Periodicity of tree growth and carbon storage in the Yangambi Biosphere Reserve

Auteur : Hicter, Pauline
Promoteur(s) : De Mil, Tom; 5442
Faculté : Gembloux Agro-Bio Tech (GxABT)
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Abstract

Congo Basin forests are crucial for sequestrating carbon from the atmosphere, notwithstanding that this key function is critically threatened. In the context of climate change, it is essential to better understand how and when carbon is fixed within the woody tissue. Carbon uptake by trees is typically a periodic process, even for tropical forests. This justifies studying both cambial activity as well as rhythms of leaf development over the seasons. Forests of Central Africa are subjected to a variety of rainfall and temperature regimes, with varying degrees of seasonality, impacting the floristic composition that makes up these forests. Nowadays, numerous studies on phenological rhythmicity are conducted in forests with clear seasonality, focusing mainly on deciduous species. However, leaf and cambial phenology of evergreen species from tropical climates with low seasonality, such in the Congo Basin are still little studied, preventing a good understanding of relationships between climate, tree growth and carbon sequestration processes.

Here, I propose an original approach aiming at characterizing cambial and foliar phenologies of 6 abundant evergreen or brevi-deciduous tree species during the onset of the rainy season in Yangambi forest: *Leplaeae thompsonii*, *Panda oleosa*, *Petersianthus macrocarpus*, *Scorodophloeus zenkeri*, *Synsepalum subcordatum* and *Trilepisium madagascariense*. The objective was also to analyse the relation between climatic variables and anatomical features of the cambial zone during the transitional season between dry and short rainy seasons from February to May 2022.

In order to meet these goals, the first objective was to determine the status of cambium for the tree species by using micro-coring technique and by studying its ring anatomy. The second objective was to characterise the leaf phenology of the trees monitored using binoculars and phenocam over the study period. The last objective was to link the cambial and leaf phenologies together and to relate them to the evolution of the weather parameters collected locally.

On average for the 6 species between 5 and 8 cells of 5 to 8 μm each are observed within the 11 μm wide cambial zone. Cambial activity was observed for *P. oleosa*, *P. macrocarpus*, *S. zenkeri* and *T. madagascariense* with an average of 4, 6 and 5 cells in the enlargement, thickening and in lignification phases, respectively. In addition, high variability of cambial status but also of leaf phenology exists traducing by different and asynchronous leaf and cambial phenomena between and within the different species. The phenological trends observed at the scale of the monitoring plots seem to be comparable to those of the forest. Finally, strong correlations are observed for some individuals between time exposure and rainfall with *P. oleosa* and *S. zenkeri*, and with temperatures for *T. madagascariense* and *P. macrocarpus*. But these parameters are insufficient to predict cells production.

To conclude, evidence was found that a detailed study of the cambial activity offers appealing perspectives for analysis of periodic tree growth and carbon sequestration. Obtained results are innovative in the field of research associated with cambial analysis and phenology in general, providing relevant elements about cambial status for the study period. It emphasises the importance of combining cambial, phenological and climatic parameters together.

Keywords: Cambium, Phenology, Tropical forests, Congo Basin, Yangambi, Wood biology, Carbon

Résumé

Les forêts du Bassin du Congo séquestrent du carbone présent dans l'atmosphère, pourtant elles sont soumises à de nombreuses menaces. Dans le contexte du changement climatique, il devient impératif de mieux appréhender comment et quand le carbone est fixé au sein de la matière ligneuse présente dans les arbres. L'absorption du carbone par les arbres est généralement un processus périodique, même dans les forêts tropicales. Ceci justifie l'étude de la phénologie cambiale ainsi que des rythmes de développement des feuilles au cours des saisons. Les forêts d'Afrique centrale sont soumises à une variété de régimes pluviométriques et thermiques, avec des degrés de saisonnalité variables, ayant un impact sur la composition floristique des forêts. De nos jours, de nombreuses études sur la rythmicité phénologique sont menées dans des forêts à saisonnalité marquée, se concentrant principalement sur les espèces à feuilles caduques. Cependant, la phénologie foliaire et cambiale des espèces à feuilles persistantes des climats tropicaux à faible saisonnalité, comme le Bassin du Congo, est encore peu étudiée, empêchant une bonne compréhension des relations entre climat, croissance des arbres et processus de séquestration du carbone.

Ce travail propose une approche originale pour la compréhension et la caractérisation des phénologies cambiales et foliaires de 6 espèces d'arbres sempervirents et semi-décidus abondants au sein des forêts de Yangambi : *Leplaeae thompsonii, Panda oleosa, Petersianthus macrocarpus, Scorodophloeus zenkeri, Synsepalum subcordatum* et *Trilepisium madagascariense*. Il propose également une mise en relation de différents paramètres climatiques et de l'anatomie cambiale au cours de la transition saisonnière depuis la saison sèche à la petite saison des pluies entre les mois de février et mai 2022.

Afin de répondre à ces manquements, un premier objectif consiste à déterminer le statut cambial des 6 espèces suivies en utilisant la technique du micro-carottage et en étudiant l'anatomie des cernes de croissance. Un second objectif est de caractériser la phénologie foliaire des individus suivis à l'échelle des parcelles à l'aide de jumelles et à l'échelle de la forêt avec des phenocams. Le dernier objectif est de comparer phénologie cambiale et foliaire, et de les mettre en relation avec l'évolution des variables climatiques locales.

En moyenne pour les 6 espèces, entre 5 et 8 cellules de 5 à 8 μm sont observées dans la zone cambiale de 11 μm de large. Une activité cambiale a été observée pour *P. oleosa* , *P. macrocarpus*, *S. zenkeri* et *T. madagascariense* avec une moyenne de 4, 6 et 5 cellules en phase d'élargissement, d'épaississement et de lignification, respectivement. Par ailleurs, une forte variabilité des statuts cambiaux et de la phénologie foliaire existe entre et au sein des espèces. Les tendances phénologiques à l'échelle des parcelles suivies semblent comparables à celle de la forêt. Finalement, de fortes corrélations sont observées pour certains individus entre le temps d'exposition et la pluviométrie pour *P. oleosa* et *S. zenkeri*, et avec les températures pour *T. madagascariense* et *P. macrocarpus*. Mais ces paramètres sont insuffisants pour prédire la production de cellules.

Pour conclure, il a été démontré qu'une étude détaillée de l'activité cambiale offre des perspectives intéressantes pour l'analyse de la croissance périodique des arbres et la séquestration carbone. Les résultats obtenus sont novateurs dans le domaine de la recherche associée à l'analyse cambiale et à la phénologie en général, fournissant des éléments pertinents sur l'état cambial pour la période étudiée. Ils soulignent l'importance de combiner ensemble les paramètres cambiaux, phénologiques et climatiques.

Mots clés: Cambium, Phénologie, Forêts tropicales, Bassin du Congo, Yangambi, Biologie du bois, Carbone

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List of abbreviations

AIC	Akaike information criterion
CZ	Cambial zone
DIC	Differential interference contrast
DRC	Democratic Republic of Congo
EZ	Enlargement zone
LZ	Lignification zone
MAB	Man and Biosphere
magn.	magnification
Ph	Phloem
RMAC	Royal Museum for Central Africa
TZ	Thickening zone

1 Introduction

1.1 Context

Forests cover about 31% of the earth's surface, and more specifically, tropical forests represent 45 % of the world's forest cover [1]. The forest as a whole contributes to many services of all kinds. They participate in the regulation of natural cycles such as water, air and soil quality regulation [2]. They support livelihoods for humans by providing food and materials; and shelter up to 80% of world's biodiversity [3]. In addition, tropical forests largely contribute to climate regulation by sequestering CO2 from the atmosphere [4].

However, major challenges are related to tropical forest management. Indeed, many threats, such as deforestation [5] and rising anthropogenic pressure [6], will weaken these ecosystems, altering services they provide [7]. As a result of climate change, we expect to observe increased dry periods and temperatures in the tropics, which will also alter dynamics of tropical forests [8].

In this context, it is paramount to find appropriate solutions for forest management and conservation on the long term. But first, we need to understand and characterise the processes of forest dynamics [9] and identify mechanisms that may change their functioning and productivity. One process of forest' dynamic is the vegetation growth which depends, in other parts, on its ability to sequester carbon in woody material. Carbon fixation into vegetation occurs during wood and bark formation through the photosynthesis process [10]. During wood formation or xylogenesis, carbon is fixed into woody materials within the newly cell walls generated by the cambium [11]. On the other hand, carbon is also used for production of leaves, flowers and fruits [12]. Thus, these processes are key elements on the understanding of carbon sequestration and forest dynamics [13].

Furthermore, as cambial and foliar phenology adopt an annual or multiannual rhythmicity over seasons [14, 15, 16], it is relevant to study these processes over time. In fact, monitoring cambial activity and phenological rhythmicity is relevant to understand carbon storage process, characterise periods when trees are forming xylem during the season and to identify factors that control it [17, 18, 19, 20]. Furthermore, foliar phenology is a good proxy for monitoring the response of vegetation to local conditions [21]. However, both endogenous and exogenous factors have been shown to influence cambial and phenological activities affecting tree growth [22, 23, 24]. For instance, the extent and the growth vegetation period are affected by climate factors [20, 25]. Likewise, relative humidity plays a role in the phenomenon of seasonal variation in trunk circumference [26]. Conversely, wood formation can be strongly influenced by tree phenology [27]. Hence the importance of characterising the wood formation process and comparing the two approaches. Unfortunately, little precision exists to explain the possible relationships between phenology and cambial activity in tropical trees [28]. This obliges us to study them precisely on a species-by-species or even tree-by-tree basis and try to identify factors that can affect the phenological rhythms.

The forests of the Congo Basin constitute the second largest forest in the world within 126 million hectares of forest are located in the Democratic Republic of Congo (DRC) [1]. Even if the Congo Basin forests shelter a large part of the world's biodiversity and millions of people depend directly or indirectly of them [29, 30], they do not escape the current threats. More specifically, these forests provide both ecological, economic and social services [30]. This is the case for Man and Biosphere Reserves (MAB) present in the DRC and more precisely in Yangambi [31]. Furthermore, we assume that 25% of the 247 Gt carbon sequestered in the world's forests is stored in sub-Saharan Africa. [32]. Paradoxically, forest of Africa present the largest net area loss and present the most important rate of deforestation in the world [1] with DRC being the second country with the highest annual loss of forest area. African forest management issues are thus global challenges to which solutions are to be found.

Unfortunately, major obstacles prevent on easily understand dynamics and working of tropical forests and more specifically forest of the Congo Basin. Even though, numerous studies have been progressively carried out in recent years, they mainly focus on South and Central America or Asian rainforests ecosystems [33]. Furthermore, the lack of information on local climate and environmental data for the tropical environments is observed. This hinders a proper assessment of the response of vegetation to climate evolution [21]. On the other hand, tropical environments are more complex to study than temperate ones due to their species diversity, structure and forest composition [34].

The forests of the DRC are a good example of this complexity. In particular, numerous studies have contributed to the understanding of vegetation growth and dynamics in the Mayombe forest. Researches address data about inter-annual wood formation [35], links between foliar phenology and climate influence [15], cambial growth seasonality in Africa [36] or about the relation between cambial activity and foliar phenology [37]. Unlike other sites in DRC, the phenology, community dynamics and growth remain unknown for Yangambi and Thsopo province in general. Nevertheless, the forest formation and the particular species composition of this forest, is intimacy related to particular ecological, edaphic and climate conditions. In semi-deciduous forests of Yangambi forests, both species are found with a distinct deciduous, semi-deciduous and evergreen temperament [38]. Yangambi presents a low seasonality, thus inter-species variation in leaf phenology, and hypothetically variation in cambial activity during the seasonal transition, can therefore be expected [39]. But this requires a thorough study of the ecology and local climate of these forests.

Even though researches on dendrochronology and ecology have been carried out in the context of Yangambi, they are only focusing on particular species such as *Pericopsis elata* (Harms) Meuwen. This species has been the subject of numerous studies, notably about the relationship between cambial activity and individual tree growth [40], but also on its ecology in the local context [41]. Other studies on the subject have focused on the impact of rainfall on growth of trees [40]. However, studies about the cambial activity, wood anatomy, the influence of seasonality on vegetation growth, ecology and phenology remain rare for a lot of abundant species from the forest in the wider Yangambi region.

1.2 Wood formation and cambial dynamics

1.2.1 Structure and wood formation

a. Wood structure and wood anatomy

Structure and composition of the phloem and the xylem of Angiosperms are complex, forming heterogenous tissues [10]. It consists of a multitude of cells with different functions, shapes and chemical compositions. In tropical woods, 3 main types of cells can be found. (i) Fibres which have a supporting role thanks to their cell wall, whose thickness and composition vary according to the stage of development. The immature fibres are surrounded by a thin non-lignified wall. During maturation, this wall is thickened and lignified until a mature fibre is observed. (ii) Parenchyma cells are composed by a single wall, mostly lignified, which fulfil several roles such as transport, water or starch storage and mechanical functions. They can be radially or axially oriented and adopt a complex network form along the xylem. For many tropical species, paratracheal axial parenchyma can be observed [42]. In tropical species, marginal parenchyma bands can delineate tree growth rings [43]. They largely participate in water and carbohydrate derivatives storage [44]. (iii) Vessel's elements form a more or less dense network which plays a role in the transport of water. The specialisation into these 3 cell types takes place during xylogenesis, a process that allows the transition from an immature cell to a mature cell that, as a result of physical and chemical changes, can fulfil its function [45]. Consequently, characterisation of the stage of cell development of wood or phloem can be distinguished both by anatomical and chemical differences.

b. Xylogenesis and cambium

Wood formation or xylogenesis results from the activity and the differentiation of a layer of undifferentiated meristematic cells called cambium that will mainly specialized into fibres, parenchyma or vessels

[46]. Periclinal division and longitudinal division of these cells occur which increase the diameter and the height of stems, respectively. The cambial zone is composed of three cell types: the cambial layer, the phloem and xylem mother cells being produced by cambium [47]. The cells of the cambial zone divide themselves by producing both secondary xylem and phloem (Figure 1.1).

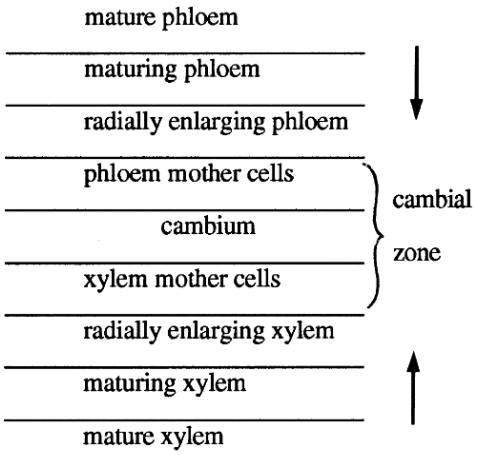


Figure 1.1: Cambium and secondary tissues production. Taken from: Lachaud (1999) [47]

The mother cells are composed by two types of cells. The initial fusiform cells are often narrow, elongated for a diameter between 5 and 8 μm with a thin wall (<0,1 μm). The short radial ones measure until 40μm [47]. They respectively create conducting cells, such as phloem and xylem, and create ray parenchyma. Most of the time, the shape and size of cells are good characteristics to identify the cambial zone. Thus, it enables scientists to observe them in cross-sections thanks to microscopy tools.

In the secondary xylem, wood formation can be resumed in four successive stages (Figure 1.2). The first stage is the production of new cells from the undifferentiated cells of the cambial zone. The second stage is the enlargement phase in which cells start to grow in a radial section. The third stage is the thickening of the cell wall, including the creation of a secondary wall for fibre cells. The fourth stage is lignification, which results from a chemical change in the composition of the cell wall through the deposition of lignin [48]. Wall thickening and the lignification are determinant for carbon sequestration by vegetation [48, 46]. An added phase is the programmed cell death [49].

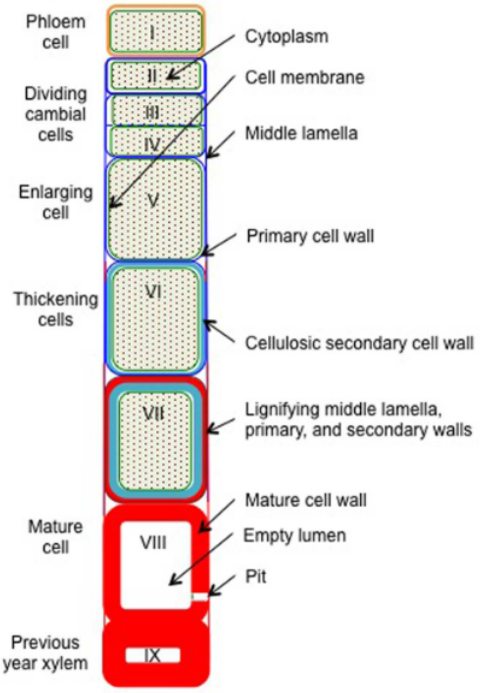


Figure 1.2: Scheme of developing radial file for tracheid cell. I Phloem cell, II-IV Dividing cambial cell, V Enlarging cell, VI-VII Thickening cells and VIII Mature cell. Taken from: Rathgeber et al. (2016)[10]

1.2.2 Control and rhytmicity of cambial activity

Cell formation is intimately linked to the rhythmicity of cambial activity. It is important to notice that many factors can affect the dynamics of cambial layers, such as environmental or genetic factors.

In temperate forests, cambial activity is mainly affected by seasonality [19, 50]. Although, seasonality is less marked than in temperate environment, climate parameters still affect both cambial and leaf phenology in tropical rainforests. Therefore, there is a variable periodicity of tree growth during the year [28]. Moreover, at a macroscopic point of view, the appearance of rings in the wood results from alternating cambial activity which itself is regulated by endogenous or exogenous factors [51]. These factors create favourable or unfavourable conditions for tree growth. Furthermore, growth can also vary from a year to year, implying indistinctness of annual tree-ring boundaries within species [52, 53]. Consequently, there is still significant variability in the interpretation of tree rings boundaries [53].

At the microscopic level, the number of cells produced at each stage and present in cambial zone, as well as their shape and the ratio between the different parts, vary between species, depending on environmental conditions or genetic variability between individuals [54, 37]. However, some characteristics allow to determine the dormancy or the activity of cambium that will be described here below.

Climate-growth relation

The relationship between climate and leaf and cambial phenology has been the subject of much researches. However, these studies are mostly concerned with semi-deciduous or deciduous species, especially in contrasting climates. Many studies have highlighted the importance of rainfall on cambial growth, with cambial dormancy often initiated by a period of drought [55, 56]. Temperature can also alter the rythmicity of cambium, it is particularly true under temperate climate [57]. Other parameters can also influence cycle of growth such as relative humidity, insolation index or day length [58]. In contrast, growth patterns and phenologies are much less well known for evergreen tropical species, especially in climates with little seasonality. As Pandey said, combining anatomical study

and environmental changes provide physiological explanations for the adaptation process and response strategies of tree growth to climate [59].

1.2.3 Studying xylogenesis and cambial activity

This strong dependence of cambial activity, and thus of wood formation, on climate conditions, underlines the importance of conducting a study over multiple intervals during the season. Studying periodicity of tree growth can be addressed in different approaches that do not provide the same level of accuracy depending on the information sought [60]. Furthermore, wood formation can be approached from inter-annual or intra-annual perspectives. Their common interest is to characterise the periods of vegetation growth, and to relate them to the evolution of climate, edaphic or ecological parameters.

The study of tree rings on an annual scale is sometimes insufficient to understand the rhythmicity of tree growth. However, dendrochronology focuses on the evolution and rhythmicity of wood formation and cambial activity on a period ranging from several years to the entire life of a tree. This approach can be used either by collecting of whole wood cores [61] or by collecting of disks [62, 63]. In tropical regions this is not evident due to several ring anomalies [35]. A new approach combining photogrammetry, high resolution image processing, and GIS tools are now also used in dendrochronological studies [64].

Moreover, other non-destructive techniques focus on stem growth in diameter. This is the case of band and electric radius dendrometers, which are chosen to collect data on diameter variation over several months or years [65, 66]. The second is more suitable in the case of the study at an intra-annual level.

To study of the cambial zone, it is sometimes necessary to reduce the study period during the growing season if known. This intra-annual perspective is well adapted to trace the cambial activity by measuring the radial increment. It often requires microscopic in-depth studies. Depending on the approach chosen, data are either relative or punctual. In the first case, the cambium has to be marked or injured. For instance, pinning is a technique based on assessing the reaction of cambium to an external impact [67]. In the second case, the measurements provide the state of the cambium in real time. In contrast to the other methods, punctual observations are not delayed results. Consequently, measurements must be repeated over several months to consider the evolution of cambial activity. Formerly, a technique involved rectangular samples of wood and bark together “Mariaux windows”, but this work was laborious and invasive for the stem [63]. Nowadays, the most suitable way to quantify and characterise cambial activity is the micro-coring method.

Micro-coring process

During micro-coring, small samples of 2 mm diameter are taken at regular intervals in the cambial zone using a Trephor (Figure 1.3)[18]. The micro-cores are preserved in an alcohol solution before being dehydrated to obtain histological sections. This sampling method is easy and less invasive [17] compared to pinning and Mariaux windows. The samples must be well oriented to the transversal plane, in order to observe the elements of the cell structure.

Figure 1.3: Micro-coring process. From the left to the right: (I) insertion of trephor with a hammer (ii) inserted micro-core ready for extraction (iii) extracting the micro-core from the trephor device (iv) trephor with micro-core showing the xylem (white tissue) and bark (darker tissue) from a *Panda oleosa* tree.

Micro-sections

After micro-coring, samples are processed into micro-sections thanks to microtomy techniques. Thin sections allow an assessment of the cambial activity through microscopic analysis of the wood formation by observing them under light of microscope. Especially the width of the zone showing cell differentiation, between the cambium and the fully lignified mature wood, is considered as an indication of cambial activity in broadleaf species.

1.3 Research questions

Following research questions were tackled:

- What is the wood anatomy of the species at the ring transition? And what is the anatomy of the cambial zone of each species over the study period?
- Can dormancy or cambium activity be observed during the study period? If so, when does it begin?
- Is there a synchronicity between cambial activity and leaf development for deciduous species?
- Is there a synchronicity between cambial activity and flowering or fructification?
- Is the trend of phenological process at the level of study plots follow the same trend than at the level of the entire stand?
- How cambial activity is related to exogenous factors (Temperature, rainfall, brightness, relative humidity)? In which range and when are they affect this activity?
- How foliar phenology processes are they affected by exogenous factors (Temperature, rainfall, brightness and relative humidity)?
- How can cambial activity, phenology processes and exogenous factors be related?

1.4 Objectives

The first objective is to describe wood anatomy of growth ring transition and of cambial zone at the study time for species. A first sub-objective is to characterise the ring transition from samples from RMCA. A second sub-objective is to identify cambial dormancy or activity for species of interest by using micro-coring processing. After identifying species for which micro-coring can be conducted, characterisation of cambium can be carried out by a microscopic approach. Then, if possible, Then, if possible, a quantitative assessment of the cambial zone is carried out. The second objective is to characterise foliar phenology of monitored stems at two scales. One at individual scale, thanks to visual assessment with binoculars. One at stand scale, through the use up of two autonomous

Wingscape timelapse cameras. Then results about cambial and leaf phenology can be related along a time axis. The third objective is to characterise the evolution of climate parameters within the seasonal transition by identifying major factors that may influence both foliar phenology and cambial processes.

1.5 Contributions and outline

The novelty of this work is the exploration of the cambial and foliar phenologies in relation to climate for brevi-deciduous and evergreen species of tropical forest under a climate with low seasonality. This aims at describing wood biology for tree species thanks to micro-coring process. This master thesis participates in the comprehension of cambium status and foliar phenology of 6 tree species over the seasonal transition between the dry season and the small rainy one. It tends to fill the blank left in literature about cambial activity for these species from tropical humid forest of Central Africa. Personal involvements in this work are the collection and processing of micro-cores at Yangambi, the collection of phenological data and their post-processing and microscopic analysis at the RMCA, followed by writing this work.

This present work is divided in 4 parts. The first part deals with the materials and methods used in the collection and processing of data. The second part presents synthetically results obtained from the different data sets. The third part is devoted to the discussion and comparison of the result. The last part proposes several ways to continue the study.

2 Material and methods

2.1 Study site

Data were collected into the Yangambi Biosphere Reserve (0°46'N -24°29'E) which is located in the Tshopo province in the north-east of the Democratic Republic of Congo (Figure 2.1A). The climate is Af equatorial [68], characterised by two dry seasons and two rainy seasons. Precipitation is well distributed over the year. Consequently, dry seasons aren't really marked (Figure 2.1C). However, minima of pluviometry occur just after the two solstices [69]. Annual rainfall reaches 1800mm and the average annual temperature is 24,9°C (Figure 2.1C).

This reserve covers 235 000 ha of forest around the locality of Yangambi, which has been included in UNESCO's Man and the Biosphere (MAB) program since 1976 (Figure 2.1A). It is home to various endangered animals such as *Loxodanta africana cyclotis*, etc hence the importance of its preservation. Moreover, there are different woody botanical families of which the most abundant are the Fabaceae, Euphorbiaceae, Aracaceae et Malvaceae [38]. The Yangambi forest can be characterised as a semi-evergreen forest both species are found with a distinct deciduous, semi-deciduous and evergreen temperament [38]. Indeed, a diversity of forest patches is found, with old growth forests reverting to *Gilbertiodendron dewevrei* mono-dominant evergreen forests and semi-deciduous mixed forets. But there are also deforested areas with varying gradients of reforestation [70].

This study focuses on two permanent sample plots MIX 3 and MIX4 from the COBIMFO project [71])[1] (Figure 2.1B). These two plots of 1ha each are us as permanent devices since 2010 for monitoring plant biology. Their stands are mature mixed forests with abundance of *Scorodophloeus zenkeri*. In 2020, the average diameter at body height (DBH>20cm), of the 11 species present within the plots, ranged 32,4cm, the basal area was of 20,28 m^2/ha for 208 trees and 17,48 m^2/ha for 147 trees in MIX3 and MIX4, respectively. A sample collection campaign was carried out there. In addition, *Wingscape* timelaps cameras have been installed on the fluxtower from the CONGOFLUX project[2] located into the Yangambi forest.

