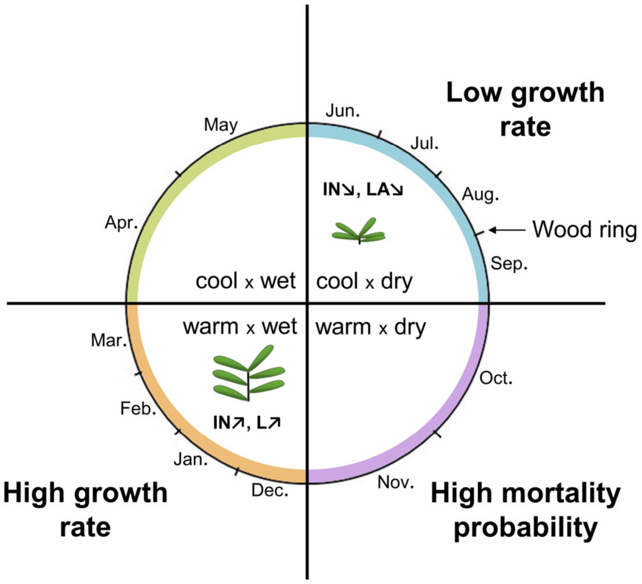


Figure 5. Results summary on the developmental phenology in a 3 years-old juvenile of the monocarpic tree species, *C. candelabra*. The growth shows an annual pattern and is characterized by (1) annual growth rings and (2) monthly variations in internode length (IN), number of leaves produced (L) and leaf area (LA).

Secondary growth (stem enlargement) is rhythmic and growth rings are produced every year in September at the end of the slow phase of primary growth. Considering the number of phytomers produced before the emergence of the first growth rings ($\bar{L}$ = 9 ± 1.7 leaves), we estimate that all plants have germinated between April and May 2019. As suggested by Read et al. (2021), our results provide new evidence that *C. candelabra* joins the 230 tropical tree species known to produce annual growth rings (Schongärt et al., 2017). In New Caledonia, only a few trees are included in this inventory, the most well-known being the endemic conifer *Agathis ovata*

(Araucariaceae) (Enright & Goldblum, 1998; Enright et al., 2003; Lieubeau et al., 2007). While in *A. ovata* the timing of tree ring production is unknown, in *C. candelabra* we suggest that growth rings are formed at the end of the cool-dry season. This result supports previous studies demonstrating that tree ring formation in tropical and subtropical regions is mainly driven by seasonal variations in rainfall (Lieubeau et al., 2007; Brienen et al., 2016; De Lara et al., 2017; Rahman et al., 2019).

Continuous primary growth with periodic variations – *C. candelabra* studied are in their third year of growth and we have measured three morphogenetical units along the trunk. As defined by Prat (1936), MUs are repetitions of structural entities identified here by a succession of long and short internodes. The short internode zones, associated with a reduction in leaf area, mark a slowdown phase of primary growth. Consequently, *C. candelabra* presents continuous growth in sense of Hallé et al. (1978). Since the “evergrowing species” concept was introduced by Koriba (1959), there is an issue concerning the boundary between continuous and rhythmic growth. This issue might be related to the lack of a clear guideline on (1) the structure-time relationship that must be observed to define the growth rhythmicity and (2) the component of growth, elongation, or organogenesis, that must be characterized. Rhythmic growth is defined as a plant development marked by rhythmic stops of elongation which structurally delimits successive "growth units" (GUs) along the axes (Hallé & Martin, 1968; Barthélémy et al., 1989; Barthélémy & Caraglio, 2007). In opposition, a continuous growth refers to an uninterrupted elongation and is suggestive of linear development (Hallé et al., 1978; Comte, 1993; Caraglio & Barthélémy, 1997). However, it is well known that some plants, such as *Camellia thea* (Theaceae) or *Rhizophora mangle* (Rhizophoraceae), show distinct MUs although their organogenesis is temporally continuous (Bond, 1942, 1945; Gill & Tomlinson, 1971). Likewise, some species don’t show visible MUs, or GUs, although their organogenesis is temporally rhythmic (Comte, 1993; Edelin, 1993). Therefore, (1) continuous growth is not suggestive of a monotonous linear development and (2) the presence or absence of MUs is not sufficient to define the growth rhythmicity of a plant. In our case, *C. candelabra* develops in a subtropical environment with distinct seasons. Its growth is suggested continuous, as its elongation is uninterrupted, but also "periodic" (i.e. of variable intensity under the influence of seasonality) and therefore, structurally characterized by a succession of MUs. This periodic development is even more remarkable at the leaf level, with continuous leaf production marked by phases of leaf area reductions at each seasonal shift.

4.3. Promising results for the reconstruction of adult tree development

At least for the juvenile stage, our results support the carbon-14 datings of Read et al. (2021), suggesting that the growth rings of *C. candelabra* are annual. In addition, we demonstrate that zones of internode length shortening along the trunk can be used as a marker of the primary growth slowdown that occurs during the cool-dry season. Since primary growth is continuous, these short internode zones don't delimit real GUs, as suggested by Veillon (1971), but they do allow us to identify annual growth limits. This remains to be validated on older adult trees. Therefore, these results suggest that it's possible to retrospectively reconstruct the whole developmental trajectory of this large rainforest tree. Such studies have only been done for a few tropical species (Heuret et al., 2002; Zalamea et al., 2008; Nicolini et al., 2012).

5. Conclusion

Our study opens a new small window in our understanding of monocarpy in *Cerberiopsis candelabra*. Although further investigations are needed to obtain a complete and comprehensive view, growth monitorings remain rare despite their critical importance for such species where stand regeneration can occur at intervals ranging from decades to centuries. Based on our results and those of previous studies (Read et al., 2006, 2008, 2021), we suggest that *C. candelabra* may be defined as a large light-gaps specialist and a fast, continuous, growing species. Since survival at the juvenile stage is a key parameter of the monocarpic life history's success (Kitajima & Augspurger, 1989; Forget et al., 1999; Read et al., 2006), the combination of these two traits can be an advantage in high-light microsites. (1) Seedlings show high population densities and survival rates, ensuring the new generation establishment. (2) Juveniles have fast, continuous primary growth rates to compete with other species and possibly reach reproductive maturity quickly. This last point has been emphasized as a potential precondition for the evolution of the monocarpic strategy in trees (Foster, 1977; Poorter et al., 2005; Burd et al., 2006). However, these two traits combined are only advantageous if the parental trees environment is (1) frequently open and (2) sufficiently open to create favorable light conditions for seedling recruitment (Martinez-Ramos & Alvarez-Buylla, 1986; Read et al., 2008; Sakai & Kitajima, 2019). Read et al. (2006, 2008) highlighted that the gaps freed up by *C. candelabra* mast events are often insufficient for the juvenile establishment unless trees are large and in dense stands. Frequent environmental disturbances, such as small-scale fires or blow-downs from tropical cyclones, may be more advantageous in creating favorable light environments for seedling recruitment than mast-dependent gaps only.

6. Additional information

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6.2. Author contributions

CReDIT authorship contribution statement - Conceptualization: *SI, PH, CS*; Funding acquisition: *SI, PH*; Investigation: *CS, VH*; Data curation and Formal analysis: *CS*; Visualization: *CS, PH*; Writing - Original draft: *CS*; Writing - Review: *PH, SI, VH*; Project administration and supervision: *PH, SI*.

6.3. Data Availability Statement

The data that support the findings of this study are openly available in Zenodo (https://zenodo.org) at http://doi.org/10.5281/zenodo.7112855.

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Chapter 5

Intertwined crowns of a fertile and sterile *C. candelabra* at Pic du Grand Kaori (New Caledonia) © C. Salmon & J.M. Bore

Chapter 5 is an original research article that quantitatively analyzes the ontogeny of adult individuals within the three *Cerberiopsis* species. We retrospectively reconstruct their developmental trajectories based on measurements of various morpho-anatomical traits. Our results highlight that each species exhibits strong structural regularities and high coordination between all developmental processes (growth, branching, and flowering). This developmental synchronicity might be a prerequisite for the evolution of the monocarpic strategy.

An integrative dendrochronological approach to reconstruct developmental trajectories in the subtropical genus *Cerberiopsis* (Apocynaceae).

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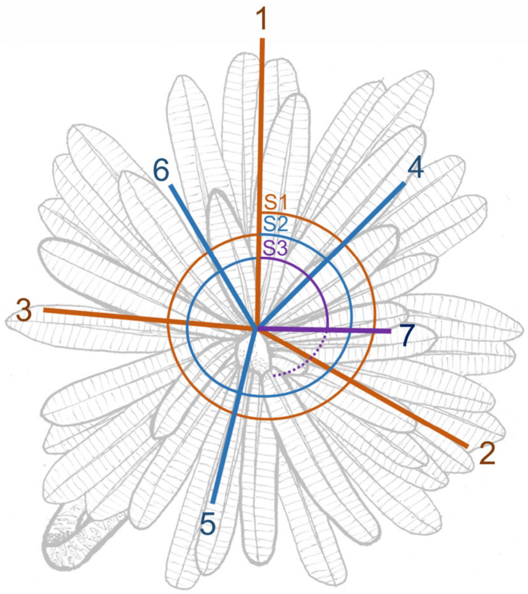


Abstract

Phenological studies at the individual scale investigate the temporality of plant developmental processes, such as leaf flushing and shedding, wood production, branching, and flowering. In this study, based on an integrative dendrochronological approach, we reconstruct the developmental trajectories and of the three subtropical species belonging to the genus *Cerberiopsis* (Apocynaceae). Variations in several morpho-anatomical traits, such as growth rings, internode lengths, pith area, branch and flower positions, and leaf mass per area (LMA), are quantitatively analyzed within the whole plant body from and interpreted a dynamic point of view and with respect to climate seasonality. Our results show that all *Cerberiopsis* species exhibit strong structural regularities, especially annual growth rings presumably formed during the cool-dry season of New Caledonia. In each species, primary and secondary growth, branching, and flowering processes are highly coordinated within the plant architecture. One of the three species studied, *C. candelabra* Vieill., is among the 29 monocarpic canopy tree species known worldwide for its monocarpic strategy (flowering once and dying). As monocarpy implies the synchronous flowering of all apical meristems, we suspect that highly coordinated developmental processes within the plant body are a prerequisite for monocarpy evolution.

Key Words

branching – growth ring – New Caledonia – phenology – pith area – polycyclism – primary growth – stem profile – synchronicity

1. Introduction

In plants, the expression of fundamental biological events, such as growth, leaf senescence, or reproduction, is determined endogenously and regulated according to seasonal regimes. They are expressed at times that maximize their fitness consequences (van Schaik et al., 1993; Sun et al., 1996; Fenner, 1998; Valdez-Hernandez et al., 2010). Phenology is the study of the temporality of these recurring biological events and phenological studies provide insight into how plants develop throughout time (Lieth, 1974; Sarmiento and Monasterio, 1983; Newstrom et al., 1994; Chapman, 1999; Sakai, 2001). Therefore, plant phenology is multilevel and could be studied at the community, population, and individual scale.

At the individual scale, phenology explores the temporality of plant developmental processes, such as leaf flushing, wood production, branching, and flowering. These processes have been widely studied, mostly in temperate species, and several morpho-anatomical traits have been identified as useful in understanding their timing. Among the most well-known plant anatomical traits, the growth rings have been the most used. The study of growth ring formation, dendrochronology, allows us to investigate the plant's secondary growth patterns (Schweingruber, 2012; De Micco et al., 2019; Quintilhan et al., 2021; Rodriguez et al., 2022). By analyzing the number of growth rings or the wood density profile, dendrochronological studies aim to estimate tree age, secondary growth rate, and productivity in various ecosystems (Worbes, 1995, 1999; Fichtler et al., 2003; Brienen & Zuidema, 2006; Brienen et al., 2016). In the last decades, they have gained momentum, especially in the tropical regions, since the presence of macroscopically distinct growth rings is known in many species (Coster, 1927; Worbes, 2002; Rozendaal & Zuidema, 2011; Schöngart et al., 2017).

The study of other morpho-anatomical traits, such as leaf, bud, and inflorescence scars, or pith size, has long lagged behind the study of growth rings, probably due to its more apparent complexity of implementation. However, the potential of these additional traits to explore plant phenology has been evidenced several times (Heuret et al., 2002; Passo et al., 2002; Baret et al., 2003; Zalamea et al., 2012; Taugourdeau et al., 2012). One of the most common morphological regularities in plants is the alternation of long and short phytomer zones all along the axes. The phytomer is the smallest botanical entity of the plant body: a leaf, its axillary bud, and its subtending internode (the stem portion separating a leaf from the next one) (Barthélémy & Caraglio, 2007). The quantitative analysis of phytomers length within the plant, and the localization of branches and flowers in this phytomer network, allows us to investigate the plant's primary growth, flowering, and branching patterns (Heuret et al., 2002; Grosfeld & Barthélémy, 2004; Zalamea et al., 2008; Nicolini et al., 2012).

In all phenological studies on tropical and subtropical species, temporality is the main issue. The quantitative analysis of morpho-anatomical traits, such as growth rings or phytomers, aims to define structural regularities within the plant that reflect a relative periodicity of development. In temperate species, this developmental periodicity is often annual due to their establishment in highly seasonal environments, but in tropical and subtropical species defining an absolute periodicity remains difficult (Détienne, 1989; Killmann & Thong, 1995; Dünisch et al., 2003; Schöngart et al., 2002, 2015). Therefore, a few studies promoted the combined use of several morpho-anatomical traits to disentangle the temporality of species development (Baret et al., 2003; Zalamea et al., 2008; Nicolini et al., 2012; Morel et al., 2015; Silva et al., 2019).

In tropical and subtropical regions, water availability and photoperiod are some of the main factors impacting plant phenology (Reich & Borchert, 1984; Wright, 1996; Borchert et al., 2002; Anderson et al., 2005; Valdez-Hernandez, 2010). As temperate species, tropical and subtropical species are likely to be affected by global changes, especially by the intensification of extreme events such as droughts, cyclones, and hurricanes (Cleland et al., 2007; Garcia et al., 2014; IPCC, 2014; Piao et al., 2019). Some of the most reported effects concern the flowering phenologies and show that individuals are shifting their flowering frequency, which may affect population regeneration (Pau et al., 2013; Kitayama et al., 2015; Chen et al., 2017; Sakai & Kitajima, 2019). Therefore, understanding plant development, especially in rare and endangered species, is an issue for tropical biodiversity conservation.

In this integrative dendrochronological study, we retrospectively reconstruct the developmental trajectories of individuals belonging to the subtropical genus *Cerberiopsis* (Apocynaceae). We quantitatively analyze their developmental processes (primary and secondary growth, branching, and flowering) thanks to the combined use of several morpho-anatomical traits. The genus *Cerberiopsis* comprises three species endemic from New Caledonia, and one of them, *C. candelabra*, is among the 29 canopy tree species known worldwide for their monocarpic strategy (Veillon, 1971; Read et al., 2006, 2008, 2021; Salmon et al., 2023). Monocarpy characterizes plants that die following a unique flowering event (Harper, 1977; Simmonds, 1980; Amasino, 2009; Davies & Gan, 2012). In trees, perennial poly-axial plants, this strategy is rare and has been variously classified as archaic (Gadgil & Bossert, 1970), suicidal (Foster, 1977), and an evolutionary bottleneck (Poorter et al., 2005). The others species of the genus, *C. neriifolia* and *C. obtusifolia*, are respectively a treelet and a shrub that flower multiple times a year (Boiteau, 1981; Salmon et al., 2023). Little is known about these two species and both are classified as vulnerable by the IUCN (IUCN, 2022).

Salmon et al. (submitted) suggested in young *C. candelabra* that growth rings are distinct and form annually during the New Caledonian cool-dry season. These results support the ^{14}C dating of Read et al. (2021), which indicated that growth rings were very close to annual. Here, we hypothesize that the three *Cerberiopsis* species, exposed to distinct wet and dry seasons, exhibit strong structural regularities and that their primary growth pattern is annual. We suspect that developmental processes are highly coordinated in *C. candelabra* since the monocarpic flowering synchronously concerned all meristems of the tree crown, independently of tree age or size (Salmon et al., 2023).

Figure 1. *Cerberiopsis* species developmental features. (**A**) *C. candelabra* tree C6 which flowered and died in October 2019; the main axis has developed rhythmically ten distinct tiers of branches. (**B**) *C. candelabra* tree C2 with two distinct branch tiers sampled along a cleared roadside at Yaté. (**C**) Branch of *C. neriifolia* treelet N2 with its visible leaf scars; arrow indicates a growth slowdown marked by a short phytomer zone. (**D**) Branch of *C. obtusifolia* shrub O3 with a sympodial construction; arrow indicates a sympodial relay that has allowed the branch development after terminal flowering. (**E**) Branch apex of *C. neriifolia* treelet N3 with an alternate spiral phyllotaxis.

2. Materials and methods

2.1. *Cerberiopsis* species

The genus *Cerberiopsis* (Apocynaceae), endemic to New Caledonia, includes three woody perennial species (Boiteau, 1981). While *C. candelabra* Vieill. is a monocarpic tree, which flowers once and dies (Veillon, 1971), the other two species, *C. neriifolia* S. Moore and *C. obtusifolia* Van Heurck & Müll.Arg., are respectively a polycarpic treelet and shrub which flower several times a year. All species grow on the ultramafic substrate characteristic of the territory (Jaffré, 2022). *C. candelabra* is a large tropical tree reaching 30m in height for a maximum observed diameter at breast height (DBH) of 79 cm (Read et al., 2006). It can establish in rainforests and in disturbed open areas (cleared roadside, trail, forest edge). *C. neriifolia* and *C. obtusifolia* are found exclusively in the shrubby maquis. These species respectively reach up to 14m and 5m for a maximal observed DBH of 24cm and 6cm (Salmon et al., 2023). All *Cerberiopsis* species have a main axis characterized by a monopodial construction (i.e. growing through a unique apical meristem) and developing successive and distinct tiers of branches (**Figure 1A, B**). Branch construction is monopodial in *C. candelabra* and *C. neriifolia*, and sympodial (i.e. growing through multiple meristems) in *C. obtusifolia* (**Figure 1D**). The flowering of all axes is terminal in each species (Salmon et al., 2023).

2.2. Plant materials and study sites

First batch sampled – 12 trees growing in natural conditions were cut down and collected in the southern ultramafic massif of New Caledonia, from March to August 2020. Individuals ranging from 1.4 to 10.3 m in height were fully described, including six *C. candelabra* (C1-C6), three *C. neriifolia* (N1-N3), and three *C. obtusifolia* (O1-O3). All plants are presented in **Table 1**. We were authorized by the North Province of New Caledonia to collect only three *C. neriifolia* and three *C. obtusifolia* because of their vulnerable status (IUCN, 2022). *C. candelabra* trees were sampled in the communes of Thio (C1, C2: 21°40'38.18"S, 166°20'13.11"E) and Mont-Dore (C3-C6: 22° 4'53,43"S, 166°37'51,15"E). *C. neriifolia* and *C. obtusifolia* were respectively collected in the communes of Thio (21°41'58.14"S, 166°19'23.51"E) and Voh (20°59'39.63"S, 164°44'24.75"E). While all *C. neriifolia* and *C. obtusifolia* were in flower during sampling, *C. candelabra* were sterile except for one dead tree (C6) that flowered in October 2019 (**Figure 1A**).

