1   **Original Article**

2   **Low functional but large soil-related variations in growth trajectories characterise the**

3   **widespread Neotropical tree *Cecropia obtusa* Trécul (Urticaceae)**

4   Running title: **Soil-related phenotypic variability for a widespread tree species**

5   Sébastien Levionnois[1*], Niklas Tysklind[2], Eric Nicolini[3], Bruno Ferry[4], Valérie Troispoux[2],

6   Gilles Le Moguedec[5], Hélène Morel[6], Clément Stahl[2], Sabrina Coste[7], Henri Caron[2, 8], Patrick

7   Heuret[2, 5*]

8

9   **1.** CNRS, UMR EcoFoG, AgroParisTech, CIRAD, CNRS, INRA, Université des Antilles,

10   Université de Guyane, 97310 Kourou, France.

11   **2.** INRA, UMR EcoFoG, AgroParisTech, CIRAD, CNRS, INRA, Université des Antilles,

12   Université de Guyane, 97310 Kourou, France.

13   **3.** CIRAD, UMR AMAP, CIRAD, CNRS, INRA, IRD, Université de Montpellier, 34398

14   Montpellier, France.

15   **4.** AgroParisTech, UMR LERFoB, AgroParisTech, INRA, 54280 Champenoux, France.

16   **5.** INRA, UMR AMAP, CIRAD, CNRS, INRA, IRD, Université de Montpellier, 34398

17   Montpellier, France.

18   **6.** CIRAD, UMR EcoFoG, AgroParisTech, CIRAD, CNRS, INRA, Université des Antilles,

19   Université de Guyane, 97310 Kourou, France.

20   **7.** Université de Guyane, UMR EcoFoG, AgroParisTech, CIRAD, CNRS, INRA, Université

21   des Antilles, Université de Guyane, 97310 Kourou, France.

22   **8**. INRA, UMR BIOGECO, INRA, Université de Bordeaux, Cestas, France

23

24   *Authors for correspondence:

25   Sébastien Levionnois, PhD student

26   Postal adress: UMR EcoFog, Campus Agronomique, Avenue de France

27   BP709 – 97387 Kourou Cedex

28   French Guiana

29   Tel: +33 760 26 73 83

30   Email: sebastien_levionnois@live.fr

31

32   Patrick Heuret, PhD

33   Postal adress: UMR AMAP, TA- A-51/PS2 Boulevard de la Lironde

34   34398 Montpellier Cedex 5 (France)

1   French Guiana

2   Tel: +33 467 61 55 14

3   Email: patrick.heuret@inra.fr

4

5   **Author contributions**

6   PH designed and led the project. PH, SL, EN, VT, HM, NT, CS, SC, BF and HC .measured

7   tree architecture and functional traits. BF and VT described soils characteristics. SL, PH and

8   GL performed data analysis. SL wrote the manuscript with contributions from PH and NT.

9   All authors contributed critically to the drafts and gave final approval for publication.

10

1 **ABSTRACT**

2 **1.** Environment-driven interspecific functional variability has been convincingly described

3 across Amazon lowland tree species. However, functional variability has rarely been

4 addressed at the intraspecific level, especially through one key environmental driver such as

5 soil composition. In this study, we assess whether patterns of soil-dependent interspecific

6 variability are retained at the intraspecific level.

7 **2.** We examined phenotypic variability for 16 functional leaf (dimensions, nutrient,

8 chlorophyll) and wood traits (density) across two soil types, Ferralitic Soil (FS) vs. White

9 Sands (WS), and on two sites for 70 adult trees of *Cecropia obtusa* Trécul (Urticaceae) in

10 French Guiana. *Cecropia* is a widespread pioneer Neotropical genus that generally dominates

11 forest early successional stages. We also examined the architectural development through a

12 temporal-scaled retrospective analysis and lifespan-level growth trajectories, in order to

13 evaluate the role of soil phenotypic variability. *Cecropia*'s unique features, such as simple

14 architecture and growth markers allowed us detailed description of temporal-scaled

15 retrospective analysis of development.

16 **3.** Functional trait responses to soil types were weak, as only two traits, namely petiole length

17 and leaf area, exhibited significant differences between the two soil types. Soil effects were

18 stronger on growth trajectories and tree architectural development, with WS trees having the

19 slowest growth trajectories -underlined by smaller internode length-, smallest trunk heights

20 and diameters for a given age, and less numerous branches.

21 **4.** Soil-related functional traits did not mirror the divergence usually found at the interspecific

22 level. By integrating a dynamic approach based on retrospective analysis of architectural

23 development to the functional approach to understand tree ecology, here, we demonstrate how

24 an improved understanding of environmental effects on tree phenotypic variance can be

25 captured.

26

27 **Key words:** architecture, *Cecropia obtusa*, ferralitic/white-sand soils, functional traits,

28 growth trajectory, intraspecific variability

1   **INTRODUCTION**

2   In the Amazon forest, abiotic factors such as edaphic conditions are habitat filters and

3   strong drivers of species distribution (Allié et al., 2015; Baraloto, Morneau, Bonal, Blanc, &

4   Ferry, 2007; Clark, Palmer, & Clark, 1999; Guitet et al., 2016; John et al., 2007; Kanagaraj,

5   Wiegand, Comita, & Huth, 2011; Pélissier, Dray, & Sabatier, 2002; Sabatier et al., 1997;

6   Stropp, Sleen, Assunção, Silva, & Steege, 2011; ter Steege, Jetten, Polak, & Werger, 1993;

7   Valencia et al., 2004). Two contrasts are generally studied as edaphic factors. First,

8   bottomland (or valley) *versus* hilltop (or plateau) microhabitats is the most used contrast to

9   study species and functional turnover. Such environmental heterogeneity is mainly driven by

10   water availability, as it is explained by topography and soil structure (Allié et al., 2015;

11   Sabatier et al., 1997). Hilltops experience higher levels of lateral and vertical water drainage

12   due to slopes and deeper soils (Sabatier et al., 1997). In contrast, bottomlands receive water

13   draining from slopes and are thus, more prone to seasonal flooding. Moreover, topographical

14   and hydrological variations are associated with nutrient differences (Allié et al., 2015; Ferry,

15   Morneau, Bontemps, Blanc, & Freycon, 2010). Hilltop-bottomland heterogeneity impacts

16   species distribution (Clark et al., 1999; Pélissier et al., 2002; Sabatier et al., 1997; ter Steege

17   et al., 1993), for which strong species-specific habitat preferences have been shown (Allié et

18   al., 2015). Evidence for directional across-community differences in functional traits

19   underlying such spatial patterns is also accruing (Cosme, Schietti, Costa, & Oliveira, 2017;

20   Engelbrecht et al., 2007; Fortunel, Paine, Fine, Kraft, & Baraloto, 2014; Fortunel, Ruelle,

21   Beauchêne, Fine, & Baraloto, 2014; Lopez & Kursar, 2003).

22   Second, the contrast between white-sand (WS) *versus* ferralitic soils (FS) has been

23   repeatedly used for explaining Amazonian spatial species diversity turnover. WS are mainly

24   quartz soils, representing 3% to 5% of soils in the Amazon basin and exist as island-like spots

25   in a matrix of other soils such as FS (Adeney, Christensen, Vicentini, & Cohn-Haft, 2016;

26   Fine & Baraloto, 2016). Generally, WS are poor in mineral nutrients and acidic, with a low-

27   usable water reserve and poor nitrogen mineralization, especially in comparison with common

28   FS. Similar to the hilltop-plateau contrast, FS-WS heterogeneity has strong impacts on species

29   distribution patterns (Daly, Silveira, Medeiros, Castro, & Obermüller, 2016; Fine & Baraloto,

30   2016; Stropp et al., 2011; ter Steege et al., 2013). At the community level, WS flora is

31   characterised by a convergence in functional strategies, particularly towards a conservative

32   nutrient use strategy (Fine & Baraloto, 2016; Fine, García-Villacorta, Pitman, Mesones, &

33   Kembel, 2010; Fortunel, Fine, & Baraloto, 2012; Fortunel, Paine, et al., 2014; Fortunel,

34   Ruelle, et al., 2014; Fyllas et al., 2009; Grubb & Coomes, 1997; Patiño et al., 2009). These

4

1 imply higher leaf mass area (LMA), higher wood density, smaller seeds, and lower leaf

2 nutrient contents associated with higher nutrient use efficiency (Fine & Baraloto, 2016), in

3 comparison with other soil types such as FS.