[1]COBIMFO project (Congo Basin integrated monitoring for forest carbon mitigation and biodiversity; contract no. SD/AR/01A) and funded by the Belgian Science Policy Office (Belspo).

[2]https://www.ugent.be/bw/gct/en/research/isofys/projects/yps-congoflux

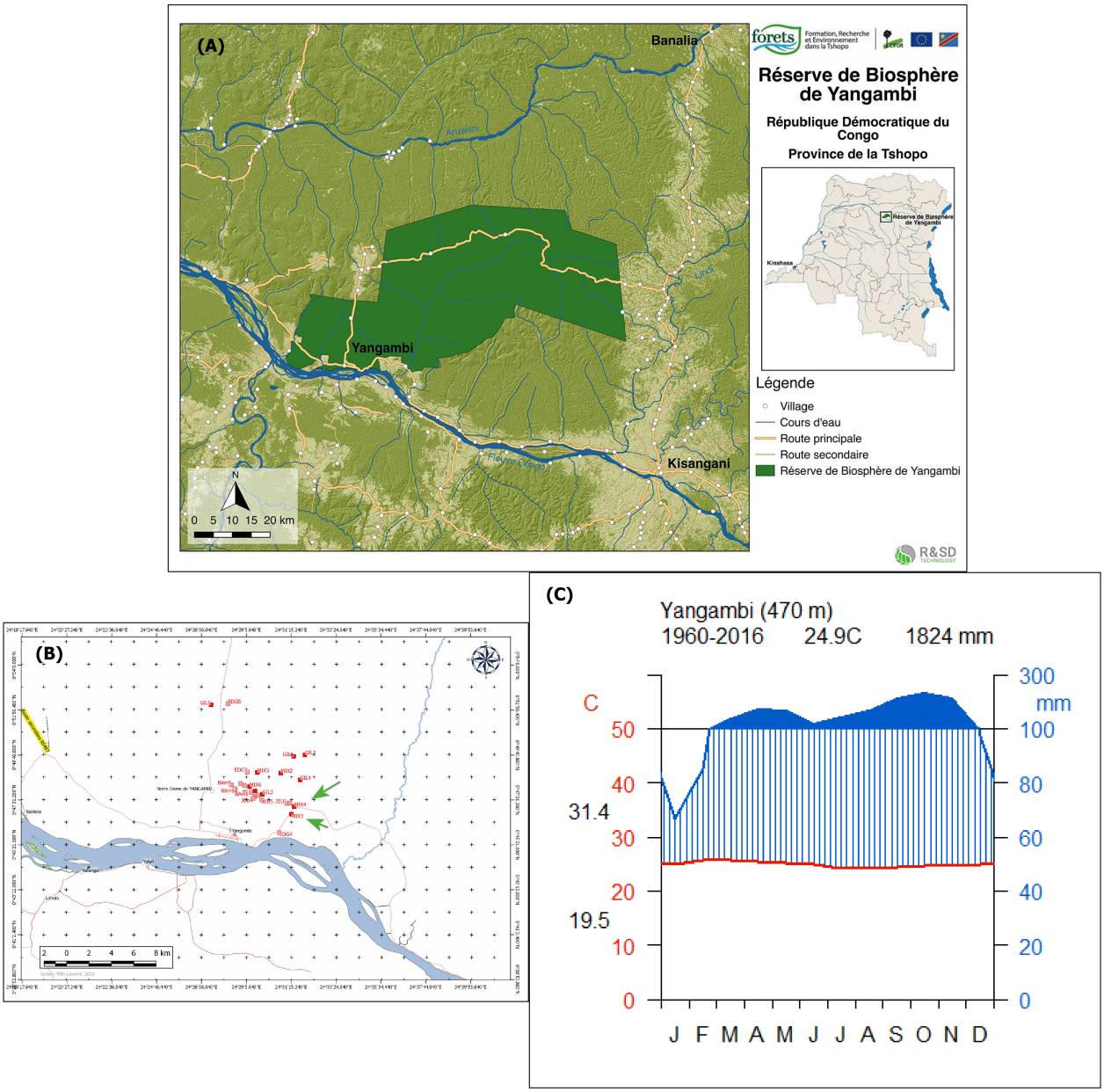


Figure 2.1: (A) Location of Man and Biosphere (MAB) of Yangambi. Source: Cifor (2022). (B) Location of plots Mix3 and Mix4 in Yangambi site (green arrows). (C) Walter and Lieth Diagram of Yangambi over from 1960 to 2016. The red line represents the mean monthly temperature, the blue line represents the mean monthly precipitations. The humid period is represented by vertical hatching. The very wet periods are represented by solid blue area. In this case, the scale is increased from 2mm/<ba>C to 20mm/<ba>C. Source: Table based on data from INERA Yangambi's Agroclimatology Department (2017).

2.2 Studied species

The selection of species was based on a list previously established on the two monitored mature forest plots MIX3 and MIX4 (Figure 2.1B). They are among the 70% most abundant species, in terms of average basal area and number of stems, in these plots. Further information such as diameter at body height (DBH), species, height, position are known for the year 2020.

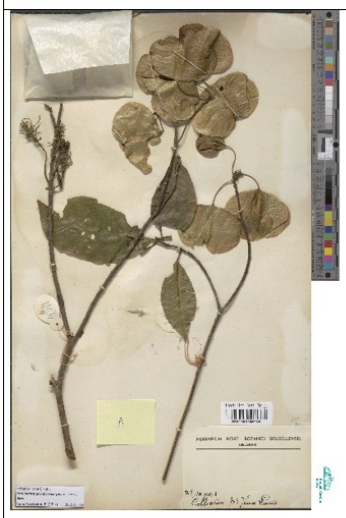
The selection of both individuals and species for micro-coring was performed on the basis on a field prospection, and the health of the stems encountered. Initially, a total of 8 species were selected, for each of which 3 average individuals were monitored (Table 2.1). After the first collection of micro-cores on 05 March, *Trilepisium madagascariense* and *Synsepalum subcordatum* were added. The selection of individuals was based on the average DBH of the species, the health status of the individuals and

the conformation of stems (straightness, cylindricity of the stem and ease of taking entire micro-cores). Furthermore, the selected individuals are contained within the same diameter class, close to the average DBH referenced in the list.

Table 2.1: Description of selected species

Leplaeae thompsonii EJ.M. Koenen & J.J. de Wilde	
(1)  	**Vernacular appellation** [3] **:** Bossé foncé, Guarea noir (Trade) **Family:** Meliaceae **Temperament:** Evergreen **Light demanding** [6]**:** sciaphilous when young and needs light when growing **Habitat and ecology** [7]**:** lowland evergreen rainforests, usually primary forests. **Phenology** [5]**:** Fruits: Jul. Flowers: NA Leaf senescence: NA
Panda oleosa Pierre	
(1)  (2) 	**Vernacular appellation** [3]**:** Afan(e) (Gabon), Afam (Cameroun), Bokale (DRC), Mahula (Kisangani, DRC) **Family:** Pandaceae **Temperament:** Evergreen **Light demanding** [2]**:** shade tolerant **Habitat and ecology** [2]**:** semi-deciduous and evergreen forests **Phenology** [5]**:** Fruits: May to Feb. Flowers: Feb. to May Leaf senescence: June, Oct.

Petersianthus macrocarpus Liben



(1)

(2)

Vernacular appellation [3]**:** Essia, Abale (Ivory Coast), Oso (DRC),
Family: Lecythidaceae

Temperament: Deciduous
Light demanding [2]**:** semi-heliophilic
Habitat and ecology [2]**:** semi-deciduous and evergreen forests

Phenology [5]**:**
Fruits: June to Oct.
Flowers: Feb. to Apr., May to June
Leaf senescence: Feb.

Scorodophloeus zenkeri Harms

(1)

(2)

Vernacular appellation [3]**:** Divida (tradename), Esum-ngang (Gabon)
Family: Fabaceae-Caesalpinoideae
Temperament: Evergreen
Light demanding [7]**:** sciaphilous when young and needs light when growing
Habitat and ecology [2]**:** semi-deciduous and evergreen forests

Phenology [5]**:**
Fruits: Ma. to Apr.
Flowers: Feb. to Ma., Apr., Aug. to Dec.
Leaf senescence: Feb.

Synsepalum subcordatum De Wild

(1)

Vernacular appellation [3]**:** Yombolo, Bonge (DRC), Wisangila (DRC)

Family: Sapotaceae
Temperament: Evergreen
Light demanding [6]**:** sciaphile but can tolerate light exposure (often dominated)

Phenology [5]**:**
Fruits: Apr., May to Jul.
Flowers: Feb., March., Apr.
Leaf senescence: Oct.

Trilepisium madagascariense Thouars ex DC.

(1)

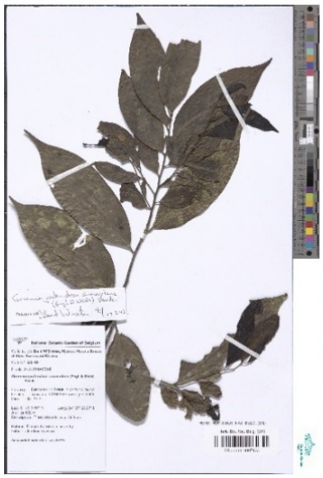
Vernacular appellation [3]: Bonge (RDC), Bonke (RDC), Bofonge (DRC), Béhio (Gabon), Fongi (Cameroon) [2]
Family: Moraceae

Temperament: Deciduous
Habitat and ecology [8]: primary or secondary forests in regions with evergreen or semi-deciduous forests; moist forest

Phenology [5]:
Fruits: March to May, Sep. to Dec.
Flowers: June, Jul., Sept. to Nov., Feb., March
Leaf senescence: Feb.

Greenwayodendron suaveolens Engl. & Diels

(1)



(4)

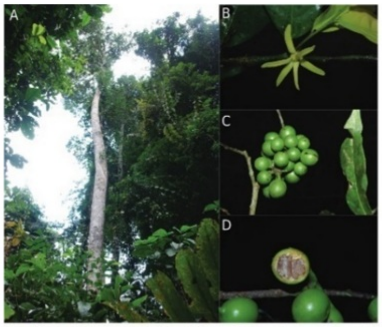


Figure 10. *Greenwayodendron suaveolens*. **A** Habit **B** Flower **C** Fruits and monocarps **D** Latitudinal section of one monocarp showing ruminate endosperm of seeds. Photos: TLP Couvreur.

Vernacular appellation [3]: Otunga (Gabon), Otungui (Cameroon), Moamba ndombe (Luki, DRC), Dolindu (Kisangani, DRC)
Family: Annonaceae

Temperament: mostly evergreen
Habitat and ecology [4]: Moist evergreen and semi-deciduous lowland and mid-altitude 30–1600 m in forests.

Phenology [5]:
Fruits: Dec. to Ju., Jul to Aug
Flowers: Feb. to Apr.
Leaf senescence: Oct.

Chrysophyllum lacourtianum De Wild

(1)

(2)

Vernacular appellation [2]: Longhi rouge
Family: Sapotaceae

Temperament [2]: Deciduous
Light demanding [2]: shade tolerant
Habitat and ecology [2]: semi-deciduous and evergreen forests

Phenology [5]:
Fruits: Feb. to Aug.
Flowers: Oct. to Dec., Jan. to Feb.
Leaf senescence: June to Aug., Jan. to Feb.

References: (1) (“Botanical Collections,” August-3-2022) (2) Les arbres utiles du Gabon (Meunier et al., 2015) (3) (“Tervuren Xylarium Wood Database | Musée royal de l’Afrique centrale - Tervuren - Belgique,” June-3-2022) (4) (Lissambou et al., 2018) (5) < junglerhythms.org > (6) (GILBERT, 1952) (7) (“PROTA4U,” June-22-2022) (8) (“African Plant Database”, June-18-2022)

Various information on each monitored individual are collected such as species, DBH, bark thickness, and geographical coordinates. In order to assess the vegetation competition of the monitored individuals, the Crown Illumination Index (CII) developed by Dawkins and Field [72] was also visually assessed (Appendice 6.1).

2.3 Processing of micro-cores

The various stages of micro-core preparation are designed to produce microsections useful for characterising the cambial zone. This preparation starts with the collection of samples and ends with histological sections that can be observed under the light microscope.

2.3.1 Sampling strategy

Samples collection was carried out in 4 times, covering the seasonal transition between the dry season and the small rainy season (from February to April 2022). Data were collected at 2-week intervals on 5 March (A), 18 March (B), 1 April (C) and 15 April (D) respectively. An additional collection was carried out the 29 April. A Trephor was used with a hammer to collect the micro-cores [17, 18] (Figure 2.3). These samples were stored in Eppendorf tubs filled with 50-% ethanol. Each tube was coded with date, species, sample number and individual.

Micro-cores collection started at 2 meters from the ground. 3 samples per individual were collected vertically and spaced 10cm apart to avoid wounding effects from previous sampling. The whole collection followed a spiral pattern, oriented northwards and then clockwise (Figure 2.2). Bark was removed for species with at least 1 cm of thickness.

Figure 2.2: Spiral scheme of micro-cores collection with from the first to the fourth collection (red arrow heads)

2.3.2 Conservation and transformation of micro-cores

Firstly, 2 samples per individual were preserved in Formalin Aceto-Alcohol (FAA) solution for 4 days, the third sample was kept in a 50% ethanol solution. After observing the first results obtained, any difference was noticed between the samples stored in FAA and ethanol. It was therefore decided to giving up the immersion of the micro-cores in the FAA solution whose handling is harmful to health.

The entire sampling process has been realised in Yangambi woodbiology lab. After, conducting the first analysis on the histological sections, the quality of obtained results was not always sufficient to conclude of the activity of the cambium. Different reasons can explain this situation. The most likely reason is the use of undistilled water during the successive bath process (Table 2.2). Therefore, it was

decided to reiterate the process of micro-cores in Tervuren woodbiology lab on the control samples. Then, part of the bark and wood were removed to only conserve the cambial area whose cross-section is marked by a line (Figures 2.3A and B). Finally, samples are placed into microcassettes which were successively immersed in different dehydration baths (Table 2.2) and two baths of paraffin at 60°C (Table 2.2)(Figure 2.3C). The passage through the baths was done manually and with the automatic STP 120 Spin Tissue processor, in Yangambi and Tervuren, respectively. Paraffin blocks are shaped into micro-cores oriented on the cross-section (Figure 2.3D).

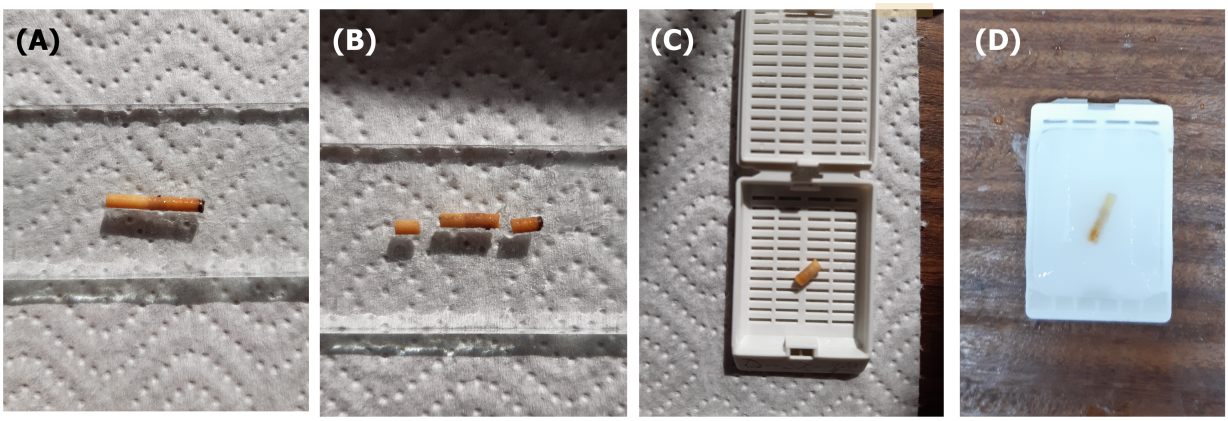


Figure 2.3: Preparation steps of micro-cores. (A) Entire sample as taken from the tree (B) Cutting of zone of interest (e.i. cambial zone) (C) Microcasette (D) Embedded sample in paraffin block.

Table 2.2: Dehydration stages and paraffin infiltration steps adapted from (Prislan et al., 2014)[73]

Dehydratation steps	
Solution	**Immersion lasting (hours)**
Ethanol (50-%)	2
Ethanol (75-%)	2
Ethanol (96-%)	2
Ethanol (100-%)	A night

Paraffin infiltration steps		
Solution in Yangambi lab	**Solution in Tervuren lab**	**Immersion lasting (hours)**
UltraClear	Histoclear	1,30
UltraClear	Histoclear	1,30
Paraffine 1 (60°C)	Paraffine 1 (60°C)	1,30
Paraffine 2 (60°C)	Paraffine 2 (60°C)	1,30

2.3.3 Preparation of anatomical sections

When the paraffin is cured, the sections of 10 to 14μm thick can be cut with the Leica RM 2235 rotary microtome. Due to the fragility of samples, several sections were obtained by affixing sticky paper to the core. This method was only used at Yangambi lab. These resulting sections were glued to a glass surface with heated albumin. Then slides were heated few minutes in order to ensure the adhesion between the different components.

The whole process includes cleaning the paraffine with UltraClear or HistoClear solution, dehydration with ethanol solutions at different concentrations and a staining phase. A mixture of Alcian Blue and Safranin was used, which bind to cellulose and lignin, respectively. Finally, the samples are fixed between slides and coverslips with Euparal (Table 2.3).

Table 2.3: Clearing, coloration and dehydration steps at Yangambi and Tervuren labs adapted from (Prislan et al., 2014)[73]

Solution in Yangambi lab	**Solution in Tervuren lab**	**Immersion lasting (minutes)**
UltraClear	Histoclear	6
UltraClear	Histoclear	6
UltraClear	Histoclear	6
Ethanol 100-%	Ethanol 100-%	3
Mix Blue alcian and Safranine	Mix Blue alcian and Safranine	3
Water	Distilled water	Few seconds
Ethanol 50-%	Ethanol 50-%	3
Ethanol 70-%	Ethanol 70-%	3
Ethanol 96-%	Ethanol 96-%	3
Ethanol 100-%	Ethanol 100-%	3

2.3.4 Cambial analysis

A combination of different microscopic tools provides complementary information about microsections. Firstly, microsections have been observed under BX60 transmission light microscope. Although staining of microsections is useful to detect lignification of cells or other elements, sometimes it is not well performed, making observations much more complicated to make. In this case, a BX60 epifluorescence microscope used in combination with a mercury lamp and filter (Olympus U-UCV, a barrier filter 420nm and a dichromatic mirror 400 nm) is the best tool to detect the autofluorescence of lignin present in the mature wood or bark tissues, by increasing the contrast between unlignified and lignified cells. It is also useful for detecting starch deposits, or other residues or crystals. Whereas with epifluorescence it is sometimes difficult to assess wall lignification, especially when the walls are thick but not lignified, differential interference contrast microscopy (DIC) U-DICT filter add on transmission microscope can be used in order to highlight tissues in lignification. In summary, epifluorescence is relevant when the cambium is dormant, whereas the DIC filter allows better characterisation of the evolution of developing cells.

Images of microsections have been taken by connecting a camera (Olympus UC30, U-TV0.5XC-3) to microscope. These data have been collected using to Toupiew® and CellBe® softwares. Different magnifications, from 4x to 40x, are used covering different levels of accuracy. Histological characterisation could be made thanks to ImageJ ® software.

Firstly, the identification of the cambial zone, the wood zone, and the bark zone are performed at a finer magnification, achieving both by the staining, the size and shape of cells. When cambial activity is detected, enlargement zone, thickening zone, and the lignification zone are sometimes observable thanks to epifluorescence and DIC filter. Secondly, description of wood anatomy has been performed at higher resolution. Finally, for each microsection, the number of cells par radius, the size of cells and the width of the successive cambial zones (bark, cambial zone, enlargement zone, wall cell thickening, lignification zone and maturity zone) are mesured at least for 3 radii [17]. By repeating this protocol over several collections, it is possible to assess and quantify the evolution of cambial activity (Figure 2.4). All measurements were made manually with the ImageJ software. The average measurements made per radius were calculated, and then compiled by date, per individual and per species. These data were analysed in Rstudio 4.0.3 version software in order to conduct statistical tests. Anova and student test or Wilcoxon test (according to the condition of appliance) have been processed to assess the difference of means, either for number and size of cells, or for width of zone of interest between the collections for each individual and for each species. These tests and statistical tests such means and standard-deviation calculation for the different variables (average number cells, average size cells or average width of zone of interest) have been computed thanks to “gridExtra”, “stats”, “dplyr”, “rstatix” packages on Rstudio.

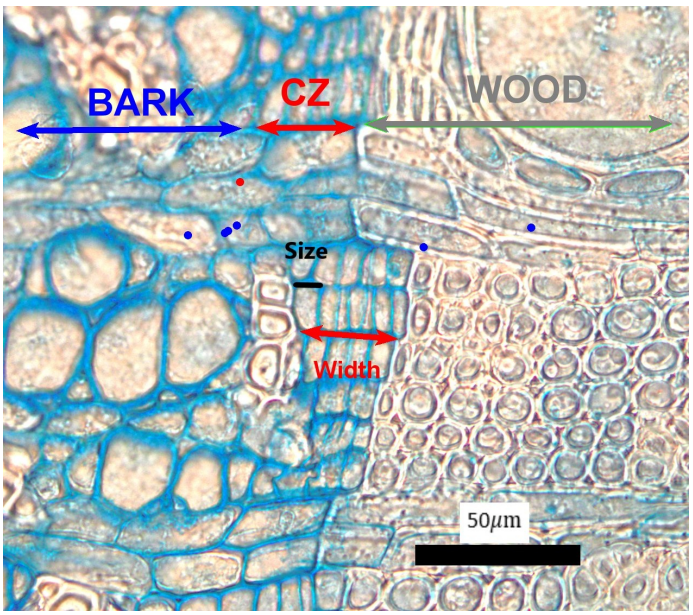


Figure 2.4: On cross-section, cambial zone is located between bark and wood. Measurement of width zone of interest is made along a radial axis (double red arrow). The number of cells in this area is counted, and each cell is measured along the axis (black line).

2.4 Growth rings analysis

As the micro-cores were too short to assess the anatomy of the growth ring boundary (from previous rings), it was decided to study a larger sample to characterise this transition zone. This approach focuses on the macroscopic study of the rings transition anatomy. However, it is not sufficient to clearly assess the stage of development of the current growth ring. Microsections were therefore analysed. In fact, these analyses serve of reference to assess the progression of xylem growth according to its anatomical characteristics and to give us a clear idea how the ring structure is built for the given species. To achieve this goal, samples such as tree cores, disks or wood sanded blocks, issued from the wood collection of the RMCA have been considered. Images have been taken thanks an Olympus SZH10 stereomicroscope in association with an Olympus UC30 camera at different levels of magnification. These images have been studied within ImageJ software.

2.5 Phenological data

A monthly visual assessment of phenological traits was carried out at the level of the individuals monitored with binoculars. Firstly, a classification of foliar phenology such as old, new and young leaves was assessed. Secondly, the flowers present were monitored and differentiated according to their developmental status as young or old flowers. Finally, the fruits are classified into 2 categories: mature and immature. These visual assessments are given as a percentage, the total sum of all the elements being 100%. observations have all been realised by the same person at each data collection.

Data of the upper canopy were acquired daily with 2 autonomous phenocam Wingscape timelapse cameras every hour from 5:00 am to 4:00 pm from 18 March to 12 May 2022. This installation allows the characterisation of the phenophase and the identification of the phenological transition period of the canopy such as flowering, fructification, leaf development [74]. They were mounted on the Congoflux, facing northwest and southeast respectively. Only one camera provided images. 4 crowns were monitored at one month interval to characterise the evolution of the leaf composition.

2.6 Climate data

Meteorological parameters such as data on temperature, relative humidity, precipitation and insolation duration, have been registered from 1th February to the 20th May 2022, over a period of 120 days, at

the Km 5 climatological station of INERA Yangambi.

On the one hand, monthly averages were made to represent the main climate trends during the seasonal transition, from February to May. On the other hand, the mean values of the monitored climate variable based on two-weeks intervals before each date of sample collection have been computed on Rstudio. In order to summarize climate data and because these climate parameters are highly related, a principal component analysis (PCA) has been processed in R environment thanks to "corrplot", "FactoMineR", "factoextra" packages. This approach allows to identify a first principal axis that explained 52,32% of the variability observed over the study period. Indeed, several parameters, such as the sum of precipitation, mean precipitation and insolation lasting for the 5 considered intervals, present a significant correlation to this first axis. This axis separates hot and sunny days from colder days with cloudiness (Appendice 6.2).

2.7 Analysis of relationships between cambial phenology and climate seasonality

Three types relation have to be considered, between: cambial activity and climate, foliar phenology and climate, cambial activity and foliar phenology.

In order to explore the relation between climate parameters and cells production over time, a regressive approach was adopted. After studying, evolution of local climate parameters, and in order to better understand the growth-climate relationship, it was decided to use the synthetic climate variable derived from the PCA as the explanatory variable. This approach is adapted from the one adopted by H. Morel [75]. The evolution of the total number of cells in the development zone over the study period have been considered as variable to explain. As shown by the PCA, the variables average precipitation, cumulative precipitation and the exposure index are correlated to this axis, so it is their effect that will be measured by the regression. Indeed, as will be shown below, the temperature variables remain rather constant, unlike the rainfall, exposure and relative humidity variables.