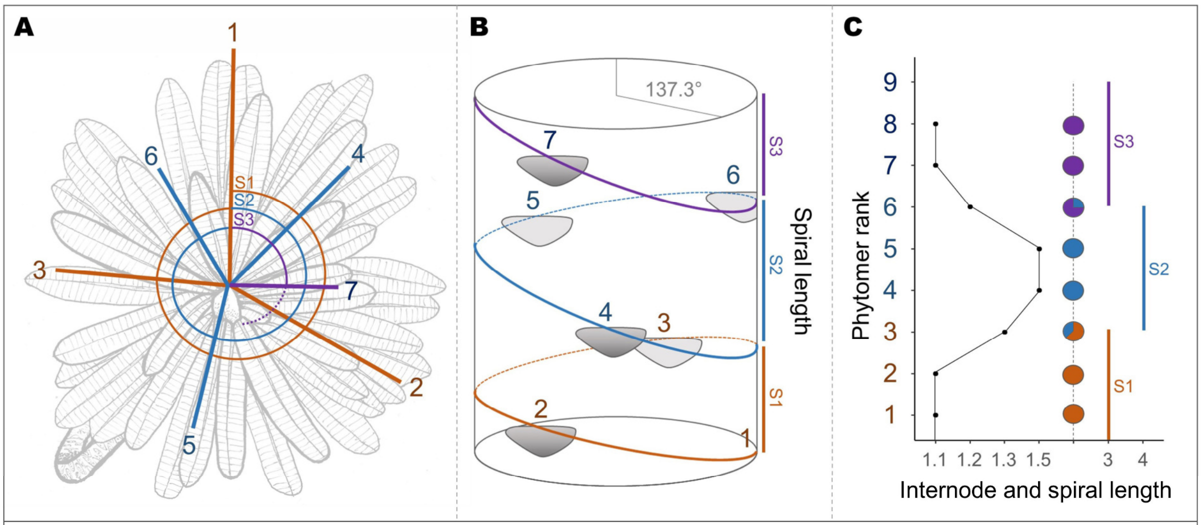
Second batch sampled – In November 2021, after a mast-flowering event at the forest patch of Baie Nord (22°19'20.65"S, 166°51'30.72"E), 10 additional *C. candelabra* trees, 5 flowering and 5 non-flowering, were sampled for complementary measurements. Trees ranged from 7 to 14m in height and each pair (1 flowered/1 non-flowered) consisted of individuals displaying the same architecture (i.e. of similar total height (H), diameter at breast height (DBH), and branch tiers number (Bt)). For all trees, we only collected a stem portion comprising the last two morphological units (MUs) produced by the first living branch carried by the trunk (see Salmon et al. (2023 and submitted) for more details on MU identification).

Table 1. Main characteristics of individuals in the first batch sampled. Six *C. candelabra*, three *C. neriifolia,* and three *C. obtusifolia* are quantitatively described. *C. candelabra* trees range from 2.7 to 10.3 m in height for a DBH of 2.6 to 19.3 cm; individual C6 is a dead tree that flowered in October 2019. *C. neriifolia* treelets range from 1.9 to 3.8m in height for a DBH of 1.7 to 3.6 cm. *C. obtusifolia* shrubs range from 1.4 to 2.2 m in height for a DBH of 0.7 to 1.1 cm. All *C. neriifolia* and *C. obtusifolia* described flowered at least one time. B/T ratio corresponds to the number of phytomeres produced by a branch relative to the number of phytomeres produced by the trunk above its insertion (B/T > 1: branches produced more phytomers than the trunk).

Species	*C. candelabra*						*C. neriifolia*			*C. obtusifolia*		
Tree ID	**C1**	**C2**	**C3**	**C4**	**C5**	**C6**	**N1**	**N2**	**N3**	**O1**	**O2**	**O3**
DBH (cm)	2.6	3.6	4.6	6.9	8.6	19.3	1.7	2.4	3.6	0.7	1.0	1.1
total height (m)	2.7	3.9	4.1	5.4	7.4	10.3	1.9	2.3	3.8	1.4	1.6	2.2
growth rings	13	14	13	15	23	23	14	17	18	10	9	8
trunk phytomers	972	553	723	784	1335	1581	528	541	518	195	258	173
B/T ratio	0.8	0.9	0.6	0.8	0.9	0.8	1.0	1.2	1.3	1.5	1.9	1.5
branch tiers	1	4	2	2	4	11	2	1	3	5	3	6
branches	6	7	13	20	24	61	3	2	4	10	9	22
leaves	117	240	393	893	1141	_	73	103	80	91	150	274
total leaf area (m^2)	1.2	2.9	3.5	9.8	11.2	_	0.4	0.7	0.5	0.2	0.9	1.3
average LMA ($g.m^{-2}$)	198	205	206	218	205	_	186	180	183	195	191	193

2.3. Plant measurements

Methodological framework – An internode is defined as the vertical distance between two successive leaves (Barthélémy & Caraglio, 2007). All *Cerberiopsis* species show an alternating spiral phyllotaxis with a phyllotactic index between 5/18 and 8/21 referring to the Fibonacci mathematical sequences (King et al., 2004; Newell & Shipman, 2005; Okabe, 2015) (**Figure 1E**). Each new leaf is produced at an angle of 137.3° to the previous one and each phyllotactic spirals consist of 2.62 phytomers (**Figure 2A, B**). In this study, we consider two measurement scales: the phyllotactic spiral and the phytomer. For each plant sample, the phyllotactic spirals of all axes (trunk and branches) were manually drawn following the successive leaf scars (**Figure 1C**). For each axis, we measured the longitudinal length of the successive phyllotactic spirals and calculate the length of the successive internodes constituting this spiral. The internode lengths were calculated by considering both the spiral length and the number of phytomers in the spiral according to its geometry (**Figure 2C, D**).



D

Estimate the length of an internode within one phyllotactic spiral (1, 2, 4, 5, 7): $\frac{137.3}{360} * H_{spiral1}$

Estimate the length of an internode within two phyllotactic spirals (3, 6): $\left(\frac{x1}{360} * H_{spiral1}\right) + \left(\frac{x2}{360} * H_{spiral2}\right)$

$x1, x2$: angles traversed by the phytomer in the phyllotactic spiral 1, 2 (in degree).

Figure 2. Internode length estimation for plants with a spiral alternate phyllotaxis. (**A**) Apical view of *Cerberiopsis* phyllotactic pattern; each leaf (1-7) is produced at 137.3 degrees from the previous one. (**B**) Lateral view of *Cerberiopsis* phyllotactic pattern; a spiral (S1, S2, S3) includes an average of 2.62 phytomers. (**D**) Graphic representation of internode length estimation; the internode length is calculated according to its length proportion in each spiral (pie charts) and the spiral heights. (**D**) Formulas used to calculate the internode lengths; if the internode is included in two different spirals, the second formula is used.

Morpho-anatomical traits measured – Plants exhibit several morpho-anatomical traits indicative of their past development. Measuring and analyzing these traits allow us to retrospectively reconstruct the functioning of meristems throughout the plant's life (Heuret et al., 2002; Grosfeld & Barthélémy, 2004; Zalamea et al., 2008; Nicolini et al., 2012). All morpho-anatomical traits considered in this study are presented in **Figure 3**. For all sampled axis, we analyzed at the scale of each phytomer: the calculated internode length (IN), the location and number of branches (B) and branch tiers (Bt), the leaf area (LA), and the leaf mass per area (LMA)

(**Figure 3A**). LMA was obtained by weighing 3cm^2 of leaf blade (excluding the main veins) dried at 70°C for a week. Subsequently, we analyzed at the scale of each phyllotactic spiral: the axis diameter (D), the number of visible growth rings (GR), and the pith area (PA) (**Figure 3B**). PA was obtained by calculating the ellipse associated with the two measured perpendicular diameters of the pith cross section ($L * l * \pi$). For fully sampled individuals, LMA and PA were measured for the trunk and for one branch of each branch tier.

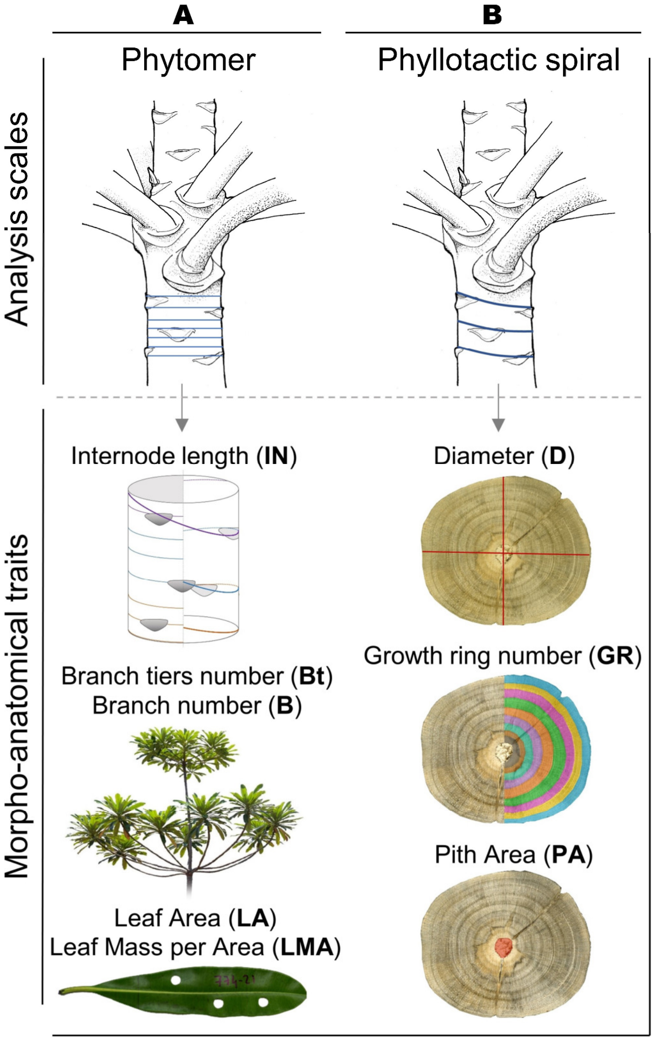


Figure 3. Morpho-anatomical traits measured for the reconstruction of developmental trajectories in *Cerberiopsis* species. Two analyses scales are considered, the phytomer and the phyllotactic spiral. (**A**) Five morphological traits are considered at the phytomer level: the internode length (mm), the branch tiers number, the branch number, the leaf area (cm^2), and the leaf mass per area (g.m^2). (**B**) Three anatomical traits are considered at the phyllotactic spiral level: the diameter (cm), the number of growth ring (GR), the pith area (PA). The growth ring area (GRA, mm^2) has been additionally measured in individual C6.

Stem profile of a dead C. candelabra after monocarpic flowering - The stem profile of *C. candelabra* C6 was built to fully reconstruct a developmental trajectory leading to the unique flowering event (**Figure 1A**). For each phyllotactic spiral, cross sections of the trunk were cut and sanded using 220-grain sandpaper. All wood disks have been digitized with an Epson Perfection V700 scanner. Growth rings were delimited and the growth ring area (GRA) was measured with the Photoshop CS3 software (Adobe Systems Incorporated, 2022). Stem profiles are classically built considering wood disks or cores sampled at fixed intervals along the trunk, providing a discontinuous age-height relationship. Here, the construction of a stem profile from a phyllotactic scale that translates the trunk developmental dynamic allows us to precisely relate the variations in internode lengths (primary growth) with the growth ring formation (secondary growth).

2.4. Data analysis

The dataset was structured in a Multi-Scale Tree Graph (MTG) format (Godin & Caraglio, 1998). This coding method allows the representation of quantitative (e.g. IN length) and qualitative data (e.g. branch position) by considering both the plant topology (i.e. the relative positions of entities within the plant) and the plant geometry (i.e. the spatial position and form of entities) (Godin et al., 1997; Godin et al., 1999; Godin, 2000). Here, we define four scales of botanical entities: the whole plant, the axes, the phyllotactic spirals, and the phytomers.

Data were analyzed and extracted with the VPlants package from the OpenAlea-2.0.0 software (Pradal et al., 2008). This package based on Python language facilitates the representation and location of structures in multi-scale plant architectures. All analyses were performed with the R-4.2.0 software (R Core Team, 2022). As our data do not satisfy the applicability conditions of standard parametric tests (no homogeneity of residuals), we use non-parametric statistics for sample statistical comparisons. We performed Wilcoxon Man Whitney tests for mean comparisons of unpaired (W) and paired (V) samples and Fligner-Killeen (FK) tests for variance comparisons (Stats package; R Core Team, 2022).

3. Results

3.1. Growth trajectories

Primary and secondary growth patterns – In each individual, we identify growth structural regularities along all axes, both from primary and secondary growth. These regularities define successive morphogenetical units (MUs) (**Figures 4, 5** and **6**). MUs are firstly defined through variations in internode length that reveal the alternation of short-long phytomer zones all along the axes. Each short phytomer zone is related to the formation of a new growth ring (**Figures 4C, 5C** and **6C**). Considering the three phyllotactic spirals developed before and after the formation of a growth ring, the internode lengths are significantly shorter than the others (*C. candelabra*: FK = 8.2, P = 0.004**; *C. neriifolia*: FK = 4.6, P = 0.032*; *C. obtusifolia*: FK = 6.7, P = 0.009**). Internode lengths vary from 0.76 to 18.31mm in *C. candelabra*, 0.76 to 15.26mm in *C. neriifolia*, and 1.14 to 19.74mm in *C. obtusifolia*. Considering the first and last three MUs develop by the main axis, all individuals show a significant decrease in internode length between the base and the apex of the trunk (*C. candelabra*: V = 10153, P < 0.001***; *C. neriifolia*: V = 10866, P < 0.001***; *C. obtusifolia*: V = 2308, P < 0.001***).

Leaf characteristics – The boundaries of the youngest MUs are secondly defined through variations in leaf area (**Figures 4D, 5D** and **6D**). Considering the three leaves develop before and after the formation of a new growth ring, the leaf areas are significantly lower than the others (*C. candelabra*: FK = 3.8, P= 0.041*, *C. neriifolia*: FK = 5.2, P= 0.027*, *C. obtusifolia*: FK = 6.1, P= 0.009**). In *C. candelabra*, leaf area varies from an average of 89 cm^2 in the short phytomer zones to an average of 135 cm^2 in the long internode zones. This species produces significantly larger leaves than *C. neriifolia* and *C. obtusifolia* ($\overline{LA}_{cand}$ = 106 cm^2; $\overline{LA}_{nerii}$ = 79 cm^2; $\overline{LA}_{obtu}$ = 43 cm^2; W = 15, P = 0.035*). *C. candelabra* shows significantly higher LMA than *C. neriifolia* and *C. obtusifolia* ($\overline{LMA}_{cand}$ = 206 g.m^{-2}; $\overline{LMA}_{nerii}$ = 183 g.m^{-2}; $\overline{LMA}_{obtu}$ = 193 g.m^{-2}; W = 15, P = 0.036*). No significant fluctuations in LMA are recorded along axes, and LMA variations are not correlated with LA variations.

Relative primary growth rates – Individuals have been developing for 8 to 23 growing cycles according to the number of MUs identified all along their main axis (**Figure 7**). We recorded an average primary growth rate of 32.4cm.MU^{-1} in *C. candelabra*, 14.1cm.MU^{-1} in *C. neriifolia*, and 17.9cm.MU^{-1} in *C. obtusifolia*. Individual C6 (the only *C. candelabra* that has flowered) shows a much higher growth rate (44cm.MU^{-1}) then other non-flowering conspecifics (t = 3.93, P < 0.01**).

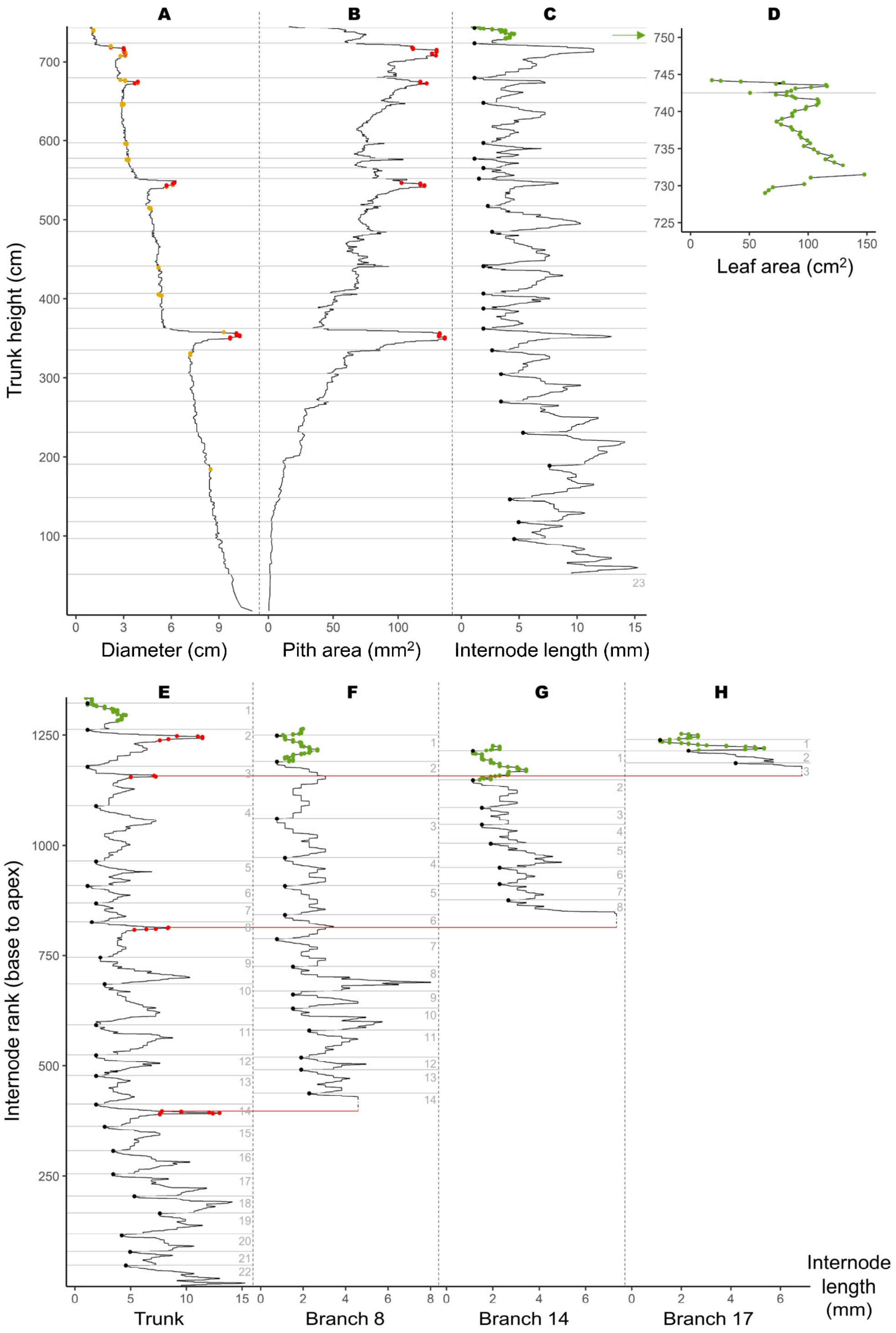


Figure 4. Quantitative analysis of *C. candelabra* development. Individual C5 is shown and representative of the other conspecifics studied. (**A-D**) Tree's construction is represented according to the trunk height growth (cm); From left to right: variations in (**A**) trunk diameter (cm), (**B**) pith area (mm²), (**C**) internode length (mm), and (**D**) leaf area (cm²). (**E-H**) Tree's construction is represented according to the trunk topological growth (internode rank); From left to right: variations in internode lengths (mm) along (**E**) the trunk, (**F**) the branch n°8 (first branch tier), (**G**) the branch n°14 (second branch tier), and (**H**) the branch n°17 (third branch tier). (**A-H**)

Grey lines show the position of each new growth ring formed along the trunk and the related grey numbers indicate the growth ring number (1 to 23); Black dots show the minimum internode lengths at the time of growth ring formation; Additional dots indicate the position of living branches (in red), aborted branches (in yellow), and leaves (in green).