4 Despite the stark community composition differences among contrasting edaphic

5 conditions, generalist species (i.e. species able to establish perennial individuals on

6 contrasting habitats) are common. Species-specific habitat preferences, linked to directional

7 variations of the functional composition, suggest habitat specialization based on the

8 evolutionary processes of selection, adaptation, and species divergence. Among the

9 mechanisms maintaining rainforest species diversity, these processes (selection, adaptation,

10 divergence) can occur within or between populations or species , even in a sympatric context

11 (e.g. ecological speciation through local adaptation and extreme competition, without a

12 geographical barrier)(Savolainen, Lascoux, & Merilä, 2013; Savolainen, Pyhäjärvi, & Knürr,

13 2007). Thus, it can be hypothesised that generalist species are composed of a mosaic of the

14 genetic and functional divergences of populations. Such divergence has been shown for the

15 Panamazonian hyperdominant (ter Steege et al., 2013) tree model species *Eperua falcata*

16 Aublet. (Fabaceae) through the hilltop-bottomland contrast, where functional trait

17 differentiation (Brousseau, Bonal, Cigna, & Scotti, 2013a) and potentially adaptive genetic

18 divergence has been found between individuals living in contrasting habitats (Audigeos,

19 Brousseau, Traissac, Scotti-Saintagne, & Scotti, 2013; Brousseau, Foll, Scotti-Saintagne, &

20 Scotti, 2015). However, generalist species are not necessarily the result of adaptive genetic

21 divergences among populations, but could be based on phenotypic plasticity, defined here as

22 the capacity of a given genotype to generate various phenotypes in response to environmental

23 variations (Bradshaw, 1965). Indeed, phenotypic plasticity is assumed to be a leading process

24 for species eco-evolutionary dynamics and species diversification (Hendry, 2016; Moczek et

25 al., 2011; Nicotra et al., 2010; West-Eberhard, 2003).

26 Conversely to the bottomland-hilltop contrast, the effects of the FS-WS contrast on

27 both genotypes and phenotypes of related generalist species remain mostly unknown. One of

28 the few published examples, studying *Protium subserratum* Engl. (Burseraceae), found

29 differentiations for genetic, and chemical traits associated to herbivory resistance between FS

30 and WS, but for rather large geographic distances (Fine, Metz, et al., 2013; Fine, Zapata, et

31 al., 2013). In the context of generalist species on the FS-WS contrast, three questions need to

32 be addressed to improve our understanding of Neotropical tree eco-evolutionary dynamics: (i)

33 are functional traits shaped by FS and WS? and if so, how? (ii) are the traits to which FS- and

34 WS-specialised species converge respectively, the same at the intraspecific level? and (iii) by

1   which eco-evolutionary processes (e.g. genetic adaptation or phenotypic plasticity) are such

2   potential divergences realised at the intraspecific level? Moreover, there are only a few

3   functional studies on trees at the intraspecific level in the Amazon rainforest, which are

4   particularly needed for hyperdominant overabundant species (ter Steege et al., 2013). Such

5   studies are desirable since hyperdominant species exhibit disproportionately large

6   intraspecific variability (ITV; Albert et al., 2010; Des Roches et al., 2018; Siefert et al., 2015;

7   Valladares et al., 2014) and can play a disproportionate role in ecosystem functioning (Fauset

8   et al., 2015). Moreover, incorporating such ITV for hyperdominant species can improve our

9   understanding of forces structuring plant communities (Violle et al., 2012).

10   Finally, we propose an improvement of functional approaches to understand tree

11   ecology, with a dynamic approach to better incorporate tree phenotypic variability (intra- or

12   interspecific). In our point of view, functional approaches are most of the time "static", since

13   trait measurements are made at a particular age of the tree, representative of a tree's

14   functional traits at a specific moment of its life. A dynamic approach considers the

15   development of the trunk for instance, described as a sequence of elementary repetitive units

16   (e.g. internode, growth unit, annual shoot), universal for vascular plants, and the accumulation

17   and fluctuation of growth, branching, and flowering processes through a tree's lifespan, in

18   reference to the tree's architectural development (Chaubert-Pereira, Caraglio, Lavergne, &

19   Guédon, 2009; Yann Guédon, Caraglio, Heuret, Lebarbier, & Meredieu, 2007; Taugourdeau

20   et al., 2012).

21   Here, we want to bridge these caveats by taking advantage of the Amazon rainforest

22   genus *Cecropia,* composed of hyperdominant pioneer trees critical in the recovery of Amazon

23   forests. We focus on *Cecropia obtusa* Trécul (Urticaceae), a widespread Guiana shield

24   generalist species, capable of growing on both FS and WS, and displaying perennial growth

25   marks, which allow for retrospective analysis of tree architectural development (growth,

26   branching, flowering) through time, making *C. obtusa* an ideal case study (Heuret,

27   Barthélémy, Guédon, Coulmier, & Tancre, 2002; Taugourdeau et al., 2012; Zalamea,

28   Stevenson, Madriñán, Aubert, & Heuret, 2008). We developed a functional ecology-based

29   approach by coupling architectural development and growth trajectory analyses for two sites

30   with both soil types in French Guiana. The ITV assessment according to the FS-WS variations

31   are fitted in the perspective of the eco-evolutionary dynamics of *C. obtusa*, without *a priori*

32   on genotype. We aim to answer the following questions:

33   (i) Do growth trajectories and architectural development patterns give us a more

34   comprehensive understanding of soil effects on tree phenotype? As growth trajectories and

6

1   architectural development vary, we hypothesise capturing soil-related variation, leading to a

2   more comprehensive understanding of overall phenotypic variation patterns.

3   (ii) Are the functional intraspecific patterns between FS and WS analogous to the

4   interspecific functional patterns observed at the community level? As WS are poor soils

5   determining particular functional traits at the interspecific level, we hypothesised to find an

6   analogous functional divergence at the intraspecific level.

7   (iii) Finally, what is the phenotypic variance strategy of *C. obtusa* to cope as a soil

8   generalist?

9

10   **MATERIALS AND METHODS**

11   *Study species: Why* C. obtusa *is an appropriate tree model species?*

12   *C. obtusa* has several characteristics that allow the retrospective construction of a

13   tree's past growth. The growth of *C. obtusa* is continuous (no cessation of elongation) and

14   monopodial (no death of meristem), the tree is made of a set of axes, where each one is

15   composed of an ordered, linear, and repetitive succession of phytomers (i.e. the set of a node,

16   an internode, a leaf, and its axillary buds; Fig. S1). Leaves are stipulated, with an enveloping

17   stipule named calyptra which has a protective function (Fig. S1). At the leaf establishment,

18   the calyptra sheds leaving a characteristic ring scar delimiting the associated internode, and

19   usable as a permanent growth marker (Heuret et al., 2002). The 10-day stable phyllochron

20   (i.e. rhythm of leaf production) associated with such permanent growth marker allows for the

21   retrospective analysis of tree growth and development, covering the tree's lifespan (Heuret et

22   al., 2002; Zalamea et al., 2012).

23   There are three lateral buds in the axil of each leaf (Fig. S1). The central bud is

24   vegetative and potentially originates a new axis. The two others are proximal lateral buds of

25   the vegetative central one and potentially originate inflorescences (i.e. borne inflorescences by

26   an A1 axis are fundamentally of order 3). The inflorescences are thus arranged in pairs

27   consisting of a common peduncle bearing spikes initially completely enclosed by a spathe.

28   The inflorescences leave permanent scars after shedding, allowing the retrospective analysis

29   of tree's lifespan flowering events. The same retrospective analysis is possible with branching

30   events since the presence of past branches remains visible.