As we can assume variability of the cambial state between individuals of the same species, a random factor has to be added to the equation both for the intercept but also for the slope of this regression line thanks to the equation (1)**(M1)**. As this approach remains theoretical and hypothetical, it is therefore necessary to evaluate whether this equation allows us to draw an acceptable conclusion with regard to our null hypothesis which is to evaluate whether climate, taking into account inter-individual variability, influences cell production. Thus, the model (M1) is compared with a theoretical null model that not taking into account the climate effect thanks to equation (2) **(M0)**. Since, for some species, the variability between individuals can be less marked, a third model which does not take into account the randomness linked to the individual was carried out with the equation (3) **(M2)**. Cambial activity, so total mean number of cells, has been log 10 transformed for linear mixed model in order to verify appliance conditions on residuals. In order to assess the quality of models to compare them together; AIC criterion, standard error around estimated parameters and also marginal and conditional R^2 or R^2 and adjusted R^2 have been computed. They are also compared 2 by 2 by ANOVA. The "lme4" and "lmerTest" packages of Rstudio have been used.

$$\ln(\textit{cambial activity}) \sim \textit{climate} + (1 + \textit{climate}|\ \textit{individual}) \quad (1)$$

$$\ln(\textit{cambial activity}) \sim (1|\ \textit{individual}) \quad (2)$$

$$\ln(\textit{cambial activity}) \sim \textit{climate} \quad (3)$$

3 Results

3.1 Data of specimen

The monitored individuals have varying heights of trunk between species, however it can be seen that access to light is not always linked with greater height as for the *S. zenkeri*. Although individuals of the same species have similar access to the light according to the Dawkin indexes, but they are slightly different between species.

Table 3.1: Summary of specimen's data with. n corresponds to the number of trees considered.

Species	**Average DBH (cm) (n=3)**	**Average timber height (m) (n=3)**	**Average bark thickness (mm) (n=3)**	**Dawkin index**	**Average wood density mean (g/cm3)**[3]
Leplaea thompsonii	33,77 ± 4,68	10,00 ± 3,05	1,87 ± 1,23	2-3	0,58 (n=31)
Panda oleosa	46,33 ± 11,36	9,20 ± 2,85	0,8 ± 0,3	3	0,57 (n=49)
Petersianthus macrocarpus	42,70 ± 5,68	19,07 ± 0,66	0,9 ± 0,15	5	0,65 (n=57)
Scorodophloeus zenkeri	39,03 ± 8,30	8,20 ± 2,00	0,63 ± 0,13	4	0,73 (n=77)
Synsepalum subcordatum	39,13 ± 13,84	7,30 ± 1,00	1,25 ± 0,27	3	0,75 (n=5)
Trilepisium madagascarinese	47,50 ± 3,00	23,33 ± 2,38	0,8 ± 0,11	5	0,53 (n=16)
Greenwayodendron suaveolens	48,93 ± 11,87	20,07 ± 2,82	1,27 ± 0,33	5	0,63 (n=27)

[3]Wood density data has been extracted from COBIMFO project (Congo Basin integrated monitoring for forest carbon mitigation and biodiversity; contract no. SD/AR/01A) and funded by the Belgian Science Policy Office (Belspo).

3.2 Anatomy and tree ring distinctiveness

a) *Leplea thomposonii*

This species has axial parenchyma in narrow bands from 2 to 3 cells thick, and confluent paratracheal axial parenchyma. Their fibres have intermediate wall thickness. The wood is diffuse-porous with vessels of diameter between 100 and 200 μm. Histological sections show a lot of starch deposits within both ray and radial parenchyma cells (Figure 3.7).

Macroscopically, it is sometimes feasible to detect growth rings transition, noticed by the absence of axial parenchyma and vessels over several micrometres (Figures 3.1A and B). In the opposite, microscopically, rings are indistinct because they remain really rare (Figures 3.1C and D).

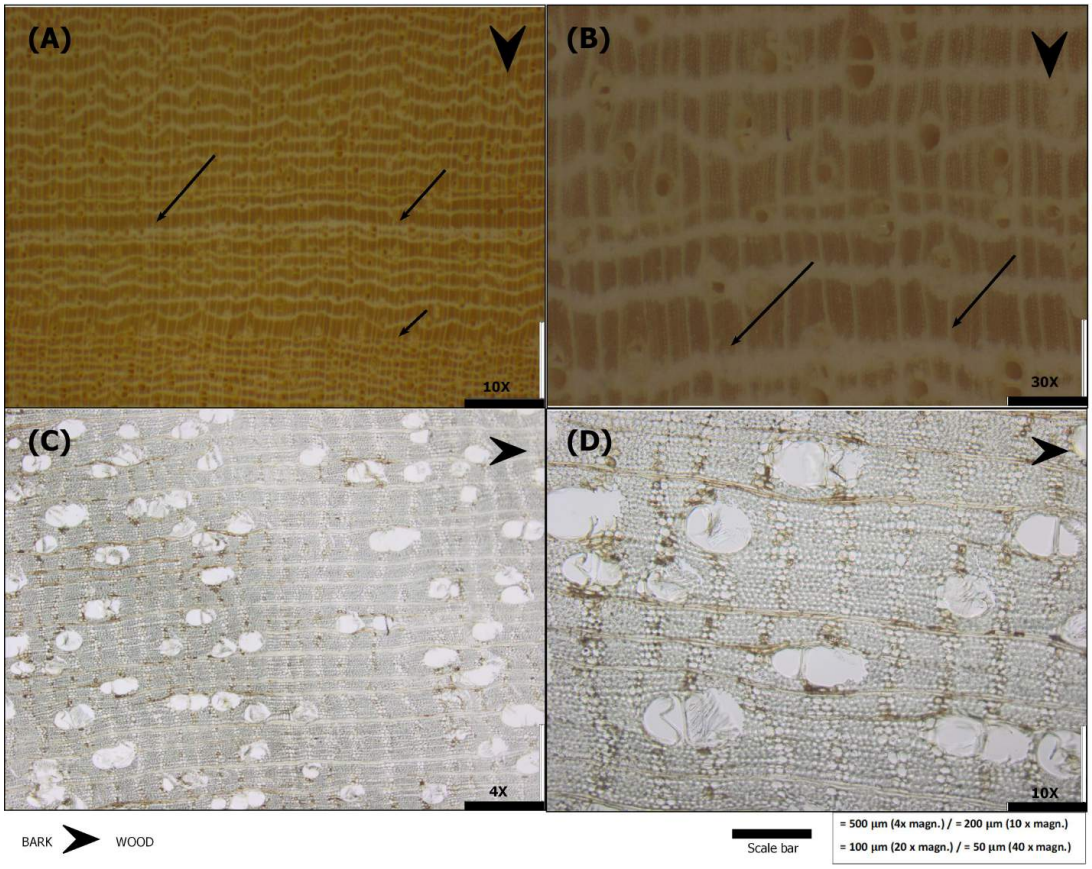


Figure 3.1: Anatomical specimen of *L. thompsoniii* (Tw_66740) under the stereomicroscope: the black arrows show the transition zone of growth rings in (A) and (B). Cross-sections of *L. thompsoniii* (Tw_63830) under light of microscope in (C) and (D). Microsections show indistinct rings.

b) *Panda oleosa*

P. oleosa has a particular bark structure with a large section of rounded cells whose walls are not lignified. This zone is adjacent to the cambial zone and to another part of the bark composed by lignified cells and sclerenchyma where many crystals are observed (Appendice 6.4A). The axial parenchyma is diffuse along the vessels, but the axial parenchyma also forms narrow bands of 3 cells wide and is scalariform (Figures 3.2B and C). The fibres have a thick cell wall. Numerous starch deposits are found within radial parenchyma cells for samples of this study (Figure 3.9).

Macroscopically, *P. oleosa* shows growth rings whose boundaries can sometimes be observed. The transition zone can be distinguished by less compact axial parenchyma (Figures 3.2A and B). Boundaries being barely distinct, these observations can be very difficult or impossible to make microscopically. Sometimes, the transition zone is composed of slightly axially flattened fibres (Figure 3.2D), without axial parenchyma (Figures 3.2B and C). After the discontinuity of axial parenchyma that occurs at the beginning of the new growth ring, the axial parenchyma becomes scalariform (Figure 3.2C).

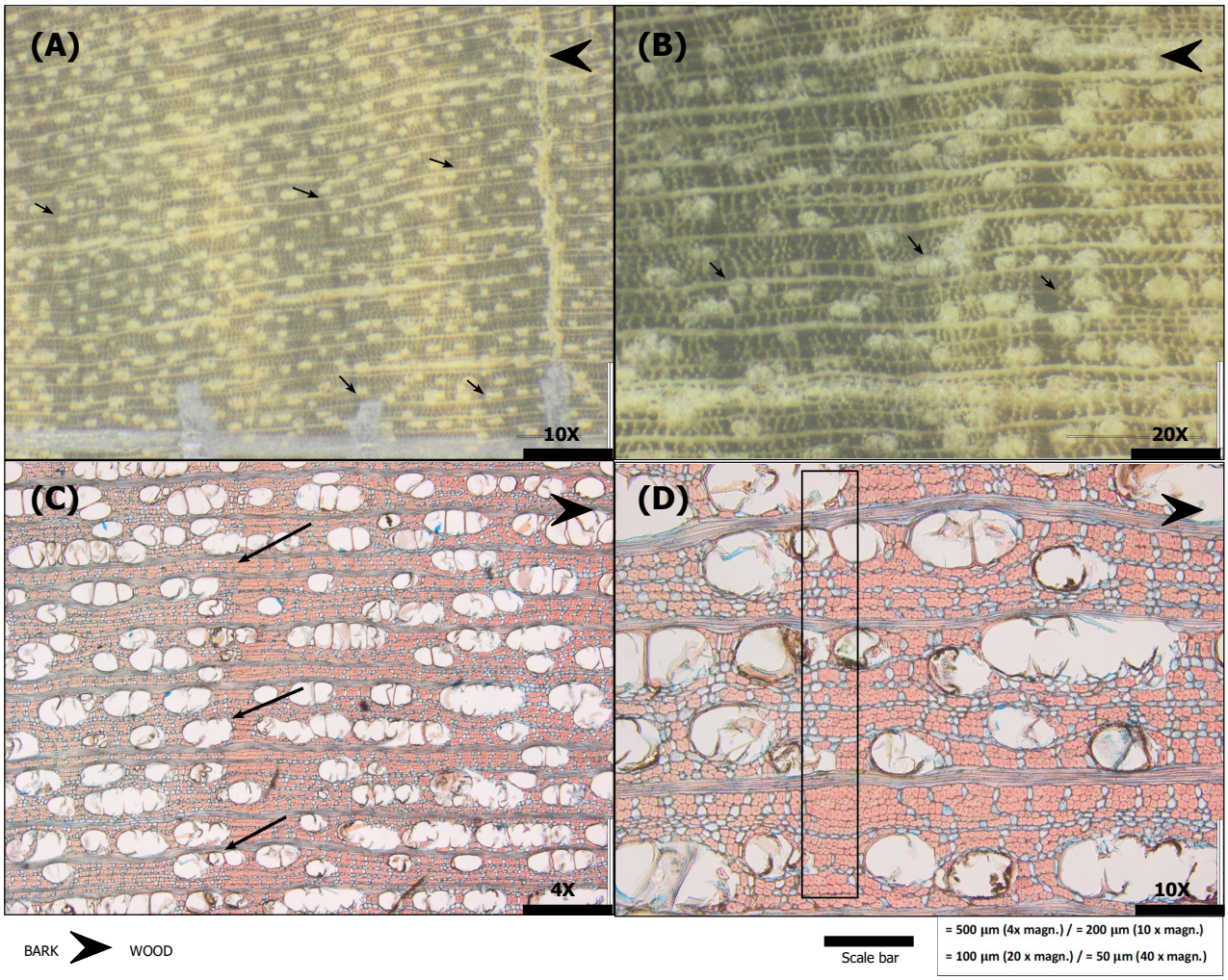


Figure 3.2: Anatomical specimen of *P. oleosa* (Tw_63819) under the stereomicroscope: the black arrows show the transition zone of growth rings in (A) and (B). Cross-sections of *P. oleosa* (TW_69583) under light of microscope: the black arrows show the transition zone of growth rings at respectively in (C) and a black frame surrounds the whole zone where fibre cells are axially flattened in (D).

c) *Petersianthus macrocarpus*

P. macrocarpus has a particular bark structure with alternating non-lignified cells and lignified sclerenchyma. Crystals are also found within these cells (Appendice 6.4B). The fibres have a thick, lignified cell wall within the mature xylem. 2 types of axial parenchyma are noticed, the first is apotracheal and diffuse along the wood. The second is paratracheal and can be structured as vasicentric, lozenge and winged aliform parenchyma, and variably confluent. Numerous starch deposits are found within parenchyma cells during the study period.

Macroscopically, ring distinctness is not always evident. Sometimes, the axial parenchyma seems to be less present, forming bands of xylem devoid from parenchyma (Figure 3.3A). In addition, at higher magnification, a thin continuous line of marginal parenchyma appeared. At microscopic level, growth rings are indistinct or absent. However, slightly axially flattened fibres can sometimes be seen adjacent to a small band of parenchyma cells (Figures 3.3C and D). In this case, discontinued bands of 1 or 2 cells width are observed adjacent to these fibres.

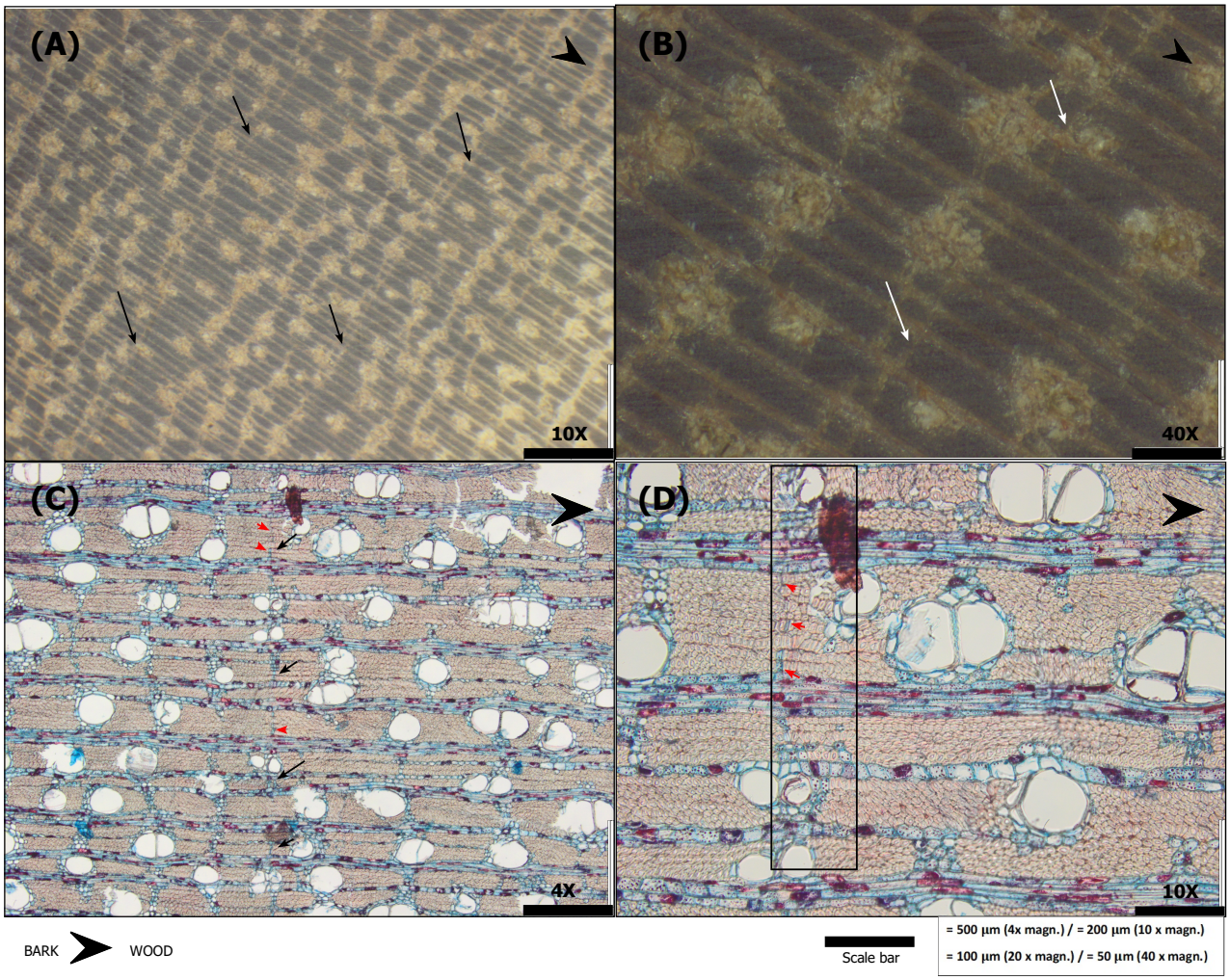


Figure 3.3: Anatomical specimen of *P. macrocarpus* (Tw_32722) under stereomicroscope the black arrows show the limits of rings (A) and white arrows show the limits of rings (B). Cross-sections of *P. macrocarpus* (Tw_9407) under light of microscope: the black arrows show the transition zone of growth rings (C) and black frame surrounds the entire zone where fibres are axially flattened (D). Red arrows show discontinuous bands of axial parenchyma cells (C) and (D).

d) *Scorodophloeus zenkeri*

S. zenkeri has a characteristic bark structure with zones of lignified sclerenchyma and progressively lignified intercellular walls as one moves away from the cambial zone (Appendice 6.4C). This species includes a diffuse-in-aggregates apotracheal axial parenchyma. There is also a sparse vasicentric paratracheal axial parenchyma and scanty, which is also confluent. Banded parenchyma is present in narrow bands of 3 cells and in marginal bands. Fibre cells have a thick wall.

At macroscopic level, wedging rings are observed for *S. zenkeri* (Figure 3.4A). Growth rings are distinguishable by a very thin band of thickened fibres (Figures 3.4B and C). Microscopic analysis is required to clearly identify these cells, although it is rarely possible to identify the boundaries of growth rings. Microsections show a region of about 4 fibre cells, which are radially flattened (Figures 3.4D and E). Instead of a mean fibre of xylem of 11,2 μm wide, these flattened cells measured 4,83 μm wide.

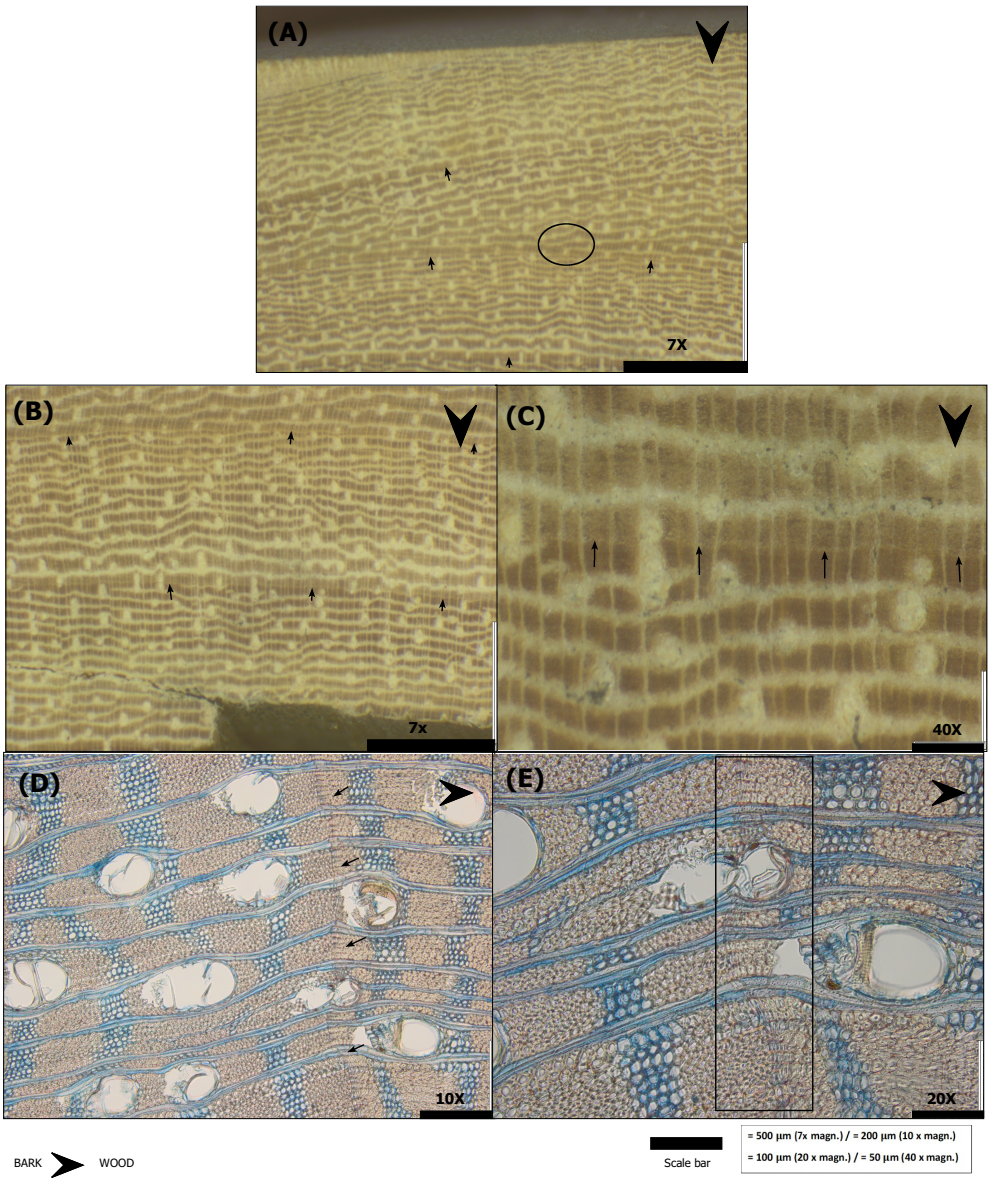


Figure 3.4: Anatomical specimen of *S. zenkeri* (Tw_41199) under stereomicroscope: the black arrows show the limits of rings (A) and black circle shows the joint of wedging rings (A), the black arrows show the limits of rings (B) and (C). Cross-sections of *S. zenkeri* (Tw_69459) under light of microscope, the black arrows show the transition zone of growth ring (D), and black frame surrounds the entire zone where fibre cells are axially flattened (E).

e) *Synsepalum subcordatum*

S. subcordatum has a bark with thin bands of lignified sclerenchyma in a matrix of rounded, unlignified cells, increasingly lignified as one moves away from the cambial zone lignified as one moves away from the cambial zone (Appendice 6.4D). Fibres of the xylem have a thick wall; they surround vessel elements. The axial parenchyma forms narrow bands of 3 cells wide, this parenchyma is also reticulated. Numerous starch deposits are found within cells of the axial parenchyma (Figure 3.15).

Macroscopically, the transitions between growth rings are visible. In these areas, the axial parenchyma is absent for several micrometres, forming a long band of xylem without large reticulated parenchyma band (Figure 3.5A). It is worth noticing that thin bands of marginal parenchyma also appear by using a higher magnification (Figure 3.5B), although this is less obvious at the microscopic level (Figures 3.5C and D).

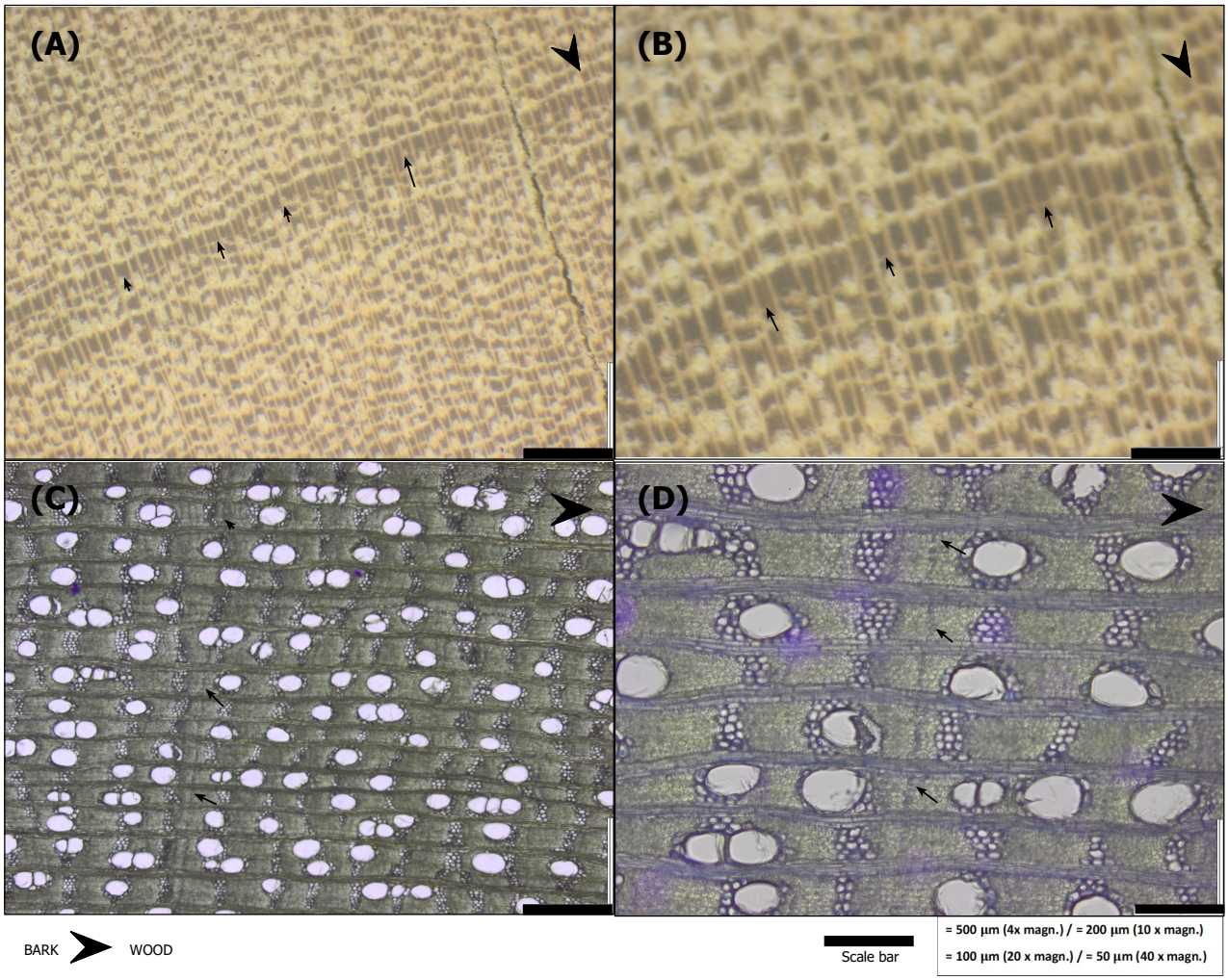


Figure 3.5: Anatomical specimen of *S. subcordatum* (Tw_1150) under stereomicroscope: black arrows show the limits of rings in (A) and black arrows show the limits of rings in (B). Cross-sections of *S. subcordatum* (Tw_1750) under light of microscope: black arrows show the transition zone of growth ring in (C) and (D).

f) *Trilepisium madagascariense*

T. madagascariense has a bark composed by rounded cells full of gums, crystals or lignified elements (Appendice 6.4E). The xylem contains apotracheal axial parenchyma, and different types of paratracheal axial parenchyma. There is axial parenchyma, scanty paratracheal and sometimes vasicentric parenchyma. This axial parenchyma forms bands of 3 to more than 3 cells wide and thus surrounds the vessels. The fibres present a thin to thick cell wall.