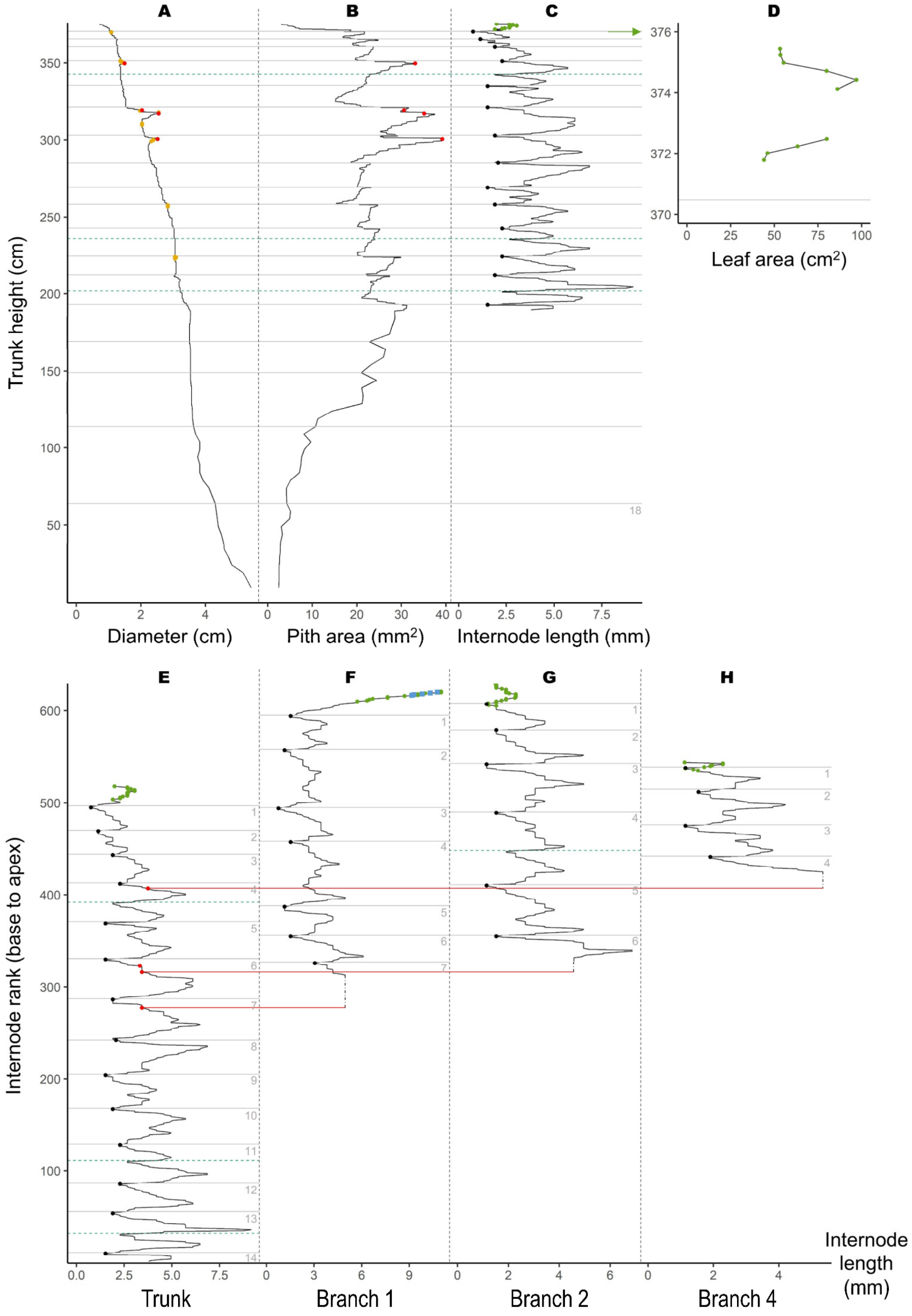


Figure 5. Quantitative analysis of *C. neriifolia* development. Individual N3 is shown and representative of the other conspecifics studied. (**A-D**) Plant's construction is represented according to the trunk height growth (cm); From left to right: variations in (**A**) trunk diameter (cm), (**B**) pith area (mm^2), (**C**) internode length (mm), and (**D**) leaf area (cm^2). (**E-H**) Plant's

construction is represented according to the trunk topological growth (internode rank); From left to right: variations in internode lengths (mm) along (**E**) the trunk, (**F**) the branch n°1 (first branch tier), (**G**) the branch n°2 (second branch tier), and (**H**) the branch n°4 (third branch tier). (**A-H**) Grey lines show the position of each new growth ring formed along the trunk and the related grey numbers indicate the growth ring number (1 to 18); Blue dashed lines indicate the position of false rings within the MUs n°4, 11, and 13. Black dots show the minimum internode lengths at the time of growth ring formation; Additional dots indicate the position of living branches (in red), aborted branches (in yellow), and leaves (in green). Blue squares show the position of inflorescences along the branches.

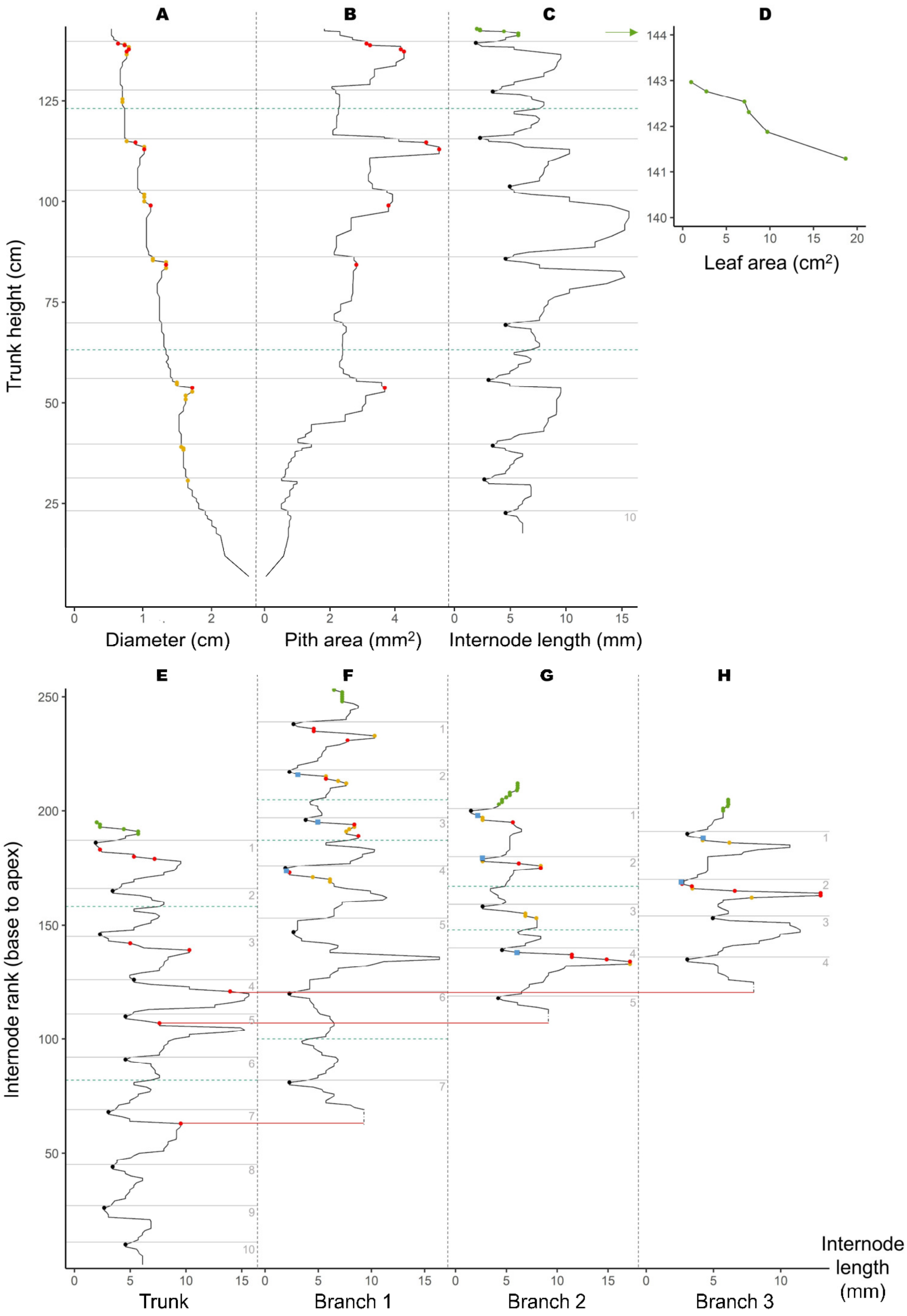


Figure 6. Quantitative analysis of *C. obtusifolia* development. Individual O3 is shown and representative of the other conspecifics studied. (**A-D**) Plant's construction is represented according to the trunk height growth (cm); From left to right: variations in (**A**) trunk diameter (cm), (**B**) pith area (mm^2), (**C**) internode length (mm), and (**D**) leaf area (cm^2). (**E-H**) Plant's construction is represented according to the trunk topological growth (internode rank); From left to right: variations in internode lengths (mm) along (**E**) the trunk, (**F**) the branch n°1 (first branch tier), (**G**) the branch n°2 (second branch tier), and (**H**) the branch n°3 (third branch tier). (**A-H**) Grey lines show the position of each new growth ring formed along the trunk and the related grey numbers indicate the growth ring number (1 to 10); Blue dashed lines indicate the position of false rings within the MUs n°2, 3, and 6. Black dots show the minimum internode lengths at the time of growth ring formation; Additional dots indicate the position of living branches (in red), aborted branches (in yellow), and leaves (in green). Blue squares show the position of inflorescences along the branches. As the branches of *C. obtusifolia* exhibit a sympodial construction, each blue square also indicates the position of a sympodial relay.

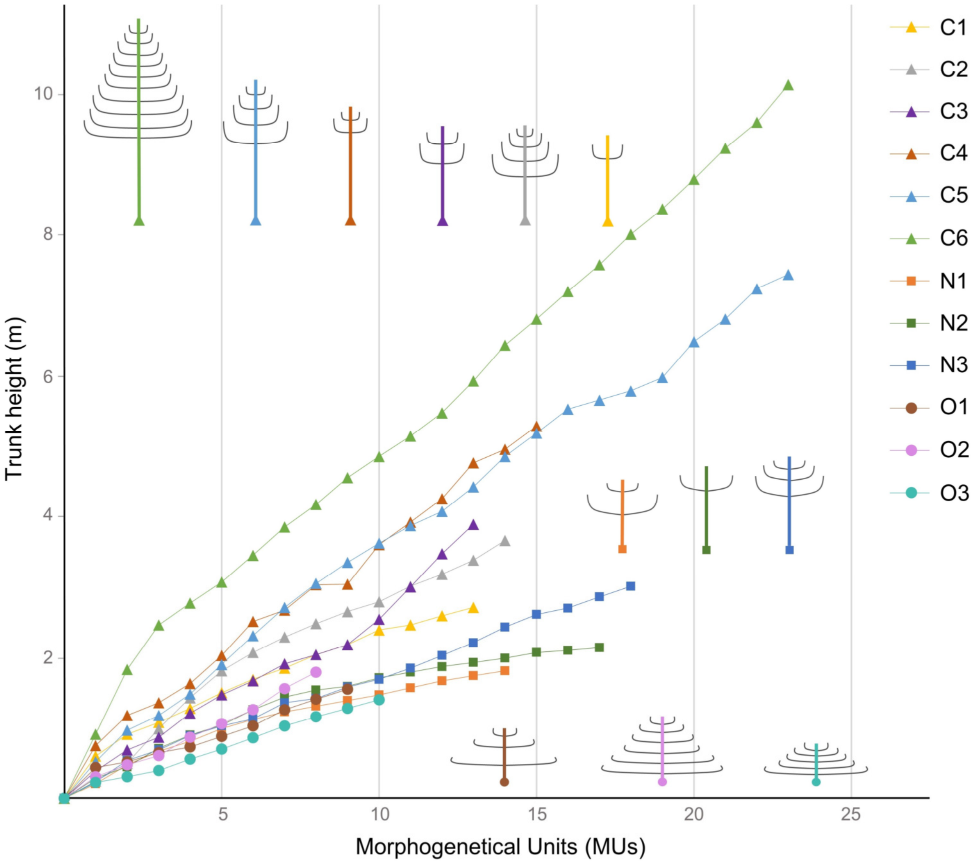


Figure 7. Primary growth trajectories in *Cerberiopsis* species. Six *C. candelabra* (triangles), three *C. neriifolia* (squares), and three *C. obtusifolia* (dots) are shown. Individuals have been developed from 13 to 23 MUs (*C. candelabra*), 14 to 18 MUs (*C. neriifolia*), and 8 to 10 Mus (*C. obtusifolia*). Tree C6 (green triangles) is the only *C. candelabra* that has flowered (monocarpic flowering). Schemes indicate the fundamental architecture of the individuals presented.

3.2. Crown development

Branching pattern – In all three *Cerberiopsis* species tiers of branches develop rhythmically along the trunk. Branches are produced before the formation of a new growth ring on the last short phytomers of the MUs (**Figures 4E, 5E** and **6E**). At the base of each branch, we observed (1) a relatively long proximal internode with a lack of proximal cataphylls and (2) the same number of growth rings between the base of the branches and the trunk portion where they initiate (**Figures 4F, 5F** and **6F**). On average, *C. candelabra* and *C. neriifolia* produce a first branch tier after more growing cycles than *C. obtusifolia* ($\overline{H}_{Bt1\_cand}$ = 2.07m, 5 ± 3MUs; $\overline{H}_{Bt1\_nerii}$ = 1.91m, 7 ± 3MUs, $\overline{H}_{Bt1\_obtu}$ = 63cm, 2 ± 1MUs). In all species, only one branch tier is produced per MU, and branching does not occur at each MU. From the development of the first branch tier, branching occurs every 2 ± 1MUs in *C. candelabra*, 6 ± 4MUs in *C. neriifolia*, and 1 ± 1MUs in *C. obtusifolia* (**Figures 4G, 5G** and **6G**). *C. candelabra* produce significantly more branches per branch tier than *C. neriifolia* and *C. obtusifolia* ($\overline{B/Bt}_{cand}$ = 6 ± 3; $\overline{B/Bt}_{nerii}$ = 2 ± 1; $\overline{B/Bt}_{obtu}$ = 3 ± 1; W = 127, P = 0.002**).

Coordination between branching, primary growth, and secondary growth – In all three species, branching occurrence is related all along the axes with variations in pith area (**Figures 4B, 5B, 6B**). Considering the phyllotactic spirals where branches initiate, the pith area is significantly higher than in the other spirals (*C. candelabra*: FK = 8.22, P = 0.004**; *C. neriifolia*: FK = 4.87, P = 0.027*; *C. obtusifolia*: FK = 1.13, P = 0.029*). Maximum pith area is 129 ± 18 mm^2 in *C. candelabra*, 33 ± 6 mm^2 in *C. neriifolia* and 5 ± 1 mm^2 in *C. obtusifolia*. In each species, the pith area increases slowly until reaching a maximum, then a tier of branches develops, and the main axis diameter increase drastically. Subsequently, the pith area and the main axis diameter decrease abruptly (**Figures 4A, 5A** and **6A**). The coordination between branching, primary growth, and secondary growth is even more noticeable in *C. candelabra* C6 stem profile (**Figure 8**). All along the trunk, the growth ring areas increase and each new growth ring has an average area equivalent to 125% of the previous one ($\overline{GRA}_3$ = 2.5mm^2; $\overline{GRA}_{13}$ = 21.1mm^2, $\overline{GRA}_{23}$ = 66.7mm^2). Only the last two rings, formed before the flowering event, have a smaller area ($\overline{GRA}_3$ = 69.39 cm^2;

$\overline{GRA}_2$ = 67.70 cm^2; $\overline{GRA}_1$ = 66.74 cm^2). When branching occurs, the axis diameter increases due to a synchronous increase in the pith area and growth ring area below the branch tier (**Figure 8C**).

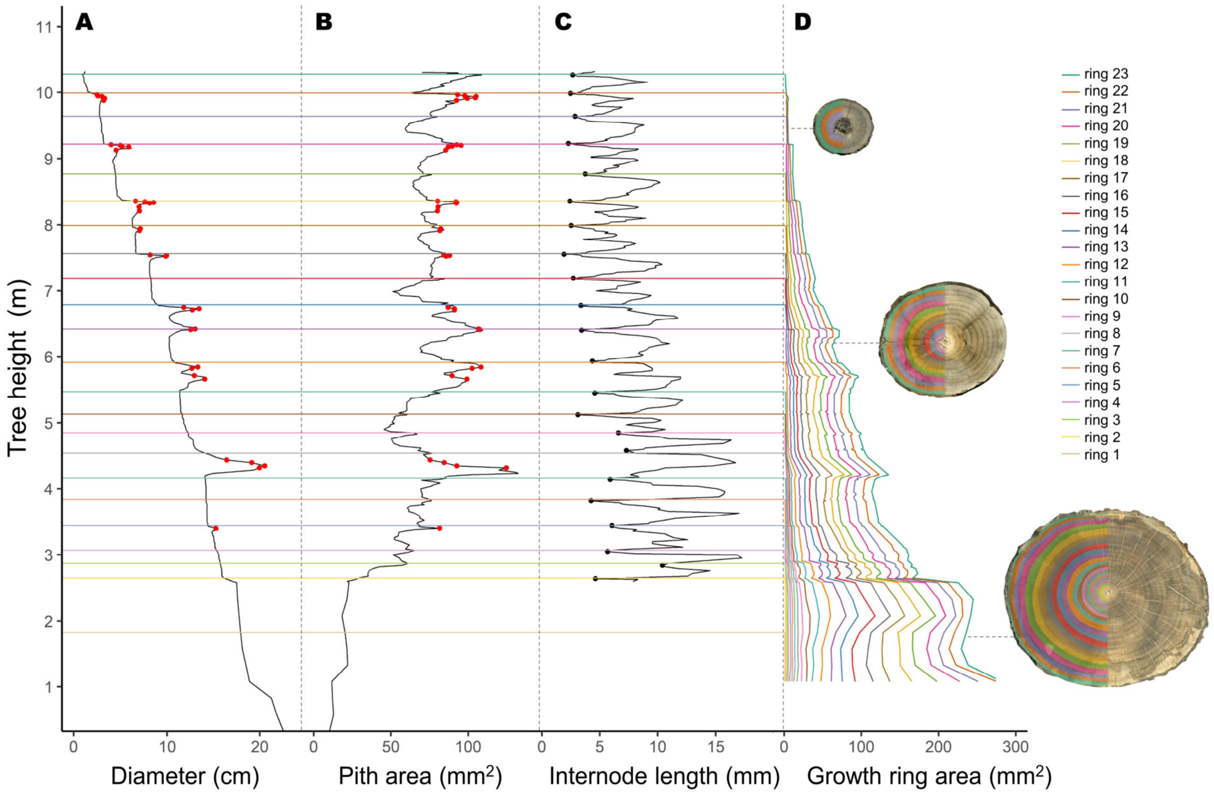


Figure 8. Stem profile of a dead *C. candelabra* after monocarpic flowering. Tree development is represented according to the trunk height growth (m). From left to right: variation in (**A**) trunk diameter (cm), (**B**) pith area (mm^2), (**C**) internode length (mm), and (**D**) growth ring area (mm^2). Colored lines indicate the position of growth ring formation along the trunk (1 to 23). Dots indicate (in black) the minimum internode lengths at the time of growth rings formation, and (in red) the position of the living branches. Ten branch tiers corresponding to a total of 61 branches have been developed along the trunk. The individual has flowered in its 24th growing cycle.

3.3. Divergences in *Cerberiopsis* species developmental trajectories

Growth dynamics – Although all *Cerberiopsis* species show similar growth and branching patterns, their developmental trajectory diverges. *C. candelabra* and *C. neriifolia* produce more phytomers per MU than *C. obtusifolia* ($\overline{MU}_{cand}$ = 36 phyt., $\overline{MU}_{nerii}$ = 33 phyt., $\overline{MU}_{obtu}$ = 22 phyt.; W = 73, P = 0.004**). In addition, *C. candelabra* and *C. obtusifolia* produce longer phytomers than *C. neriifolia* ($\overline{IN}_{cand}$ = 6.75 mm; $\overline{IN}_{nerii}$ = 4.35 mm; $\overline{IN}_{obtu}$ = 6.79 mm; W = 29593, $P < 0.001$***). In all three species, slight decreases in phytomer lengths are punctually observed within the MUs (i.e. between the two short phytomer zones) (**Figure 4C**: MUs n°3, 4, 5, 13; **Figure 5C**: MUs n°2, 5, 9, 10; **Figure 6C**: MUs n°2, 6). These additional short phytomers do not delimit MUs as they result from (1) less than 3 internodes of reduced length and (2) are not anatomically related to the formation of a new growth ring. However, in *C. neriifolia* and *C. obtusifolia*, the production of additional short phytomers is punctually related to the formation of a false ring within the MU (**Figures 5** and **6**). False rings are at most visible along 3±1 phyllotactic spirals. In *C. candelabra*, no false rings are observed (**Figures 4** and **8**).

Trunk versus branches development – In each three species, different growth dynamics are recorded between the trunk and the branches (**Table 1**). In *C. candelabra* branches produce fewer phytomers than the trunk per MU ($\overline{B/T}_{cand}$ = 0.81) (**Figure 4H**). In contrast, in *C. neriifolia* and *C. obtusifolia*, branches develop more phytomers than the trunk per MU ($\overline{B/T}_{nerii}$ = 1.17; $\overline{B/T}_{obtu}$ = 1.63; W = 10, P = 0.036*) (**Figure 5H** and **6H**). Thus, when the trunk produces 10 phytomers, the branches produce an average of 8 phytomers in *C. candelabra*, 12 phytomers in *C. neriifolia*, and 16 phytomers in *C. obtusifolia*. No significant differences in internode lengths are found between the trunk and the branches of all species. Therefore, in *C. candelabra* branches are shorter than the trunk portion above their insertion while in *C. neriifolia* and *C. obtusifolia,* branches are longer. For instance, in *C. obtusifolia* O3, the first branches developed by the trunk were of the same size as the trunk itself (**Figure 6B**).