31

32   *Study site*

33   Two sampling sites were selected in French Guiana: (1) Counami, along the Counami forestry

34   road (N5.41430°, W53.17547°, geodesic system WGS84); and (2) Sparouine, along the

7

1   national road 5 (RN5) that connects the municipalities of St-Laurent-du-Maroni and Apatou

2   near Sparouine Municipality (N5.27566°, W54.20048°). It is difficult to find locations with

3   both FS and WS populated by *C. obtusa* stands, so we had to incorporate a potential site

4   effect. The warm and wet tropical climate of French Guiana is highly seasonal due to the

5   north-south movement of the Inter-Tropical Convergence Zone. Annual rainfall is 3,041 mm

6   year^{-1} and annual mean air temperature is 25.7 °C at Paracou experimental station (Gourlet-

7   Fleury, Guehl, & Laroussine, 2004) situated nearly at 30 km and 150 km to the east of

8   Counami and Sparouine sites respectively. There is one long dry season lasting from mid-

9   August to mid-November, during which rainfall is < 100 mm month^{-1}. The two studied sites

10   (Counami and Sparouine) are characterised by rainfall differences (Fig. S2). Counami shows

11   higher levels of rainfall and higher contrasts between the long rainy and the long dry seasons.

12   For each of the two sites, two micro-localities are identified corresponding to two soil types:

13   ferralitic soils (FS) and white-sand soils (WS). Local sites were chosen to be well drained and

14   on upper slopes. Each micro-locality supports individuals of *C. obtusa*.

15

16   *Plant material, study conception, and sampling*

17   Individuals have grown in clearings and form a secondary forest where they are the dominant

18   species together with *C. sciadophylla*. A total of 70 trees were selected in September and

19   December 2014 respectively for Counami and Sparouine sites: 32 in Counami and 38 in

20   Sparouine. Soil samples were taken at the same time for pedological analysis. On the

21   Counami site, where individuals are widely spaced, a soil sample was taken at the base of

22   each individual tree. On the Sparouine site, where individuals where clustered, 9 soil samples

23   were taken, as each soil sample was representative of 4-6 individuals located no further than

24   30m from the soil sample spot. We acknowledge that the link between an individual and the

25   associated soil sample remains approximate as root system of *C. obtusa* can colonise a zone

26   of 15 m around the tree (Atger & Edelin, 1994).

27   As *C. obtusa* is dioecious, only pistillate trees were felled to avoid potential sex-

28   related variability in the measured traits. Trees were not felled according to the same scheme

29   in the two sites. Trees were preselected to have as close as possible comparable diameters at

30   breast height (DBH), and age was estimated with binoculars according to the method

31   described by Zalamea et al. (2012). By counting the number of internodes we were able to

32   estimate the age of trees as each internode is produced in 10 days (Heuret et al., 2002;

33   Zalamea et al., 2012). In Sparouine, all individuals correspond to a single colonisation pulse:

34   all individuals have similar age (7-10 years), with DBH of 11.94 to 25.70 cm, and heights of

1   13.85 to 23.20 m (Fig. S3). Both soil types were represented by 19 individuals and all

2   individuals were felled and measured between the 14th and the 19th of September 2015. Thus,

3   season-, size-, and age-related effects on traits are controlled for soil and individual

4   comparisons.

5   The experimental design at Counami was different. The forestry road was opened

6   gradually, and therefore the age of the trees differed according to the road section (Zalamea et

7   al., 2012). All individuals assigned to WS at Counami were selected at a single small WS

8   patch located 6 km after the entrance of the road. Thus, trees also represented a single

9   colonisation pulse and were of similar age (14-16 years), except one significantly older

10   individual of 22.8 years old), with DBH from 6.21 to 15.18 cm, and heights from 10.27 to

11   16.18 m, (Fig. S3). It was not possible to choose trees on FS on a single restricted area

12   because of the perturbation of soil structure by the logging machines and because we

13   excluded trees on down slopes. Consequently, FS trees were sampled between km 6 to 11 of

14   the forestry road and included different cohorts with different ages (7-23 years), DBH of 9.55

15   to 22.44 cm, and heights of 12.16 to 22.63 m (Fig. S3). Eleven and eighteen individuals were

16   sampled on FS and WS respectively. Counami trees were felled at different dates, from

17   September 2014 to April 2016. The contrasted protocol was chosen to study seasonal and

18   ontogenetic effect on leaf traits, but the results of such analysis will not be addressed here.

19

20   *Soil properties*

21   Pedological analyses included granulometry, moisture content, acidity, organic matter

22   contents, and contents of exchangeable cations (Appendix S1, with detailed abbreviations).

23   The complete sampling procedure is described in the Appendix S1. Exchangeable cations

24   were analysed divided by cation-exchange capacity (CEC) to avoid autocorrelations between

25   the former and the latter. We also calculated a soil index of fertility as: $Index_{Soil} =$

26   $\frac{K+Ca+Mg+Na}{CEC}$.

27   The *a priori* classification of soil types (FS-*versus*-WS) was confirmed by pedological

28   analyses of the soil properties within each site. The described pattern of soil properties is

29   congruent with that reported in the literature (Adeney et al., 2016; Fine & Baraloto, 2016).

30   WS consist of a large proportion of coarse sand with high Ca:CEC and C:N ratios. FS consist

31   of a large proportion of clay and silt with high moisture, N, C, MO P_{tot} contents and a high

32   Al:CEC ratio. Based on water availability, N content, and Index$_{soil}$, the site fertility can be

33   ordered as COU-FS > SPA-FS > COU-WS = SPA-WS. Sparouine WS are characterised by

9

1 higher H:CEC and Fe:CEC ratio than Counami WS. The related results are presented in

2 Appendix S1. Within sites, the difference between soil types is more contrasted in Counami

3 than in Sparouine.

4

5 *Architectural and functional traits*

6 For all individuals, we measured a suite of architectural traits at phytomer and whole-

7 tree levels to characterise growth, branching and flowering dynamics and the resulting tree

8 architecture. Retrospective analysis of development allows us to consider tree developmental

9 trajectories as growth performance traits (i.e. the height-age relationship). Such dynamical

10 approach considers the development of the trunk only (no branches) described as a sequence

11 of phytomers. Three variables were measured for each phytomer: (1) internode length (2)

12 vegetative bud state coded as: 0 not developed or aborted; 1 developed, present or pruned, (3)

13 inflorescence bud state coded as: 0 no inflorescence; 1 pruned or present inflorescences.

14 Features for bud states are treated as binary values: presence or absence. As suggested by

15 Davis (1970), Heuret et al. (2002), and Zalamea et al. (2008), we analysed periodical

16 fluctuations in internode length as well as the rhythmic disposition of inflorescences and

17 branches to infer the past development of the tree and model its growth dynamic (section

18 statistical analysis and Appendix S2). The measured and estimated traits presented as

19 longitudinal sequences, associated with abbreviations, are shown in Table 1. Whole-tree

20 dimensional traits complete the dynamic analysis to define the tree's ecological performance

21 (Table 1, with detailed abbreviations)

22 Functional traits were measured especially at the leaf level (Table 2, with detailed

23 abbreviations) indicative of leaf resource capture and defence against herbivores (Baraloto et

24 al., 2010). Trunk wood specific gravity is indicative of stem transport, structure and defence

25 against parasites (Baraloto et al., 2010). As *Cecropia* trees bear only few, but very large

26 leaves, we measured leaf-level traits for only one leaf per individual: either the third or the

27 fourth leaf positioned under the apex of the A1 axis. In this way, potential effects of plant

28 spatial structure and phenology on variation of leaf-level traits are controlled. Leaf lifespan

29 was derived on the postulate of a constant 10-day phyllochron (i.e. rhythm of leaf production)

30 as shown by Heuret et al., (Heuret et al., 2002), by multiplying the number of leaves of the A1

31 axis by 10 days (i.e. interval between the emergence of two successive leaves). The complete

32 sampling procedure for functional traits is described in Appendix S3.

33

34 *Statistical analyses*

10

1   Topology of trees and the different pedological, dimensional, and functional features

2   associated with each repetitive unit are coded in sequences in Multi-scale Tree Graph format

3   (MTG; Godin & Caraglio, 1998; Godin, Costes, & Caraglio, 1997).

4   Statistical analyses relative to developmental dynamics were conducted with

5   AMAPmod (*op. cit*), now integrated in the OpenAlea platform, re-engineered and named

6   'VPlants' (Pradal, Coste, Boudon, Fournier, & Godin, 2013), and the R programming

7   language (R Core Team, 2018).