Macroscopically, rings transitions are visible thanks to the absence of axial parenchyma within an area that is accolated to a thin non-continuous band of parenchyma (Figures 3.6A and B). Microscopically, axially flattened fibres are observed (Figures 3.6C and D).

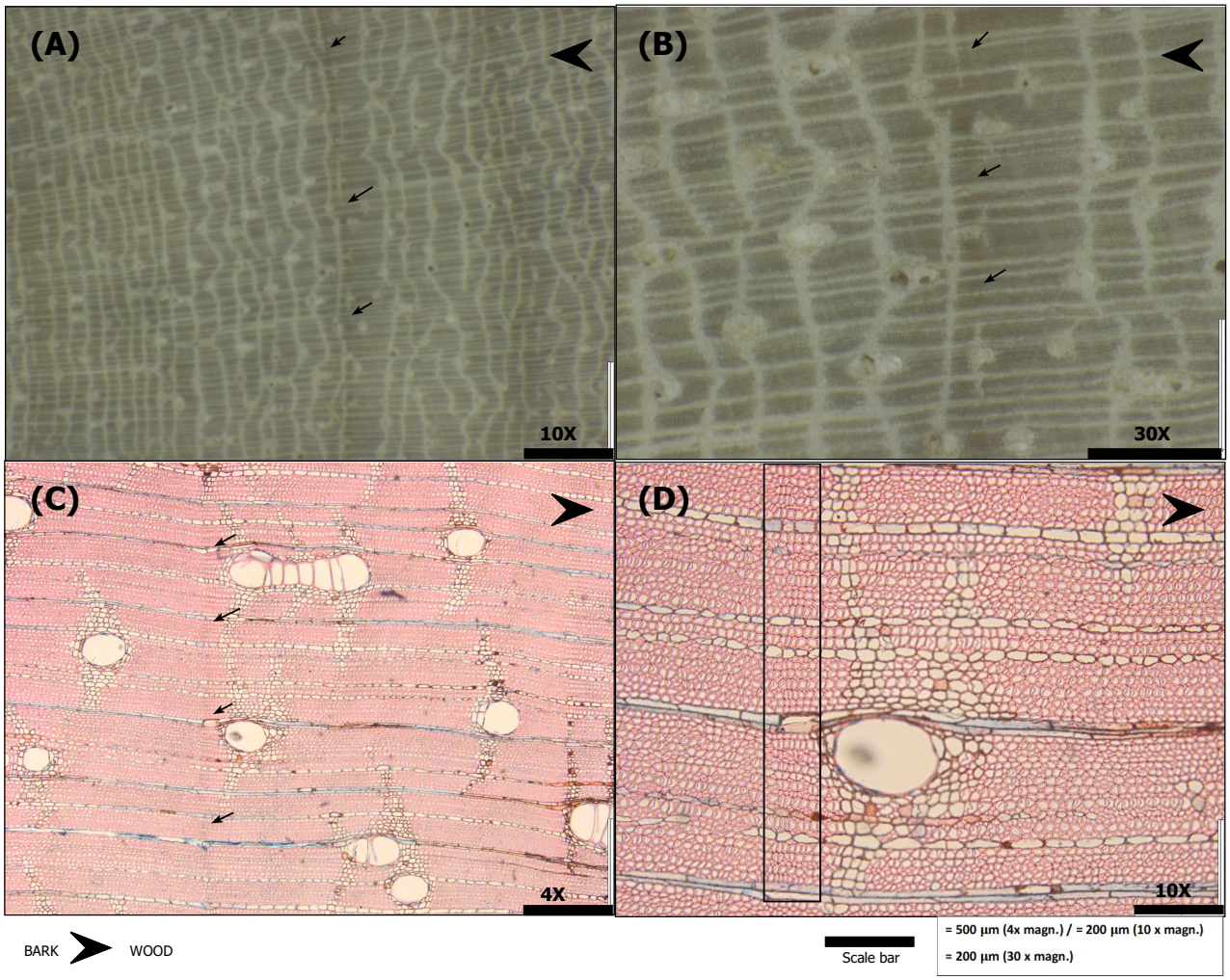


Figure 3.6: Anatomical specimen of *T. madagascariense* (Tw_63829) under stereomicroscope: black arrows show the limits of rings in (A) and, black arrows show the limits of rings in (B). Cross-sections of *T. madagascariense* (Tw_32669) under light of microscope: black arrows show the transition zone of growth ring in (A) and a black frame surrounds the entire zone where fibre cells are axially flattened in (D).

3.3 Cambial data

a) *Leplea thomposonii*

Observations on *L. thompsonii* suggest the existence of cambial activity from the first collection on 5 March. In fact, the cambial zone is sometimes rather large, composed by many cells. In addition, some cells of the CZ adjacent to the xylem appeared larger and more rounded than cells of CZ or mature fibres especially in samples of the individual3 (Figures 3.7A, B and C). These could be radial parenchyma cells. Indeed, most of the time for this species, within the study period, a band of radial parenchyma is directly adjacent to the cambial zone (Figures 3.7B and C). Furthermore, these cells have a thickened, but not lignified cell walls, which could be interpreted as new young xylem cells. This leads us to conclude of a low cambial activity at the moment of sampling.

However, under DIC filter, the transition of non-lignified to lignified elements is directly visible by both the demarcation between blue and red cells and the brightness of mature cells. Under blue light, the epifluorescence shows the lignification of intercellular spaces between the different cells of mature wood directly after the CZ, confirming this hypothesis of a low cambial activity (Figure 3.7C).In addition, and despite some variations, from a quantitative point of view, the size and the number of cells that composed the cambial zone by considering both thinner and larger cells are not significatively different from one data collection to another (Figure 3.8). For the three individuals the cell size is a bit larger for the second collection, it can be explained by the recurrent presence of axial parenchyma for which cells have been counted and measured within cambial zone.

To conclude, *L. thompsonii* does not present all 4 phases of development from juvenile to mature cells. However, it can be considered that there is no cambial activity which is limited to the multiplication of the cambial cells without them entering in enlargement and thickening phases. But most of the time a band of radial parenchyma is directly adjacent to the dormant cambial zone.

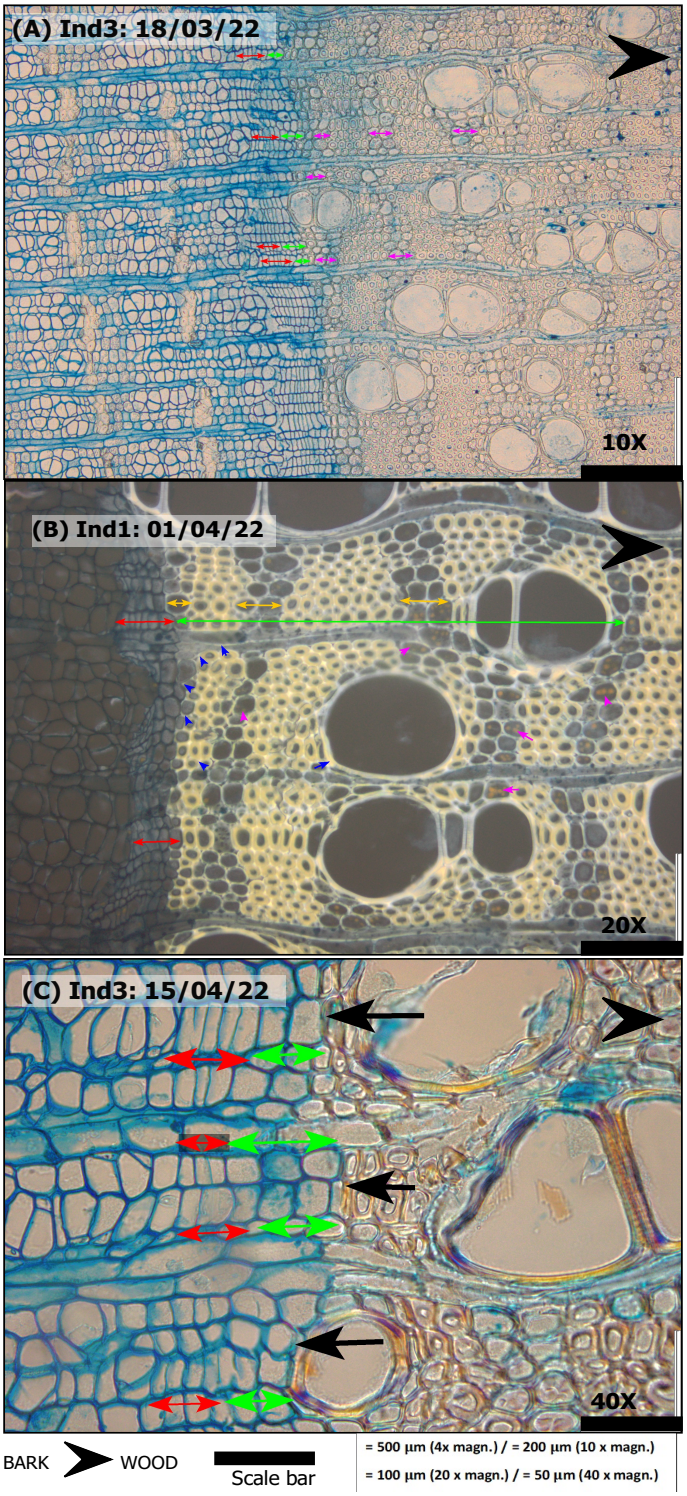


Figure 3.7: (A) Cross-sections of *L. thompsoniii* under light of microscope (A), blue light (B) and DIC filter (C). The cambial zone is composed by a multitude of cells in division (red arrows), with 2 or 3 cells wider adjacent to both the cambial zone and the mature wood (green arrows in A and B). These cells look like parenchyma that, in comparison to mature parenchyma cells (purple arrows in A), do not have lignified walls. Mature axial parenchyma are full of starch deposits (purple arrows in B). In addition, the lignification of intercellular spaces and of cells walls (such as fibres and vessels) start directly after the cambial zone (blue arrows in B).

The quantitative approach can be summarised in a graph of the distribution of mean values.

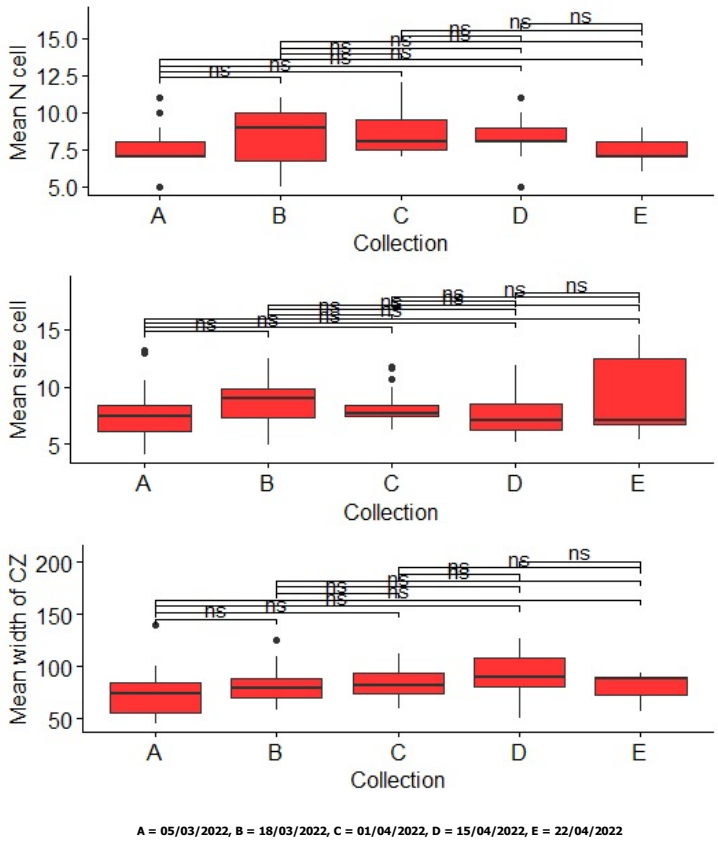


Figure 3.8: Boxplots considering all individuals of *L. thompsoniii* indiscriminately. Mean value of number and size of cells in CZ (Mean N cell, Mean size cell), and also the average total width of ZC (Mean width of CZ) are computed for each data collection T-test were performed to compare the means, but only one of them has been significant (*).

b) *Panda oleosa*

Only one individual of *P. oleosa* shows cambial activity from the first collection on 5 March. Micro-sections under blue light and DIC filter illustrate the beginning of lignification of cells wall and inter-cellular spaces directly after the cambial zone (Figure 3.9C). Moreover, mature fibres have thick walls, easily distinguished, notably by the coloration differentiation under light microscope (Figure 3.9A). Furthermore, no significant differences about the mean number or the size of cells that composed cambial zone are observed (Figure 3.10A). However, the evolution in average of cells' number or their size seems to be more important for the collections B and E, on 18 March and 15 April, respectively. These results are confirmed both for the second and the third individuals.

It is therefore possible to observe each stage of the cell development for the individual1 (Figures 3.9D and F). In addition, new vessels are produced within the cambial zone without any lignified walls (Figure 3.9F).

The quantitative approach confirms the cambial activity. Indeed, firstly, the total number of cells in the considered zone of development increases (Figure 3.10C). Secondly, the mean number and size of cells for each zone on interest slightly varies over time for each part of the developing zone although these mean values are not significantly different between collections (Figures 3.10B). In average, the number of cells in CZ decreases over time with the size of these cells, whereas the number of cells in EZ and TZ increase while the size decreases and remains constant, respectively. As the relative part of the number of cells of EZ and TZ and the width slightly vary, the relative parts occupied by the cambial zone, in terms of cell's number or width of the CZ, are decreasing in favour of their LZ that increased over time (Figures 3.10D). The variability of the width measurements, especially for

the LZ, is related to the difficulty of interpreting the lignification limit between cells in thickening and lignification phase.

Globally, the cambial zone is more represented in terms of mean cells number before the lignification zone. But, in terms of width, the lignification zone and the thickening zone are more represented than the cambial zone.

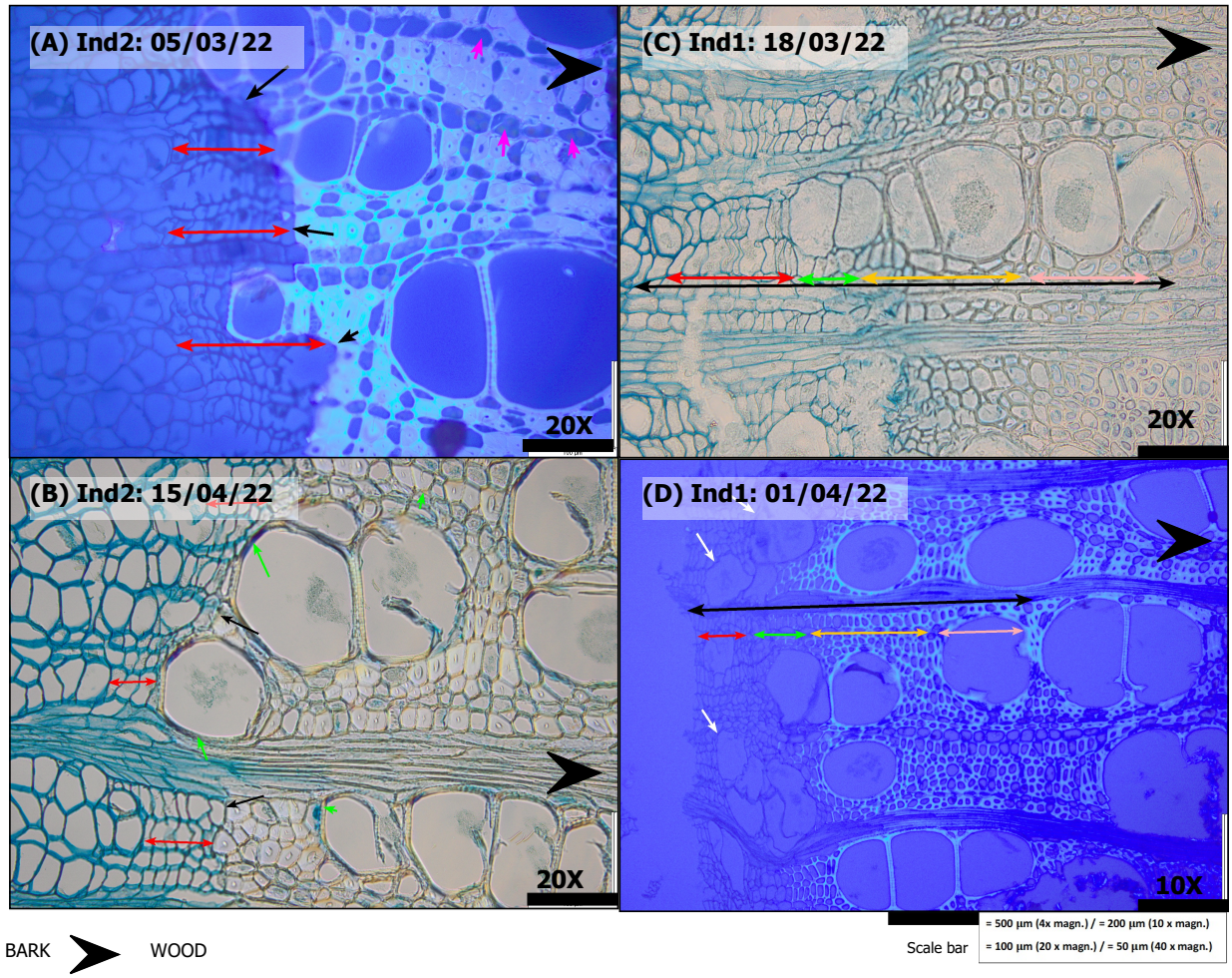


Figure 3.9: Cross-sections of dormant cambial zone of *P. oleosa* under blue light (A), and under the DIC filter (B). Cross-sections of active cambial zone of *P. oleosa* under light of microscope (C), and under blue light (D). The cambial zone is composed by several narrow cells (red arrows). The transition between CZ and the mature xylem is represented blue cells and light grey or shiny cells respectively (black arrows). Lignified walls are well visible thanks to the holographic effect (green arrows in B). Starch deposits also detected under blue light (magenta arrows in A). For active cambium (C and D), the development zone (black arrows) is composed of 4 zones: CZ (red arrows), EZ (green arrows), TZ (orange arrows) and LZ (pink arrows). In addition, developing, non-lignified vessels appeared (white arrows).

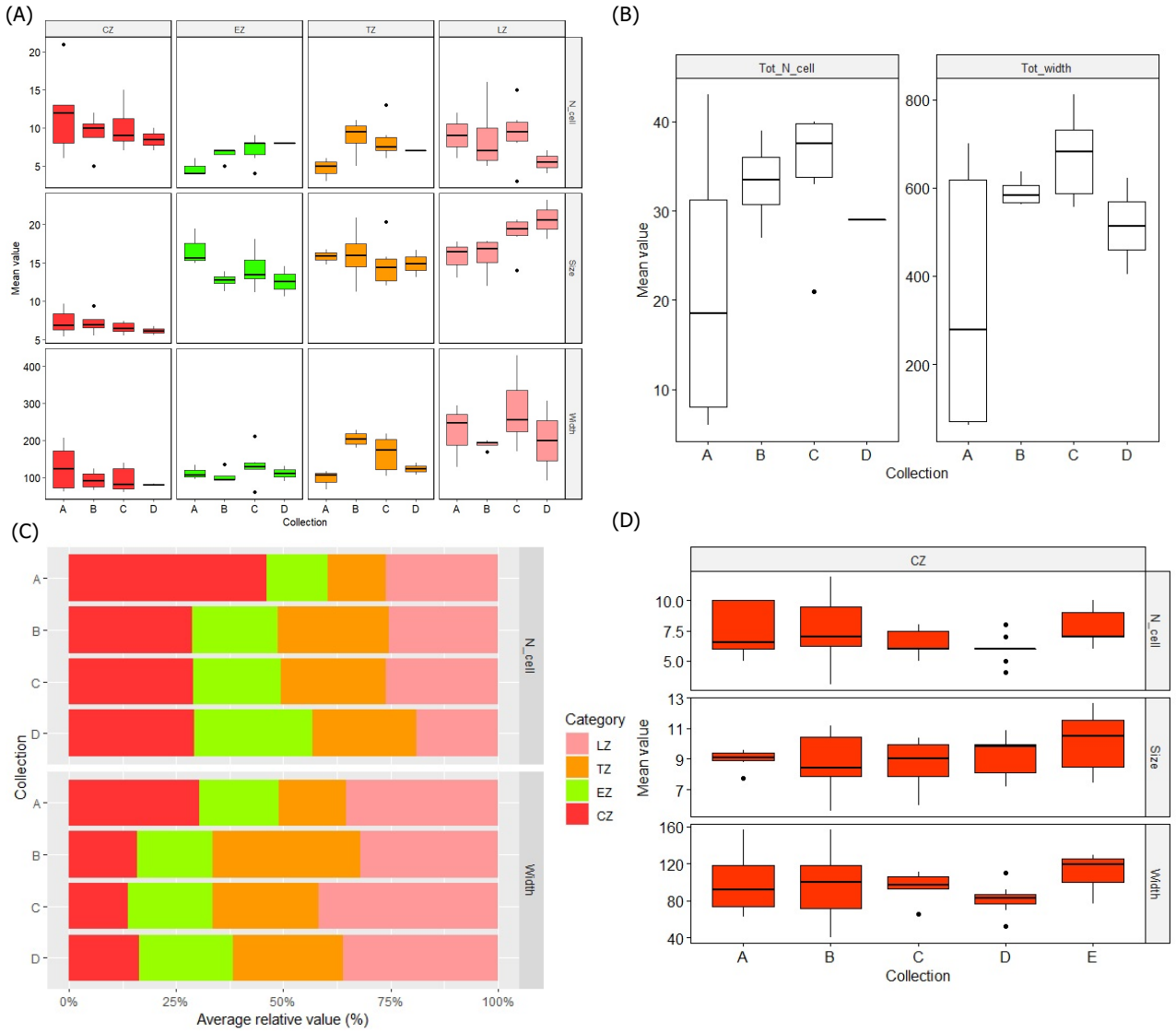


Figure 3.10: (A) Boxplots considering active individual1 of *P.oleosa.* Mean number of cells counted by radius (N_cell), radial width of these cells (Size) and mean width of each entire zone of interest (Width) are computed for Cambial Zone (CZ), Enlargement Zone (EZ), Thickening Zone (TZ) and Lignification zone (LZ). Wilcoxon tests show any significant differences of mean between collections. The total mean number of cells and the total mean width of the zone in development increases over collection (B). The average relative part occupied by each zone of interest within the zone of development in terms of number of cells or width fluctuate over data collection (C). (D) Boxplots considering mean value for number and size of cells and width of CZ for dormant individuals of P.oleosa.

c) *Petersianthus macrocarpus*

An important variability is observed between observations from different collections and between individuals of *P. macrocarpus*.

The thinness of the walls of the fibres present and adjacent to the cambium, particularly for individuals 1 and 3, is a characteristic of the growth rings transition. Most of the time axial parenchyma is directly adjacent to the cambial zone.

Globally at the scale of the fourth samples collections, no distinct cambial activity is visually observed for the individual1. The transition between CZ and mature wood is clear (Figures 3.11A and C). However new cells in formation are observed in places within samples of the second collection (Figure 3.11B). Epifluorescence shows that intercellular spaces are lignified between parenchyma elements, fibres or vessels. It is also the case for walls fibres and vessels. Furthermore, numerous starch deposits are observed within (radial and axial) parenchyma cells. However, the quantitative approach shows that the mean number of cells of CZ and their mean size increase between collections A and B and between C and D (Figure 3.12D).

Some areas of the individuals 2 and 3 of *P. macrocarpus* show an activity of the cambium for the first collection in March 5th. In fact, different stages of xylem development are observable, but these observations are not always recurrent over time. New cells in development are located, but the activity of cambium seems to be non-uniform, i.e. the developing cells are observed only on a few cell rays. Cambial activity is more sustained in individual 2 for which cells are observed to be developing until the collection C on 1April. On the other hand, individual 3 only shows little cambial activity for the two first collections, with few cells in enlargement and thickening phase. From the second collection to the last one, we observed that the number of cells composing the development zone is reducing (Figure 3.12C), no cells in thickening zone are observed (Figure 3.11E). Indeed, for the last sample collections any cambial activity is observed (Figures 3.11F and G). They have thinner cell wall than mature wood but lignified.