Flowering patterns – In all three species, the flowering of the trunk and the branches is terminal. In the two polycarpic species, *C. neriifolia* and *C. obtusifolia*, the flowering of the branches occurs concomitantly with an increase in pith area (**Figures 5F** and **6F**). Considering the phyllotactic spirals where inflorescences initiate, the pith area is significantly higher than in the other spirals (*C. neriifolia*: FK = 12.40, P = 0.023*; *C. obtusifolia*: FK = 16.59, P = 0.01**). This coordination between flowering and primary growth is even more noticeable in *C. obtusifolia*, where it also coordinates with branching. Following the development of 2 ± 1 MUs, the pith area increases, then branching occurs followed by terminal flowering (**Figure 6F, G, H**). Subsequently, the branch development continues through the most terminal twig produce (i.e. sympodial construction, Figure 1). In *C. candelabra*, the flowering occurrence is also correlated with an increase in pith area but leads to the death of the whole individual (**Figure 9**). In pairs A to D, flowering trees have higher pith areas within the last MU developed, and individuals show an average pith area equivalent to 190% of the non-flowering trees ($\overline{PA}_{fertile}$ = 112 mm^2; $\overline{PA}_{sterile}$ = 70 mm^2; W = 16, P = 0.029*). In pair E, both trees have high pith areas ($PA_{fertile}$ = 101.9 mm^2; $PA_{sterile}$ = 105.3 mm^2). They are the largest individuals considered in terms of total height and DBH (**Figure 9E**).

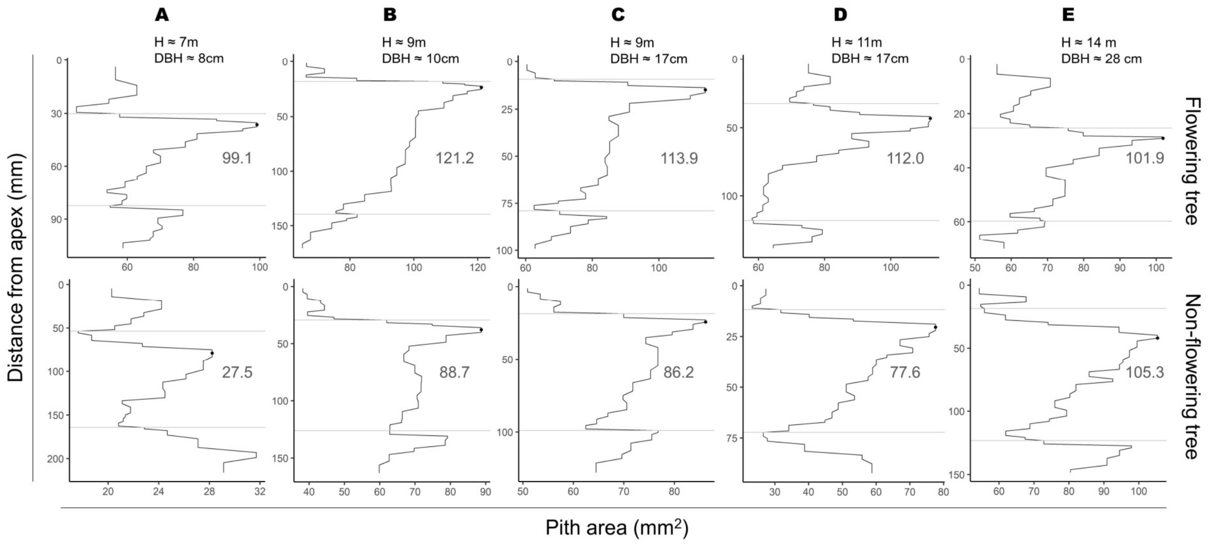


Figure 9. Pith area variations within branch apexes of ten *C. candelabra* trees. Pith area variation (mm^2) is recorded along the two last MUs develop by the axis. Grey lines indicate the position of growth ring formation along the branch. Grey numbers indicate the maximum pith area measured in each branch. Five pairs (**A-E**) of flowering versus non-flowering individuals of the same size are considered; Top figures show branches of flowered individuals and bottom figures show the branches of their related non-flowered conspecifics. (**A**) Trees of 6.1 - 7.3 m total height for a 7.3-7.9 cm DBH; (**B**) Trees of 8.3 -9.4 m total height for a 10.2-10.5cm DBH; (**C**) Trees of 8.9 - 10.9 m total height for a 16.1 - 17.5 DBH; (**D**) Trees of 9.2 - 11.6 m total height for a 16.6 - 17.5 cm DBH; (**E**) Trees of 13.9 - 14.1 m total height for a 26.7 - 29.9 cm DBH.

4. Discussion

4.1. *Cerberiopsis* species show strong structural regularities

Based on an integrative dendrochronological approach, we found that all three *Cerberiopsis* species show strong structural regularities. All along the trunk and the branches, we identified successive morphogenetical units (MUs) thanks to (1) variations in internode length and leaf area, and (2) the formation of growth rings. These MUs are the results of the individual's ontogeny and reflect the temporality of its development (Prat, 1936; Caraglio & Barthélémy, 1997; Barthélémy & Caraglio, 2007). Reductions in internode length and leaf area are the consequences of primary growth slowdowns (Heuret et al., 2002; Zalamea et al., 2008; Nicolini et al., 2012), while the formation of growth rings results from secondary growth slowdowns (Krepkowski et al., 2011; Worbes 2002; Brienen et al., 2016; Schöngart et al., 2017). The climate in New Caledonia is seasonal, with a 4-month cool-dry season from June to September and a 4-month warm-wet season from December to March, both interspersed by short transitional periods (MétéoFrance, 2022a). Several studies have underlined that temperature and water availability are the main factors limiting primary and secondary growth in tropical and subtropical species (Reich & Borchert, 1984; Worbes, 1995; Wright, 1996; Borchert et al., 2002; Anderson et al., 2005; Valdez-Hernandez, 2010). Therefore, we suggest that MUs correspond to the stem portions developed between two cool-dry seasons and that the periodicity of the primary and secondary growth is annual in all three *Cerberiopsis* species. This result supports previous studies suggesting that the growth periodicity in *C. candelabra* is annual (Read et al., 2021, Salmon et al., 2023).

By attributing an absolute temporality to species development, we show that *C. candelabra* exhibits a faster primary growth rate (c.a. 32.4 cm.y-1), develops a higher leaf area, and produces more branches per year than *C. neriifolia* and *C. obtusifolia*. This faster growth rate results from (1) a higher production of phytomers and (2) phytomers with higher internode lengths. This is in line with the growth forms and habits of the three Cerberiopsis species. While *C. candelabra* is a large tree preferentially growing in the rainforest, *C. neriifolia* and *C. obtusifolia* are respectively a treelet and a shrub growing in the bushy maquis (Veillon, 1971; Boiteau, 1981; Read et al., 2006; Salmon et al., 2023). On the resource acquisition spectrum, tall trees in light-limiting environments have more acquisitive traits (indicating their ability to compete for light and nutrient acquisition) while smaller trees or shrubs in restrictive habitats have more conservative traits (promoting their resistance to stresses like drought and soil infertility) (Reich, 2014; Diaz et al., 2015; Zhao et al., 2017; Maracahipes et al., 2018; Maynard et al., 2022).

4.2. A primary and secondary growth pattern with polycyclism

In all three *Cerberiopsis* species, the shoot apical meristems and the vascular cambium operate synchronously in the whole plant body, and their synchronous slowdown of activity presumably occurs each year during the cool-dry season. However, during these annual growing cycles, we identified additional primary growth slowdowns not related to the formation of growth rings. These intra-annual variations in shoot apical meristem activity are indicative of polycyclism (Lanner, 1976; Barthélémy & Caraglio, 2007; Girard et al., 2011). An intra-annual slowdown or cessation of growth allows plants to cope with environmental stresses, such as nutrient or water limitation, and a few studies suggested that polycyclism is an adaptive trait to drought (Cabanettes et al., 1995; Sabatier et al., 2003; Girard et al., 2012; Hover et al., 2017). Subtropical species are confronted with climate seasonality, and their development can be affected by each seasonal change (Killman & Thong, 1995; Fenner, 1998; Schöngart et al., 2002; Dié et al., 2012). For instance, Salmon et al. (submitted) demonstrated that young *C. candelabra* trees show a reduction in leaf area twice a year at each seasonal shift.

In *C. neriifolia* and *C. obtusifolia*, this polycyclism extends to secondary growth and is structurally identified through the formation of intra-annual growth rings. They are only visible in the stem portions developed at the time of intra-annual slowdowns of primary growth. In both species, the presence of these intra-annual growth rings within stem portions produced at the same time suggests that environmental factors are implicated. *C. neriifolia* and *C. obtusifolia* develop in harsh environments frequently exposed to drought (Morat, 1993; Grandcolas et al., 2008; Isnard et al., 2016). In all *C. neriifolia* studied, polycyclism was expressed within MU n°4 of the trunk and several branches. This MU corresponds to the stem portion developed from 2016 to 2017. In New Caledonia, May-July 2017 was marked by the most intense drought event since 1961. The commune of Thio, where *C. neriifolia* is endemic, was particularly affected with no rainfall recorded for 14 consecutive weeks (MétéoFrance, 2022b).

4.3. Value of integrative dendrochronological studies

Dendrochronological studies (/*Dendron*/: tree; /*Khronos*/: time) traditionally rely on the quantitative analysis of growth rings to investigate the periodicity of plant development. However, growth rings are structural regularities only reflecting the vascular cambium activity which supports the plant's lateral enlargement (secondary growth) (Schweingruber, 2012; Schöngart et al., 2015; Brienen et al., 2016). In contrast, phytomers are structural regularities reflecting the primary meristems activity which support the plant's apical elongation (primary growth) (Heuret et al., 2002; Nicolini et al., 2012; Mangenet, 2013). In this study, we promoted the combined use of several morpho-anatomical traits to retrospectively reconstruct species developmental trajectories. Quantitative analysis of other traits, such as leaf and inflorescence scars, allows us to explore additional aspects of plant developmental processes and to obtain a more comprehensive view of their meristematic activity over time. Plant phenological patterns are highly diverse within and among tropical and subtropical ecosystems (van Schaik et al., 1993; Fenner, 1998; Sakai, 2001; Sakai & Kitajima, 2019). As a result, several species are likely to express polycyclism, such as we observe in the *Cerberiopsis* species. The study of the structural regularities of primary growth or secondary growth alone cannot detect this polycyclism without long-term monitoring of the apical meristems or vascular cambium. However, combined, they lead to its detection by considering the synchronization between (1) primary and secondary growth and (2) trunk and branch development (Lanner, 1976; Barthélémy & Caraglio, 2007; Girard et al., 2011).

4.4. A high synchronicity between developmental processes

All three *Cerberiopsis* species show high coordination between distinct developmental processes: (1) a synchronism between primary and secondary growth (axes elongation and enlargement) and (2) a synchronism between primary growth, branching, and flowering patterns. In each species, branches develop the same number of MUs as the trunk portion above their insertion. Therefore, the branching process and crown construction are immediate during trunk development (Caraglio & Barthélémy, 2007). As branch tiers are produced in the acrotonic position on MUs (i.e. just before the formation of a new growth ring), the branching process expresses at the end of the growing cycle. In all species, the number of phytomers produced by the trunk and branches during the same growing cycle diverges. In *C. candelabra*, the trunk produces 1.2 times more phytomers than the branches, leading to its tree habit, while in *C. obtusifolia*, the branches produce 1.6 times more phytomers than the trunk, leading to its shrubby habit. In agreement with Salmon et al. (2023), these results emphasize that variations in primary growth rates at the individual scale may contribute to the divergence of growth form within the genus *Cerberiopsis*.

The coordination between primary growth, branching, and flowering patterns, has been evidenced through variations in pith areas all along the axes. In all three species, the branching and flowering processes occur concomitantly with an increase in pith area. Fluctuations in pith area are anatomical regularities of the primary growth and reflect the tree vigor or leaf carbon stocks at the time of axis development (Lauri, 1988; Edelin, 1993; Kaplan, 2001; Larios Mendieta et al., 2021). Only a few studies have examined this anatomical trait but, as a proxy for apical meristem size, it could be an indicator of the plant's ability to branch and flower (Baret et al., 2003; Longuetaud & Caraglio, 2009; Buissart et al., 2015; Hover et al., 2017). In addition, high increases in axis diameter were recorded at the time of branch development, underlining that the branching pattern has substantial consequences on the secondary growth rate of *Cerberiopsis* species. According to the so-called 'pipe model theory', wood formation is intrinsically related to the total leaf area carried by the plant (Shinozaki et al., 1964; Lehnebach et al., 2018). By increasing the overall leaf area, branching patterns will retroactively influence the vigor of apical meristems (primary growth) and the intensity of cambial production (secondary growth).

5. Conclusion

Based on a quantitative analysis of several morpho-anatomical traits we retrospectively reconstructed the developmental trajectories in the subtropical genus *Cerberiopsis*. Our results show that all species exhibit strong structural regularities, especially annual growth rings presumably formed during the cool-dry season of New Caledonia. Although the periodicity of primary and secondary growth processes is annual, both can express polycyclism. Plant developmental phenology is suggested to be sensitive to seasonal changes and drought. In all three *Cerberiopsis* species, we highlight that developmental processes such as primary and secondary growth, branching, and flowering, are highly coordinated within the plant body. *C. candelabra*, a large monocarpic canopy tree, is known for the massive synchronization of all its apical meristems when flowering (Salmon et al., 2023). Therefore, we suspect that highly synchronous developmental processes at the individual scale might have been preconditions for the evolution of the monocarpic strategy within the genus *Cerberiopsis*.

6. Additional information

6.1. Acknowledgments

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6.2. Author Contributions

Conceptualization: *PH, SI, CS*; Funding acquisition: *SI, PH*; Investigation: *CS, PH, JF, SI*; Data curation and Formal analysis: *CS, PH, JF, CG*; Visualization: *CS, PH; SI*; Writing - Original draft: *CS*; Writing - Review: *PH, SI, JF, CG*; Project administration and supervision: *PH, SI*.

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Chapter 6

The tallest *C. candelabra* tree – 32m in height – observed in a rainforest patch at Yaté (New Caledonia) © C. Salmon

Chapter 6 is an original research article introducing a new type of annual growth ring in *C. candelabra*. Our previous studies have led us to analyze what distinguishes and characterizes growth rings in *C. candelabra*, both at macroscopic and microscopic scales. We show that trees exhibit growth rings with annual increments of circular tension wood. We suspect this anatomical feature to be a functional adaptation to the New Caledonian cyclonic season.

Circular tension wood: A new type of annual growth ring.

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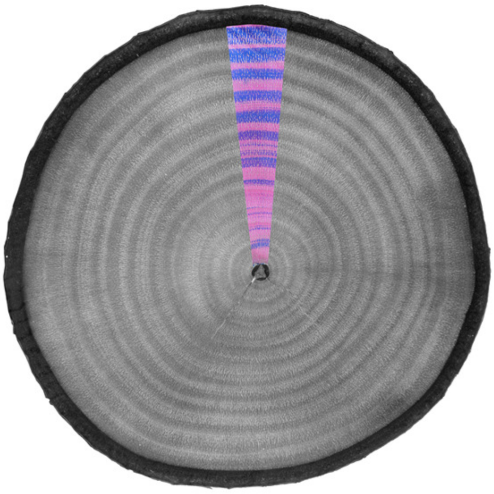
Running head

Salmon et al. — Circular tension wood.



Abstract

Growth rings are structural and temporal markers of plant development and the anatomical markers responsible for their distinctness have been widely investigated. In this study, we present a new type of growth ring formed by the alternation of circular bands of gelatinous fibers and lignified fibers. Wood anatomy is described and wood traits, including micro-density, vessel lumen fraction, vessel diameter, and cellulose microfibril angle (MFA), are analyzed from trunk wood disks and cores. Our results show that growth rings are bounded by narrow bands of axial parenchyma and formed of alternating concentric bands of tension wood and normal wood. Wood MFA and micro-density are very low and tension wood bands show higher micro-density due to reductions in vessel size and density. It's the first time that annual growth rings composed of circular tension wood bands are reported. We suggest that tension wood in *Cerberiopsis candelabra* (Apocynaceae) may be an adaptive feature allowing the species to maximize its resistance to multidirectional winds, such as those experienced during the cyclonic season of New Caledonia. While many tropical and subtropical trees are increasingly exposed to high wind disturbances and cyclones, little is known about the influence of wind seasonality on vascular cambium activity.

Key words

Cerberiopsis candelabra – gelatinous layer – marginal parenchyma – MFA – vessel lumen fraction – reaction wood – thigmomorphogenesis – winds – xylogenesis

1. Introduction

A growth ring is a structural and temporal marker of vascular cambium activity. According to Silva et al. (2019), it's a tangential portion of the secondary xylem tissue, in which one or more cell show modifications along the dimension of radial growth. At the macroscopic scale, growth rings are recognized as concentric circular bands of varying coloration and bulk density. At the microscopic scale, they could be identified using various anatomical features such as vessel density, fibre wall thickness, cell chemistry profile, and tangential continuity of longitudinal parenchyma cells (Wheeler et al., 1989; Tarelkin et al., 2016; Quintilhan et al., 2021). These anatomical modifications reflect the periodicity of the secondary growth (Lisi et al., 2008; Krepkowski et al., 2011; Pérez-de-Lis et al., 2021, Ortega Rodriguez et al., 2022) as well as evolutionary and phylogenetic issues (Nath et al., 2016; Silva et al., 2020).

Growth ring formation has long been exclusively associated with the growth phenology of temperate species in highly seasonal environments. Since Coster (1927), an increasing number of studies reported growth rings in tropical and subtropical species including trees, shrubs, and lianas (Détienne, 1989; Rozendaal & Zuidema, 2011; Brandes et al., 2022; Quesada-Roman et al., 2022). Evidence of annually formed rings is now well documented in some of these species (Worbes, 1999; Dié et al., 2012; Brienen et al., 2016; Schöngart et al., 2017). However, dendroecologists face substantial difficulties in tropical and subtropical contexts, the main one being the difficulty of identifying growth rings at macroscopic and microscopic scales. Other difficulties included: (1) the greater anatomical diversity of woods in tropical rainforests (Worbes, 2010; Tarelkin et al., 2016; Islam et al., 2018), (2) the transposition of knowledge from the temperate to the tropical and subtropical contexts without a readjustment of the concepts used (Martinez-Ramos & Alvarez-Buylla, 1998; Worbes, 2002; Silva et al., 2019), and (3) a missing universal definition of the growth ring (Tarelkin et al., 2016; Silva et al., 2019).

In temperate regions, the cambial activity slows down or stops during winter in conjunction with lower temperatures and reduced photoperiod. In tropical and subtropical regions, the cambial activity is more impacted by the rainfall regime (Reich & Borchert, 1984; Worbes, 1999; Dunisch et al., 2003; Fichtler et al., 2003; Lisi et al., 2008; Dié et al., 2012) or specific seasonal shifts as flood-pulse or soil salinity increase in the floodplain and mangrove forests (Schöngart et al., 2002; Chowdhury et al., 2008). These recent studies emphasize that even in these regions growth ring formation is influenced by seasonality (Worbes, 2002; Brienen et al., 2016; Schöngart et al., 2017, Quesada-Roman et al., 2022).

The wood formation process, the xylogenesis, is influenced by a broad range of environmental factors resulting in a wide diversity of growth rings (Schweingruber, 2007; Rathgeber et al., 2016; Beeckman, 2016; De Micco et al., 2019). For instance, wood anatomy can reflect the response of trees to mechanical constraints through the production of reaction wood, known as tension wood in hardwood species (Dadswell & Wardrop, 1955; Clair et al., 2006; Ruelle, 2014; Groover, 2016). Tension wood is composed of fibres whose physicochemical properties generate tensile stress and allow the tree to continuously adjust its position to the multiple disturbances that occur throughout its life (Ghislain & Clair, 2017).

We consider in this study the intriguing subtropical species *Cerberiopsis candelabra* (Apocynaceae). This rainforest tree is endemic to New Caledonia, a biodiversity hotspot located in South Pacific. This species is among the few rare monocarpic trees worldwide (Veillon, 1971; Read et al., 2006, 2008; Salmon et al., 2023). Monocarpy, also known as big-bang reproduction (Humphries & Stevens, 2001), is a life history strategy characterized by the death of the whole plant soon after its unique and massive flowering (Gadgil & Bossert, 1970; Foster, 1977; Poorter et al., 2005; Amasino, 2009). In the case of *C. candelabra*, trees live for more than a century before flowering once (Read et al., 2021). Because the monocarpic strategy implies that the persistence of the species relies on a single reproductive event at the individual scale, this large tree is supposed to show resilience to a wide range of environmental constraints to lower its probability of pre-flowering mortality.