8   We relied on sample autocorrelation coefficients to point out a potential periodicity on

9   the stand level (i.e. soil x site) for growth, branching, and flowering process. Thereafter, such

10   stand periodicity would help to improve retrospective analysis of tree development with a

11   temporal scale. The use of sample autocorrelation coefficients for all trees together allows

12   measurement of the correlation between observations of sequences of quantitative variables

13   separated by different distances. The autocorrelation function measures the correlation

14   between Xt and $Xt+k$ as a function of the internode lag k. The sample autocorrelation function

15   is an even function of the internode lag and hence needs to be plotted for $k = 0, 1, 2, …, n$. We

16   applied auto-correlation analysis to residual sequences obtained from internode length

17   sequences after removing the ontogenetic trend, to binary branching, and flowering sequences

18   (Y. Guédon, Barthélémy, Caraglio, & Costes, 2001; Y. Guédon, Heuret, & Costes, 2003).

19   To analyse fluctuations of internode length, we used classical methods of time series

20   analysis relying on a decomposition principle. The different sources of variation, such as

21   long-term changes in mean level and local fluctuations, are identified by the application of

22   various types of filters that were initially analysed for individual trees (Yann Guédon et al.,

23   2007). Firstly, we calculated a moving average to extract the trend of internode length

24   sequences in a similar way as Zalamea et al. (2008). Having extracted the trend, we looked at

25   local fluctuations by examining the residuals. Residuals were generated by dividing for each

26   internode, its length by its moving average. Such standardization allowed us to give the same

27   status to fluctuations of both small and large amplitudes, which is pertinent in old trees that

28   have very short internodes at the apex of axes compared to the first nodes at the trunk base

29   (Appendix S3 for details). Analysis of generated internode residuals allows the identification

30   of the limits of the long dry season in September/October for successive years, since shorter

31   internodes are elongated during this period as demonstrated in (Davis, 1970), for *C.*

32   *obtusifolia* Bertol. and *C. peltata* L., and (Zalamea et al., 2013), for *C. sciadophylla* Mart..

33   Year delineation for each individual allows estimation of a mean phyllochron for each year

34   according to the node rank (Appendix S3). Knowing the phyllochron allows conversion of the

11

1   rank node to a temporal scale. Finally, a higher organizational level can be interpolated at the

2   year scale considering the length or the number of nodes elongated between two successive

3   dry seasons (Table 1). Although the growth is continuous (Zalamea et al., 2013), we use the

4   term "annual shoot" (AS; Table 1) in the text to refer to the growth between two successive

5   dry seasons.

6   Based on cumulated tree height according to age, two linear growth phases were

7   identifiable, with a slope rupture nearly at the age of 6-7 for all trees. As the first phase was

8   fully described for all individual trees, and all trees were older than 7 years old, we calculated

9   quantitative growth rates (m $^{-1}$) for each tree as the slope of the linear regression of the

10 relationship between the cumulated tree height and tree age, for the first seven years only.

11   Existence of clusters defined by signatures of developmental trajectories are

12 characterised with a clustering method on the generated longitudinal data (Table 1), with the

13 *kml* R package (Genolini & Falissard, 2009). It is a classification method based on an

14 implementation of "k-means", itself based on a minimization function of distances. As for

15 classical k-means, KML deals with the choice of a distance, cautions against local maxima,

16 and the criterion of partition choice (*op. cit)*. For each trait, 100 simulations are used, and

17 decisions are based on the Calinski-Harabasz criterion. The dependency of defined clusters on

18 soil types is evaluated with a Pearson's chi-squared test.

19   Analyses relative to pedological, dimensional, and functional data are realised in R

20 language. Principal Component Analysis (PCA) were conducted with the *ade4* (Chessel,

21 Dufour, & Thioulouse, 2004) and *Factoextra* (Kassambara & Mundt, 2016) R packages. A

22 comparison of factorial coordinates of individuals was conducted for each axis based on a

23 nested-ANOVA and a *post-hoc* Tukey's HSD test. Comparisons of means between the four

24 conditions (soil types x sites) for soil properties, functional traits, and growth rates were

25 conducted with a nested-ANOVA and a *post-hoc* Tukey's HSD test. For a proper soil

26 comparison, season and ontogeny-related effects on leaf trait variation for Counami trees were

27 tested with a multiple regression analysis. No season-related effects were detected based on a

28 total of 70 leaves. Only ontogeny-related effects were filtered for each trait when a signal was

29 detected based on a linear regression analysis.

30

31 **RESULTS**

32 *Dynamic approach: architectural development and growth trajectory*

33 Autocorrelation functions calculated for the internode length residues as well as branching

34 and flowering binary sequences all showed significant periodicity regardless of the site or soil

1   type (Fig. 1). In Counami, the correlogram calculated for internode residues sequences

2   yielded significant positive maxima at lags 30, 58, 88 in WS and 30, 52, 64, 88 in FS (Fig.

3   1a). In Sparouine, a similar pattern was observed with significant positive maxima at lags 17,

4   34, 79 in WS and 19, 36, 68, 88 in FS (Fig. 1b). Similar overall patterns are observed for

5   flowering event sequences. In Counami, the correlogram yielded significant positive maxima

6   at lags 12, 27, 52, 77, 88 in WS and 27, 53, 73, 89 in FS (Fig. 1c). In Sparouine, significant

7   positive maxima were at lags 16, 32, 63, 74 in WS and 19, 33, 48, 64, 89 in FS (Fig. 1d).

8   Considering the first 50 lags, a bimodal pattern (lags 12-19 and 27-36) is more pronounced in

9   Sparouine and on WS for internode length and flowering variables. In Counami, the

10   correlogram calculated for branching event sequences yielded significant positive maxima at

11   lags 38, 60 in WS and 29, 60, 88 in FS (Fig. 1e). In Sparouine, the correlogram calculated for

12   this variable yielded significant positive maxima at lags 30, 40, 70 in WS and 28, 38, 100 in

13   FS (Fig. 1f).

14   Based on rhythms relying on autocorrelation coefficients and the knowledge on *C.*

15   *obtusa* (Heuret et al., 2002) and *C. sciadophylla* (Zalamea et al., 2008), we delineated years,

16   trying to respect the following rules: 30-35 trunk nodes per year, 1 to 2 trunk flowering events

17   per year, and 0 or 1 trunk branching event (i.e. tiers of branches) per year. Based on such

18   diagnosis, we calculated the date of the formation of each node and switched from a

19   topological scale, the rank of the node, to a temporal scale (Appendix S5). Phyllochron

20   according to node rank showed the same trend in both sites (Fig. 2). It initially decreased to

21   the 100th node rank and then linearly and continually increased for both sites (Fig. 2a, b). For

22   both sites, there were no significant difference between FS and WS based on confidence

23   intervals (Fig. 2).

24   The variation of trunk internode length according to age showed a hump-like trend for

25   both sites (Fig. 3a, c), with an initial increase to the 8-9th year preceding a decrease and a

26   plateau phase. In Counami, FS trees had significant longer internodes than WS ones the first 5

27   years, based on confidence intervals (Fig. 3a). In Sparouine, there were no significant

28   difference between FS and WS mean trajectories based on confidence intervals. The cluster

29   analysis defined two clusters for both sites (Fig. 3b, d). The clusters significantly matched the

30   soil types in Counami (P = 0.003) but not in Sparouine (P = 0.328).

31   For both sites, the number of nodes per AS initially increased over the first 3-5 years

32   and then continually decreased (Fig. 3e, g). There were no significant differences between FS

33   and WS based on confidence intervals. The cluster analysis defined two clusters for both sites

1   (Fig. 3f, h). In Counami the two clusters were not related to soil type (P = 0.401), whereas in

2   Sparouine the clusters were significantly associated with soil-type (P = 0.008).

3   For both site, the variation of AS length followed the same trend as the internode level

4   (Fig. 3a, c, i, k). AS length initially increased over the 3 fist years and then decreased, except

5   for WS Counami trees where AS length decreased from the first year. There was a significant

6   difference in AS length between Counami FS and WS for trees between 2 and 4 years old.

7   There was no significant difference between Sparouine FS and WS based on confidence

8   intervals. The cluster analysis defined for both sites two clusters (Fig. 3j, l). At Counami they

9   were related to soil types (P = 0.003), while they were not in Sparouine (P = 0.283).