The quantitative approach confirms this trend by showing the decrease of the number and the size of cells in LT and EZ over time (Figure 3.12A). In addition, a significant difference of the mean number of cells of EZ and TZ, and also the mean size of cells are observed between the collections A and D. In the opposite the number and the size of the cambial cells remain constant over the study period. Consequently, the proportion of the development zone occupied by cambial zone increases over time at the expense of the enlargement and thickening zone (Figure 3.12C). Overall, there is a slowdown in cambial activity for individuals 2 and 3, through a reduction in the total number of cells forming and the width of the developing zone.

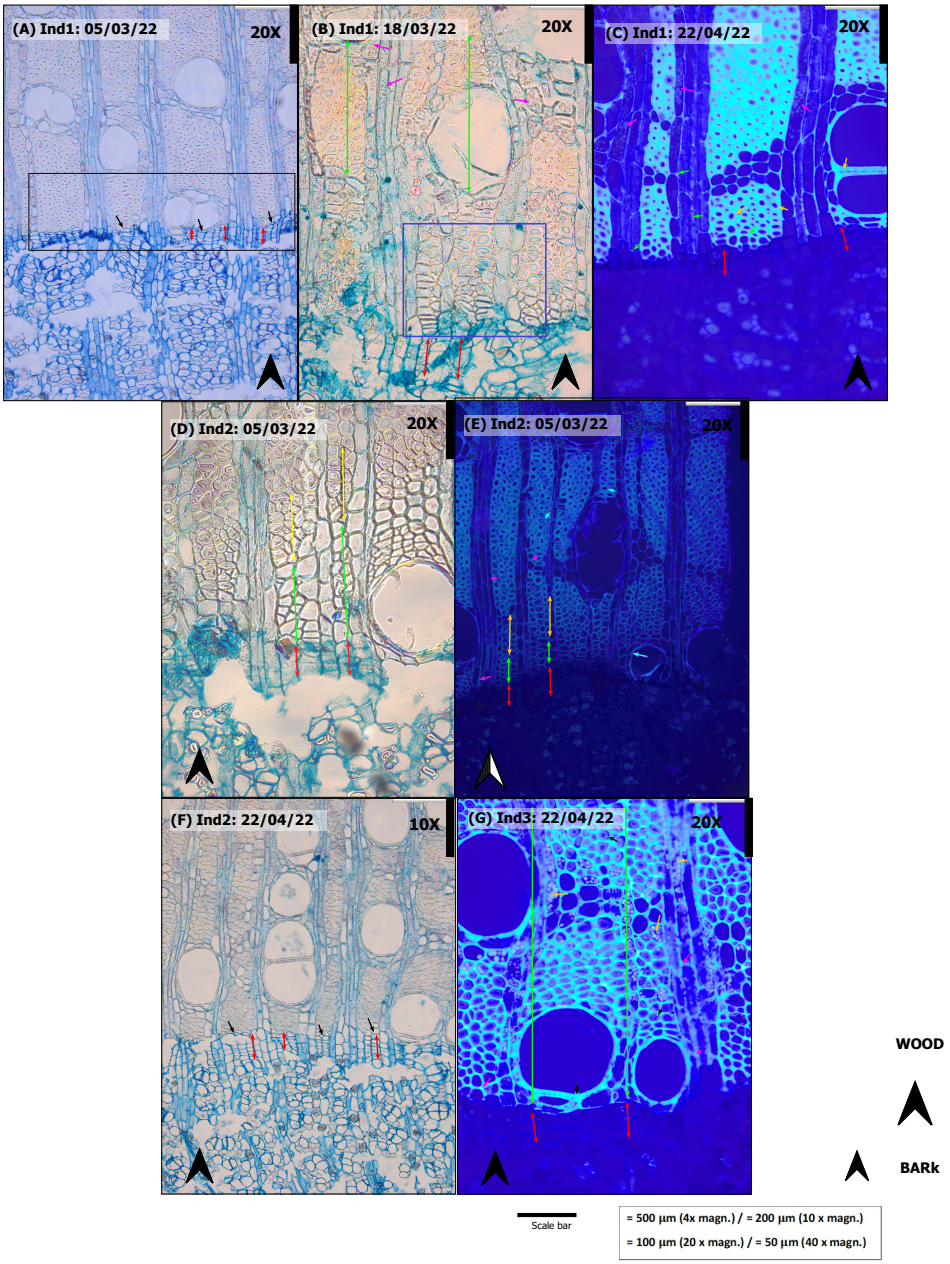
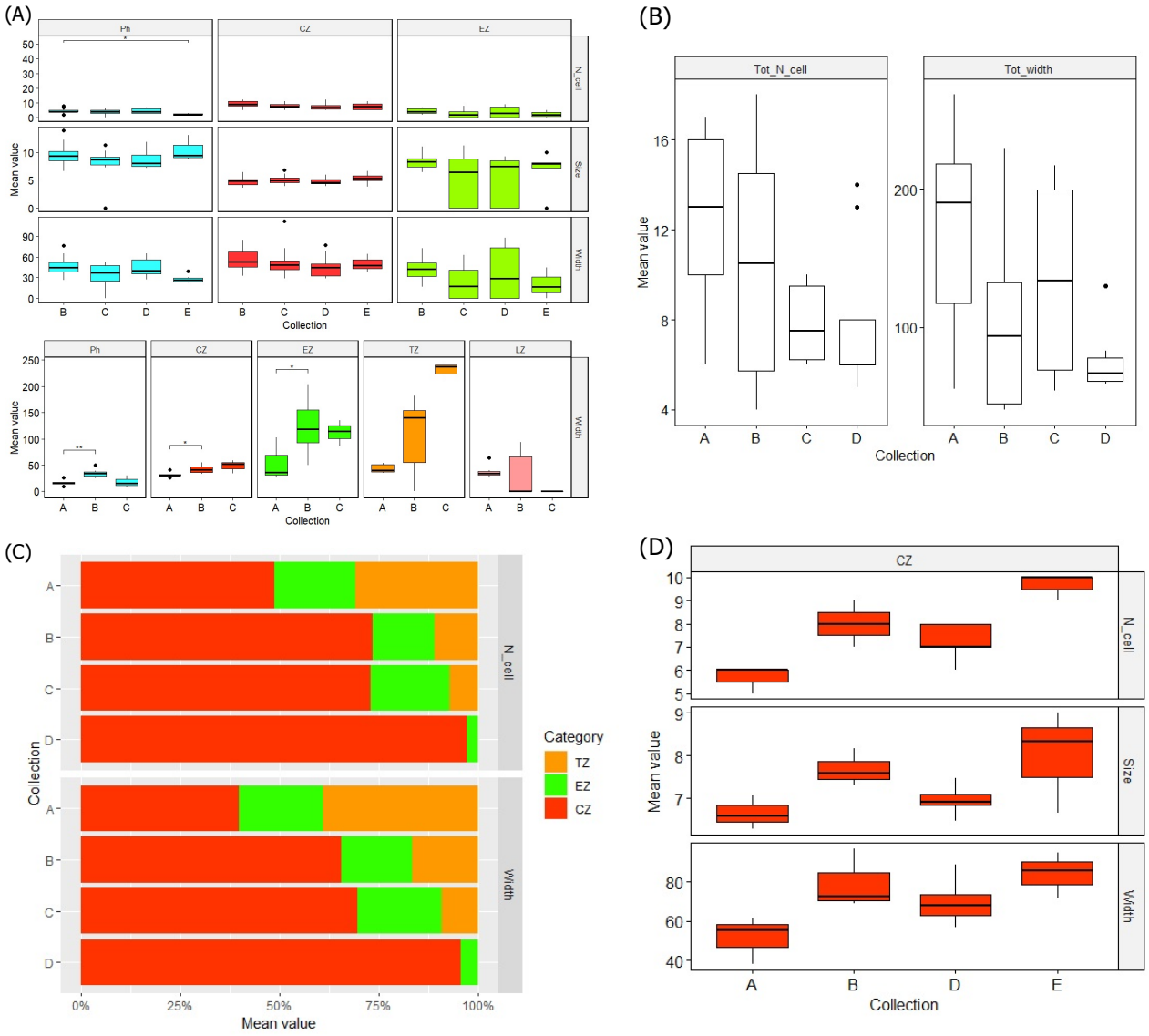


Figure 3.11: Cross-sections of dormant cambial zone of individual1 of *P. macrocarpus* under the light of microscope (A), under the DIC filter (B) and under blue light (C). CZ is composed by several narrow cells (red arrows) represented by blue cells. Light grey (A) or shiny (B) cells correspond to mature cells of xylem (black arrows). (B) Lignified walls are well visible thanks to the holographic effect (green arrows) in opposite to the CZ (red arrows). Under blue light, starch deposits are also detected (magenta arrows), intercellular spaces are lignified from de CZ (purple arrows). Black (A) and blue (B) boxes surround space where fibres are axially narrower. Cross-sections of active CZ of the individual2 of *P. macrocarpus* under the DIC filter (D and F) and under blue light (E and G). The development zone is composed of 3 zones: the CZ (red arrows), the EZ (green arrows), the TZ (orange arrows), no LZ was observed. For the same individual2 observed at different dates, the cambium active on 05/03 is perceived inactive on 22/04.



A = 05/03/2022, B = 18/03/2022, C = 01/04/2022, D = 15/04/2022, E = 22/04/2022

Figure 3.12: (A) Boxplots considering active individuals 2 and 3 of *P. macrocarpus*. Mean number of cells counted by radius (N_cell), radial width of these cells (Size) and mean width of each entire zone of interest (Width) are computed for Cambial Zone (CZ), Enlargement Zone (EZ) and Thickening Zone (TZ). Wilcoxon tests show on significant differences of mean number of cell in EZ and in TZ between 05/03 and 15/04. The total mean number of cells and the total mean width of the zone in development decreases over collection (B). The average relative part occupied by each zone of interest within the zone of development in terms of number of cells or width fluctuate over data collection (C). (D) Boxplots considering mean value for number and size of cells and width of CZ for dormant individual of *P. macrocarpus*.

d) *Scorodophloeus zenkeri*

Intraspecific variability in cambial activity is observed for *S. zenkeri*. Two individuals show no activity of their cambium characterized by few, narrow cells (Figures 3.13A and B). Epifluorescence shows that lignification occurs directly after the cambial zone on mature wood (Figure 3.13B). Furthermore, for several samples, limits of growth ring, characterised by flattened fibres directly adjacent to the CZ are visible (Figures 3.13B and C). The microscopic observations are confirmed by statistical analysis. There are no any significant differences, neither in terms of number of cells, nor in terms of size of the cells that compose the cambial zone between the different collections (Figures 3.14D).

In the opposite, a high cambial activity is observed for the individu2 of *S. zenkeri*. Thanks to the combination of the different microscopic approaches, each stage of cell development, from their division to the lignification process are detected (Figures 3.13C and D). New vessels are also present (Figure 3.13D).

Globally, few significant differences have been observed for the different variables over time. The number of cells increase for CZ, EZ and TZ, in the opposite it decreases for LZ (Figure 3.14B). However, the size of each type of cells seems to decrease over the study period (Figure 3.14A).

In a quantitative point of view, the mean number and the mean size of cells that composed the cambial zone either for individual 2 either for individuals 1 and 3, follow the same increasing trend. In addition, the respective mean values of cambial cells number are almost equal if we consider each data collections for active or inactive cambium (Figures 3.14A and D). However, in the opposite to individuals 1 and 3, for the individual 2 other cells in development are observed. Globally, few significant differences have been observed for the different variables over time. The number of cells increases for CZ, EZ and TZ, but the size of each of EZ and TZ cells seems to decrease over the study period (Figure 3.14A). Cells of LZ seem to become less numerous and narrower over time. Furthermore, while the total number of cells present in the development zone increases, the relative parts occupied by cells in EZ and TZ rise at the expense of CZ and LZ (Figures 3.14B and C). In fact, in the particular case of *S. zenkeri*, it remains difficult to distinguish cells in lignification process to mature fibres. Moreover, the wall is thin to thick, it is therefore difficult to really separate the thickening and the lignification processes. The decrease in the number of cells in EZ and TZ may be related to their maturation.

Relatively considered, the thickening zone is more represented within the zone of development than cambial and enlargement zones in terms of the mean number of cells or the width of the zone (Figure 3.14C). Then it is the enlargement zone and the cambial zone, the lignification zone and the juvenile phloem.

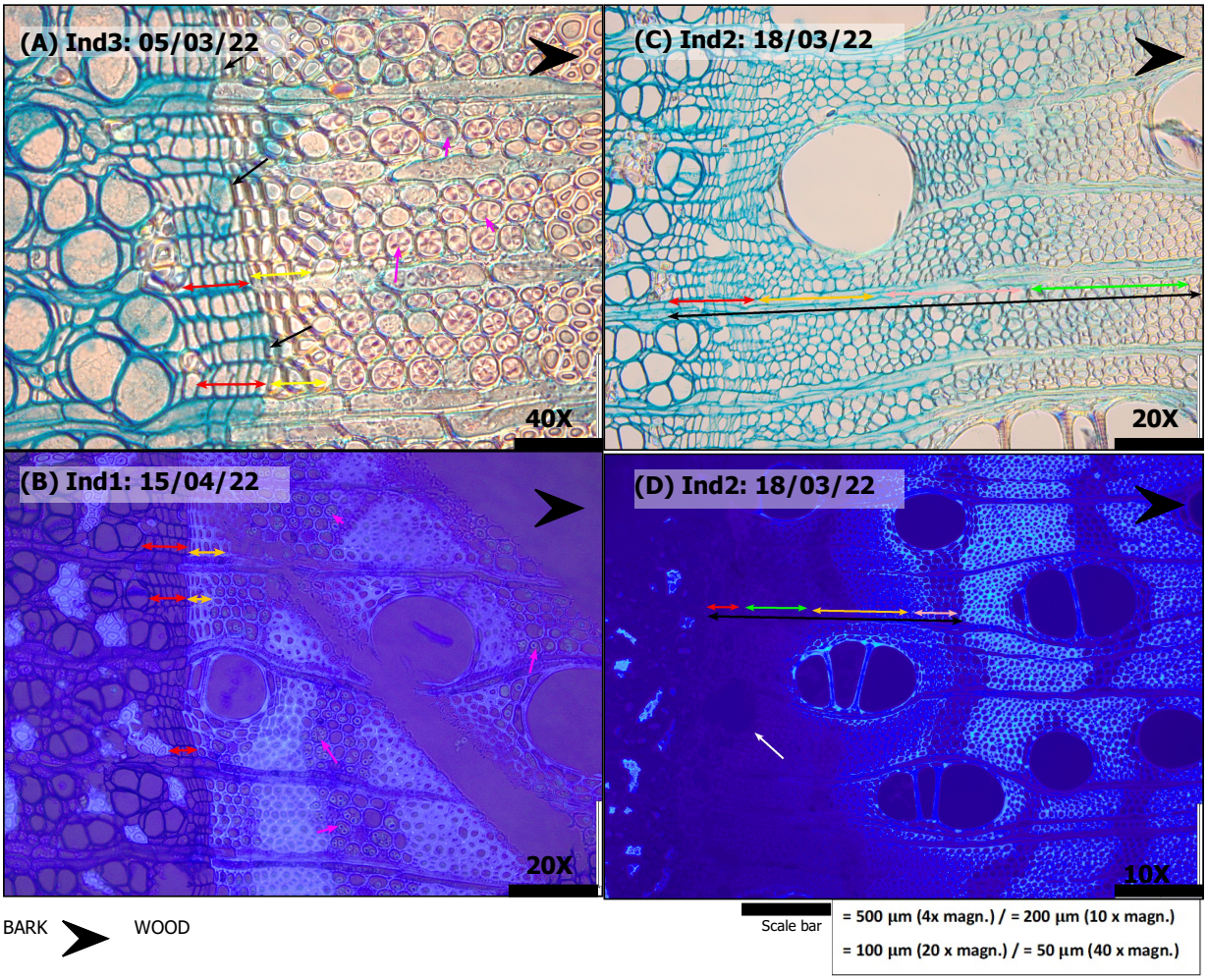


Figure 3.13: Cross-sections of dormant cambial zone for individuals 1 and 3 of *S. zenkeri*, under the DIC filter (A) and under blue light (B). CZ is composed by several narrow cells (red arrows). The transition between CZ and the mature xylem is represented blue cells and light grey or shiny cells respectively (black arrows). In addition, axially flattened fibres are directly adjacent to CZ (yellow arrows). In (A) lignified walls are well visible thanks to the holographic effect (green arrows), starch deposits are detected under blue light (magenta arrows). Cross-sections of active cambial zone of *S. zenkeri* (individual 2) under the DIC filter (C) and under blue light (D). The development zone (black arrows) is composed of 4 zones: the cambial zone (red arrows), the enlargement zone (green arrows), the thickening zone (orange arrows) and the lignification zone (pink arrows). In addition, developing, non-lignified vessels appeared (white arrows).

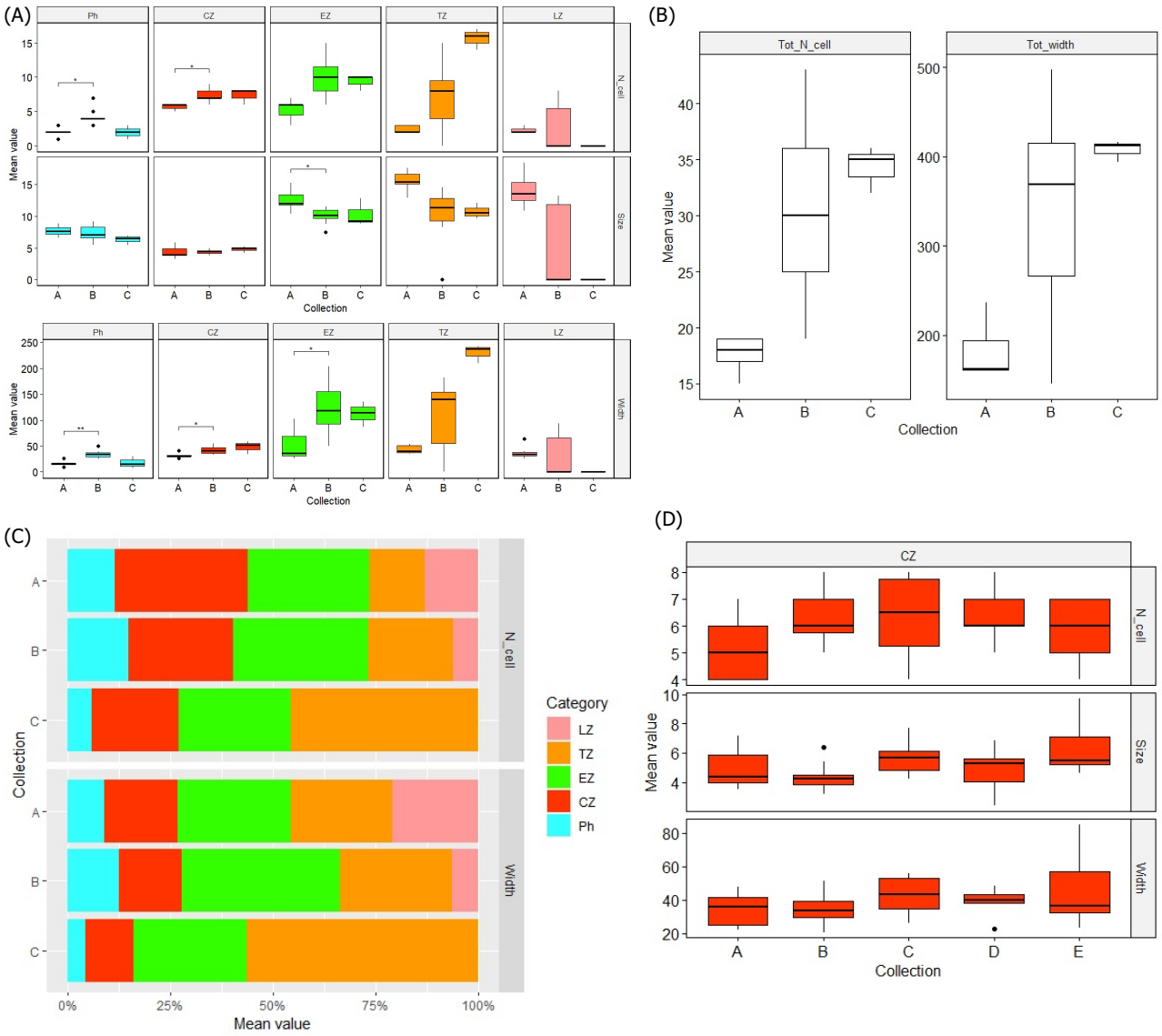


Figure 3.14: (A) Boxplots considering active cambium of individual2 of *S. zenkeri*. Mean number of cells counted by radius (N_cell), radial width of these cells (Size) and mean width of each entire zone of interest (Width) are computed for Cambial Zone (CZ), Enlargement Zone (EZ), Thickening Zone (TZ), Lignification zone (LZ), and juvenile phloem (Ph). Wilcoxon tests have been realised and show on significant difference (*) of mean number of cambial cells between collections A and B. (The total mean number of cells and the total mean width of the zone in development increases over collection (B). The average relative part occupied by each zone of interest within the zone of development in terms of number of cells or width fluctuate over data collection (C). (D) Boxplots considering mean value for number and size of cells and width of CZ for dormant individual of *S. zenkeri*.

e) *Synsepalum subcordatum*

Individuals of *S. subcordatum* show no cambial activity and generally have a narrow dormant cambial zone. The followed pattern of growth is similar for the three individuals, that are thus indiscriminately considered. A band of axial parenchyma, whose cells have a lignified wall, is often found adjacent to the CZ (Figures 3.15A and C). In addition, the fibres walls directly adjacent to the CZ are often thinner than the other fibres of the mature xylem.

The quantitative analysis, based on the measurements calculated for the 3 individuals, shows that no significant differences of means neither for number of cells neither for size of cells that composed the cambial zone are observed (Figures 3.16). There is a more marked increase in the number of cells in collection E, which could mark the beginning of activity but no conclusion can be drawn without measurements taken later in the season.

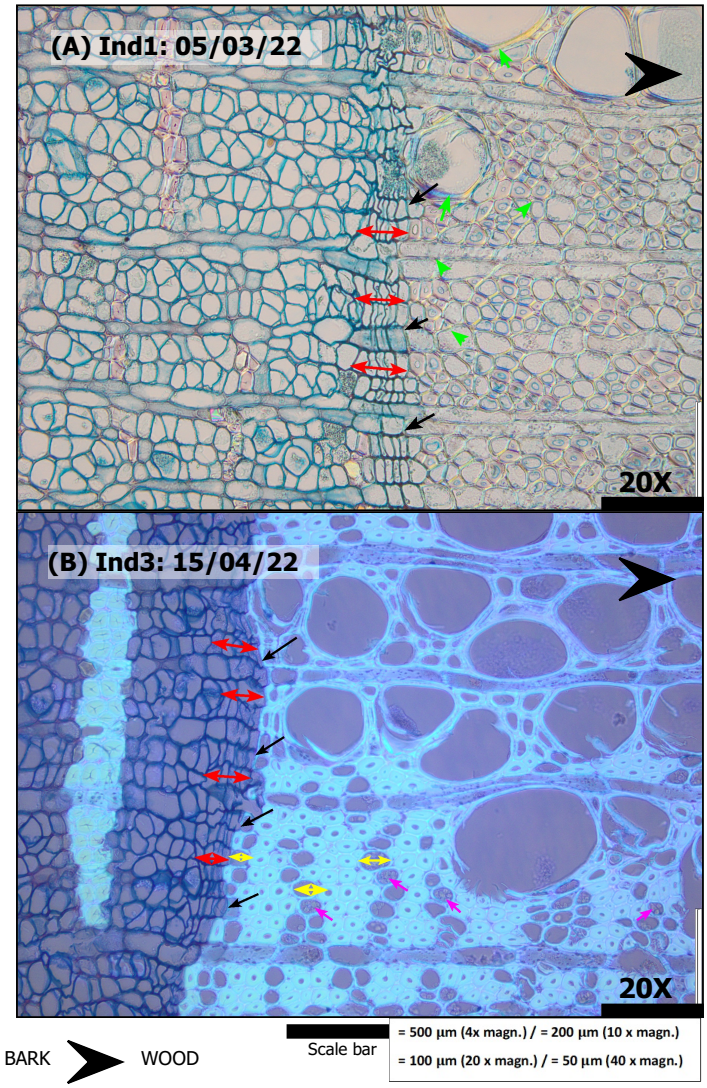


Figure 3.15: Cross-sections of *S.synsepalum* under DIC filter (A) and under blue light (B). The cambial zone is composed by several narrow cells (red arrows). Limit of lignification is observed thanks to the difference of brightness and colours. Blue cells and elements are non-lignified as opposed to the bright elements that are lignified (black arrows). Under blue light, radial parenchyma is distinguishable and sometimes accolated to the CZ (yellow arrows). Starch deposit are visible within parenchyma cells (magenta arrows).