C. candelabra is suggested sensitive to New Caledonia seasonality and forming growth rings annually, its primary meristems and vascular cambium alternating phases of high activity during the warm-wet season and low activity during the cool-dry season (Salmon et al., submitted a, b). Here, we analyze what distinguishes and characterizes *C. candelabra* growth rings at macroscopic and microscopic scales. Since this intriguing tree is exposed to annual cyclonic seasons, we question how seasonal high-wind regimes may influence its cambial activity and impact growth ring formation.

2. Materials and methods

2.1. Species description

Cerberiopsis candelabra Vieill. (ex. Pancher & Sebert) (Apocynaceae) is a subtropical species endemic to New Caledonia (Veillon, 1971). The species occurs in the main island's ultramafic massif, predominantly in the low and mid-elevation rainforest and sporadically in the open maquis (Salmon et al., 2023). Trees can reach 30m in height for a maximum observed diameter at breast height (DBH) of 79 cm (Read et al., 2006). The trunk rhythmically develops distinct tiers of branches, forming a massive pyramidal crown (**Figure 1**). *C. candelabra* is one of the most intriguing plants in New Caledonia as it belongs to the 29 monocarpic canopy tree species reported worldwide (excluding unbranched, i.e. monocaulous, palm-like trees) (Foster, 1977; Kitajima & Augspurger, 1989; Forget at al., 1999; Poorter et al., 2005; Sharma et al., 2008).

2.2. Wood sampling

Five trees, representing different ontogenic stages, from sapling to adult tree (see Salmon et al., (2023) for *C. candelabra* ontogenic stage identification), were cut down and collected (**Figure 1A-C**). Trees were sampled in two localities in the Southern region of the Grande Terre, at Thio (C1, C2) and Mont-Dore (C3, C4, C5) and (**Table 1**). These two localities are respectively located on the west (leeward) and east (windward) coastal plains of the island. Three wood disks, ranging from 1 to 4cm thick, were collected per tree: at 1.3m height (DBH) and under the first and second tier of branches developed by the trunk (**Figure 1B**). In addition, two wood cores at the trunk's DBH, in orthogonal position, were sampled using a Pressler auger from 60 individuals located at Mont-Dore, with diameters ranging from 7.3 to 48.1cm. (**Appendix 1**).

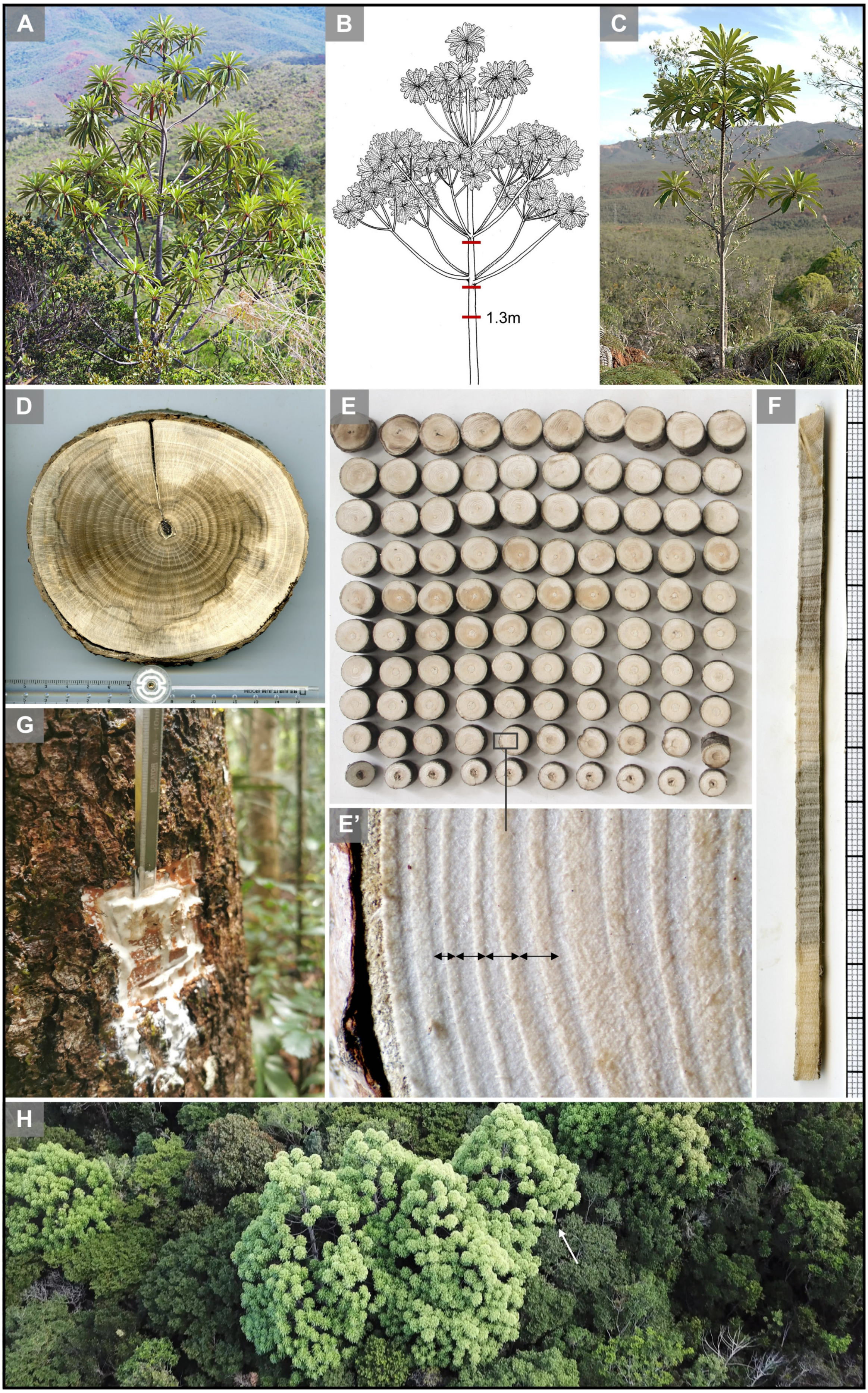

A
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Figure 1. Methods behind *Cerberiopsis candelabra* (Apocynaceae) anatomical description. (**A-C**) Trees at different ontogenic stages are considered, with all individual showing at least two distinct tiers of branches – from right to left: trees C5, C3, and C4; (**B**) In young trees (C1-C5) wood disks were sampled at 1.3m height (DBH) and under the first two tiers of branches developed by the trunk; (**D**) At the macroscopic scale growth rings show distinct boundaries marked by alternating coloration; (**E**) Dry wood shows alternation of concentric bands of high and low longitudinal depression – **E'**: most rings are formed of a high and then low depression band; (**F**) Visible growth rings in the wood cores of adult tree CA; (**G**) Wood cores have been collected at 1.3m height (DBH) after removal of the bark containing an abundant latex; (**H**) *C. candelabra* flowering in a the rainforest patch of Mouirange located at Mont-Dore in October 2021 – arrow indicates tree C6.

For all wood cores, growth rings were distinguishable at the macroscopic scale but their boundaries were unidentifiable. One adult tree in flower (C6) was selected for this study, and wood cores correspond to 10.9 and 11.2cm long sections, from bark to pith (**Figure 1F, G, H**). All wood samples were dried at 40°C for 1 to 6 weeks, sanded to 220 grain, and high-resolution scanned (6400 PPI) with an Epson Perfection V700.

2.3. Data analysis

Anatomical description – Wood anatomy has been described according to the IAWA list of microscopic characteristics for hardwood identification (Wheeler et al., 1989). For all samples, 20-µm-thick anatomical sections were obtained using a wood microtome (HM 440E or LEICA RM2245). Sections were colored with FASGA (Safranin 1% / Alcian Blue 8 GX 0.5 double stain) and photographed with a Keyence VHX-7000 digital microscope. FASGA stains lignified tissues in red, whereas unlignified or poorly lignified tissues are stained in blue (Legland et al., 2017). Wood disks sampled at DBH have been additionally digitized with a scanning electron microscope (SEM) Zeiss-Sigma HD.

For wood disks, anatomical descriptions were carried on two perpendicular radii. Transversal and longitudinal descriptions were both performed. For wood cores, anatomical descriptions were carried along the entire length of the core, from pith to bark.

Wood micro-density and microfibril angle – Wood micro-density (d) has been measured along two perpendicular radii of each wood disk and one radius of the wood cores (**Table 1**). Radii are 2-mm-thick and were measured after stabilizing at 11% moisture content. Digital radiographs were obtained with an Itrax multi-scanner (Cox Analytical Sys., 2016) and analyzed with the Cerd software (Mothe et al., 1998) at the SILVATECH platform (INRAE, Nancy, France). The radial density was recorded every 20µm. Cellulose Microfibril Angle (MFA) has been additionally measured along the wood cores at the SILVATECH platform. Average MFA was estimated using an X-ray diffractometer (Supernova, Oxford-Diffraction). The Supernova system consists of a kappa geometry including a sample holder, CCD detector, and X-ray tube, with a copper source. The tangential face of the samples was exposed to an X-ray beam (Cu-Kα X-rays. wavelength λ = 1.542Å, beam diameter 300µm) and the 002 equatorial reflection was measured. The evaluation of MFA is extracted from the 002-arc intensity curve using the method given in Verrill et al. (2006), as: $\mathrm{MFA} = 0.8 \times 0.6 \times (\sigma 1 + \sigma 2)$, where $\sigma 1$ and $\sigma 2$ are the widths of the Gaussian fits of the diffraction.

Table 1. *C. candelabra* trees characteristics and sampling data. Five saplings / young adult trees were collected at Thio (C1, C2) and Mont-Dore (C3, C4, C5) from April to October 2021. A flowering adult tree (C6) was collected at Mont-Dore in December 2021. For each tree, wood samples (2 or 3) have been collected at DBH (C1-C5, C6) and under the two first branch tiers develop by the trunk (C1-C5). DBH indicates the diameter at breast height (1.3m). GR indicates the number of growth rings recorded at 1.3m in height.

tree	**height** (m)	**DBH** (cm)	**branch tiers**	**GR**	**sampling**	**samples**	**GPS**
C1	2.5	2.6	1	9	Oct. 2020	disks (2)	21°40'38.18"S 166°20'13.11"E
C2	3.9	3.6	4	11	Oct. 2020	disks (3)	21°40'07.31"S 166°19'57.09"E
C3	4.1	4.6	2	10	Apr. 2020	disks (3)	22°12'25.52"S 166°40'46.12"E
C4	5.4	6.9	2	14	Apr. 2020	disks (3)	22°12'49.01"S 166°39'57.21"E
C5	7.4	8.6	4	22	Jun. 2020	disks (3)	22°11'29.29"S 166°42'38.87"E
C6	16,2	25.6	13	52	Dec. 2021	cores (2)	22°12'17.86"S 166°42'15.79"E

Vessel characteristics – Vessels have been measured for the 20 last growth rings formed of the wood cores (≈ 1515 vessels). Vessel diameter (VD), vessel density (Vd), vessel area (VA), and vessel lumen fraction (LF) were obtained by measuring all vessels occurring in 2 zones of each growth ring: (1) in the tension wood band located at the beginning of the growth ring and (2) in the normal wood band located at the end of the growth ring. Zones measured varying from 1.5 to 2.5mm^2, depending on the growth ring area. Measurements were performed with the Photoshop CS3 software (Adobe Systems Inc., 2007). Vessel properties statistical comparisons were conducted with the R-4.2.0 software (R Core Team, 2022) using t-tests (t) with a Welch correction.

3. Results

3.1. *C. candelabra* wood anatomy

On a macroscopic scale, all trees show distinct, circular, and concentric growth rings. On freshly cut wood disks, growth rings are marked by the alternating coloration of light and dark bands (**Figure 1D, F**). Once dry, high longitudinal depressions are observed in the lighter bands (**Figure 1E, E'**). Based on these macroscopic characteristics, the number of growth rings can be estimated from the wood disks, and the sampled trees show 9 to 22 growth rings at DBH (**Table 1**). This observation could not be made on the wood cores, and the estimation of the number of growth rings required additional microscopic analyses.

At the microscopic scale, the alternations of high-low depression bands are associated with two types of fibres revealed by the FAGSA-stained cross-sections (**Figure 2**). While low depression bands (the darkest) correspond to lignified fibres (i.e. normal wood), high depression bands (the lightest) are composed of low-lignified fibres (**Figure 2D, E**).

Growth rings are microscopically delineated by narrow tangential bands of axial parenchyma. These bands are characterized by poorly lignified cells whose diameter and wall thickness are reduced compared to the others fibres produced by the vascular cambium (**Figure 2B, C**). Axial parenchyma is generally, but not always, followed by a tangential band of low-lignified fibres (i.e. blue stained) and then normal wood. The bleu-stained bands consist of fibres with a thick extra layer at the inner side of the secondary wall (S-layer). This additional layer is not cohesive with the other cell wall layers and corresponds to a cellulosic gelatinous layer (G-layer) (**Figure 2F, F'**). The observation of (1) a high wood longitudinal depression after drying and (2) fibres with a characteristic G-layer, are indicative of tension wood. *C. candelabra* growth rings are bounded by axial parenchyma bands and formed of alternating circular bands of tension wood and normal wood (**Figure 2A**). Wood anatomy is further detailed in **Appendix 2**.

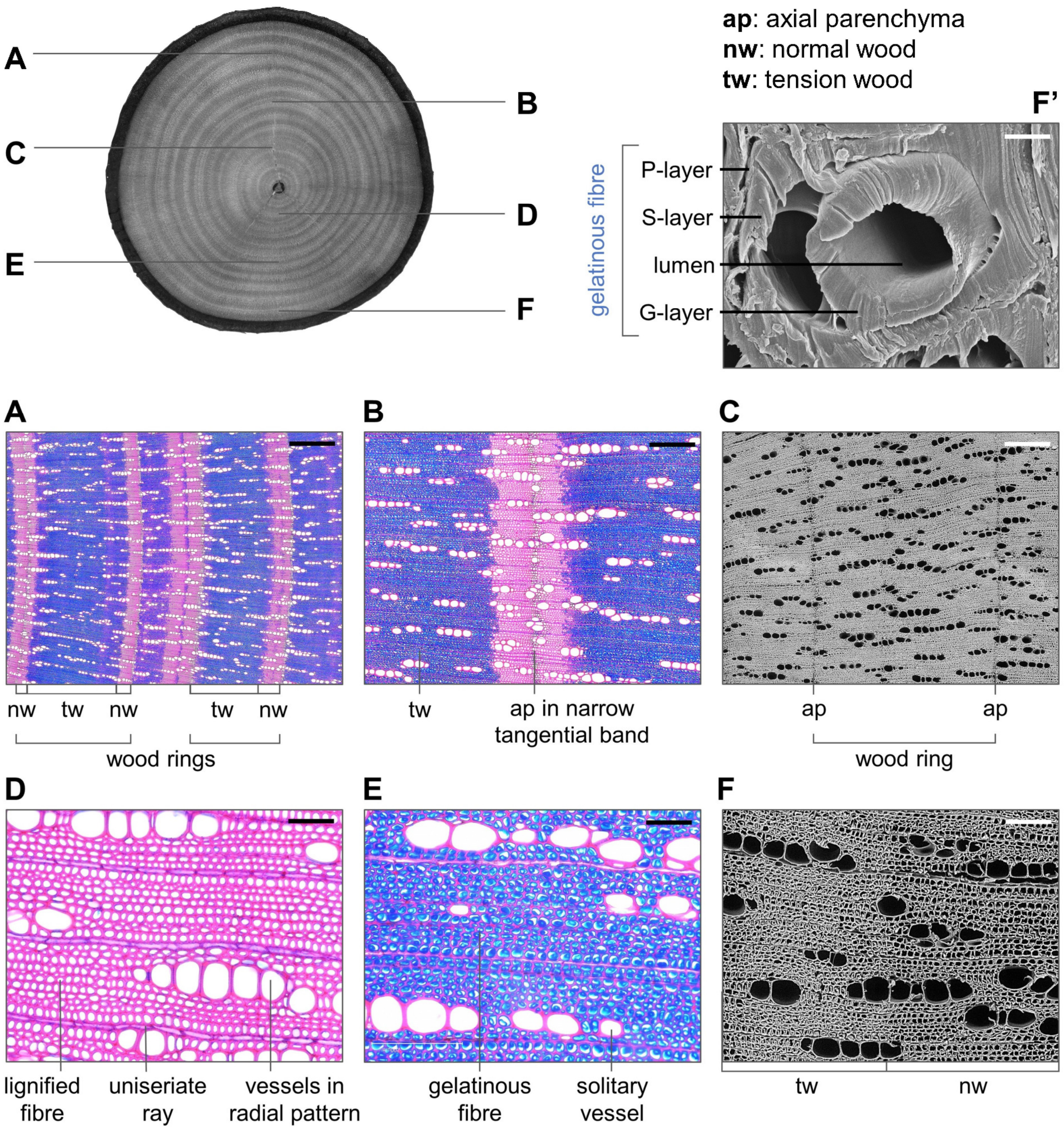

Figure 2. Wood anatomy of *Cerberiopsis candelabra* (Apocynaceae). Images are from tree C4 and are representative of the anatomy of all individuals described - Tree C4 was in its 14th year of growth. Annual growth rings are macroscopically visible thanks to the production of circular tension wood (lightest bands) differing from the normal wood (darkest bands). (**A-F**) All pictures are oriented from bark (left) to pith (right). (**A**) At the microscopic scale growth rings are marked by the alternation of tension wood and normal wood bands – growth rings are mostly composed of one circular band of tension wood followed by normal wood; (**B**) Axial parenchyma is produced in narrow tangential bands and shows cells with a reduced diameter and wall thickness; (**C**) Bands

of axial parenchyma delineates successive growth rings; (**D**) Normal wood is composed of lignified fibres crossed by uniseriate rays and large vessels in radial patterns; (**E**) Tension wood is composed of low-lignified fibres with characteristic G-layer (**F**) Fibre lumen size allows the distinction between normal and tension wood in electron microscopy; (**F'**) tension wood fibres show three distinct cell wall layers (P: primary, S: secondary, G: gelatinous), with the G-layer being punctually detached from the S-layer. Scales: (**A**) 1000µm; (**B-C**) 300µm; (**D-F**) 100µm.

3.2. Tension wood specificities

Tension wood in circular bands – In all trees, growth rings are composed of at least one circular (i.e. continuous) band of tension wood. Their tangential thickness varies independently of their position in the radial growth dimension of the secondary xylem and is not uniform throughout the band circumference. For instance, of the 21 growth rings formed at DBH in tree C5, the thickest tension wood bands are included in the growth rings 11 and 12 (**Figure 3**). These bands are respectively 1480 and 2210µm thick along radius A, while they are 1760 and 1720µm thick along radius B. For all trees, only in the first 3 to 4 growth rings produced, tension wood fibres are absent or organized in discontinuous bands. These rings are only discernable through the axial parenchyma bands.

Timing of tension wood production – Considering all wood samples collected at DBH, and excluding the first four rings, we identify four growth ring types according to the arrangement of the tension wood band (**Figure 3**). 'T1' corresponds to growth rings with a tension wood band bound to the axial parenchyma (61% of the growth rings analyzed). 'T2' are rings with a diffuse tension wood band (8%). 'T3' corresponds to rings with a main tension wood band bound to the axial parenchyma and additional bands incremented in the normal wood (14%). 'T4' are growth rings with a tension wood band not bound to the axial parenchyma (17%). Therefore, tension wood in *C. candelabra* is mainly produced from the beginning of the growth rings (types T1 and T3: 75%). As growth ring formation is annual and initiates in September, tension wood bands are annual and mainly produced from September. These results are supported by tree sampling dates (**Table 1**). In trees C1, C2, and C6, collected from October to December (warm season), the last fibres produced by the vascular cambium are tension wood. In trees C3, C4, and C5, collected from April to June (cool season), the last fibres produced are normal wood.