10   For both sites, there was a pattern for FS trees to be higher than WS trees for a given

11   age (Fig. 3m, o). Within the Counami site, FS trees covered the largest range of trajectories

12   and reached the highest height (Fig. 3m). Within the Sparouine site, WS trees covered a larger

13   range of trajectories and the WS highest trees were as tall as the highest FS ones (Fig. 3o). For

14   both sites, it was possible to identify two main growing phases. The phases were

15   differentiated by variations in growth rates over the tree's lifespan. The first phase covered the

16   first 5-7 years, except for FS Counami trees where it was the first 9-10 years. The second

17   growing phase was defined by a slower growth rate, which remained constant for all

18   individuals. The cluster analysis defined three clusters for both sites, which were significantly

19   associated to soil types (P < 0.01; Fig. 3n, p). For Counami, the cluster C was composed of FS

20   trees with the highest growth rates whereas in Sparouine, cluster C was composed of WS trees

21   with the slowest growth rates.

22   The analysis of the cumulated number of pairs of inflorescences on the trunk indicated

23   that there was no significant difference between FS and WS for both sites based on

24   confidence intervals (Fig. 4a, b). In Counami trees, there was a significant difference in the

25   cumulated number of branches of the trunk between FS and WS after 5-6 years old based on

26   confidence intervals (Fig. 4c). In Sparouine trees there was no significant difference in the

27   cumulated number of branches on the trunk between FS and WS based on confidence

28   intervals (Fig. 4d).

29   The height growth rate, calculated for the first seven years of growth, was significantly

30   different between FS and WS on both sites (P < 0.001; ANOVA; Fig. 5), with highest growth

31   rates always exhibited by FS trees.

32   When comparing all four conditions in term of performance traits at whole tree level,

33   significant differences were identified for tree height, DBH, the branching order, the height of

34   the first flowering and first branching, and the node rank for first branching (Table 3; P <

14

1 0.05; ANOVA). No significant differences appeared for any trait within Sparouine between

2 FS and WS trees (P > 0.05; ANOVA). Significant differences between FS and WS trees

3 within Counami were found for tree height, the branching order, the height of first flowering,

4 and the node rank of first branching (P < 0.05; ANOVA). Between-site differences were

5 found for DBH and the height of first flowering (P < 0.05; ANOVA).

6

7 *Characterization of functional traits*

8 The first and second axes of the multivariate analysis of correlations for functional traits

9 explained 47.0 % of the inertia (Fig. 6a). The first axis (28.5 %) clustered individuals for

10 $C:N_{leaf}$, L_{pet}, A_{pet}, A_{leaf} and N_{leaf}. The second axis (18.5 %) clustered individuals for $H_2O_{res,leaf}$,

11 and K_{leaf}. Conditions (soil types x sites) were differentiated along the first axis (Fig. 6b; P <

12 0.05; ANOVA) with significant differences (i) between FS and WS within Counami and (ii)

13 between Counami and Sparouine when only considering FS. Conditions were more strongly

14 differentiated along the first axis (P < 0.001; ANOVA) with Counami trees in WS differing

15 from Sparouine trees in both FS and WS. When comparing soil types and sites for each trait

16 separately, significant average heterogeneity appeared only for L_{pet} and A_{leaf} (Table 4). Trees

17 on FS had longer petioles (L_{pet}) and larger leaves (A_{leaf}) than those on WS in Counami but not

18 in Sparouine (P < 0.05; Tukey's test).

19

20 **DISCUSSION**

21 To our knowledge, our study is the first that compares both tree architectural development and

22 functional traits (i.e. measured leaf and trunk traits) for a generalist tree species able to

23 colonise starkly contrasting soil types: FS and WS. Our pedological analysis clearly

24 demonstrates strong contrasts in soil characteristics between FS and WS, opening the

25 possibility of soil-related phenotypic variance. Contrary to our proposed hypothesis, the

26 functional variance between FS and WS is low and does not mirror the interspecific variance

27 in functional composition. Nevertheless, significant soil-related phenotypic variance is mainly

28 mediated by the architectural development entailing carbon saving. These points are discussed

29 below.

30

31 *Variance in* C. obtusa *architectural development between soil types*

32 The autocorrelation function for all trees together confirms a high degree of periodicity across

33 all individuals for growth, flowering, and branching processes. For growth, the period is a

34 multiple of 15-18 internodes, consistent with a bi- or an annual periodicity and the production

15

1   of nearly 30-35 nodes per year associated with an approximatively-10-day phyllochron, as

2   previously shown (Heuret et al., 2002; Zalamea et al., 2012). Such strong pattern of

3   periodicity strengthened and justified the year delineation method.

4   The effect of soil types on the ontogenetic component of growth is dependent on the

5   trait considered. Here, there is no significant effect of soil types on growth rhythm traits such

6   as phyllochron and the number of nodes per AS. Similarly, Zalamea et al. (2013) found no

7   difference in phyllochron between *C. sciadophylla* from two distanced locations with

8   contrasting rainfall and our results indicates that phyllochron and leaf production are not

9   prone to vary with environment. Soil type shows a significant effect on both internode length

10 and AS length in Counami for the first 6 years, but not in Sparouine. When the soil effect is

11 strong enough, the differences in AS length between soil types correspond mainly to

12 variations in internode length rather than variations in number of nodes per AS. Reducing the

13 number of nodes per AS would imply the increase of the phyllochron, thus reducing the

14 number of leaves produced per year. Such mechanism would critically affect tree carbon

15 balance and probably is avoided as the contribution of a given leaf to the carbon balance is

16 disproportionate in comparison to most of species: *C. obtusa*'s leaves are large (1,000-5,000

17 mm², Levionnois *et al.*, *data not published*) but few (100-600 leaves on one tree, Table 3).

18 Soil type has significant effects on tree cumulated height at age, mirroring the lifespan

19 cumulated effect of soil type on internode length. Such pattern is less noticeable on Sparouine

20 trees, where there were fewer significant contrasts in height between FS and WS (Appendix

21 S2 and Fig. S4).

22   WS trees in Counami had significantly less cumulated branches, and lower branching

23 order, than those in FS. WS trees in Counami have, therefore, reduced space and light

24 foraging capacities, probably hindering their competitive abilities. Even if WS trees may have

25 reduced space foraging capacities compared to FS trees, maybe the space and light

26 competition between individuals in WS is also reduced, since tree species diversity and stem

27 density are lower on WS (Fine & Baraloto, 2016). Or on the contrary, it could posit that as

28 WS are water and nutrient limiting, intra- and interspecific competition becomes more severe.

29 Because flowering is synchronous on all crown axes (Heuret et al., 2003), the production of

30 inflorescences and seeds is exponentially related to the number of our measured main

31 branches. Therefore, WS trees in Counami must also have comparatively reduced

32 reproductive and dispersive abilities, leading to a reduced overall fitness compared to their FS

33 conspecifics under the assumption that FS and WS trees form a unique population. The

34 population genetic structure of *C. obtusa* in French Guiana, and whether individuals found in

16

1   FS and WS belong to single populations, is still unknown. Such information is essential to

2   interpret the eco-evolutionary implications of reduced seed output of WS trees.

3   WS imposed strong and significant limitations on growth trajectories. Nonetheless,

4   trees in Counami FS have access to the richest soils based on water, clay and N contents, and

5   the $Index_{soil}$ (Appendix S2 and Fig. S4), whereas the highest growth trajectories are observed

6   in Sparouine FS. Such incongruence could be explained by other factors, such as: (i) variance

7   in *C. obtusa* genetic local adaptations; (ii) cloud-shading variability (Wagner, Rossi, Stahl,

8   Bonal, & Hérault, 2012) between sites; (iii) intra- or interspecific competition, as stand

9   structures are different between sites in terms of tree density, and proportion and composition

10 of other tree species; and finally, (iv) the slightly larger rainfall during the dry season for the

11 Sparouine site (Fig. S2). Clay and silt, which drive water reserves, do not differ between sites

12 for a given soil type (Appendix S2 and Fig. S4), so under the fourth hypothesis, water

13 availability would be the leading constraining factor explaining growth differences across

14 sites, with an accruing sensitivity during the dry season for Counami trees (Wagner et al.,

15 2012).

16   Our results are consistent with those of previous studies (Charles-Dominique, Edelin,

17 & Bouchard, 2009; Charles-Dominique, Edelin, Brisson, & Bouchard, 2012; Nicolini,

18 Barthélémy, & Heuret, 2000; Stecconi, Puntieri, & Barthélémy, 2010; Taugourdeau et al.,

19 2012; Taugourdeau, Chaubert-Pereira, Sabatier, & Guédon, 2011), where limiting or stressful

20 conditions are associated with smaller geometric features (e.g. length, diameter…) or slower

21 growth rates (Coomes & Grubb, 1998). But the precise soil physico-chemical determinants

22 that explain intra- and inter-site differences in trees developmental trajectories remain difficult

23 to understand and have to be investigated.