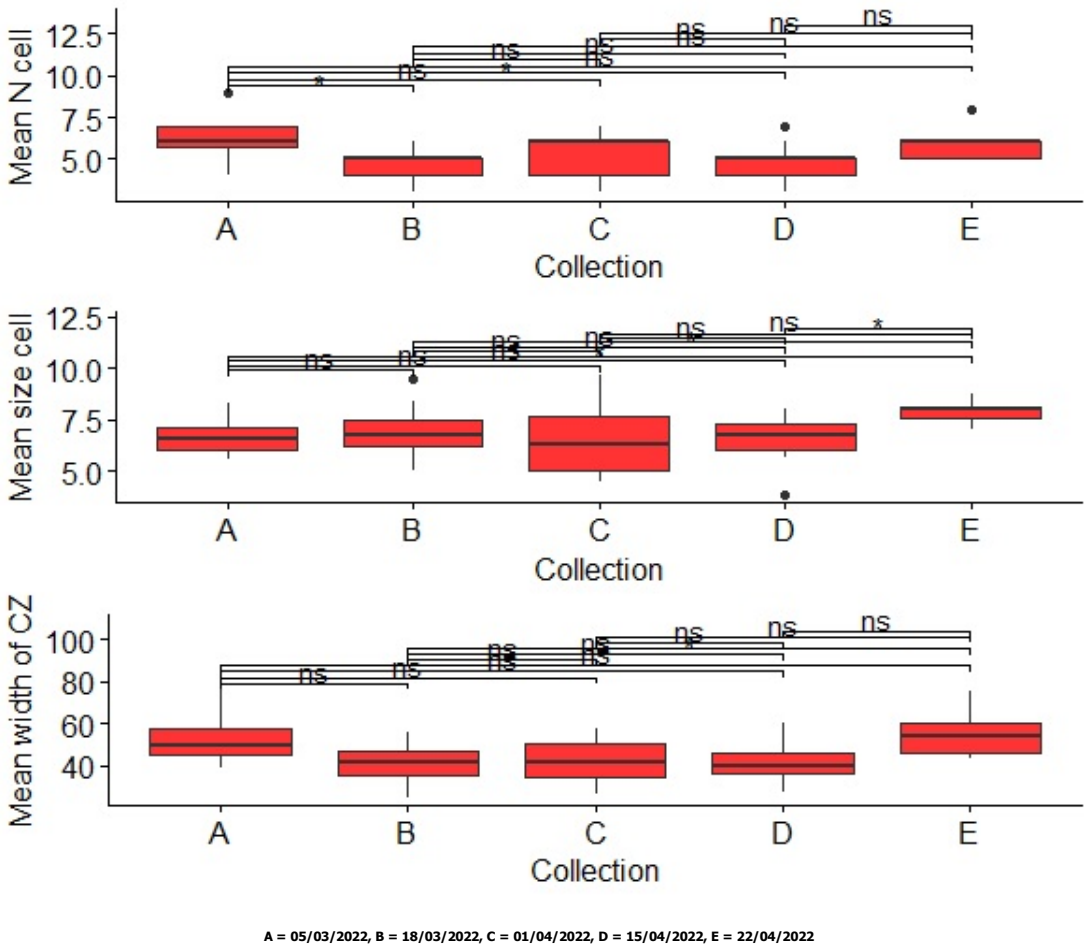


Figure 3.16: Boxplots considering all individuals of S. subcordatum indiscriminately. Mean number of cells counted by radius (Mean N cell), radial width of these cells (Mean size cell) and mean width of each entire zone of interest (Mean width of CZ) are computed for Cambial Zone (CZ). T-test were performed to compare the means, but only one of them has been significant (*), the others are non-significant changes (NS).

f) *Trilepisium madagascariense*

Samples of *T. madagascariense* have been collected from the second, on 18 March, micro-coring collections to the five one on 29 April. Cambial activity is observed within each sample of each individual of T. madagascariense over the study period. In addition to xylem development observations, development of secondary phloem is observable (Figure 3.17A and C). Therefore, the cambial zone is quite large, composed by many cells.

Visually, the three individuals show a cambial activity along the 4 collections especially for the individuals 1 and 3. But in the case of the individual2, the cambial activity is more important during the second collection notably apparition of new vessels, and during the third collection and seems to stop after that (Figures 3.17A). This is also reflected in the fact that the boxplots for the number and size of cells for the enlarging cells have interval boundaries of 0 (Figure 3.18A). In addition, even if cambial activity is observed, only cells in division and in enlargement phase are noticeable. No lignification is thus observed.

Quantitatively, only one significant difference of the means, both in terms of number and cell size, for each considered part is noticed between collections B and E (Figure 3.18A). The average width and number of cells of each of the tree part of interest seems to slightly decrease over time (Figure 3.18B). Relatively considered, the cambial zone is more represented both in terms of number of cells and by the

width of CZ, proportionally to EZ and Ph which are less represented within the zone of development (Figure 3.18C). However, the proportions occupied by each type of cells remain constant over the study period.

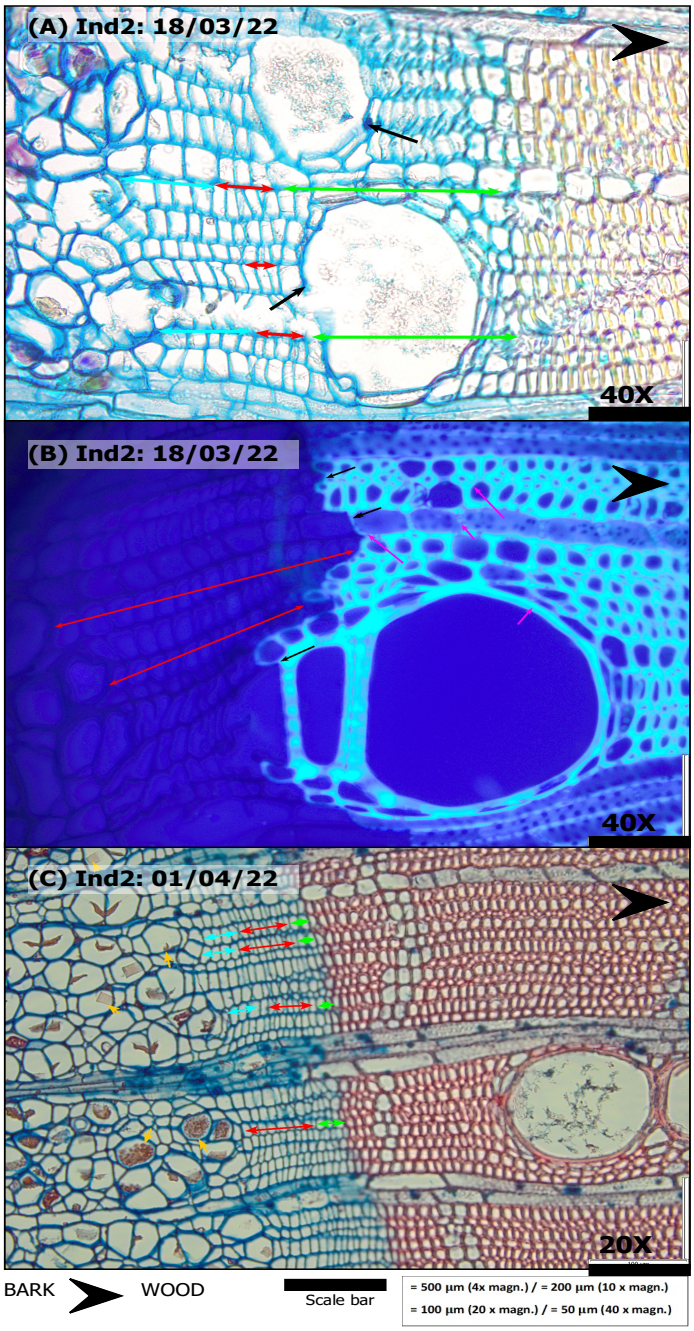


Figure 3.17: Cross-sections of *T. madagascariense* under DIC filter (A), under light of microscope (B), and under light microscope (C). The cambial zone is composed by numerous narrow cells (red arrows). The limit of lignification is observed thanks to the difference of brightness (A) and colours (C). Blue cells and elements are non-lignified as opposed to the bright or red elements that are lignified. Sometimes new non-lignified vessels are observed (A) (black arrows). Under blue light, the limit between lignified and non-lignified elements is clear (black arrows), intercellular spaces are lignified from the end of CZ and walls of mature cells such as fibres and fibres are lignified (magenta arrows).

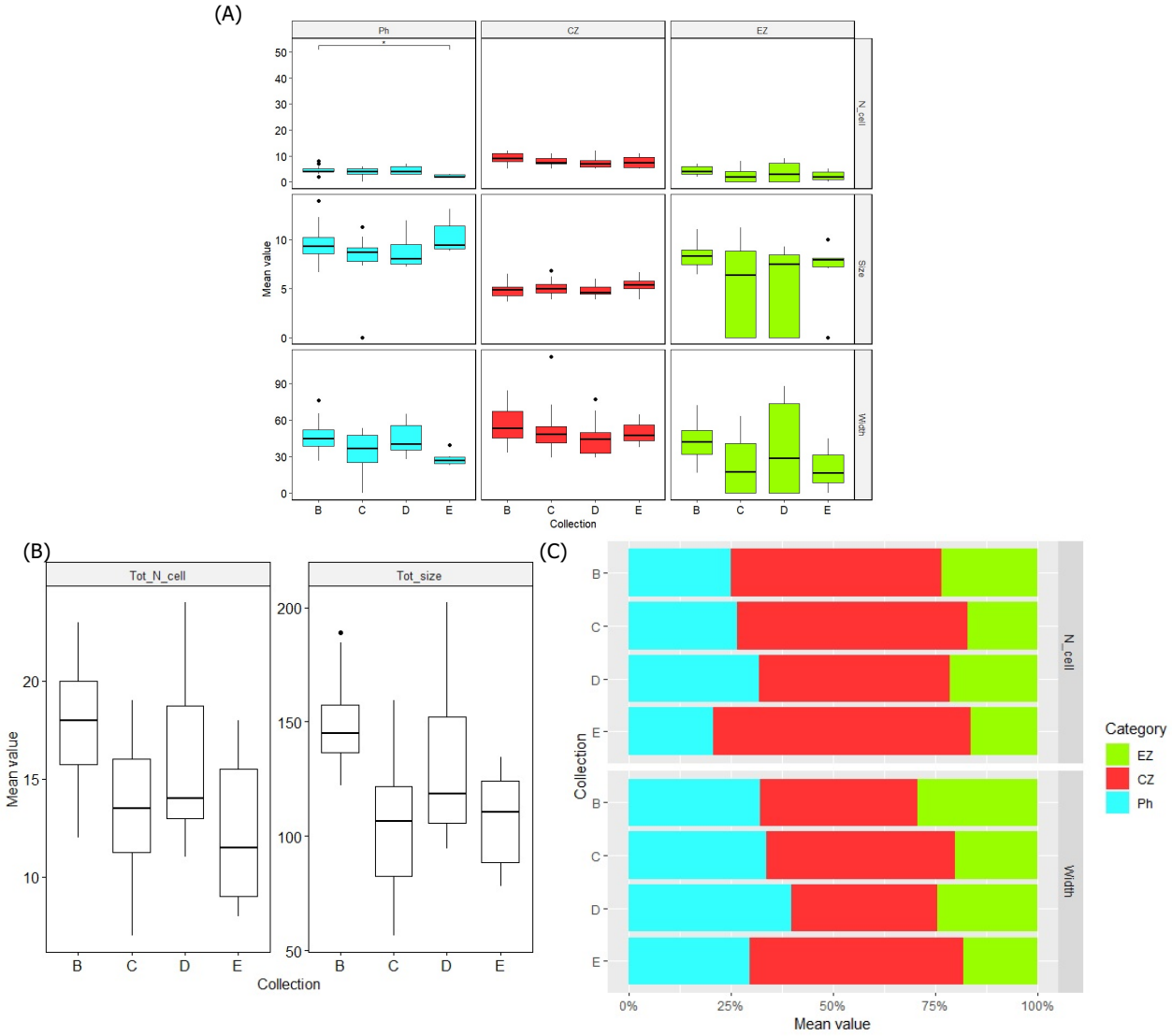


Figure 3.18: Boxplots considering active cambium of the 3 individuals of T. madagascariense indiscriminately. Mean number of cells counted by radius (N_cell), radial width of these cells (Size) and mean width of each entire zone of interest (Width) are computed for Cambial Zone (CZ), Enlargement Zone (EZ) and Phloem (Ph) (A). T-test were performed to compare the means, but only one of them has been significant (*) between the first and the fourth collection, the others are non-significant changes (NS). The total mean number of cells and the total mean width of the zone in development decreases over collection (B). The average relative part occupied by each zone of interest within the zone of development in terms of number of cells or width fluctuate over data collection (C).

3.3.1 Summary of observations

Overall, the growth ring transition is most easily seen at the macroscopic scale, with areas devoid of parenchyma and vessels. However, on a microscopic scale, when the transition is visible, radially flattened fibres, sometimes with thickened walls, are often observed (Table 3.2).

L. thompsonii and *S. subcordatum* show any cambial activity, and the mean number of cells in CZ remains constant over the study period. *T. madagascariense* present active cambium but the total number of cells decreases over time. *P. oleosa* and *S. zenkeri* present only one individual with cambial activity but the total number of cells produced over time increases for them while it remains constant for inactive individuals. *P. macrocarpus* shows a cambial activity for 2 of the 3 individuals, but the average total number of cells in development decreases whereas the cells number of cells of CZ is increasing for inactive individual.

Table 3.2: Summary of characteristics of ring transition for 6 species of Yangambi forest at macroscopic and microscopic level.

Characteristics of rings transition		
Species	**Macroscopically**	**Microscopically**
L. thompsoniii	Absence of axial parenchyma , Absence of vessels	/
P. oleosa	Less compacted axial (scalariform) parenchyma	Sometimes axially flattened fibres Absence of axial parenchyma, Absence of axial parenchyma
P. macrocarpus	Absence of axial parenchyma over several micrometers, Marginal band of parenchyma	Small discontinuous bands of parenchyma, Axially flattened fibres
S. zenkeri	Very thin band of fibres, Thickened fibres wall, ! wedging rings	/ , Sometimes flattened fibres
S. subcordatum	Absence of reticulated parecnhyma bands, Marginal band of parenchyma	/
T. madagascariense	Very thin band of fibres, Thickened fibres wall, ! wedging rings	/ , Sometimes flattened fibres
S. subcordatum	Absence of axial parenchyma, Absence of vessels, Discontinous band of parenchyma	Axially flattened fibres

Average values can be extracted from the measurements in Fig 3.8, Fig 3.10, Fig 3.12, Fig 3.14, Fig 3.16, Fig 3.18. Mean number of cells for each zone of development have been calculated by computing results for the 3 individuals, considering both dormancy or activity of the cambium. In average, the cambial zone is mainly represented within the zone of development.

Table 3.3: Data and measurements of cambial zone elements for monitored species. N is the number of radii considered. Mean values have been calculated based on the mean value obtain for each considered radius.

Mean number of cells (SD)						
Species	**Ph**	**CZ**	**EZ**	**TZ**	**LZ**	**Total**
L. thompsoniii	-	8,07 ± 1,67	-	-	-	8,07 ± 1,67
P. macrocarpus	-	6,54 ±1,62	1,30 ± 2,01	1,28 ± 2,44	-	8,85 ± 3,78
P. oleosa	-	7,98 ±2,92	1,55 ±2,93	1,77 ±3,44	2,02 ±4,08	6,54 ±11,74
S. zenkeri	3,12 ± 1,42	6,27 ±1,18	2,56 ±4,21	2,1 ±4,37	1,67 ±2,96	7,98 ±11,02
S. subcordatum	-	5,25 ±1,18	-	-	-	5,25 ±1,18
T. madagascariense	4,07 ± 1,47	8,21 ±2,13	3,51 ±2,46	-	-	15,79±1,23
Total average species	3,65 ± 1,67	7,09 ± 2,18	4,64 ± 3,15	5,83 ± 4,40	4,75 ± 4,49	10,57 ± 7,81

For various reasons, it was decided that certain species should no longer be considered. Indeed, wood of *A. mannii* stains rapidly when stored in ethanol. Therefore, visual identification of the cambial area is made almost impossible. *C. lacourtianum* was also left out because the individuals were very variable in morphology, notably by a very different DBH and difficult to find in the plots. After several treatments for the first three collections, the quality of the microsections for *G. suaveolens* are not satisfying (Appendice 6.3). Consequently, we did not further consider this species.

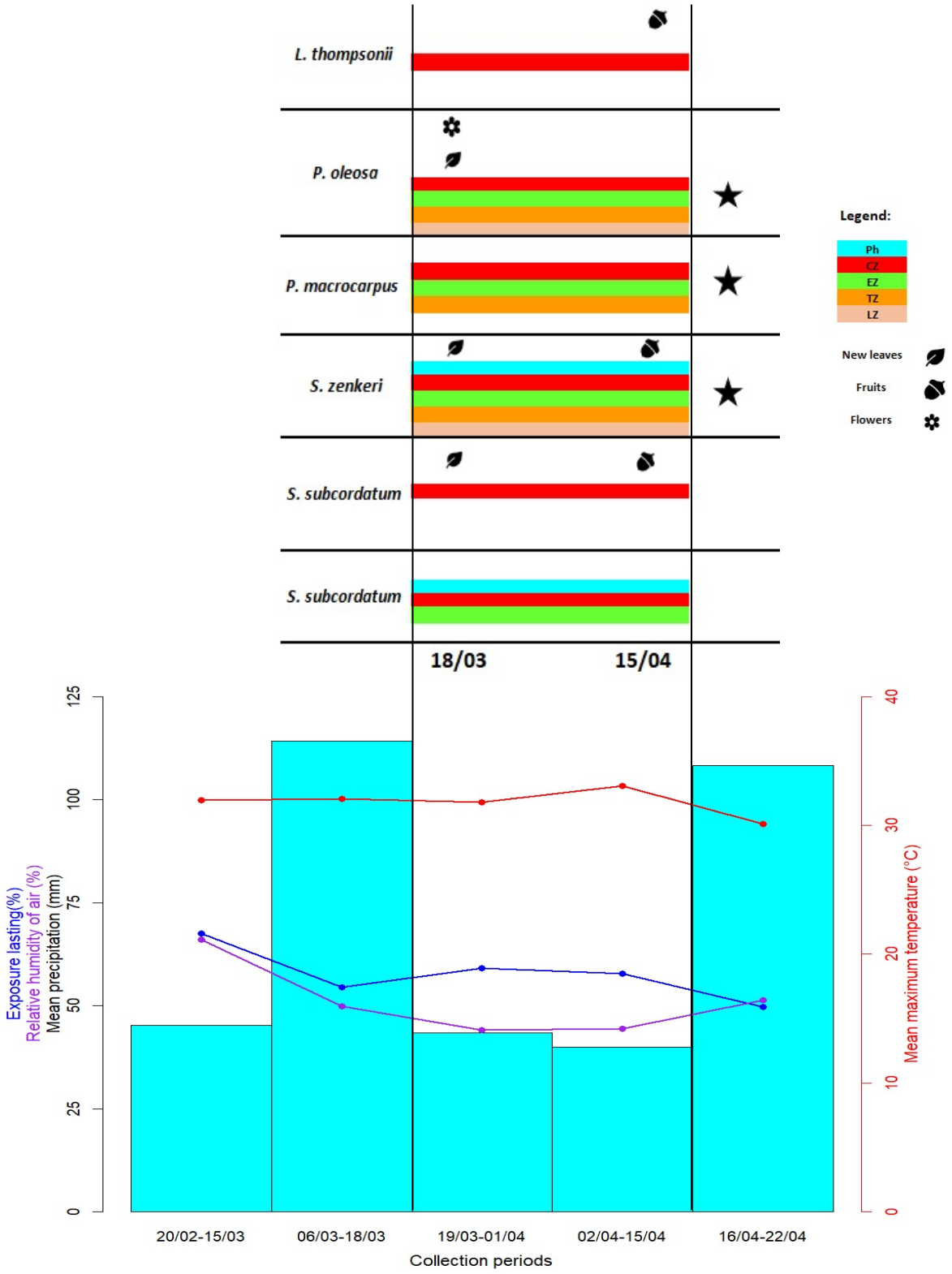


Figure 3.19: Phenology and cambial development rythms of studied trees, and climate data between March and April 2022 for study site. The star indicates that there is high intra-species variability in cambial and leaf phenology. Phloem (PH), Cambial Zone (CZ), Enlargement zone (EZ), Thickening Zone (TZ) and Lignification zone (LZ) are estimated.

3.4 Phenological data

3.4.1 At plot scale

Some species seem to have a more developed foliar phenology than others. Globally, individuals within a same species follow the same trend of foliar phenology over the study period. Over the study period, *P. macrocarpus, S. subcordatum, S. zenkeri* and *T. madagascariense* show no significant changes in their leaf phenology, mainly composed of old leaves. However, *S. subcordatum* produces fruits during the seasonal transition from 18 March to 15 April. The fruiting phenology of *S. zenkeri* changes little but the appearance of mature fruits, thus also of immature fruits, occurs within 1 month during the seasonal transition when no new leaves are produced. In the opposite, few intraspecific variations are observed for *P. oleosa* and *L. thompsonii. P. oleosa* also shows a decrease in leaves production. In contrast, *L. thompsonii* and *G. suaveolens* seem to produce more leaves during this transition.

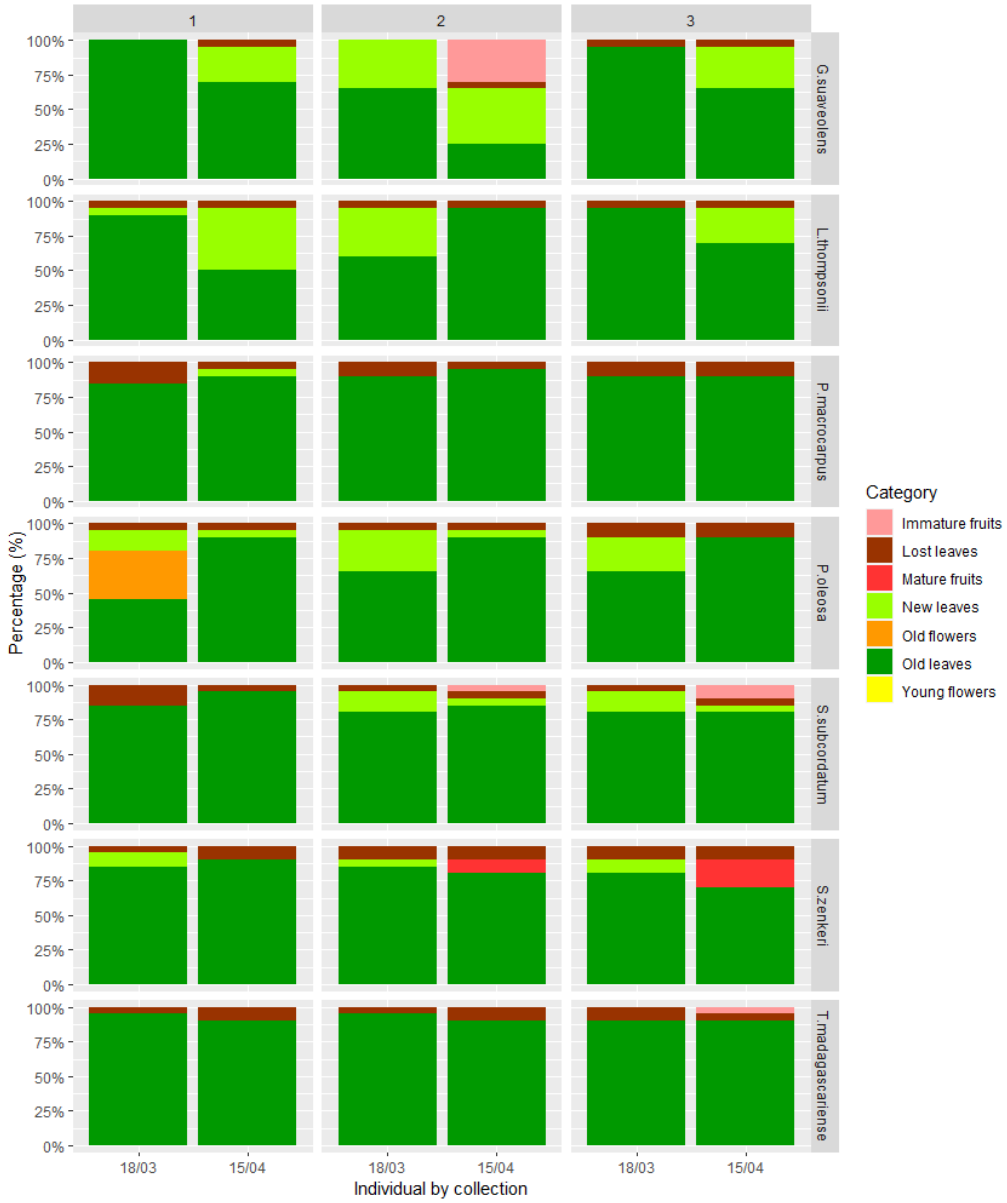


Figure 3.20: Stacked barplots of the evolution of foliar phenology from the 18 March to the 15 April2022 for the three monitored species. 1, 2 and 3 correspond to the number of the individual followed.The relative parts of each category of leaves, fruits and flowers are cumulated for each individual of each species.

3.4.2 At forest scale

The phenocam images were briefly studied. However, monitoring of the 4 circled cymes showed that some deciduous species (Red circle in figure 3.21) produced new leaves during the 2 months of observation. Other trees maintained a developed foliage (Blue circle in figure 3.21). Others appear to have produced new leaves and/or fruits (Purple and brown circles in figure 3.21).

Figure 3.21: Images taken by Wingscape autonomous phenocam on 3 dates with 1 month interval. 4 crowns were marked with a coloured circle showing deciduous species (red and purple circles), developed foliage (blue circle) and production of fruits or new leaves (purple and brown circles).

3.5 Climate data

Climate data were collected from February to May, corresponding to the transition from the dry season to the short rainy season. While the observed maximum and minimum temperatures are rather constant, parameters such as relative humidity or precipitations vary over the considered period (Figures 3.22A and C). This is confirmed by, firstly, the small standard-deviation of the average minimum and maximum temperature; and secondly by the higher standard-deviation of the humidity of air and precipitation (Figure 3.22C). Two peaks of precipitation occurred during the study period in March and in April, corresponding to the second and the fifth collection, respectively. A lower relative humidity and a less important insolation index are also observed over a period of 5 weeks between these extremes (Figures 3.22A and B), during the third and the fourth collections (Figure 3.22D).