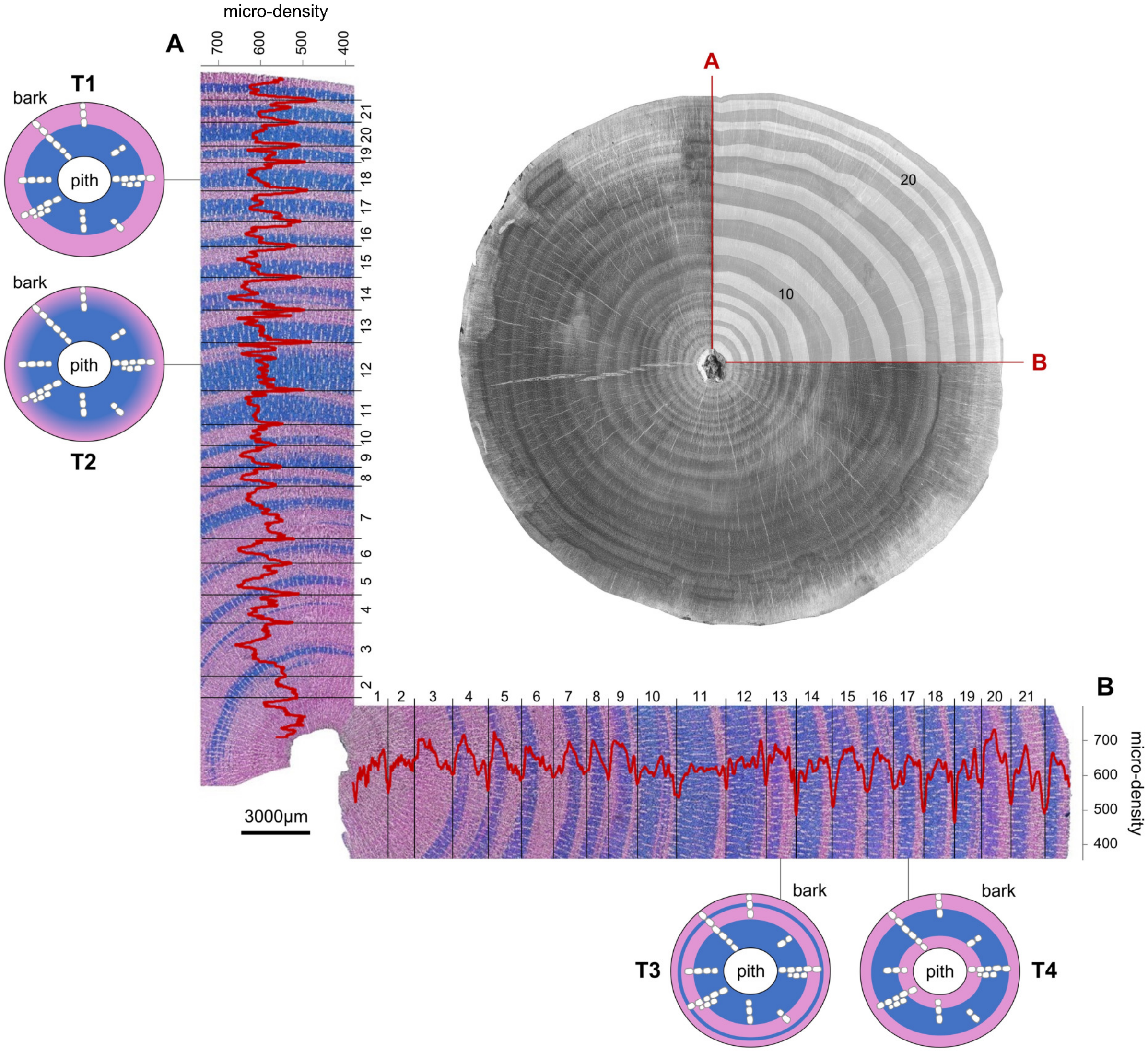

Figure 3. Transversal anatomical sections from wood disks collected at DBH in tree C5. Anatomical descriptions are carried on two perpendicular radii (**A** and **B**), from bark to pith. Black lines indicate the position of axial parenchyma bands along the dimension of the radial growth of the secondary xylem. Red curves show the variations of wood micro-density. According to the number of axial parenchyma bands, tree C5 was in its 22nd year of growth. Except for growth rings 1-3, circular bands of tension wood are observed in all rings and show distinct arrangements. **T1**: tension wood is bound to the axial parenchyma, **T2**: tension wood is diffuse in the growth ring, **T3**: tension wood is bound to axial parenchyma and additional bands are present in the growth ring; **T4**: tension wood is not bound to the axial parenchyma. In all case tension wood band thickness is variable and not uniform throughout the growth ring circumference.

Tension wood micro-density and microfibril angle – Variation in wood micro-density is in agreement with the microscopic delineations of growth rings using axial parenchyma localization. For all wood disks, we recorded the same number of growth rings at the macroscopic and microscopic scales. While axial parenchyma has a low density, resulting in several abrupt density decreases in a radial direction, normal wood and tension wood show higher densities (**Figure 3**). Only the wood micro-densitometric profile combined with the visualization of the stained fibres allow us to measure the number of growth rings in the wood cores samples. Tree C6 is estimated to be 52 years old (**Figure 4**).

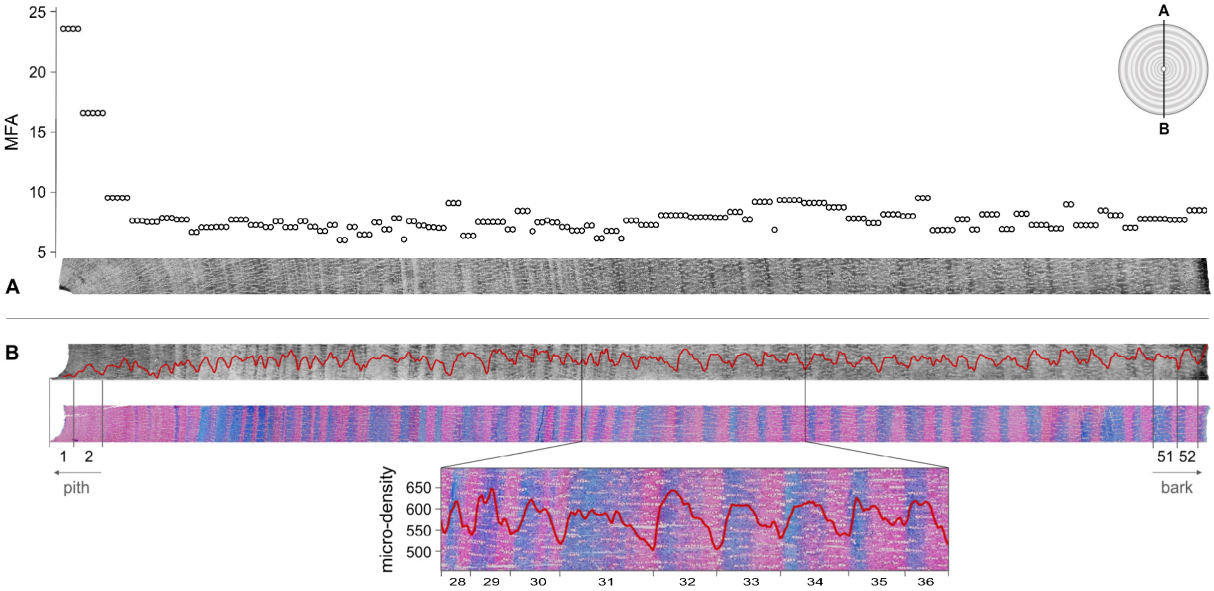

Figure 4. Transversal anatomical sections from wood cores collected at DBH in tree C6. (**A**) cellulose microfibril angles variations (in degree) from pith to bark – MFA decrease along the radial dimension of the secondary xylem growth. (**B**) Wood micro-density variations (in kg.m^{-3}) from pith to bark; lightest bands on a macroscopic scale correspond to tension wood bands (blue-stained fibres) on a microscopic scale; abrupt density decreases are recorded when forming axial parenchyma. Only the wood micro-densitometric profile combined with the visualization of the stained fibres allow us to measure the number of growth rings in the wood cores samples. Tree C6 is estimate in his 53nd years of growth.

Considering all trees studies, *C. candelabra* wood density at 11% moisture content is about 620.5 ± 56.3 kg.m^{-3}, with axial parenchyma being less dense ($\bar{d}_{AP}$ = 566.6 kg.m^{-3}) than normal wood ($\bar{d}_{NW}$ = 637.9 kg.m^{-3}) and tension wood ($\bar{d}_{TW}$ = 657.6 kg.m^{-3}) ($t = 34.4$, $p < 0.001$***). Despite poorly lignified, tension wood is significantly more dense than normal wood ($t = 12.2$, $p < 0.001$***)

(**Figure 4B**). In addition, the average cellulose microfibril angle of the wood fibres is low ($\overline{MFA}$ = 8.3°), and decreases along the radial dimension of the secondary xylem growth (**Figure 4A**). Considering the first and last five growth rings produced by tree C6, MFA ranges from 13,4° in old rings to 7.9° in newly produced rings. Although some abrupt decreases in MFA are visually related to the occurrence of tension wood bands, no significant MFA difference is found between normal wood and tension wood.

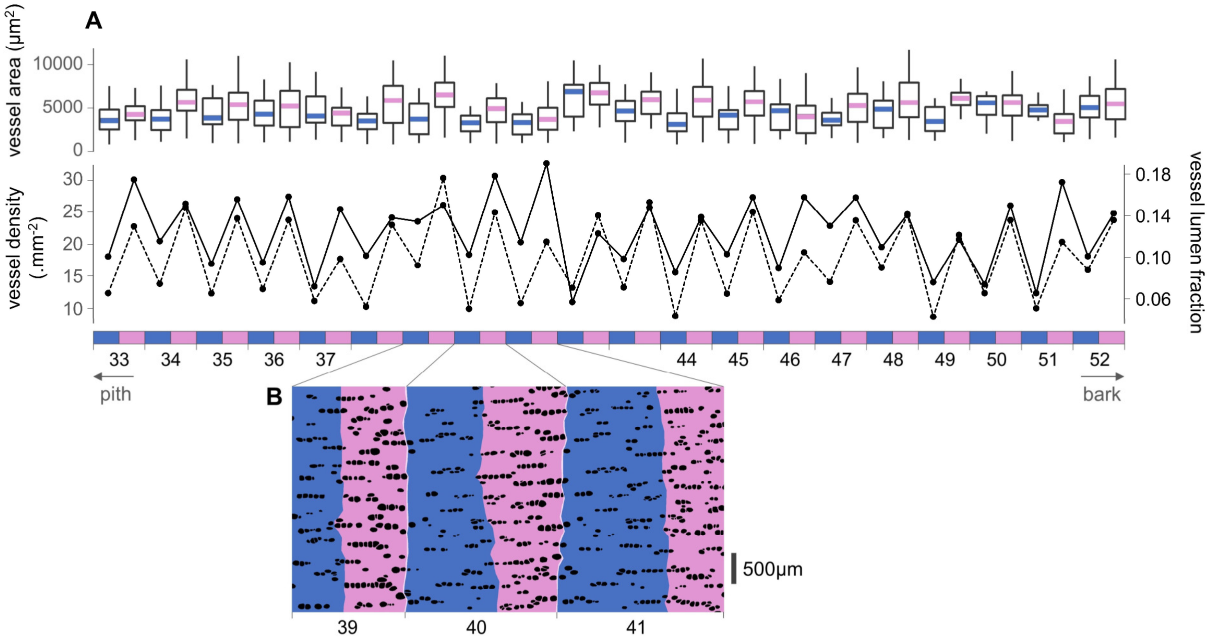

Figure 5. Vessels characteristics of *C. candelabra* according to their position in the growth ring. Measures are realized on wood cores sample at DBH in tree C6. (**A**) vessel area, vessel density, and vessel lumen fraction mean values are indicated for each band of tension wood (blue) and normal wood (pink), in the 20 last growth rings formed by the vascular cambium (33-52). (**B**) Anatomical profile of growth rings 39 to 41 – tension wood is characterized by a lower vessel area and density compared to the normal wood.

3.3. Vessel contribution to tension wood density

C. candelabra wood is characterized by vessels organized mainly in long and short radial patterns, and sporadically isolated (**Figure 2D, E**). The vessel lumen fraction ranged from 4.9% and 17.4%, with significant variations depending on whether tension or normal wood is considered ($\overline{LF}_{TW}$ = 6.9% ; $\overline{LF}_{NW}$ = 13.4% ; t = 13.7, p < 0.001***) (**Figure 5A**). These variations result from two substantial differences between the vessels of the tension wood and the normal wood. Tension wood shows a low vessel density compared to normal wood ($\overline{Vd}_{\mathrm{TW}}$ = 17.2 vessels.mm^{-2} ; $\overline{Vd}_{\mathrm{NW}}$ = 26.5 vessels.mm^{-2} ; t = 9.4, $p < 0.001$***). Vessel diameter is significantly smaller in the tension wood than in the normal wood ($\overline{VD}_{\mathrm{TW}}$ = 71µm ; $\overline{VD}_{\mathrm{NW}}$ = 80µm; t = 9.7, $p < 0.001$***) (**Figure 5B**).

4. Discussion

4.1. Circular tension wood in *C. candelabra*.

Growth rings are structural and temporal markers of cambial activity and reflect the succession of favorable and unfavorable growing cycles that affect the tree's growth throughout its life (Schweingruber, 1996; Worbes, 2002; Schöngart et al., 2017; Silva et al., 2019). In *C. candelabra*, our results show that growth rings are distinct at both microscopic and macroscopic scales. Microscopically, the growth rings are bounded by a tangential band of axial parenchyma and alternatively composed of two types of wood fibres. Each one, except the first 3-4, is composed of concentric tangential bands of tension wood (gelatinous fibres) and normal wood (lignified fibres). Tension wood in *C. candelabra* is suggested of type A1 according to Ghislain & Clair's classification (Ghislain & Clair, 2017), with characteristic low-lignified fibre walls and G-layers suspected exclusively composed of crystalline cellulose (Norberg & Meier, 1966; Côté et al., 1969; Pilate et al., 2004; Ruelle et al., 2006). These tension wood increments are responsible for the distinctness of the growth rings on a macroscopic scale through a higher longitudinal depression after drying than normal wood.

The growth ring structure and distinctness may reflect evolutionary strains and species phylogeny (Nath et al., 2016; Silva et al., 2020; Ortega Rodriguez et al., 2022). In some tropical Apocynaceae, narrow tangential bands of axial parenchyma have already been identified as an anatomical feature for growth rings delineation (Lens et al., 2008, 2009; Beckers et al., 2022), and variations in cell lignification or diameter are well-known structural changes marking the low activity phase of the vascular cambium (Détienne, 1989; Tarelkin et al., 2016; Islam et al., 2018;

Quintilhan et al., 2021). Tension wood in circular (i.e. continuous) bands has never been reported. This cambial production is exclusively described as asymmetrical and punctual (Pilate et al., 2004; Clair et al., 2006; Ruelle et al., 2006; Ghislain & Clair, 2017), and is not considered an anatomical feature for hardwood identification (Wheeler et al., 1989). However, our results show that tension wood production is a recurring anatomical characteristic of *C. candelabra* growth rings and a periodic production of the vascular cambium.

4.2. Periodicity of tension wood production

Growth ring formation is known to respond to environmental factors such as seasonal regimes (Worbes, 2002; Evert, 2006; Rathgeber et al., 2016; Perez-de-Lis et al., 2022). Previous work has suggested that *C. candelabra* forms annual growth rings in conjunction with the cool-dry season in New Caledonia, with distinct growth ring boundaries in September (Salmon et al., submitted a, b). Since tension wood bands are mainly bound to the axial parenchyma, we suggest that their production is annual and start as early as September. Therefore, seasonal factors might influence the production of tension wood in *C. candelabra*: (1) Tension wood band thickness does not correlate with their position along the radial growth of the secondary xylem and does not suggest an ontogenic pattern, and (2) G-layers composed exclusively of cellulose are known to result from fibre maturation under high tensile growth stress (Washusen et al., 2003; Clair et al., 2003; Ghislain & Clair, 2017).

Most of the dendroecological studies in tropical and subtropical contexts link the periodicity of cambial activity to changes in seasonal regimes such as precipitation and temperature (Worbes, 1999; Dié et al., 2012; Brienen et al., 2016; Tarelkin et al., 2019; Quesada-Roman et al., 2022). Little is known regarding the influence of wind regimes but a few studies have suggested that extreme events, such as high wind disturbances and tropical cyclones, may be an additional environmental factor influencing growth ring formation (Schweingruber, 2007; Bräuning et al., 2016; De Micco et al., 2019). As the main function of tension wood is biomechanical, we underline that its production in *C. candelabra* occurs each year and a few months before the beginning of the South Pacific cyclonic season (November – March). In New

Caledonia, cyclones are an integral part of the climate, with 21 tropical cyclones (winds > 118 km.h-1) and 9 tropical storms (winds > 89 km.h-1) recorded over the last 30 years, making these extreme events nearly annual (Ibanez et al., 2019; Delaporte et al., 2022; MétéoFrance, 2022).

4.3. Tension wood functions as a seasonal cambial production

Wind influence on secondary xylem – Wind influence on vascular cambium production has been evidenced several times (Niklas, 1998; Nicoll et al., 2008; Moulia et al., 2015; Bonnesoeur et al., 2016). The diversity of tree responses to mechanical disturbances, called thigmomorphogenesis, ranges from changes in tree shape to modifications in wood properties, such as the production of flexure wood or tension wood (Jaffe, 1973; Telewski 2006, 2012; Gardiner et al., 2016; Moore et al., 2018; Roignant et al., 2018). Tension wood allows the axes of the plant to recover their initial orientation by generating asymmetrical tensile stress (Dadswell & Wardrop, 1955; Clair et al., 2006; Groover, 2016; Ghislain et al., 2019). This gravitropic movement results from the higher tensile potential of gelatinous fibres whose G-layer cellulose microfibrils are almost aligned with the fibre axis (Fujita et al. 1974; Chaffey 2000; Daniel et al., 2006). In *C. candelabra,* wood is characterized by a density of 621kg.m^{-3} and a low cellulose microfibril angle (8.3°). These results are in agreement with Read et al. (2011). We found that the higher density of tension wood was driven by a lower vessel lumen fraction compared to normal wood, resulting from both vessel size and density reduction. Previous studies have demonstrated that axes submitted to mechanical stimulations, as winds, produce more fibres and fewer vessels, underlining a well-known adjustment between mechanical and hydraulic safety (Jourez et al., 2001; Ruelle et al., 2006; Badel et al., 2015; Telewski, 1989, 2016). *C. candelabra* is additionally known to exhibit a high longitudinal modulus of elasticity (MOE; c.a. 18.5 GPa) compared to other New Caledonian trees (Read et al., 2011). Considering its wood's density and low MFA we suggested that tension wood is responsible for the trunk's high resistance to bending (directly proportional to MOE). According to previous studies which explore tree biomechanical responses to winds (Fournier et al., 2013; Moulia et al., 2015; Roignant et al., 2018; Niez et al., 2019, 2020), we suspect that the last circular band of tension wood produced generates a tensile stress that lower the trunk resistance to compression but raise its resistance to tension, regardless of the wind direction.

Towards a broader definition of tension wood function – In *C. candelabra*, the novelty is the periodic production of tension wood in circular bands. We found some evidence that it may be an adaptive feature allowing the species to maximize its resistance to multidirectional winds, such as those experienced during storms. (1) Tension wood production is annual from the 3rd - 4th year of growth, which corresponds to the timing of branch development by the sapling (Salmon et al., submitted a, b), (2) its observation is systematic and is suspected independent of tree location or wind exposure, and (3) its production is independent of cyclone occurrence, with gelatinous fibres recorded in growth rings formed in non-cyclonic years. Therefore, these results suggest that expanding our definition of tension wood function is needed. In *C. candelabra*, tension wood is not only a response to punctual disturbances but might also be a prevention to frequent disturbances such as tropical cyclones.

5. Conclusion

In monocarpic trees, adaptations to maximized fitness have already been reported (Kitajima & Augspurger, 1989; Forget et al., 1999; Poorter et al., 2005; Read et al., 2006) and are expected, because species persistence relies on a very low probability of mortality before flowering. This article aimed to present a new type of growth ring due to the production of circular tension wood in the subtropical monocarpic tree *C. candelabra*. This finding suggests that, as precipitation and temperature, wind and cyclone regimes could be an additional seasonal factor influencing the growth ring structure and the dynamic of the vascular cambium. We argue that *C. candelabra* is an appropriate biological model to refine our understanding of (1) the vascular cambium response to mechanical stimulation and (2) the dynamics of wood production and maturation in tropical and cyclonic environments. Furthermore, this endemic species offers promising prospects for dendroclimatological studies in New Caledonia.

6. Additional information

6.1. Acknowledgments

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6.2. Author Contributions

CReDIT authorship contribution statement - Conceptualization: *PH, SI, CS*; Funding acquisition: *SI, PH*; Data Curation: *CS, JR, JF*; Formal analysis: *CS, JF*; Investigation: *CS, PH, SI, JF*; Vizualization: *CS*; Writing-original draft: *CS*; Writing – Review & Editing: *CS, PH, SI, RJ;* Project administration and Supervision: *PH, SI*.