24

25 *Variance in* C. obtusa *functional traits between soil types*

26 Contrasting soil properties, such as FS-*versus*-WS, have strong impacts on species

27 community structure in the Amazon rainforest, both at local and regional scales (Daly et al.,

28 2016; Fine & Baraloto, 2016; Stropp et al., 2011; ter Steege et al., 2013). At the community

29 level, WS flora is characterised by a convergence in functional strategies, particularly towards

30 a conservative nutrient use strategy (Fine & Baraloto, 2016; Fine et al., 2010; Fortunel et al.,

31 2012; Fortunel, Paine, et al., 2014; Fortunel, Ruelle, et al., 2014; Fyllas et al., 2009; Grubb &

32 Coomes, 1997; Patiño et al., 2009). These imply high LMA, high WSG, small seeds, and low

33 leaf nutrient contents associated with high water use efficiency for WS tree species (Fine &

34 Baraloto, 2016), on the contrary of FS tree species. Such well-defined trait optima according

1   to species soil-specialization lead to the assumptions that (i) the phenotype range that trees are

2   capable of expressing to match the environment they live in is bounded, and that (ii) such

3   boundaries would shape functional ITV for species colonizing both FS and WS. To our

4   knowledge, no study has focused on the effect of FS-vs-WS soil properties on the

5   intraspecific functional variability.

6   Contrary to our hypothesis, a striking result is that the soil was not a strong enough

7   driver across the area we spanned to make any measured *C. obtusa* trait responsive to soil

8   composition variance. Only two functional traits are differentiated between soil types and

9   only for the Counami site: petiole length and leaf area. Even this weak response does not

10   mirror the interspecific functional level composition, where rather high LMA, high WSG, and

11   low leaf nutrient contents are generally found (Fine & Baraloto, 2016). The higher

12   pedological contrasts between FS and WS at Counami is probably the reason why it is the

13   only site where we found significant differences in leaf traits (Appendix S2 and Fig. S4). One

14   explanation is that larger leaves are associated with larger vessels (Gleason et al., n.d.), and

15   thus potentially larger water supplies. Moreover, larger leaves are self-sufficient for

16   generating higher evaporative demand and thus higher tension and driving force (Whitehead,

17   Edwards, & Jarvis, 1984). Limiting water demand with smaller leaves could be an efficient

18   way to prevent drought-related embolism, especially in a water-limited environment as WS.

19   Such findings of low functional responses are in contrasts with intraspecific variance

20   associated to maternal habitats in most functional traits in *Eperua* juveniles (Brousseau et al.,

21   2013a). However, the patterns of genetic structure and the occurrence of highly divergent

22   alleles among bottomland and hilltop *Eperua,* suggest that individuals could be locally

23   adapted to micro-habitats which explains the habitat-dependent variance in functional traits

24   (Audigeos et al., 2013; Brousseau et al., 2013a, 2015). Such habitat-genome associations have

25   not yet been tested in *C. obtusa*. These findings of low trait response are also in contrast with

26   the results of (Fine, Metz, et al., 2013) which found differences in leaf chlorophyll content

27   and leaf defence chemical traits against herbivores for *Protium subserratum* between FS and

28   WS. However and contrary to our Counami site where we found the higher trait contrast, the

29   *P. subserratum* FS and WS ecotypes in (Fine, Metz, et al., 2013) were from different

30   locations tens to hundreds of kilometres apart, potentially introducing other distance-related

31   effects such as population genetic structure.

32   The pedological analysis indicated that water availability and N content were limited

33   on WS (Appendix S2 and Fig. S4). Therefore, the development of *Cecropia* trees on WS is

34   allowed by two unexclusive explanations in our point of view. First, there are relevant

1 functional traits we did not consider in this study. It has been shown that water availability is

2 the leading climate driver of Amazonian rainforest tree growth (Wagner et al., 2012), thus

3 hydraulic architecture and drought-resistance traits, such as drought-induced vulnerability to

4 cavitation, stomatal sensitivity, leaf turgor loss point, root depth, crown area to sapwood area

5 ratio, may have played a central role in ensuring growth and survival on the different soil

6 types (Adams et al., 2017; Anderegg et al., 2016; Eller et al., 2018; Urli et al., 2013). Greater

7 hydric stress is expected on WS, but $\delta^{13}C_{leaf}$, which is a proxy for plant water-use efficiency,

8 did not vary with soil types. One explanation would be that water-use efficiency starts to

9 change when trees are effectively water-stresses, i.e. at the end of the dry season (November

10 in French Guiana, Fig. S2), when soil water content is exhausted (Bonal, Barigah, Granier, &

11 Guehl, 2007; Wagner, Hérault, Stahl, Bonal, & Rossi, 2011). Since most of our trees were not

12 sampled at this time, we can hypothesised that they were not stresses enough for detecting

13 contrasting $\delta^{13}C_{leaf}$. The variance in soil characteristics can also impact the root system

14 properties (Freschet et al., 2017), including mycorrhizal fungi associations (Roy et al., 2016).

15 Such processes were not captured by the functional traits analysis.

16

17 *The phenotypic variance strategy for being a soil generalist*

18 We showed that soil heterogeneity across sites does not affect the functional traits of *C.*

19 *obtusa* we selected, but rather drives a divergence on growth trajectory and total biomass

20 between FS and WS. Indeed, we showed that WS trees exhibit shorter internodes and annual

21 shoots for a given age, and lower height and DBH, leading to lower aboveground biomass for

22 a given age. Also in terms of biomass, we showed that Counami WS trees have less

23 cumulated branches over their lifespan, which entails exponential carbon savings by reducing

24 the number of total leaves as also the quantity of flowers and fruits, if everything else remains

25 equal (flower and fruit size, number of flowering and fruiting events in a year). We also

26 identified that Counami WS trees bear petioles ~27% shorter than their FS conspecifics,

27 which lead to substantial carbon savings per phytomer. Minimizing carbon expenses in

28 resource-limiting environments is consistent with the growth strategy of heliophile species

29 facing strong competition for light, where they prioritise growth in height (Poorter, Bongers,

30 & Bongers, 2006; Poorter & Rozendaal, 2008; Westoby, Daniel S. Falster, Angela T. Moles,

31 Peter A. Vesk, & Wright, 2002).

32   Across soil types and sites, growth and survival on WS is optimised by buffering leaf

33 and wood traits values, at least for the traits we measured, but by saving carbon through

34 smaller internode, less branches, and lower wood increments; rather than just adjusting

1　functional traits as generally and implicitly posited or awaited (Brousseau, Bonal, Cigna, &

2　Scotti, 2013b; Fine & Baraloto, 2016). One striking result strengthening this idea is the

3　gradient of overall phenotypic response with soil contrasts. Indeed, we clearly showed, based

4　on soil analysis, that soil differences were more contrasted in Counami than Sparouine. In the

5　same way, no functional trait difference was found in Sparouine between FS and WS,

6　whereas two traits were different in Counami between FS and WS. Moreover, our

7　architectural analysis demonstrated higher contrast for Counami trees between FS and WS,

8　based on cumulated height with age, internode length, annual shoot length, and cumulated

9　branching.

10

11　**CONCLUSION**

12　Our study provides to our knowledge the first evaluation of FS-*versus*-WS soil effects on the

13　phenotypic variability at the intraspecific level. Our findings point to the improvement made

14　by integrating together functional traits, and whole-tree growth trajectory and architectural

15　development, to detect the leading phenotypic adjustments involved at the intraspecific

16　response to different soil types Functional traits divergence did not necessary occur at the

17　intraspecific level in the same pattern as documented at the interspecific level. The main

18　phenotypic differences between FS and WS trees were (i) height growth rates and trees

19　heights at age –through the variation of internode length instead of phyllochron-, and (ii)

20　branching when integrated on the tree's lifespan. A better description of the soil-dependent

21　phenotypic adjustments between FS and WS trees could be achieved by including mechanistic

22　and physiological traits such as anatomical, photosynthetic, and hydraulic traits, and should be

23　incorporated into future work. Our study provides a key insight into *C. obtusa*'s phenotypic

24　variance associated with intraspecific soil heterogeneity, and future lines of research should

25　address (i) the impact of phenotypic variability between FS and WS trees on the eco-

26　evolutionary dynamics of the widespread species *C. obtusa*, as a model generalist tree species,

27　(ii) the evolutionary process involved in the tolerance of environmental variation - phenotypic

28　plasticity and/or genetic adaptation -, and thus (iii) whether there are neutral and adaptive

29　genetic differences between individual *C. obtusa* established in FS and WS. Future prospects

30　on phenotype-genotype-environment relationships are thus desirable in this way, especially

31　for the hyperdominant tree species *C.obtusa* playing a key role in natural reforestation after

32　disturbance in the Guiana shield and facing climate change.