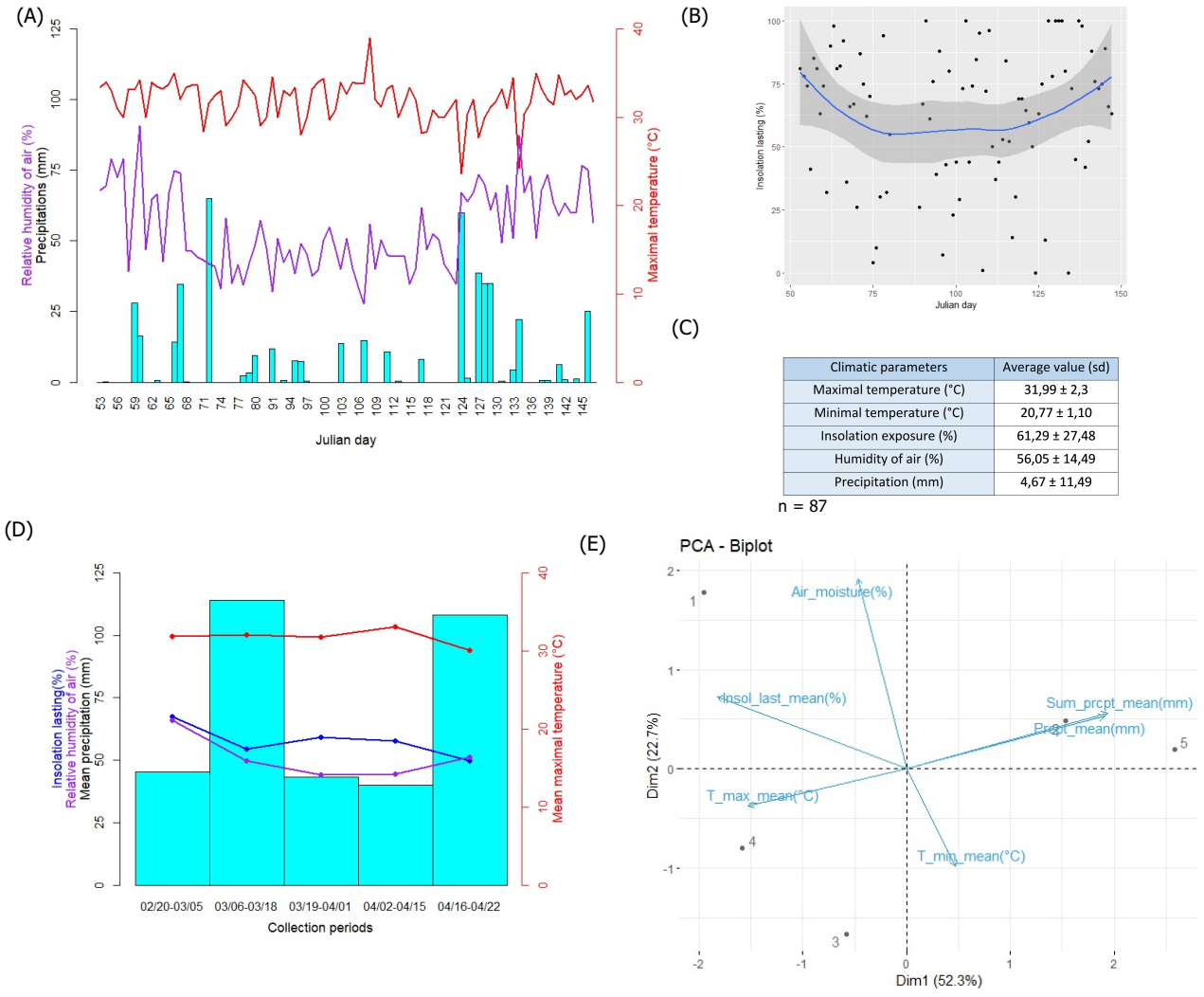


Figure 3.22: (A) Umbrothermal diagram over February to May 2022 for Yangambi. (B) Plots of the evolution of insolation index from February to May 2022 for Yangambi. Blue line is a fitted curve based on Loess regression. (C) Average climate parameters for the study period (D) Umbrothermal diagram from February to April 2022 for Yangambi, considering an interval of 2 weeks before each data collection. (E) PCA graph made on the average climate parameters obtained by intervals of 2 weeks over the study period (from 22/02/20 to 22/04/22) for the values of air humidity, sustained insolation, maximum and minimum temperatures (°C), precipitation (mm) and sum of precipitation (mm).

Resulting from the PCA, 3 groups are formed: the first with collections 2 and 5, the second with collections 3 and 4 and the last one for the first collection (Figure 3.22E). Indeed, when comparing these results with barplot considering two weeks intervals (Figure 3.22D), the intervals before the collections 2 and 5 are marked by higher precipitations, and a lower exposure index. The group

of collections 3 and 4 is marked by a lower air humidity rate, lower rainfall and higher maximum temperatures. Collection 1 is therefore characterised by air humidity and higher exposure time, but with lower rainfall.

3.6 Relation between climate parameters and cambial/leaf phenology

3.6.1 Cambial and foliar phenology relation

As the leaf phenology data were only collected twice at monthly intervals, it is possible to relate these data to the cambial data but not with a quantitative approach. The general status of the cambiums of each individual and each species observed for the study period is described in the following table. In addition, the status of the leaf parameters is assessed as a trend between the first and second foliar phenological collection dates, i.e. "Is there production of new leaves between the first and second collection dates? A "Yes" indicates that there is a positive evolution of the parameter, a "No" indicates that no significant positive evolution has been observed (Table 3.4).

No direct link between fruit, flower or new leaf production and cambial activity appears. Some individuals show cambial activity, but no change in crown composition. Conversely, other individuals are in cambial dormancy while leaves, fruits or flowers are produced (Table 3.4). Active individual of *P. oleosa* produces flower, and dormant individuals of *S. subcordatum* produce fruits over the study period.

L. thompsonii and *S. subcordatum* show no cambial activity reflected by a number of cambial cells that remains constant over the study period. But they produce new leaves, and immature fruits for *S. subcordatum*. In the opposite *S. subcordatum* presents a dormant cambium but produces fruits, flowers and leaves. The inter-individual variability of the 2 phenologies is important implying a difficulty to draw a trend for the species.
Dawkin index seems to be the same more generally identical for individuals within each species.

Table 3.4: Cambial status over the study period, and flowers, leaves and fruits production over the study period between the 18 March and 15 April, Dawkin index over the study period.

Species	Individual	State of cambium	Leaves prod.	Flowers prod.	Fruits prod.	Dawkin index
L. thompsoniii	1	Dormant	Yes	No	No	2-3
	2	Dormant	No	No	No	2-3
	3	Dormant	Yes	No	No	2-3
P. oleosa	1	Active	Yes	Yes	No	3
	2	Dormant	Yes	No	No	2
	3	Dormant	Yes	No	No	3-4
P. macrocarpus	1	Dormant	No	No	No	5
	2	Active	No	No	No	5
	3	Active	No	No	No	5
S. zenkeri	1	Dormant	Yes	No	No	5
	2	Active	Yes	No	Yes	3
	3	Dormant	Yes	No	Yes	5
S. subcordatum	1	Dormant	No	No	No	5
	2	Dormant	Yes	No	Yes	2-3
	3	Dormant	Yes	No	Yes	2
T. madagascariense	1	Active	No	No	No	5
	2	Active	No	No	No	5
	3	Active	No	No	Yes	5

3.6.2 Cambial activity and climate relation

3 models M0 (2), M1 (1) and M3 (2) were tested to assess the potential influence of climate on cambial growth. Generated mixed models using M1 almost all agree that there is no significant influence of climate on cell production (Table 3.5). But, the relevance of the model can be questioned by comparing this model with other models (M0 and M2).

M1 seems to be uniquely suitable to *P. oleosa* and *S. zenkeri* and to a lesser extent to *P. macrocarpus* (Table 3.5). Indeed, as we compare M1 and M0 that does not take the climate factor in account, the integration of climate factor and random « Individual » factor makes the model more sensitive for *P. oleosa* and *S. zenkeri*. It is traduced by a lower AIC, a significant difference for the ANOVA of the 2 models and a high conditional R^2 for M1 (Table 3.5). Thus, a tendency to increase the number of cells can be observed with increasing rainfall and decreasing exposure time for both species. Moreover, a higher interval is observed around the intercept of fix factor for these 3 species, traducing a high variability of the cells number between individuals. The significant difference observed between M1 and M2, and the higher standard error of random effects confirm the importance to take in account the random effect related to individual for these 3 species. Therefore, it can be said that the proposed M1 model is more relevant for species that show marked cambial activity for at least 1 of the monitored individuals.

On the other hand, M1 seems to be unsuitabled for the other species due to rather low marginal and conditional R^2. In addition, integration of climate in M1 and M2 for *L. thompsonii, S. subcordatum* and *T. madagascariense*, do not provide further information in comparison to M0 explained by a unsignificant difference observed between models by the ANOVA, but also by a higher AIC for M0. It is understandable that it is the case of *L. thompsonii* and *S. subcordatum* for which no cambial activity was observed. But it is problematic for T. madagascariense that present cells in division and in enlargement phase.

Table 3.5: Summaries of linear mixed model analyses of the relationships between cambial activity and climate taking into account the randomness of individuals (M1)

		L. thompsonii	*P. macrocarpus*	*P. oleosa*	*S. zenkeri*	*S. subcordatum*	*T. madagascariense*
M1 : ln(cambial activity) ~ climate+(1+climate| individual)							
		Coefficient [95 CI]					
Fixed effects	Intercept $\beta 0$	0,896 [0,849 ;0,938]	0,929 [0,781 ;1,083]	1,043 [0,56 ;1,52]	0,982 [0,499;1,464]	0,709 [0,686;0,733]	1,172 [1,089;1,254]
	Climate $\beta 1$	0,005 [-0,009;0,018]	0,014 [0,781;1,083]	0,034 [-0,024;0,099]	0,021 [-0,024;0,067]	-0,005 [-0,018;0,009]	0,015 [-0,009;0,037]
Individual random effects (SD)	Intercept 0	0,033	2,72	0,364	0,365	0,00	0,057
	Climate 1	0,003	0,25	0,037	0,031	1,339 e-02	0,004
Goodness-of-fit	Marginal R^2	0,007	0,014	0,0217	0,009	0,006	0,029
	Conditional R^2	0,125	0,327	0,846	0,939	0,006	0,23

Table 3.6: Results of the ANOVA tests performed between the different regression models by species. The level of significance is marked: significant (*), highly significant (**) and very highly significant (***).

All individuals considered						
Species	*L. thompsonii*	*P. macrocarpus*	*P. oleosa*	*S. zenkeri*	*S. subcordatum*	*T. madagascariense*
M0 VS M1	0,895	0,889	0,051	6,2 e-4(***)	0,933	0,487
M1 VS M2	0,419	0,178	2,2 e-16(***)	2,2 e-16(***)	1	0,179
M0 VS M3	-	0,06	-	-	-	4,94 e-05(***)

Consequently, it is interesting to better characterise relationship between climate factors and cells production, and thus better understand the differences observed from these regressions. For this purpose, Spearman correlations have been calculated between the total number of cells generated over the growing zone for each species, considering individuals indistinctly, and each climatic parameter. In the first row of the next table, we find the synthetic climate factor and the Spearman correlation indices for the different climate variables. The results obtained are similar to those identified by the PCA, i.e. the main axis is well correlated with precipitation, relative humidity and the insolation index. The correlations index for the species indicates that the correlations between the variables are very weak and that only a few are significantly correlated. In addition, several species show negative correlations.

However, if we only look at individuals that clearly show cambial activity, the correlation indices show a high correlation with the pattern of insolation, rainfall and the synthetic climate variable. This is particularly true for *P. oleosa* and *S. zenkeri*. But cells production is more correlated with rainfall and temperature for *T. madagascariense* and with temperature for *P. macrocarpus*.

As it can be seen that cells production of *P. macrocarpus* and *T. madagascariense* are not strongly correlated with the climate variable, but more so for the temperature variables and rainfall. It is interesting to generate alternative predictive model taking into account the variables for which a significant correlation has been identified via the Spearman test. Thus a third model M3 similar to M1 in which the climate variable was replaced by the temperature variables was proposed for *P. macrocarpus* (4) and *T. madagascariense* (5).

$$\textbf{M3-PM} : \ln(\textit{cambial activity}) \sim Tmax + Tmin + HR + (\mathbf{1}|Individual) \quad (4)$$

$$\textbf{M3-TM} : \ln(\textit{cambial activity}) \sim Tmax + Tmin + HR + Prcptsum + Prcpt + (\mathbf{1}|Individual) \quad (5)$$

M3 provide much more information than M0, as significant results of ANOVA between M3 and M0 shows (Table 3.6), AIC of M3 is lower than M0, M2 or M1. In addition, the conditionnal R^2 of these models are also more important, M3 thus seems to explain more of the variability around the observations than M0 or M1 (Appendice 6.1). These models allow to identifiy significant effects of different climate parameters.

Table 3.7: Spearman correlation indices for climatic data and the average total number of cells observed within the development area by species. The level of significance of the values for an alpha =0.05 is noted in brackets: (*) significant, (***) very highly significant. Average total number of cells (Tot N cell), synthetic climate variable (Climate), maximum mean temperature (Tmax), maximum mean temperature (Tmin), insolation lasting (insol), relative humidity (RH), precipitations (Prcpt), sum of precipitation (Sum Prcpt).

All individuals considered								
Species		**Tmax (°C)**	**Tmin (°C)**	**insol (%)**	**RH (%)**	**Prcpt (mm)**	**Sum Prcpt (mm)**	**Climate**
	Climate	-0,73	0,23	-0,88	-0,23	0,92	0,93	-
L. thompsoniii	Tot N cell	0,14	-0,05	-0,07	-0,32 (**)	0,05	-0,12	0,09
P. oleosa	Tot N cell	-0,16	0,21	0,08	-0,02	0,13	0,09	0,03
P. macrocarpus	Tot N cell	-0,57(***)	0,57(***)	0,43	(*) 0,21	0,23	0,25	-0,18
S. zenkeri	Tot N cell	0,15	-0,09	0,02	-0,14	0,25(*)	0,20	0,15
S. subcordatum	Tot N cell	-0,33(*)	0,30	0,19(*)	0,32 (***)	-0,09	-0,01	-0,13
T. madagascariense	Tot N cell	0,35(**)	-0,33 (**)	-0,29 (*)	0,29(*)	0,35(**)	0,35(**)	0,19
Individuals with active cambium								
Species		**Tmax (°C)**	**Tmin (°C)**	**insol (%)**	**RH (%)**	**Prcpt (mm)**	**Sum Prcpt (mm)**	**Climate**
P. macrocarpus	Tot N cell	-0,36(*)	0,35 (*)	0,12	0,17	0,14	0,15	-0,01
P. oleosa	Tot N cell	-0,26	0,26	-0,25	-0,44	0,35	-0,11	0,37
S. zenkeri	Tot N cell	0,32	-0,32	-0,68(***)	-0,76(***)	0,68(***)	0,32	0,68 (***)
T. madagascariense	Tot N cell	0,35(**)	-0,33(**)	-0,29(*)	0,29(*)	0,35(**)	0,35(**)	0,19

4 Discussions

4.1 Cambial data

The obtained results offer many valuable information on the cambium and its anatomy, on the particular case of Yangambi forest over the seasonal transition. More particularly about cells in enlargement and thickening phases for which studies remain rare. It also provided relevant information on the laboratory methods and tools to be used in the case of studies following the approach described in this work.

Growth rings transition
Regarding the characterisation of the transition zone macroscopically, numerous monitored species present a zone devoid of axial parenchyma on several micrometres, sometimes with discontinuous parenchyma band (Table 3.2). Microscopically, most species show a band of several radially flattened cells. Observation of flattened cells with thicken walls is characteristic for rings transition of temperate species even if the transition is more marked [39] or for other tropical species [76]. In the present case, these observations have been made on sections issued from the RMAC collection. Only a few of these could be observed on the samples collected in Yangambi especially for *S. zenkeri* in the vicinity of the cambial zone (Figure 3.13A) or sometimes for *L. thompsonii* (Figure 3.7). No other cases could be observed for the other species, even for individuals with inactive cambium. Hypothetically, either the ring transition zone was cut out during the preparation of the cores or it is located much further into the wood, showing that the start of the ring formation observed has started some time ago.

Globally, growth ring transition remains difficult to observe. But it can be explained by the local seasonality. Indeed, this is confirmed by Tarelkin who has demonstrated the anatomical variations of deciduous species are not significantly different according to the seasonality [39]. But these variations are much more important for evergreen and semi-deciduous species for well-marked precipitations [53]. She noticed that it seems more probable to observe an homogeneous wood with less variations of diameter fibres, and less abrupt thickening of cells for evergreen species under a low seasonality. In addition, the cambial dormancy induced by a period of drought implies important anatomical variation resulting in the appearance of annual growth ring for evergreen species. As the annual rainfall is rather well distributed over the year in Yangambi (Figure 2.1C), the growth rhythmicity is less regular than in other climate regime, involving less distinct anatomical variations. This statement corroborates the observations that have been made on the RMCA samples and on the collected samples.

Cambial zone
Visually, many observations and characterisations of cambial anatomy can be made for each species. The results detected cambial activity for 4 of the 6 monitored species for, at least, one of the 3 studied individuals (Table 3.4). *L. thompsonii* and *S. subcordatum* show no cambial activity. Moreover, any onset of the cambial activity has been detected during the study period. But different developmental stages were detected depending on the species ranging from dividing cambial cells to cells in the lignification phase (Figures 3.7, 3.9, 3.11, 3.13, 3.15 3.17).

The variable quality of the samples and sections affects the visual interpretation. In addition, using adapted tools is essential to conduct relevant analyses of active cambium. For individuals for which xylem and cambial zone demarcations are well marked, notably thanks to coloration, an analyse under a light microscope can be sufficient (Figures 3.17). In contrast, study of individuals with active cambium is much more complex and more subjective despite the used tools. It is the reason why filters (DIC filter and Epifluorescence) should be used (Figures 3.9, 3.11, 3.13). Characterisation of wood anatomy can be extended to the phloem but this part has not been detailed on this work.

For several species, bands of axial parenchyma were directly encountered the cambial zone, especially for *L. thompsonii* (Figures 3.17). These bands seem to be mature wood, signifying that dormant

cambium is sometimes accolated by band of parenchyma. It can be a limit of growth rings such as observed for *S. parahyba* [76]. In *Cedrela fissilis* this marginal band of parenchyma is produced just before the dormancy [77], it is also the case for *Carapa guianensis* and *Swietenia macrophylla* [78]. This could confirm the conclusion made for LT where a dormant cambium is observed but where parenchyma adjacent to the CZ is often found.

The characterisation and counting of cells in the different development zones can be influenced by different factors. Firstly, the distinction between thickening and lignifying cells is complex and subjective, especially when using unsuitable tools. Secondly, lignification can start while the walls of the fibres thicken (Figures 3.13D). This complexity in separating the two phases is reflected in a larger interval around the calculated mean value of the cell size or cell number variables in *T. madagascariense* and *L. thompsonii* (Table 3.4). Consequently, it might be more relevant to consider these areas indiscriminately. Thirdly, some species have a much more developed network of vessels, such as *P. oleosa* near the cambium. As these vessels were not taken into account in the measurements made, it is likely that the number of cells observed per ray for these species is affected (Figure 3.9). This also induces more variability around the average zone width values (Table 3.4).

Quantitatively, the results show that dormant cambiums, observed for *L. thompsonii* (Figure 3.7) and *S. subcordatum* (Figure 3.15), are characterised by a constant mean number of cambial cells over time. For *P. oleosa* and *S. zenkeri* the total number of cells evolves for the active individuals, but remains constant for inactive individuals (Figures 3.14A, 3.10A). Numbers of cells varies for all the individuals of *P. macrocarpus* (Figure 3.12A).

Globally, *S. zenkeri* and *T. madagascariense* show both secondary xylem development, and secondary phloem development (Figures 3.13, 3.17). It is interesting, because information about development of phloem remains rare. On average 4 cell layers were observed for these species. Marcati also observed 2 to 5 immature phloem cells next to active cambium for *Schizolobium parahyba* [76].

Significant differences of the mean number or size of cells between collections have been rarely occurred. However, the data sets generated for each individual and species remain quite reduced, test may be subjective or unrepresentative. Furthermore, as the cambium study is a punctual measure it is really important to multiply measurements and collection over time. The number of cambial cells between active and inactive individuals is only slightly different for *P. oleosa, S. zenkeri* and *P. macrocarpus* (Figures 3.9, 3.13, 3.11). The average number of cambial cells is around 6-7 cells, although *S. subcordatum* has a reduced CZ with 5 cells and *L. thompsonii* a larger CZ with 8 cells, with small increments for active individuals. Although some studies have shown that cambial zone can be reduced to only 2 or 3 cells [79], number of cambial cells is from 5 to 11 cells for dormant cambium, with an average increase of 2-3 cambial cells during cambium activity [80, 81, 82, 57]. But in some cases, number of cells can raise until 15 to 20 cells at the peak of cambial activity [83, 77, 76]. Most of the time the more numerous cells within the zone of development of active individuals are cambial cells. However, the cumulated cells located outside the cambial zone are more numerous (Table 3.4). The same observation was made by Morel on *Parkia velutina* and *Parkia nitida* [75]. Number of cells in development located outside the CZ can reach 30 cells in differentiation phase [76, 80]. Although the time steps considered in these studies are much larger than the one considered in this curent work, our obtained results seem following the same trends as observed for tropical and temperate trees.

Finally, in order to assess the state of cambium, it is important to combine the quantitative and visual approaches which provide complementary information. Most of the time, if cambial activity is visually observed, the quantitative approach confirms these observations. On the other hand, it happens that visually no differences, especially in terms of cell number, are detected while quantitative analysis show an increase in cell number. This is particularly the case when the cells of the CZ are dividing but have not yet entered the enlargement phase. On the other hand, it is important to note that only the characterisation of the shape, size and number of cells within the developing zone were

considered as indicators of cambial activity. Indeed, the ultrastructure of a cambial cell consisting of a vacuole, the wall or the mytotic apparatus evolves during cambial activity and can be used as proxy for detect onset of cambial activity [84].

4.2 Phenological data

Obtained results globally confirm the information gathered in the literature (Table 2.1). 3 of the 6 species show very little change (*P. macrocarpus, S. subcordatum, T. madagascariense*) and 3 others show a slight (until 20%) increase (*L. thompsonii, P. oleosa*) or decrease (*G. suaveolens*) in mature leaf composition as well as anecdotal fruit and flower production for *S. zenkeri* and *P. oleosa* (Figure 3.20). This variability of cases and situations is also reflected in the phenocam images that show the production of new leaves and fruits for some trees, and a maintenance of leaf abundance over the 3 months of observations (Figure 3.21). The senescence observed in March seems to be gradually disappearing (blue circle in Figure 3.21). As the species have not been identified on the images and not observed with binoculars, their exact temperament cannot be known. However, some of them do not seem to be completely deciduous (purple circle in Figure 3.21). This is confirmed by the fact that some senescence can be observed even in evergreen species [39, 9].

4.3 Relation between climate parameters and cambial/foliar phenology

4.3.1 Variability of cambial and foliar phenology

As the previous results show, important variabilities of foliar and cambial status exist between and within species (Figure 3.19, Table 3.4). Many studies have confirm these important interspecies and inter-individual variabilities [39], sometimes observed even under similar environmental conditions [85]. Many justifications can be put forward. Firstly, phenological activities can be synchronous [86] but also asynchronous [37]. For numerous evergreen or semi-deciduous species, leaves of flowers or at least buds flushing start several weeks before the onset of cambial activity [87, 79, 37]. Secondly, it has been recognised that cambial activity is not uniform in all directions. Study on *Robinia pseudoacacia* has shown that the solar radiation can lead to an increase in temperature at the periphery of the trunk and promote cambial growth depending on the direction of the light received [88]. Indeed, in one hand, as a reminder the collection of samples started in the northern direction. On the other hand, numerous monitored individuals present a Dawkin index of 2 or 3 signifying that one side of the tree receives light preferentially. Unfortunately, the direction from which individuals receive this light has not been determined, so this hypothesis cannot be concluded. But hypothetically, the sampling process realised can be unrepresentative of the major trend of the entire individual. Thirdly, according to Rathgeber, differences in status related to diameter, height or exposure of the crown can influence the intra-annual cambial dynamics of species [89]. As all individuals are broadly in the same diameter class, it seems unlikely that differences between individuals of the same species are related to this variable but it can be true to explain differences between species. The height of monitored stems is variable, but the higher individuals, dominant, which have more access to light, are not systematically those with an active cambium. However, this must be contextualised according to the respective light requirements and the development stage of the species. In addition, some non-dominant trees have significant access to light, as shown by *S. zenkeri* (Table 3.1). Our results do not really seem to follow Rathgeber's observations. Finally, sometimes growth abnormalities such as momentary cessation of cambial activity can occur. According to Detienne this could be caused by phenological events [62]. Otherwise, intraspecific variability can be explained by the accessibility to other resources such as water and minerals within the soil. Indeed, the influence of soil moisture on the cambial activity has been several times proved [56, 86, 75]. In addition, the interspecies variability can be related to the lack of knowledge on species phenology, especially about the interannual variability of growth cycles of trees. Indeed, some species adopt an biannual cycle of growth [14, 15, 16]. Finally, endogenous factors can influence phenophases of cambium differently for the individuals [22, 23, 24].

4.3.2 Cambial activity and climate

Spearman correlations between climate parameters and production of cells are low when the individuals of the same species are considered indistinctly. However, they are more important and also have a more significant effect on growth when tested only on active individuals. As for the variability of correlations between climatic variables and cells development of species, predictive models of the cell production must take into account different climatic parameters (Tables 3.5, 3.6). This inter-species variability, even when considered under the same climate conditions, seems to be confirmed in many cases [90].