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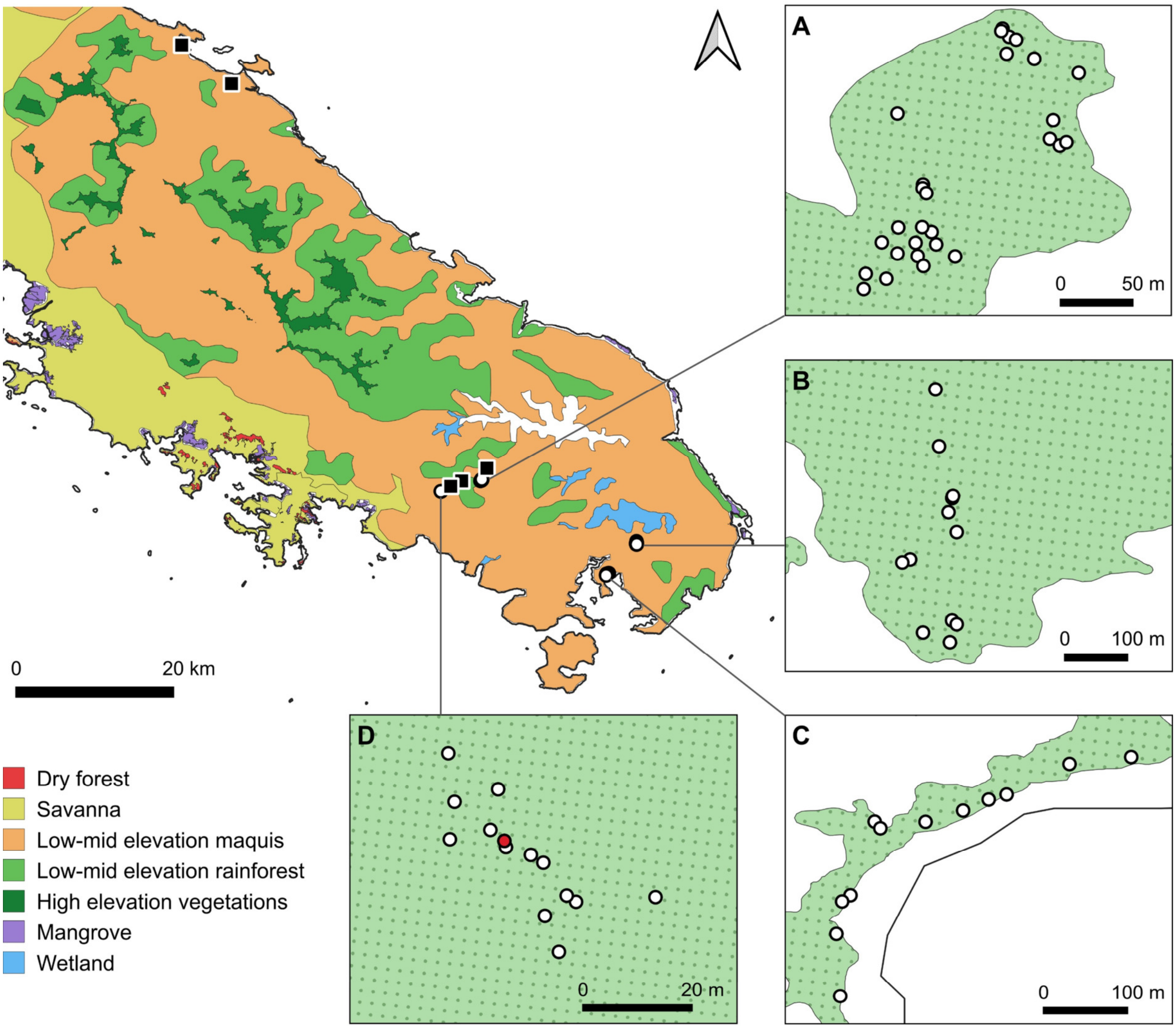
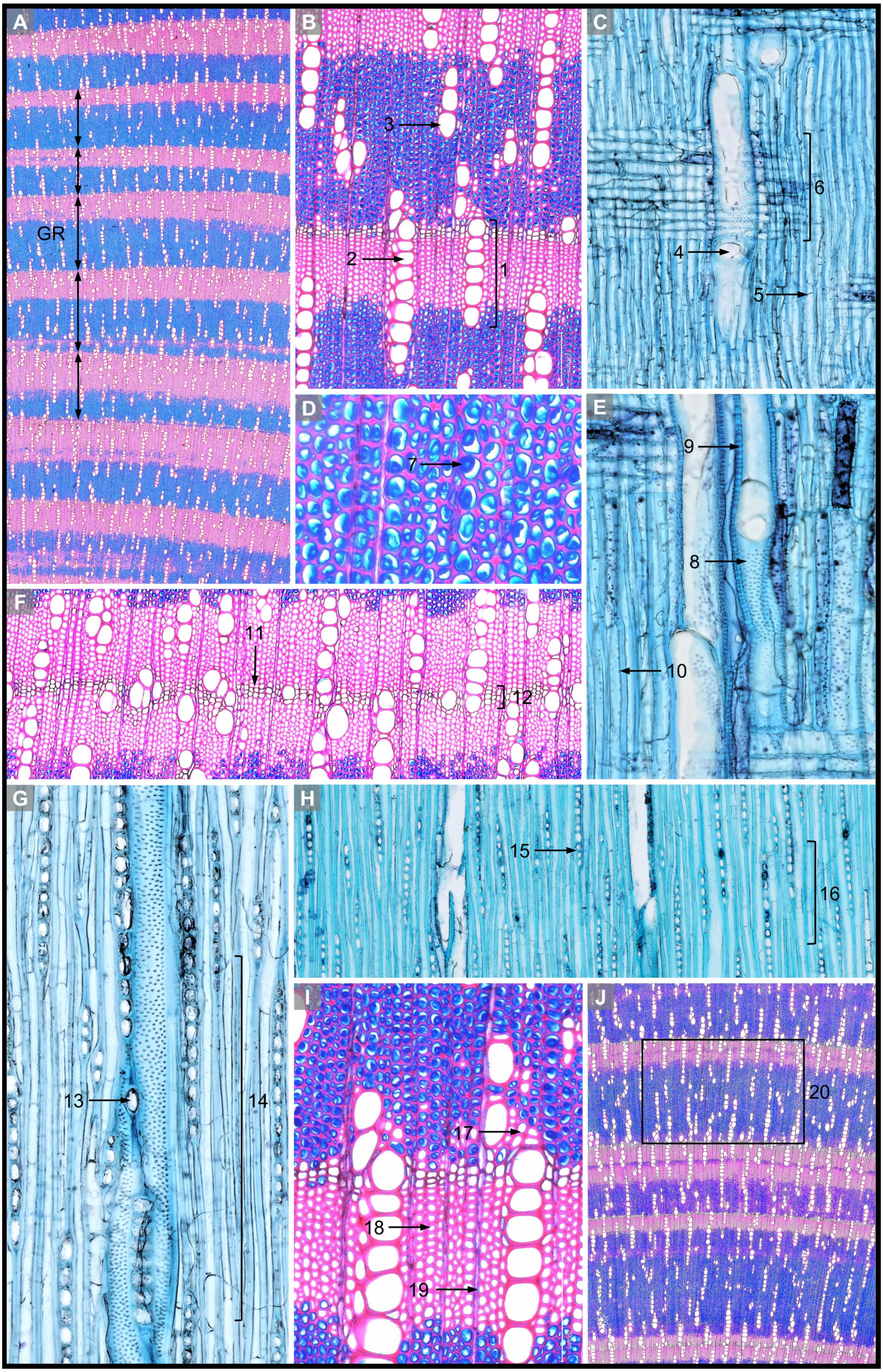
Appendix 1. Localization of *C. candelabra* trees sampled for wood anatomical description. Black squares indicate the localization of the five trees cut down for wood disks sampling (C1-C5). All trees are located in the Southern region of the Grande Terre, at Mont-Dore (western coastal plains; C1, C2, C3) and Thio (eastern coastal plains; C4, C5). White dots indicate the localization of the 60 trees sampled for wood cores analyses. Four forest patches are studied: Col des deux tétons (**A**), Pic du Grand Kaori (**B**), Baie Nord (**C**), and Mouirange (**D**). The red dot indicates the localization of tree C6 whose cores are analyzed in detail in this study.



Appendix 2. Table. Wood anatomy of *Cerberiopsis candelabra* (Apocynaceae), according to the IAWA list of microscopic features for hardwood identification (Wheeler et al., 1989).

	IAWA anatomical features	**no.**	**Definition**	**Figure**
GR	Growth rings	1	growth ring boudaries distinct	A, D
Vessels	Porosity	5	wood diffuse-porous	A
	Vessel arangement	7	vessels in diagonal and/or radial pattern	B
	Vessel groupings	10	vessels in radial multiples of 4 or more common	B
	Solitary vessel outline	_	*vessel outline not angular*	B
	Perforation plates	13	simple perforation plates	C
	Intervessel pits arrangement	22	intervessel pits alternate	E
	Vesstured pits	_	*no vestured pits*	C
	Intervessel pits size	24	minute	E
	Vessel-ray pitting	30	with distinct borders, similar to intervessel pits	E
	Helical thickenings	39	helical thickening only in narrower vessels	G
	Tangential diameter of lumina	41+42	50-200 µm	J
	Vessels per square millimeter	48	20-40 vessels per square millimiter	J
	Mean vessel element lenght	53	350-800 µm	G
	Tyloses and Deposites	_	*no tyloses and deposites*	B
	Wood vesselless	_	*no wood vesselless*	A
Fibres	Ground tissue fibres	62	fibres with distinctly bordered pits	E
	Septate/Parenchyma-like fibres	65+66	septate and nonseptate fibres present	C
	Fibre wall thickness	69	fibres thin- to thick-walled	I
	Mean fibre lenghts	73	900-1600 µm	G
AP	Paratracheal axial parenchyma	78	axial parenchyma scanty paratracheal	F, I
	Banded parenchyma	86	axial parenchyma in narrow bands or lines	F
	Axial parenchyma cell type	92	Four (3-4) cells per parenchyma strand	F
Rays	Ray width	96	rays exclusively uniseriate	I
	Aggregate rays	_	*no aggregate rays*	H
	Ray height	102	rays height > 1mm	H
	Rays of two distinct sizes	_	*no rays of two distinct sizes*	C
	Rays: cellular composition	104	all ray cells procumbent	C
	Rays per millimeter	115	4-12 / mm	H
	wood rayless	_	*no wood rayless*	J
SS	Stroried structure	119	low rays storied, high rays nonstoried	H
Secretion	Oil and mucilage cells	_	*no oil and/or mucilage cells*	_
	Intercellular canals	_	*no intercellular canals*	_
	Tubes / tubules	132	Laticifers or tanniniferous tubes	_
	Cambial variants	_	*no cambial variants*	_


A
GR
B
3
2
1
C
6
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5
D
7
E
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G
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14
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J
20

Appendix 2. Figure. Wood anatomy of the subtropical monocarpic tree *C. candelabra*. (**A**) growth rings (GR) show distinct boundaries marked by a thin tangential band of axial parenchyma; each GR included at least one tangential circular band of tension wood formed at the beginning of the dimension of the ring's radial growth. (**B**) 1: vessel elements are arranged in a radial pattern and organized in radial multiples of 4 or more common vessels; 2: vessel outline is circular; 3: vessels show no tyloses or deposits. (**C**) 4: vessel perforation plates are simple; 5: normal wood fibres are both septate and nonseptate; 6: all rays cells are procumbent and do not show distinct sizes. (**D**) tension wood fibres show a characteristic gelatinous layer (G-layer) composed of crystalline cellulose; 7: G-layer is frequently detached from the wall secondary layer. (**E**) 8: intervessel pits are alternate and < 4µm ('minute'); 9: vessel-ray pitting shows distinct borders; 10: normal wood fibres show distinctly bordered pits. (**F**) 11: growth rings are delineated by axial parenchyma; 12: Axial parenchyma is in narrow bands of 3-4-cells-thick. (**G**) 13: helical thickening is not observed or only in narrower vessels; 14: normal wood fibres are 900-1600µm long. (**H**) 15: rays are > 1mm tall and not aggregate; 16: most rays are non-storied. (**I**) 17: axial parenchyma is scanty paratracheal; 18: normal wood fibres are thin to thick-walled; 19: rays are exclusively uniseriate. (**J**) 20: Normal wood show 20-40 vessels per square millimeter with a tangential diameter of lumen ranging from 50-200µm.

Chapter 7

Fertile and sterile *C. candelabra* at Baie Nord, three months after cyclone Niran (New Caledonia) © C. Salmon & J.M. Bore

Chapter 7 summarizes the developmental trajectories of *C. candelabra* with consideration of its sister species (*C. neriifolia* and *C. obtusifolia*) and its environment. From the evolution of the branched growth form to the expression of the monocarpic strategy in canopy trees, we provide new insights into the morpho-anatomical bases of monocarpy, its underlying ecological implications, and its functional adaptations. We discuss the contributions of this study to our understanding of monocarpy in trees and suggest further research perspectives.

General discussion

Keeping in mind our initial research questions, 'What are the developmental patterns of a monocarpic tree?' and 'What are the morpho-anatomical bases of monocarpy, its underlying ecological implications, and functional adaptations', we provide hereafter some original insights into the monocarpic life history of *Cerberiopsis candelabra* Vieill. We will discuss the growth, branching, and senescence patterns of *C. candelabra* compared to those of its closely related polycarpic species (**sections 1, 2**), the phenology of these patterns in relation to New Caledonia climate (**sections 3, 4**), and the functional adaptations that may be required to sustain *C. candelabra* monocarpic strategy at the individual scale (**sections 5, 6**). Lastly, we will provide further research perspectives (**section 7**).

1. Insights into the developmental trajectories of *Cerberiopsis* species.

Monocarpic trees are rare worldwide and known from only two genera and twenty-nine species. The evolution of this reproductive strategy, based on a single flowering event followed by the individual's death, confronts us with a series of questions about the selective pressures that led to its evolution and persistence (Foster, 1977; Kitajima & Augspurger, 1989; Poorter et al., 2005, Read et al., 2006, 2008, 2021). In this study, we have dissected the bases of this strategy at the individual scale through an extensive morpho-anatomical diagnosis. First, we sought to understand the topological and geometrical construction of *Cerberiopsis* species throughout time (**Chapters 3, 4, 5**). All *Cerberiopsis* species develop an architecture organized according to the repetition of three axis categories: the main axis, the branches, and the twigs. These axes differ in (1) their orientation, (2) their monopodial or sympodial construction and their ability to branch, and (3) their synchronous or non-synchronous flowering patterns. Therefore, while *Cerberiopsis* species share an architecture of a rather similar nature, their growth form divergences only rely on the combination of these three architectural traits (**Chapter 3**). These results were in line with previous studies underlining that only a few variations in the plant growth forms may lead to a wide diversity of life histories (Isnard et al., 2012; Chomicki et al., 2017; Bruy et al., 2018; Anest et al., 2021). In these latter studies, the relationship between plant growth form and their underlying strategies was investigated in light of dated phylogenies to estimate the evolvability of plant architecture in different taxa and environments. In this thesis, we were confronted with the absence of a *Cerberiopsi*s phylogeny (Alvarado-Cárdenas & Ochoterena, 2007; Endress et al., 2014). Nevertheless, the quantitative analysis of species architecture and their interpretation from a dynamic point of view helped us to formulate hypotheses on the evolution of monocarpy within the genus *Cerberiopsis* (**Chapter 5**).

The conceptual framework provided by architectural analysis allowed us to study the apparent structural complexity of plants and to decompose the plant body into several structural units comparable between individuals of the same and different species (Hallé & Oldeman, 1970; Barthélémy et al., 1989; Edelin, 1984; Barthélémy & Caraglio, 2007). Within the genus *Cerberiopsis*, we demonstrate that species-specific temporal synchronism (i.e. the paces of axis development) was a fundamental feature explaining their divergences of growth forms: from a polycarpic shrub growing in the bushy maquis to a monocarpic canopy tree growing in the rainforest (**Chapter 5**). Compared to its two polycarpic sister species, the monocarpic tree *C. candelabra* exhibits a specific combination of only two architectural traits: (1) the complete synchronization of flowering at the individual scale, with flowering extending to all apical meristems of all axis categories, and (2) the inability of delayed branching, preventing regrowth after terminal flowering. Respectively, its polycarpic sister species share one of these architectural traits but never both (**Chapter 3**). Furthermore, *C. candelabra* is the *Cerberiopsis* species whose architecture is the most derived from the generic architecture of the Apocynaceae (axis development by apposition of plagiotropic modules; Prévost, 1967; Tomlinson & Zimmerman, 1978; Mueller, 1985). Both of these results suggest that this monocarpic tree exhibits the most derived growth form, and therefore life history, within the genus *Cerberiopsis*. In addition, they support the hypothesis that only a few architectural variations may contribute to monocarpy evolution. Moreover, previous studies have suggested that only a few genetic mutations were required to evolve monocarpic in branched perennial plants (Young & Augspurger, 1991; Amasino, 2009; Hugues & Simons, 2014; Kakishima et al., 2019).

2. Do monocarpic trees senesce?

While a few architectural variations can lead to the evolution of the monocarpic strategy, what inherently distinct closely related monocarpic and polycarpic species at the individual scale? We suggested that the answer relies on their diverging senescence patterns. Tree lifespan is limited by biotic factors (e.g. herbivores, parasites, competitors) and abiotic parameters (e.g. water and nutrient limitations, light availability), but also by age-related structural constraints such as height-related hydraulic limitations and vascular discontinuities (Westing, 1964; Cailleret et al., 2016; Munné-Bosch, 2018; Piovesan & Biondi, 2021). With aging (i.e. increasing age and size), primary and secondary growth slow, and individuals are more likely to die. Aging and senescence are concepts often interchangeable in plant biology and mistakenly used as synonyms for deterioration. Firstly, aging is a multilevel concept that may apply to cells, organs, or whole-organism (Peñuelas, 2005; Munné-Bosch, 2007; Gan, 2018). Secondly, senescence is a physiological consequence of aging and although death is inevitable, senescence is not (Peñuelas, 2005; Thomas, 2004, 2013). Senescence is an evitable physiological process involving a fitness decrease with age, such as lower fertility and greater vulnerability to disease or damage (Munné-Bosch, 2008; Salguero-Gómez et al., 2013; Klimesová et al., 2014). Therefore, senescence depends much more on the tree's developmental trajectory than on its strict age or size (Baudisch & Vaupel 2012; Caswell & Salguero-Gómez, 2013; Miryeganeh, 2021), and there is little consensus on whether or not it is programmed (Jansson & Thomas, 2008; Brutovská et al., 2013; Lee & Muzika, 2014).

Our results on *C. candelabra* developmental trajectories demonstrate that trees (1) preferentially flower at the adult stage (i.e. individuals that have completed their architectural unit) but can also flower at the seedling and sapling stages, regardless of an age-size threshold, and (2) never show signs of senescence (e.g. crown dismantling) at the individual scale (**Chapters 3, 5**). Therefore, *C. candelabra* trees confront us with two main issues. On the one hand, the delayed flowering of this monocarpic species questions the notion of juvenility. The transition from the juvenile to the mature phase often refer as the moment when individuals express sexuality (Zimmerman, 1972; Borchert, 1976; Barthélémy et al., 1989; Jones, 1999). In *C. candelabra* we have defined the transition from the sapling to the adult stage as the time of architectural unit completion that is not related to the expression of sexuality. Therefore, while at the adult architectural stage, the trees remain in the juvenile phase, and this phase is record-breaking as it can extend more than a century. In this regard, the few individuals that flower and consequently die before reaching this adult stage show one of the most important heterochronic alterations known in plants: progenesis (i.e. the conservation of juvenile traits for faster reproductive development) (Alberch & Blanco, 1996; Li & Johnston, 2000; Box & Glover, 2010; Olson, 2007).

On the other hand, the delayed flowering of monocarpic trees questions the notion of automatic (i.e. endogenously programmed) flowering. Previous studies have suggested that the reproductive output of monocarpic perennials increases with age and size as more resources are allocated to reproduction (Schaffer, 1974a, b; Bell, 1980; Young & Augspurger, 1991; Noodén et al., 2004). Therefore, we suspect that the tree death following the unique flowering event is not the result of programmed or age-size-related senescence but the consequence of an extreme resource reallocation. In *C. candelabra*, post-flowering leaf senescence, a well-known mechanism for nitrogen reallocation (Guiboileau et al., 2010; Davies & Gan, 2012; Pérez-Llorca & Munné-Bosch, 2021), supports this hypothesis. The whole-tree death might be caused by the auxin-inhibition of axillary meristems, preventing any regrowth after the massive reallocation of carbohydrates and nitrogen to the apical meristems determined to produce seeds. This death pattern has been proposed in other branched perennial species (Guo & Gan, 2011; Davies & Gan, 2012; Thomas, 2013).