33

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Table 1. List of measured growth and dimension architectural traits.

Trait	Abbreviation	Unit
Architectural growth traits		
Internode length	IN	mm
Internode length residuals		-
Phyllochron		day
Annual shoot length	AS	cm
Number of nodes per AS		-
Cumulated tree height		m
Architectural dimension traits		
Age after determination	Age	year
Tree height	Height	m
Diameter at breast height	DBH	cm
Number of trunk internodes	IN_{A1}	-
Number of A2 bearing branches	Br_{bear}	-
Number of A2 dead branches	Br_{dead}	-
Total number of A2 branches	Br_{tot}	-
Branching order	Order	-
Total number of inflorescences	Fl_{tot}	-
Total number of leaves	$Leaf_{tot}$	-
Total estimated crown area	A_{crown}	m²
First branching height	Br1stH	m
First flowering height	Fl1stH	m
First branching node rank	Br1stIN	-
First flowering node rank	Fl1stIN	-
First branching age	Br1stAge	year
First flowering age	Fl1stAge	year

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1   **Table 2.** List of measured functional traits and the infered growth rate.

Trait	Abbreviation	Unit
Leaf content traits		
Residual moisture content	$H_2O_{res,leaf}$	%
$\delta^{13}C$ content	$\delta^{13}C_{leaf}$	‰
Carbon content	C_{leaf}	$g\ kg^{-1}$
Nitrogen content	N_{leaf}	$g\ kg^{-1}$
Carbon/Nitrogen ratio	CN_{leaf}	-
Phosphorus content	P_{leaf}	$g\ kg^{-1}$
Potassium content	K_{leaf}	$g\ kg^{-1}$
Chlorophyll content	Chl_{leaf}	$mg\ ml^{-1}$
Leaf morphological traits		
Leaf lifespan	LL	day
Petiole length	L_{pet}	cm
Petiole cross-sectional area	A_{pet}	mm²
Number of lobes	N_{lobe}	-
Leaf mass area	LMA	$g\ cm^{-2}$
Leaf thickness	Th_{leaf}	µm
Estimated leaf area	A_{leaf}	cm²
Wood trait		
Wood specific gravity	WSG	$g\ cm^{-3}$

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1   **Table 3.** Nested-ANOVA for measured architectural dimension traits between soil types and sites.

Abbreviation	Unit	$P_{ontogeny}$	P_{ANOVA}	Counami FS (N = 13)		Counami WS (N = 19)		Sparouine FS (N = 19)		Sparouine WS (N = 19)		Range
Height	m	-	**0.001**	16.13 ± 1.92	a	13.31 ± 1.10	b	18.98 ± 0.65	a	17.27 ± 0.99	ab	10.05 – 21.99
DBH	cm	-	**0.049**	15.02 ± 2.24	ab	12.44 ± 2.33	a	19.30 ± 0.97	b	18.24 1 ±.52	ab	6.21 – 30.49
IN_{A1}	-	**0.001**	0.760	429.2 ± 87.0		457.9 ± 35.0		289.5 ± 10.1		277.9 ± 14.8		221 - 765
Br_{bear}	-	**0.001**	0.139	7.85 ± 1.75		4.32 ± 1.55		10.74 ± 1.79		11.11 ± 1.82		0 - 19
Br_{dead}	-	-	0.428	10.23 ± 6.02		7.47 ± 1.97		12.84 ± 2.35		10.58 ± 2.81		0 - 33
Br_{tot}	-	**0.023**	0.373	13.62 ± 4.07		6.79 ± 2.90		21.47 ± 3.80		24.16 ± 8.17		1 - 75
Order	-	-	**0.006**	2.92 ± 0.41	a	2.32 ± 0.26	b	3.16 ± 0.17	ab	3.26 ± 0.20	ab	1 - 4
Fl_{tot}	-	-	0.330	55.54 ± 17.11		46.42 ± 12.31		75.68 ± 24.95		121.9 ± 68.0		0 - 657
$Leaf_{tot}$	-	-	0.167	140.6 ± 37.6		75.74 ± 31.54		170.74 ± 31.35		200.3 ± 72.7		25 - 674
A_{crown}	m²	**0.001**	0.188	16.44 ± 6.11		6.893 ± 3.472		21.79 ± 4.17		26.78 ± 7.89		1.656 - 74.10
Br1stH	m		**0.001**	9.04 ± 0.80	a	8.20 ± 0.80	a	10.45 ± 0.50	b	9.05 ± 0.85	b	5.27 – 14.56
Fl1stH	m		**0.001**	11.29 ± 1.38	a	9.12 ± 0.89	b	18.67 ± 0.71	c	16.71 ± 0.94	c	6.62 – 20.99
Br1stIN	-		**0.048**	141.8 ± 22.6	a	178.7 ± 32.1	b	117.0 ± 6.8	ab	113.7 ± 8.6	ab	81 - 358
Fl1stIN	-		0.079	188.6 ± 26.3		198.6 ± 32.7		284.2 ± 7.9		264.1 ± 13.9		101 - 412
Br1stAge	year		0.092	4.272 ± 0.752		5.297 ± 1.053		3.358 ± 0.220		3.263 ± 0.275		2.332 – 11.94
Fl1stAge	year		0.124	5.709 ± 0.821		8.833 ± 0.986		8.307 ± 0.231		7.699 ± 0.406		3.132 – 11.49

$P_{ontogeny}$ refers to the p-value associated with a test of the effect of ontogeny on the trait based on a linear regression. P_{ANOVA} refers to the p-value associated with a test of soil and site effects on traits based on a nested-ANOVA. Bold values are for significant correlations ($P < 0.05$). Letters refer to differences in average based on Tukey's HSD (Honest Significant Difference) test. See Table 3 for definitions of abbreviations. See Table 1 for definitions of abbreviations.

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Table 4. Nested-ANOVA for measured functional traits between soil types and sites.

Abbreviation	Unit	$P_{ontogeny}$	P_{ANOVA}	Counami FS (N = 13)	Counami WS (N = 19)	Sparouine FS (N = 19)	Sparouine WS (N = 19)	Range
$H_2O_{res,leaf}$	%	**< 0.001**	0.057	9.921 ± 0.557	10.18 ± 0.26	7.823 ± 0.132	8.255 ± 0.124	7.38 – 11.50
$\delta^{13}C_{leaf}$	‰	-	0.296	-29.61 ± 0.38	-29.74 ± 0.50	-29.30 ± 0.19	-29.78 ± 0.31	-32.12 - -28.41
C_{leaf}	g kg^{-1}	-	0.303	46.99 ± 0.39	46.27 ± 0.41	47.12 ± 0.22	46.74 ± 0.84	39.11– 48.04
N_{leaf}	g kg^{-1}	**< 0.001**	0.582	2.531 ± 0.253	2.312 ± 0.170	2.649 ± 0.111	2.743 ± 0.177	1.630 – 3.200
CN_{leaf}	-	**< 0.001**	0.706	19.13 ± 1.87	20.52 ± 1.52	17.95 ± 0.85	17.16 ± 0.67	14.84 – 28.01
P_{leaf}	g kg^{-1}	-	0.367	1.687 ± 0.305	1.698 ± 0.205	1.322 ± 0.231	1.178 ± 0.059	0.588 – 2.42
K_{leaf}	g kg^{-1}	-	0.065	16.31 ± 2.98	14.56 ± 2.43	12.30 ± 2.32	9.099 ± 0.865	4.88 – 27.50
Chl_{leaf}	mg ml^{-1}	**< 0.01**	0.851	62.16 ± 9.73	53.50 ± 6.51	101.4 ± 20.6	110.7 ± 31.5	31.1 – 309.0
LL	day	**0.016**	0.352	117.3 ± 16.8	110.3 ± 10.8	79.96 ± 0.542	83.82 ± 0.626	58 - 181
L_{pet}	cm	**< 0.001**	**0.015**	37.19 ± 4.60 b	27.34 ± 3.32 a	42.79 ± 3.62 ab	47.5 ± 2.70 ab	14.2 – 62.0
A_{pet}	mm²	**< 0.001**	0.216	67.78 ± 12.36	47.90 ± 7.22	77.07 ± 12.41	81.35 ± 8.88	25.1 – 126.3
N_{lobe}	-	-	0.160	7.923 ± 0.268	7.353 ± 0.316	7.667 ± 0.267	8.000 ± 0.218	6 - 9
LMA	g m^{-2}	**0.002**	0.141	97.42 ± 10.41	96.43 ± 7.95	99.55 ± 3.74	89.06 ± 5.30	63.49 – 130.3
Th_{leaf}	μm	**< 0.001**	0.505	366.2 ± 23.7	397.8 ± 19.9	314.7 ± 17.6	302.9 ± 29.8	213 - 482
A_{leaf}	cm²	**< 0.001**	**0.047**	1860 ± 393 b	1094 ± 215 a	2043 ± 362 ab	2587 ± 472 ab	321 - 4916
WSG	g cm^{-3}	**< 0.01**	0.099	0.389 ± 0.029	0.352 ± 0.019	0.325 ± 0.018	0.319 ± 0.014	0.252 – 0.516