For this study, the most explanatory factor of the cells production is the synthetic climate variable for *P. oleosa* and *S. zenkeri*. As a reminder, both the average rainfall and the duration of exposure underlie the synthetic variable, thus it is their combined effects that measure the influence of cell production. Even if its effect is not significant, the synthetic climate variable seems to be an acceptable predictor of cell production for these 2 species for the study period. However, the conditional R^2 values remain rather low, the model only offers a partial answer for the cells production of both species when considering indistinctly dormant and active individuals. Indeed, some studies have shown the complexity of growth-climate relationships due to the frequent correlation of climateparameters [91]. On the other hand, the synthetic climate variable is a much more reliable predictor when only active individuals are considered (Table 3.5).

As observed for *S. zenkeri* and *P. oleosa*, many studies have proven the importance of precipitation on cambial activity for many climatic and ecological contexts in tropics and subtropics [92, 75]. Most of the time radial growth is correlated to the average daily precipitation and cumulative precipitation. A positive correlation between the annual growth of trees and annual precipitation has been verified for species of the Thsopo [39]. More particulary, Iluanga and al. have shown that M.excelsa is correlated to the first rainy period (from April to May) while *P.elata* is correlated to the second rainy period (from September to octobre) (Ilunga et al., 2022). As with these two species, it is possible that some species such as *T. madagascariense, S. zenkeri* and *P. oleosa* may be more susceptible to the short rainy season (Feburary to June), while *L. thompsonii* and *S. subcordatum* may be more susceptible to the second rainy season (July to December) (Figure 2.1C). Furthermore, we only consider 2-weeks intervals of precipitations, but we do not evaluate the influence of precipitation cumulated over a longer period. Indeed, Worbes notably proved that the cambial activity was not only due to the rainfall of the few weeks preceding the collection of the samples, but rather to the yearly rainfall accumulation [43]. In the same vein, Brienen showed that for *Amburana cearensis* cambial activity was indeed correlated with the amount of precipitation observed during the cambial activity period [93]. But for cedrela odorata, the start of the cambial activity depends on the amount of the last precipitations that took place during the previous activity period [93]. Moroever, Brochert has shown that in tropical dry forests, although a correlation is observed between rainfall and cambial growth for deciduous forest, semi-deciduous and evergreen species are more dependent to water reserve of the soil [56]. In this case, growth is strongly dependent on the water reserve of the soil [56]. In particular, vascular tissue differentiation is associated with soil moisture and rainfall [91]. Marcati also found that cambial activity was highest when excess water was present in the soil [76]. This emphasizes the importance, not only of rainfall at a "T" time, but especially of the availability and quantity of the soil water reserve. These assumptions should be reconsidered in this case study.

If the model M1 that consider the synthetic climate variable is the most acceptable of the proposed models for *P. oleosa* and *S. zenkeri*, others models taking temperature variable seem to be more suitable for *T. madagascariense* and *P. macrocarpus.* The alternative models proposed for *P. macrocrpus* and *T. madagascariense* seem to offer a better prediction of cell growth due to lower residual error and higher R^2. Maximum and minimum temperatures as well as relative humidity are to be considered for *P. macrcarpus* (M3_PM), in addition to these variables average and total rainfall are to be considered for *T. madagascariense* (M3_TM)(Appendice 6.1). Although the influence of these parameters is much more significant and offers a better predictive model, they therefore require more

variables. However, all the proposed models show that there is a significant gain in incorporating the random effect of individuals, especially when there are few individuals that show very different cambial status. The effect of temperature on the resumption of cambial activity is well known in temperate climates [81, 50]. In addition, Pandley has also reviewed the state of knowledge on the climat-growth relationship for many case studies [59]. Conversely, the impact of temperature seems to be less obvious in tropical climates [94]. Temperature is sometimes correlated with other climate variables such as exposure time or evapotranspiration, which means that its lonely effect on growth is rarely established [91, 95] .

Furthermore, S. *zenkeri, T. madagascariense* and *S. subcordatum* growths are negatively correlated with time exposure. The exposure time tends to decrease over the study period. However, exposure thime, or photoperiod, may play a role in the recovery of cambial activity. Indeed, Clark et al. have shown that beyond a certain water availability, the limiting factor for growth is photosynthetic radiation [9]. Moreover, cambial dormancy in a tropical evergreen species is long-lasting, and the initiation of cambial activity can be related to day length [79]. Therefore, some of the species considered may be more sensitive to this variable.

The results obtained by linear mixed models should be considered with reservations. Indeed, on the one hand, the set of cellular data is rather reduced because of the shortness of the study period and the number of individuals considered for each species. On the other hand, the climate variable used only explains 52% of the variability observed between data collections. Thus it is very likely that other factors than those retained by the main axis of the PCA have an influence on cells production that is not measured by the regression. Furthermore, as has been shown, variation in cell numbers between collections is rarely significant. Therefore, the non-expression of the regression may not be due to the fact that climate has no influence on cell production but rather that there is statistically no cell production during the study period. Moreover, these calculations were made considering individuals with very different cambial states. It therefore seems logical that for species and individuals which do not show any cambial activity during the study area, that the climate does not explain the cells production. Finally, mean climate parameters consider a two weeks interval before the micro-cores collection. This means that even if the effect of climate is insignificant at the scale of the interval considered, the hypothesis that variables considered over a longer period of time may have an effect on cell production.

In conclusion, we note that growth-climate relationships differ from one species to another. This is a phenomenon also observed by Yanez-Espinoza, who explains this variability by the fact that the species manage to coexist by adopting different growth-climate relationships [91].

4.3.3 Foliar phenology and climate

On the scale of the study period, leaf production, fruiting and, to a lesser extent, flowering are noticeable for certain species (Figures 3.20, 3.21, 3.19 and Table 3.4). No significant senescence was observed. We see that for *G. suaveolens* and *L. thompsonii* there is a decrease in old leaves and an increase in new ones (Figures 3.20). For *P. oleosa* there is leaf maturation. This production of leaves implies that senescence must have occurred previously. If it is true that the leaf fall and production of evergreen species is less marked, caducity is possible under certain conditions [39]. However, Yanez-Espinosa has shown that in subtropical environments these species can adopt a certain seasonal phenology [86]. In addition, leaf loss of deciduous species occurs during the drought period for Thsopo. Indeed, some evergreen species can show periods of senescence in strong climates, but in weak climates this phenomenon is much less intense and shorter [53]. However, leaf production could be positively correlated with rainfall, especially for *P. oleosa*, *S. zenkeri* and *S. subcordatum* which show the appearance of new leaves following the first peak of rainfall observed during the study period (Figures 3.20). This phenomenon has been observed in particular for species forming the canopy [90]. Our trees are dominant or sub-dominant so this could be the case. Consequently, if we assume that leaf loss is initiated by the drought period at the beginning of the year (Figure 2.1C), by

producing new leaves, the species show a more or less rapid or important reaction to the short period of senescence induced by this drought. However, Borchert has shown that rainfall is rarely in deficit at the equator and does not coincide with phenological strategies [96]. But the phenological previous data for February are missing to confirm any of these hypotheses.

Moreover, it seems that the observations made at the plot level illustrate well the diversity of cases observed at the forest level. The phenocam images illustrate some greening from March to May, with new leaves production in many crowns. This observation was also made in February in tropical Africa by Borchert [96].

Moreover, results show that species and individuals seem adopt different reproductive strategies such as flowering and/or fruiting cycles by producing asynchronous fruits or flowers (Figures 3.19, 3.20). Adamescu studied this variability of strategies across Africa and found that although these processes are often annual, especially for West African species; they are mostly irregular, and can also be sub-annual for East Central African species [97]. Moreover, it shows that these processes take place throughout the year even when there is a marked seasonality [90, 97]. Thus, although environmental conditions fluctuate annually, they have an impact on seasonal growth, they do not seem to be identical throughout Africa. This observation shows the importance of understanding locally or regionally the relationships between phenology and climate.

A slight decrease of the time exposure is observed over the study period (Figure 3.22B). But overall, an increase in leaf mass and crown turnover was observed for the species monitored as well as at the forest scale (Figures 3.21, 3.19), perhaps excepted for *G. suaveolens*. In temperate regions, the decrease in photoperiod often leads to a loss of leaves [98]. In the tropics, leaf loss can be related to the photoperiod but also to the rainfall pattern. Furthermore, some semi-deciduous species from Central America renew their leaves following an increase in photoperiod [58], which seems to not corroborate our results. It is possible, however, that cloud cover was less important during the dry season preceding the data collection. Due to lack of data, this hypothesis cannot be excluded. But other studies have shown that leaf loss is more related to water stress than to reduced photoperiod [99].

5 Conclusion and perspectives

5.1 Conclusion

This work made it possible to characterise the tree-ring transitions for six species that are abundant in the Yangambi forests. In addition, the micro-core processing proved to be relevant for the targeted study of the cambial zone for these species. This approach is feasible and produces a huge quantity of relevant information. Furthermore, this study demonstrated the importance of using adapted tools for the interpretation of cells development for active cambiums. We confirm the importance of following the cambial activity of many species through periodic micro-coring during a complete growing season.

Significant variabilities in growth patterns but also in leaf phenology were detected both between and within species. During the transition period between March and April, cambial activity was observed for *P. oleosa, S. zenkeri, T. madagascariense* and *P. macrocarpus. L. thompsonii* and *S. subcordatum* showed dormancy. The brief timelapse camera approach gives a more accurate view of leaf phenology, taking into account the phenological variability of species. But the phenological observations made at the individual scale seem to be a representative sample of the observations made at the forest scale.

The comparison of foliar and cambial results could not demonstrate that activity or dormancy is directly related to the appearance or loss of fruits, flowers or fruits. However, it can be said that even if the cambial status is different between individuals, the leaf phenology is rather similar within species. The production of fruits, flowers or leaves does not seem to occur at the same time for species and individuals whether their cambium is dormant or active.

The species also show different sensitivities to meteorological parameters such as temperature or precipitation. Cambial growth of *P. oleosa* and *S. zenkeri* is partly explained by precipitation and exposure time while that of *P. macrocarpus* and *T. madagascariense* are mostly explained by temperature and exposure time.

5.2 Perspectives

As the number of individuals considered by species is smaller, the inter-species variability is sometimes high. In order to extract a more representative trend of cambial and foliar phenology at the species level, we need to consider more individuals to better take into account intraspecific diversity.

Anatomical sections analysis should be continued. Indeed, obtained results from conducted collections are highly satisfactory but the analysis made offers a first approach of the collected data. It is to be considered to deepen the anatomical study of the sections by focusing on one species at a time, in particular to be interested in the evolution of the size of the vessels, the shape and composition of the cell rays, the structure of the parenchyma but also the anatomy of the phloem.

About climate-growth relation, it can be relevant to consider other exogenous factors that may affect vegetation growth by expanding this study to other environmental parameters such as the soil nature and composition, the mineral richness, the water reserve of the soil, cumulation of precipitation over several months among others. It would be relevant to consider the amount of water present in the soil by measuring this over a year.

The results and discussions carried out must be considered with hindsight. Indeed, while the approach followed was relevant, the study period was short in terms of the cambium cycle. Indeed, it was tested to establish a relationship between climate and cell production, but mainly focusing on an interval of a few weeks. As it seems unlikely that the whole cambium cycle is limited to this interval, it cannot be excluded that the conclusions drawn are inadequate for a longer period considered.

A last, a critical element of this study is the measurement period. This work provides many information about cambial and foliar phenologies of species within forest of the Congo Basin. Nevertheless, in order to better understand the evolution of these process at inter-annual scale, to relate biological processes and evolution of local climate; we need to expand the period of study. It will be useful to better covering the entire season of growth, and obtain further information about foliar and cambial phenology on the scale of the dry period that precedes this short rainy season or on an entire year.

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6 Appendices

Encadré 10. Statut de dominance selon Dawkins[17]

La lumière disponible pour l'arbre est estimée à partir de la position de sa couronne en utilisant cinq indices de « statut social de l'arbre » mis au point par Dawkins. La signification des indices 1, 2, 3, 4 et 5 sur la Figure 19 est détaillée ci-dessous :

1) Indice 1 : arbre de la strate inférieure, couronne non exposée à la lumière directe.
2) Indice 2 : arbre de la strate inférieure, couronne exposée potentiellement à la lumière indirecte.
3) Indice 3 : arbre de la strate intermédiaire, couronne exposée à la lumière directe verticale.
4) Indice 4 : arbre de la strate supérieure, couronne totalement exposée à la lumière directe verticale.
5) Indice 5 : arbre dont la couronne est totalement exposée à la lumière directe.

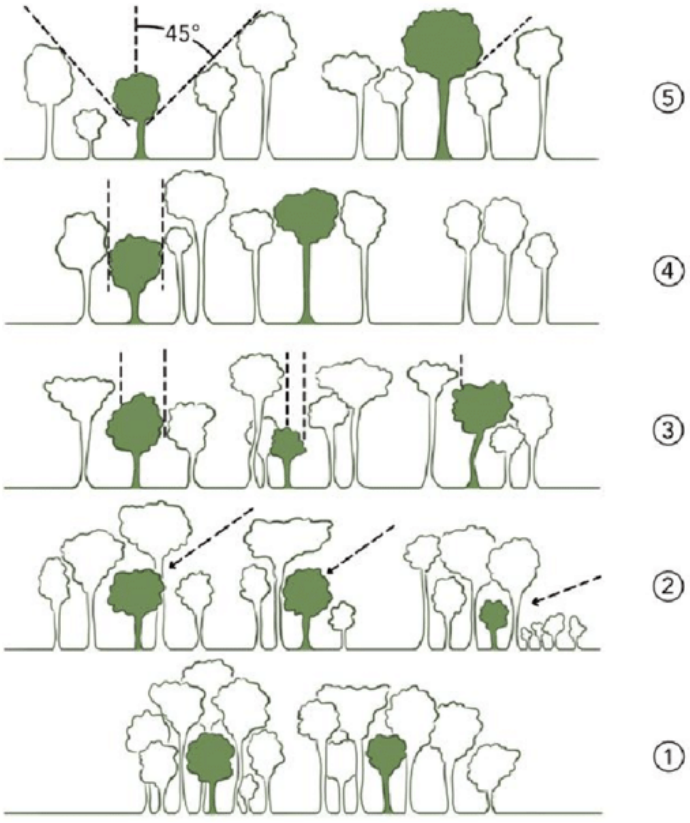

Figure 6.1: The Crown Illumination Index (CII) developed by Dawkins and Field (Dawkins et al., 1978). Taken from : (Tosso et al., 2020).

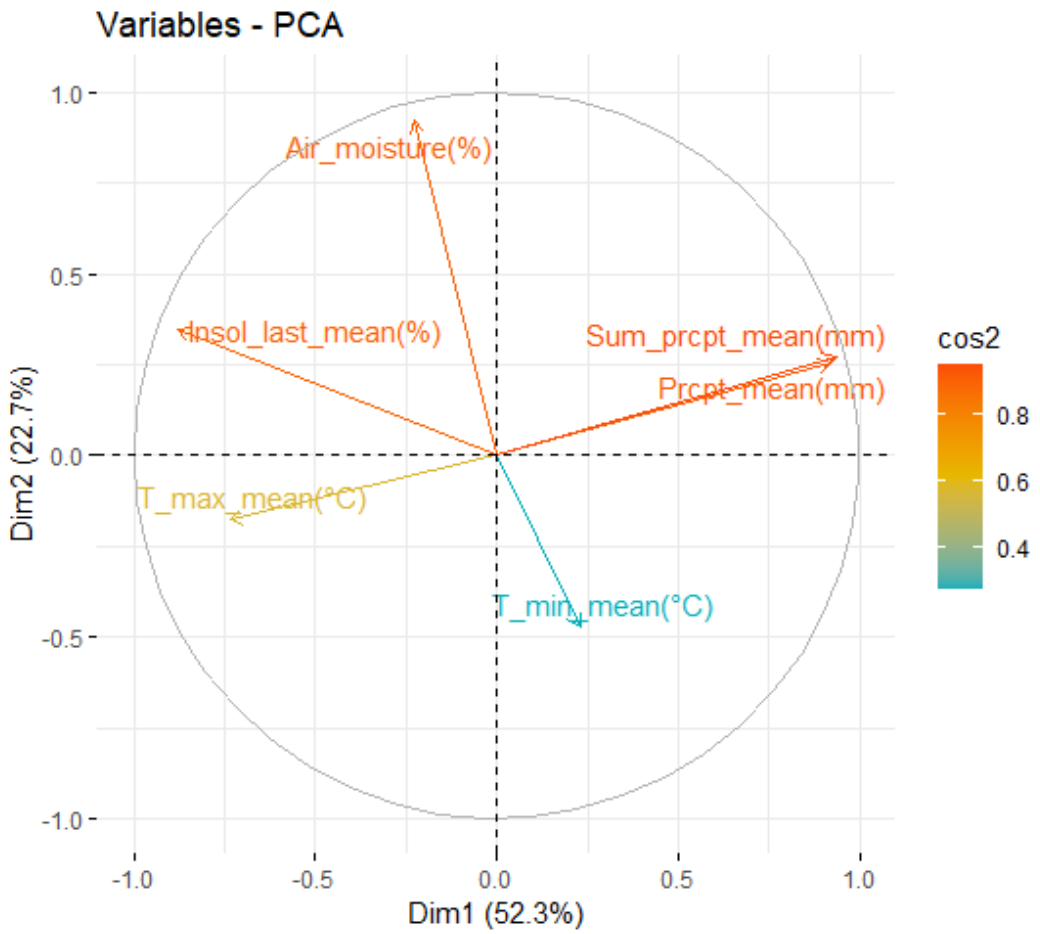

Figure 6.2: PCA chart of mean climate parameters for 2 weeks intervals considered over the study period (from 22/02/20 to 22/04/22) for the values of air humidity, sustained insolation, maximum and minimum temperatures (°C), precipitation (mm) and sum of precipitations (mm). The cos2 indicates the quality of representation of variables on the PCA graph with an increased quality from blue to red.

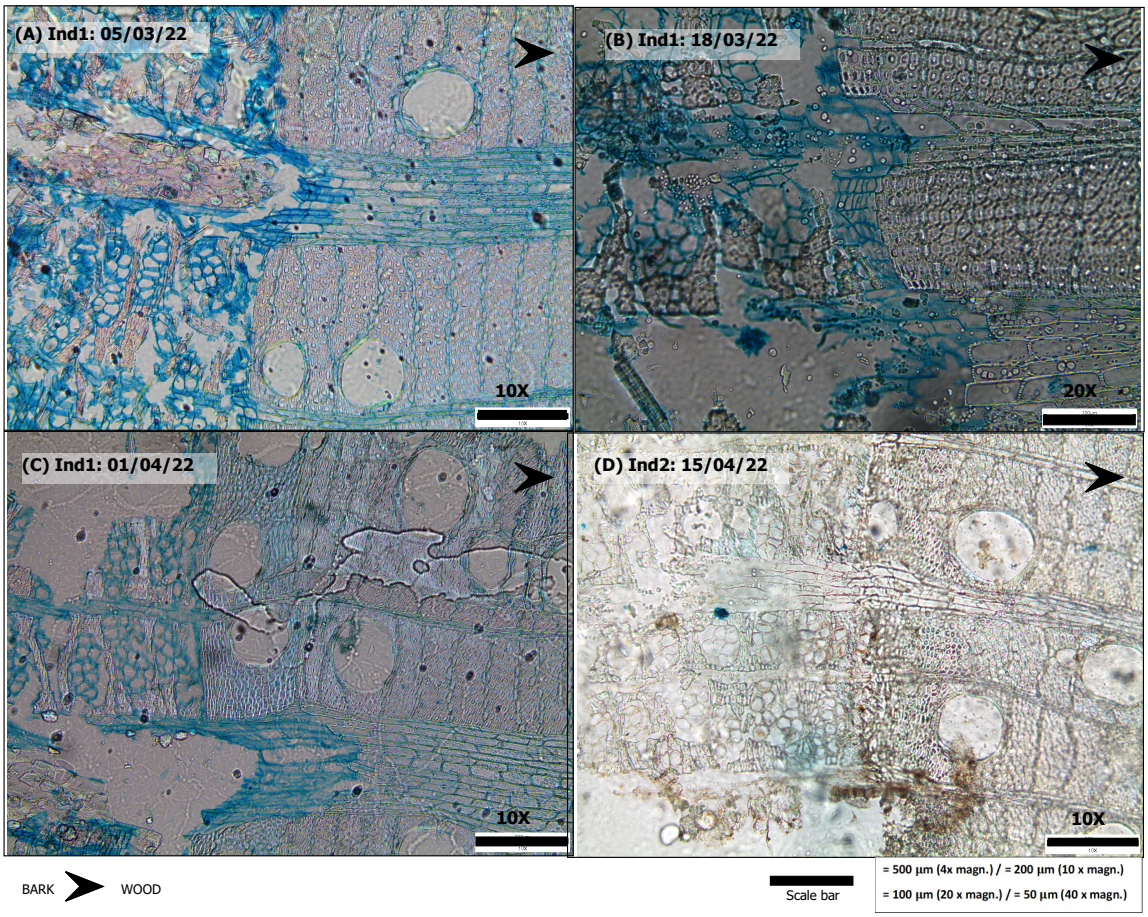

Figure 6.3: (A), (B), (C), (D) are cross-sections of the cambial zone of G. suaveolens under light microscope.

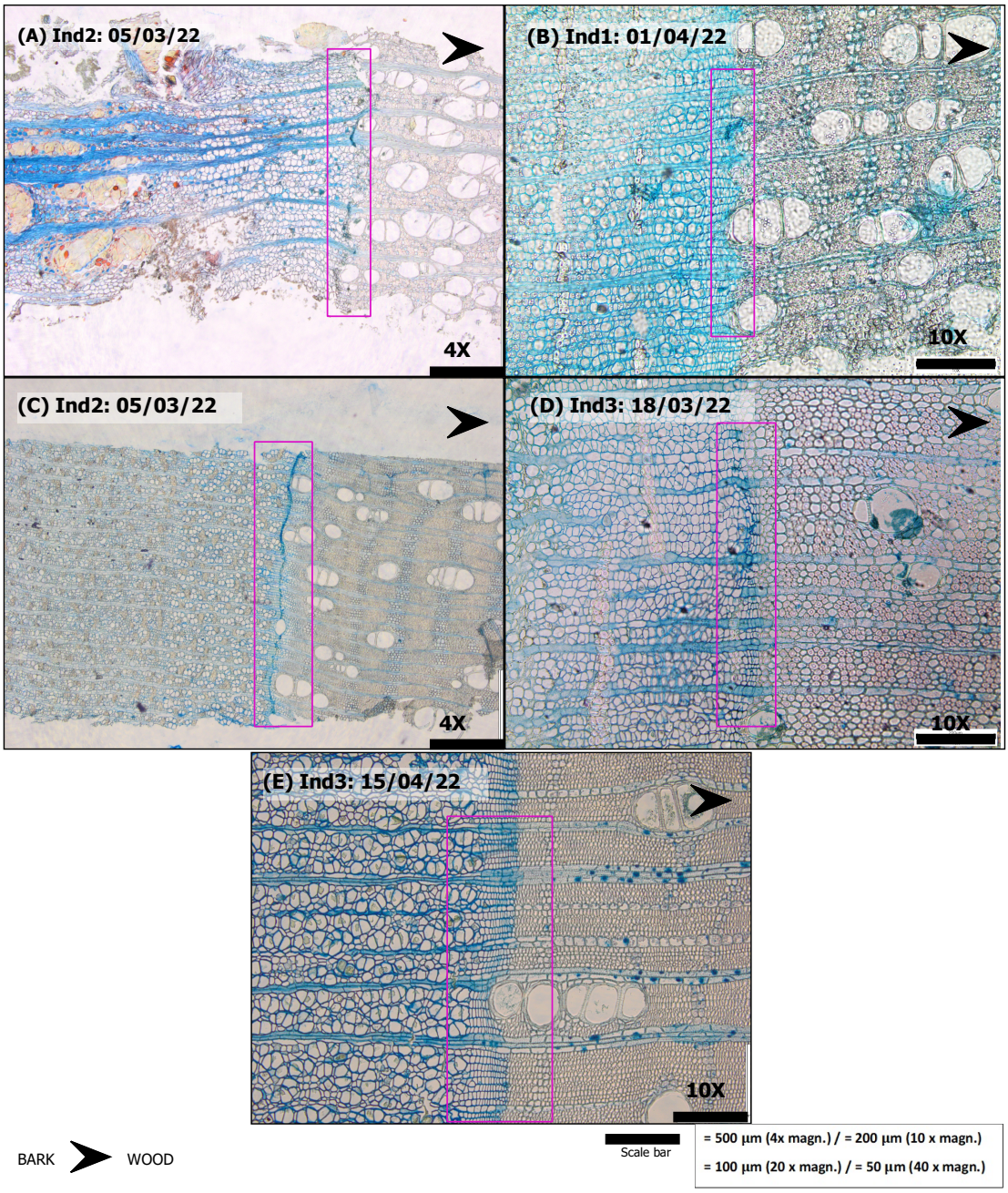

Figure 6.4: Cross-sections of P. oleosa (A), P. macrocarpus (B), S. zenkeri (C), S. subcordatum (D) and T. madagascariense (E) under light microscope. The purple frame corresponds to the transition zone between bark and wood.

Table 6.1: Goodness-of-fit of linear mixed model analyses of the relationships between cambial activity and climate parameters taking into account the randomness of individuals (M3)

$\ln(cambial\ activity) \sim Tmax + Tmin + HR + (\mathbf{1}\|Individual)$		
P. macrocarpus	Marginal R^2	0,252
	Conditional R^2	0,581

$\ln(cambial\ activity) \sim Tmax + Tmin + HR + Prcptsum + Prcpt + (\mathbf{1}\|Individual)$		
T. madagascariense	Marginal R^2	0,251
	Conditional R^2	0,386