3. Developmental phenology of *Cerberiopsis* species

Plants are known to synchronize their growth, branching, flowering, and reiteration processes with seasonal regimes. These developmental processes are interdependent and expressed at a time that maximized individual fitness (Van Schaik et al., 1993; Fenner, 1998; Valdez-Hernández et al., 2010; Miryeganeh, 2021). In this thesis, we have demonstrated that *Cerberiopsis* species exhibits strong structural regularities, and thanks to an integrative dendrochronological approach, we achieved to associate an absolute temporality to these regularities (**Chapters 4** to **6**). In each species, growth slowdowns were marked by a reduction in phytomer length, a decrease in leaf area, and the formation of a new growth ring. In *C. candelabra*, while primary growth is continuous (i.e. individuals continuously elongate), the tree's developmental patterns follow an annual schedule. The primary and secondary growth slowdowns occur each year during the cool-dry season (from June to September) and underline *C. candelabra*'s sensitivity to rainfall variations (**Chapters 4, 5**). Therefore, our results show that the shoot apical meristems and the vascular cambium activity are coordinated within the plant body. In all three species, (1) primary and secondary growth and (2) primary growth, branching, and flowering processes were highly synchronized (**Chapter 5**). As monocarpy implies the synchronous flowering of all apical meristems, we suspect that highly coordinated developmental processes within the plant body are a prerequisite to its evolution.

In this thesis, we have discussed the value of retrospective approaches, especially if polycyclism is expressed during plant development as it's the case in all three *Cerberiopsis* species (**Chapter 5**). Hereafter, we take a critical look at this approach. The combined use of several morpho-anatomical traits at the phytomer scale allows the investigation of tree developmental trajectories at a high temporal resolution and to precisely relate the variations in primary growth (internode lengths) and secondary growth (growth ring formation) (Heuret et al., 2002, 2003; Zalamea et al., 2008; Nicolini et al., 2012; Mangenet, 2013). Integrative dendrochronological approaches pave the way to better assess tree phenology in tropical regions where phenological patterns are megadiverse and permanent monitoring plots are recent. However, node-by-node characterization faces multiple constraints. (1) It relies on the legibility of structural regularities that, even if observed, may not be visible on the oldest parts of the tree because of their overlap with the bark. (2) It requires extensive and time-consuming measurements, which (3) significantly limit the number of individuals studied. (4) It may result in an unresolved developmental timeline if primary and secondary growth patterns show high desynchronization. Therefore, further research could combine quantitative dendrochronological approaches with modeling. Plant modeling has become an integral research activity and has increased our understanding of the structure-function-time relationships in plants (De Reffye et al., 1997; Godin & Caraglio, 1998; Godin, 2000). The methodological framework provided by stochastic and mechanistic models allows (1) to simulate alternative developmental trajectories and (2) to explore how the topological and geometrical organization of the plant body may vary in space and time under varying environmental conditions (Guédon et al. 2001; Barczi et al. 2008; Costes et al., 2008; Mathieu et al. 2009). For instance, in *C. candelabra*, it may be valuable to explore the rate of meristem multiplication at the tree scale to explore how the branching process retroactively affects primary and secondary growth rates and the timing of flowering.

4. Why some trees are monocarpic?

In previous sections, we have discussed the structural and temporal features characterizing *C. candelabra*'s developmental trajectory and sustaining its monocarpic life history. But what supports such an unusual strategy in an ecological framework? According to Darwinian fitness, a life history is selected if it allows individuals to colonize new habitats or to gain an advantage in their habitats (Schaffer & Rosenzweig, 1977; Stearns, 1992; Roff, 1993). Within the genus *Cerberiopsis*, as *C. neriifolia* and *C. obtusifolia* grow exclusively in the maquis, the monocarpic strategy of *C. candelabra* is inherently related to the forest habitat. Hereafter, we provide some hypotheses on the selective advantages to be a monocarpic tree in New Caledonian rainforests.

Even though a unique flowering event appears risky, the majority of monocarpic perennials occur in unpredictable environments, either successionally (i.e. frequently disturbed) or edaphically (i.e. physiologically restrictive) (Baskin & Baskin, 1979; Klinkhamer & De Jong, 1987; Young, 1990; Munné-Bosch et al., 2016). Therefore, a single, massive flowering event may be advantageous if its success outweighs the success of multiple reproductions under uncertain and unfavorable conditions (Harper, 1977; Young & Augspurger, 1991; Metcalf et al., 2003; Vaupel et al., 2013). The evolution of plant life histories is driven by disturbance frequency and environmental stresses such as resource availability (Stearns, 1976; Grime, 1977; Kleyer, 2002; Zhu et al., 2018). In New Caledonia, *C. candelabra* populations grow on soils derived from the alteration of an ultramafic substrate, one of the most constraining substrates to plant development (Pillon et al., 2010; Isnard et al., 2016; Jaffré, 2022). In addition, they are frequently exposed to large scale-disturbances such as fires, tropical cyclones and storms, or anomalies in rainfall regimes due to Southern Pacific climate oscillation (el Niño and la Niña events) (Nicet & Delcroix, 2000; Moron et al., 2016; Dutheil et al., 2021). Read et al. (2008) suggested that masting and monodominance may be necessary preconditions for the evolution of monocarpy in *C. candelabra*. This trait syndrome has been underlined in several other monocarpic branched perennials within *Tachigali*, *Strobilanthes*, *Issoglossa*, and *Stenostephanus* genera (Kitajima & Augspurger 1989; Wood, 1994; Tsvuura et al., 2011; Daniel, 2006; Kakishima et al., 2011). The selective advantage of a masting-monodominance syndrome is (1) to increase cross-pollination and seed survival thanks to predator satiation (Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002; Schauber et al., 2002) and (2) to facilitate seedling recruitment by the opening of canopy gaps following the parental trees death (Janzen, 1976; Foster, 1977; Struhsaker, 1997; Read et al., 2006a, 2008, 2021). This assumption is in sharp contrast to the Janzen-Connell hypothesis, which predicts higher survival rates away from the parental tree due to lower proximity to natural enemies (Janzen, 1970; Connell, 1971; Clark & Clark, 1984). However, in New Caledonia, this trait syndrome is widely recorded in vegetations occurring in fire and cyclone-prone areas (Pillon et al., 2021). Seedling recruitment of monodominant species, like *C. candelabra*, is favored in disturbed and poor-nutrient areas since their low regeneration capacities in shaded understories are offset by (1) the wide canopy gaps opened by disturbances and (2) the slow rates of successional change (Read et al., 2006b, 2008; 2015; Ibanez & Birnbaum, 2014). Therefore, we suspect that the selective advantage of a monocarpy-masting-monodominant syndrome is maximized in frequently disturbed and physiologically restrictive environments.

5. Functional adaptations sustaining *C. candelabra* monocarpic strategy

Although the monocarpic strategy in perennials branched species is suggested of selective advantage when combined with masting and monodominance, its persistence fundamentally relays on a very low probability of pre-flowering mortality at the individual scale (Kitajima & Augspurger, 1989; Poorter et al., 2005; Burd et al., 2006). In this thesis, we have explored some functional traits (as defined by Violle et al., 2007) that may explain *C. candelabra*'s success in New Caledonian secondary forests (**Chapters 3** to **6**). As expected for a monocarpic gap-specialist tree, juveniles show high density and survival rates in full light conditions (c.a. 88.2 %.y^{-1} at 2 years old), with individuals exhibiting an average growth rate of 60 cm.y^{-1} (**Chapter 4**). As *C. candelabra*'s primary growth is continuous and expresses polycyclism, high growth rates are maintained at the adult stage (c.a. 32 cm.y^{-1}) (**Chapter 5**). On the one hand, continuous growth patterns are suggested to promote faster growth rates in shade-intolerant species (Ackerly, 1996; Osada et al., 2012; Reich, 2014). On the other hand, polycyclic growth patterns are suspected preserving apical meristem integrity by compensating for nutrient or water limitations through timely growth slowdowns (Cabanettes et al., 1995; Sabatier et al., 2003; Girard et al., 2012; Hover et al., 2017).

Although *C. candelabra* growth rates may appear paltry compared to those of some neotropical pioneer plants (Dalling & Hubbell, 2002; Zalamea et al., 2008, 2012), this species does exhibit high growth rates for a New Caledonian tree growing on ultramafic soils water-deficient, poor in nutrients (P, K), and rich in metals and trace metals (Ni, Mn, Cr, Co, Fe) (Isnard et al., 2016; Jaffré, 2022). For instance, *C. candelabra* relatively thick leaves with high LMA values (c.a. 206 g.cm^{-2}) are indicative of a conservative strategy on the worldwide leaf economic spectrum (Wright et al., 2004; Reich, 2014; Díaz et al., 2016) (**Chapter 5**). In the context of New Caledonian flora, these LMA values suggests an acquisitive strategy and underlines its adaptation to ultramafic substrates (*Isnard S., personal communication*).

Throughout this thesis, we have identified traits that might explain *C. candelabra*'s biomechanical resistance to disturbances. Our results show that the so-called "candelabra physiognomy"(Veillon 1971, Read et al., 2006, 2011), with reduced branching order, open crown, and intense branch self-pruning, may contribute to reducing the drag and mechanical damage caused by high winds (Valinger et al., 1993; James et al., 2006; Peltola et al., 2013; Loehle, 2016). In addition, the tree slenderness factors (H/DBH) were always in a high stability range, ensuring the biomechanical safety of individuals regardless of their size or habitat openness (**Chapter 3**). Among the outstanding particularities of *C. candelabra*, our analyses revealed a new type of annual growth ring due to alternating layers of normal and tension wood. This tension wood is seasonally produced in circular bands and is suspected an adaptive cambial production allowing trees to reinforce their resistance to multidirectional winds, such as those experienced during tropical cyclones (**Chapter 6**). The originality of this anatomical feature relies on the lower energetical cost of cellulose synthesis (i.e. tension wood cell wall production) versus lignin synthesis (i.e. normal wood cell wall production) (Whetten & Sederoff, 1995; Hatfield & Vermerris, 2001; Beck, 2005). Circular tension wood might be a functional adaptation enhancing *C. candelabra* fitness at a lower cost.

6. Is *C. candelabra* a highly mechanosensitive tree?

Environmental disturbances may enhance the selective advantage of *C. candelabra* monocarpic-masting-monodominant syndrome, and trees are suggested to be highly resistant to wind disturbances. Therefore, as suspected by Read et al. (2006, 2008, 2021), tropical cyclones could be the main triggers of *C. candelabra*'s flowering events. The timing of flowering is a critical trait for a long-lived monocarpic tree, as it ensures the successful establishment of the next generation and the survival of the species (Cohen, 1976; Putterill et al., 2004; Mouradov et al., 2002; Amasino & Michaels, 2010). As suggested by previous studies, we suspect that monocarpic reproduction in *C. candelabra* is dependent on a minimum resource threshold necessary to sustain the production of flowers and seeds (Simonds, 1980; Burd et al., 2006; Metcalfe, 2003). Once this minimum threshold is reached, flowering is delayed until an external cue, such as a tropical cyclone, triggers its initiation.

All plants perceived mechanical stimulations from their environments, such as gravity, raining, snowing, and winds (Jaffe, 1984; Braam, 2005; De Langre, 2008; Moulia et al., 2022). The diversity of tree responses to mechanical simulations, called thigmomorphogenesis, ranges from modifications in cell walls to changes in tree shape (Telewski, 2006, 2012; Monshausen & Haswell, 2013; Braam & Chehab, 2017; Moore et al., 2018). According to Lichtenthaler (1998), these mechanical stimulations are perceived as stresses if they affect the plant's developmental processes. Therefore, plant sensitivity and response to stresses mostly rely on (1) their developmental trajectories and (2) the strength of the stress and the duration of its action (Bohnert et al., 1995; Alscher & Cumming, 1990; Kranner et al., 2010; Raza et al., 2020). The physiology of plants frequently exposed to wind disturbances has been well studied, and most physiological responses imply variations in growth rates (Telewski, 1995; Mitchell, 1996; Dongmo et al., 2022), a change in wood composition (Gardiner, 2016; Roignant et al., 2018), and inhibition of flowering (Jaffe, 1973; Braam, 2005). However, a few studies have underlined that mechanical stimulations, including strong winds, may also promote flowering initiation (Wada & Takeno, 2010; Takeno, 2012, 2016; Kazan & Lyons, 2016). Stress-induced flowering events have been reported at a large scale in a few tropical lowland rainforests after extreme climatic events, such as tropical cyclones (Hopkins & Graham, 1987; Hamann, 2004; Novaes et al., 2020; Afifah et al., 2022). We suggest that a similar stress-induced response is involved during mass-flowering events of *C. candelabra*. In 2021, we witnessed a mass-flowering of several populations three months after the passage of Niran, a category-five tropical cyclone (**Figure 1**). The last three *C. candelabra* mass-flowering events were also documented in years of severe tropical cyclones (Read et al., 2021).

Figure 1. Mass-flowering events in four *C. candelabra* populations from June 2021 to January 2022. Flowering occurred three months after the tropical cyclone Niran. Populations are located at (**A**) Pic du Grand Kaori, (**B**) Col des deux tétons, (**C**) Mouirange, and (**D**) Baie Nord.

7. Conclusion and perspectives

Among the life history strategies of trees, the one that implies flowering only once after decades and then dying, namely monocarpy, has long intrigued botanists and evolutionary biologists. This thesis aimed to dissect the developmental trajectories that sustain monocarpy in *C. candelabra*, one of the 29 species of monocarpic canopy tree known worldwide. While most studies investigating tree strategies focus on the structure-function relationships underlining their development, we show that the examination of timing was of great value for understanding *C. candelabra's* life history. In particular, my work highlights that synchronism at different scales, from meristem to population level, is a key determinant of monocarpy evolution.

C. candelabra show high seedling density and survival rates and can be considered a large-gaps specialist. These ecological features combined with a masting-monodominant syndrome might explain its success in secondary forests. In addition, the selective advantage of *C. candelabra's* life history may be enhanced by the disturbance regimes (fires and tropical cyclones) of New Caledonia. As the persistence of monocarpy also relies on the ability of individuals to survive such events, we have shown that trees exhibit several architectural and functional adaptations that are likely to improve their biomechanical resistance. In particular, we have highlighted an intriguing new type of annual growth ring characterized by the succession of tension wood and normal wood layers.

Recruitment rates of gap-dependent trees depend on the frequency and intensity of habitat disturbances (Martinez-Ramos & Alvarez-Buylla, 1986; Sakai & Kitajima, 2019). Facing the evidence that global changes will increase the Southern Pacific climate oscillations and therefore the frequency of droughts and cyclones (IPCC, 2013), it is critical to understand how changes in disturbance regimes will affect the pace and the shape of *C. candelabra* developmental trajectories. In this regard, it will be necessary to extend our dendrochronological analysis of trees' developmental chrono-sequences.

A substantial data set collected during this thesis, but not analyzed in this manuscript, should allow us to address these issues shortly. We sampled a batch of 130 wood cores from mature *C. candelabra* trees ranging from 6.1 to 24.5m in height and 7.3 to 48.1cm in DBH, with complete overlap between flowering and non-flowering individuals (**Appendix 1**). Analysis of these data should allow us to better understand whether particular developmental trajectories preferentially lead to flowering initiation. With this dataset, we can also explore the correlations between tension wood band thickness and tropical cyclones intensities to better assess whether tension wood formation results from phenotypic plasticity or functional adaptation. Many exciting issues remain to be explored about the role of tension wood from a biomechanical perspective. For instance, how do layers of tension wood affect the wood's tensile and compressive strength and its resistance to wind damage?

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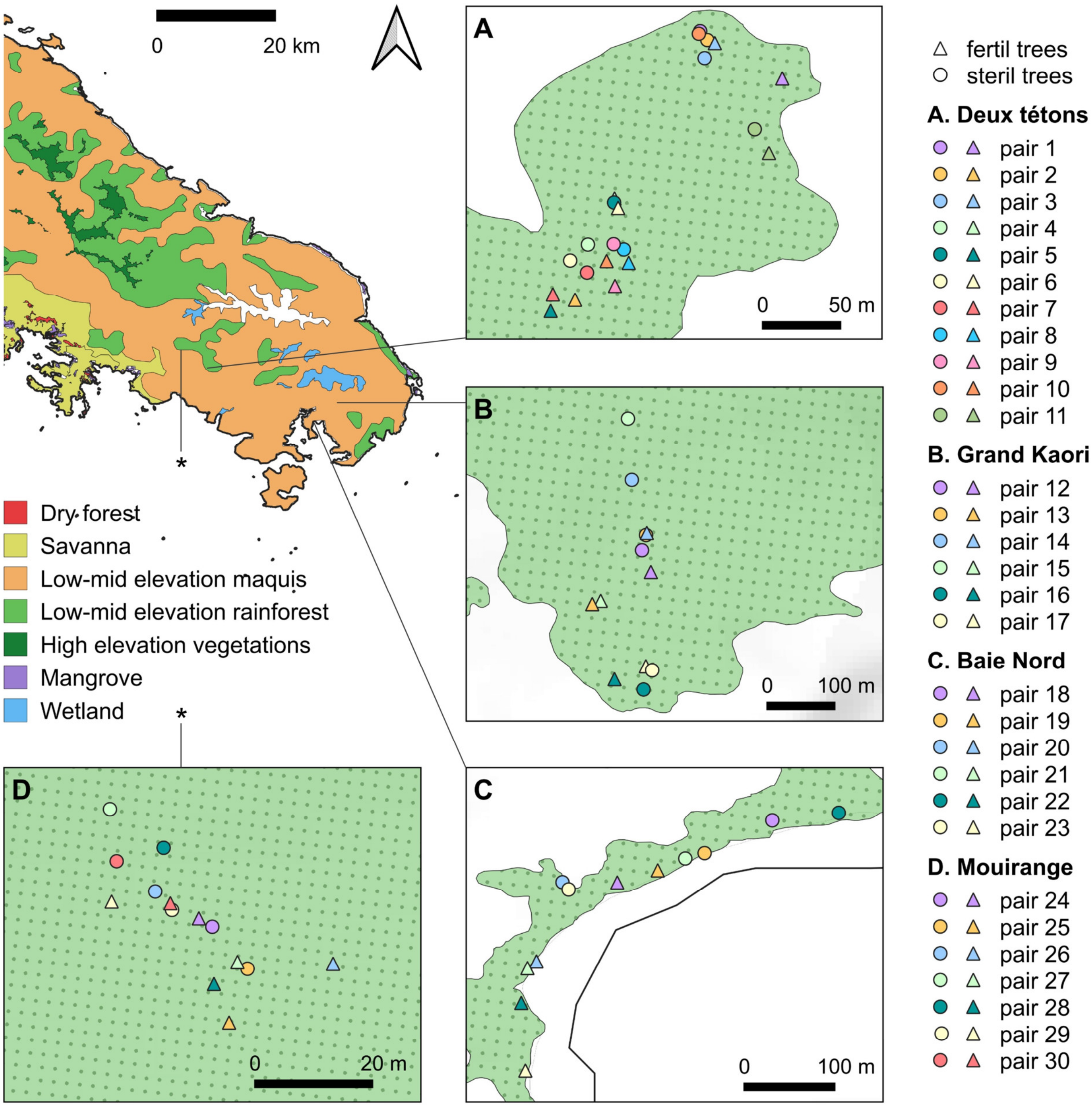
Appendix 1. Sampling protocol for further dendrochronological analyses. After the passage of the tropical cyclone Niran in March 2021, massive flowering events have occurred in several *C. candelabra* populations in the Southern region of New Caledonia's main island. 130 wood cores have been sampled in fourth of these populations, at (**A**) Col des deux Tétons, (**B**) Pic du Grand Kaori, (**C**) Baie Nord, and (**D**) Mouirange. Individuals of similar dimensions (in terms of total height, DBH, and branch tier number), respectively fertile and sterile, have been paired. 30 pairs have been formed and trees range from 6.1 to 24.5m in height and 7.3 to 48.1cm in DBH, with complete overlap between flowering and non-flowering ones. Two wood cores, from bark to pith, in orthogonal positions were collected per tree.



Flowering *C. candelabra* trees around a canopy gap opened by a dead conspecific (New Caledonia) © C. Salmon & J.M. Bore