$P_{ontogeny}$ refers to the p-value associated with a test of the effect of ontogeny on the trait based on a linear regression. P_{ANOVA} refers to the p-value associated with a test of soil and site effects on traits based on a nested-ANOVA. Bold values are for significant correlations ($P < 0.05$). Letters refer to differences in average based on Tukey's HSD (Honest Significant Difference) test. See Table 2 for definitions of abbreviations.

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1 **FIGURE LEGENDS**

2 **Fig. 1.** Autocorrelation function according to growth, flowering, and branching processes. (a)

3 Internode length residuals for Counami, (b) Internode length residuals for Sparouine, (c)

4 Flowering presence for Counami, (d) Flowering presence for Sparouine, (e) Branching

5 presence for Counami, (f) Branching presence for Sparouine. Red: ferralitic soils; black:

6 white-sand soils.

7 **Fig. 2.** Phyllochron (day) according to the node rank from the base. (a) Counami, (b)

8 Sparouine. Red: ferralitic soils; black: white-sand soils. Thick lines: means; thin lines: each

9 individual; dashed lines: confidence intervals at 95%.

10 **Fig. 3**. Architectural growth traits according to age (years). Main boxes represent features

11 according to soil types. Inboxes represent mean trajectories after clustering longitudinal

12 analyses (*kml*). The left column represents Counami trees, the right column represents

13 Sparouine trees. Distributions between soil types and kml-trajectories are represented with

14 Pearson chi-squared test. Red: ferralitic soils; black: white-sand soils. Blue: trajectory A;

15 green: trajectory B; orange: trajectory C. Thick lines: means; dashed lines: confidence

16 intervals at 95%.

17 **Fig. 4.** Cumulated number of trunk nodes with pairs of inflorescences and number of branches

18 per annual shot according to the age (year). (a) and (b) Means for inflorescences for Counami

19 and Sparouine respectively. (c) and (d) Means for branches for Counami and Sparouine

20 respectively. Red: ferralitic soils; black: white-sand soils. Thick lines: means, dashed lines:

21 confidence intervals at 95%.

22 **Fig. 5.** Principal component analysis (PCA) on functional traits for the two sites for 70 trees.

23 (a) Correlation circle of data with the histogram of inertia. (b) Individual factor map of data

24 according to soil types and sites. In (a), the colour gradient indicates the contribution of each

25 variable to the axis. See Table 3 for definitions of abbreviations. "Res" prefixes indicate

26 residuals after removing the ontogenetic effect. In (b), significant differences in coordinates

27 ($P < 0.05$; ANOVA) between soil types and sites are indicated by letter according to the

28 considered axis. Red: ferralitic soils; black: white-sand soils; COU: Counami; SPA:
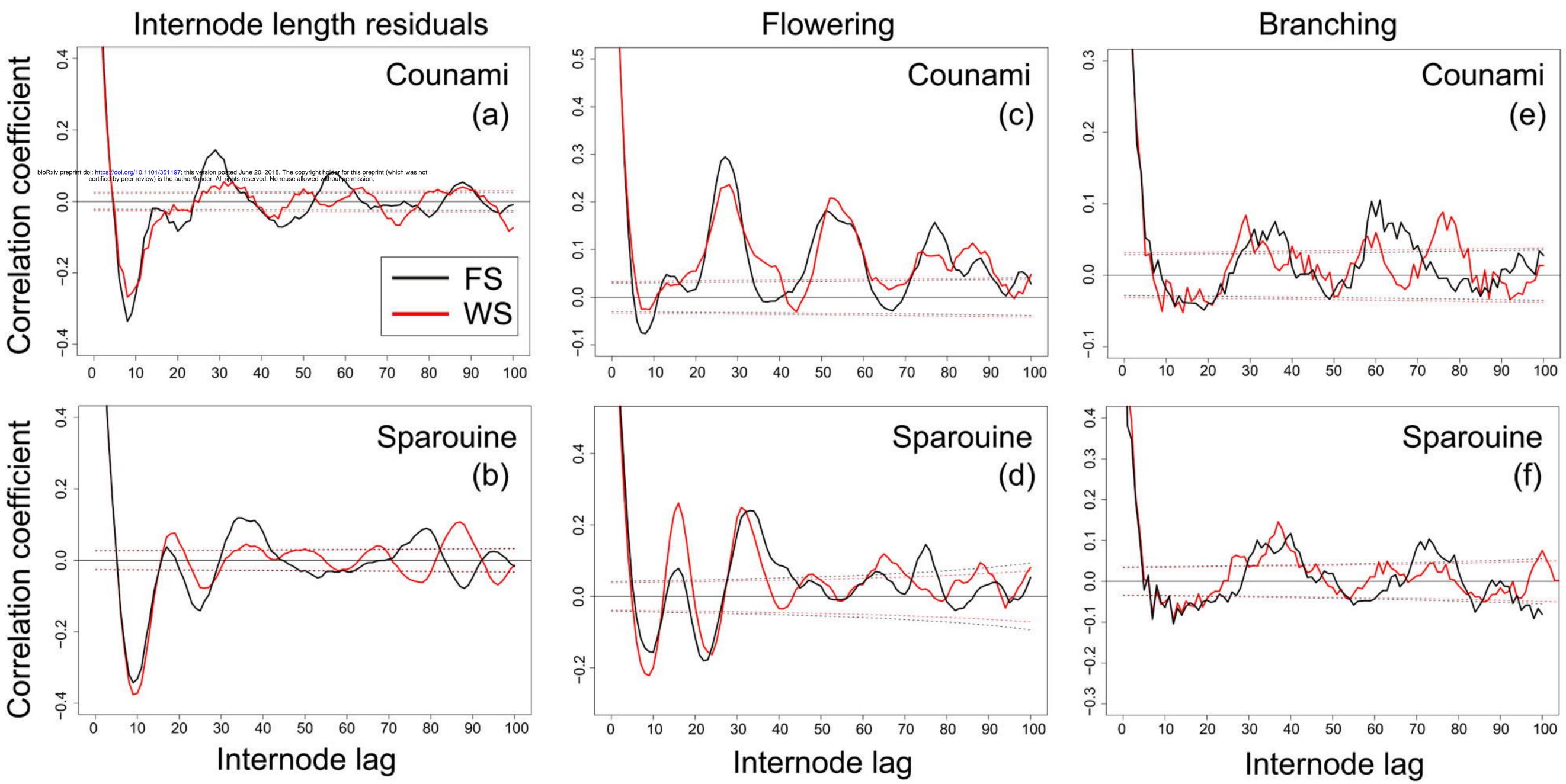
29 Sparouine.

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SUPPORTING INFORMATION LEGENDS

Appendix S1. Pedological characterization: Materials and methods, and results.

Appendix S2. Materials and methods: residuals, year delineation and inference of age.

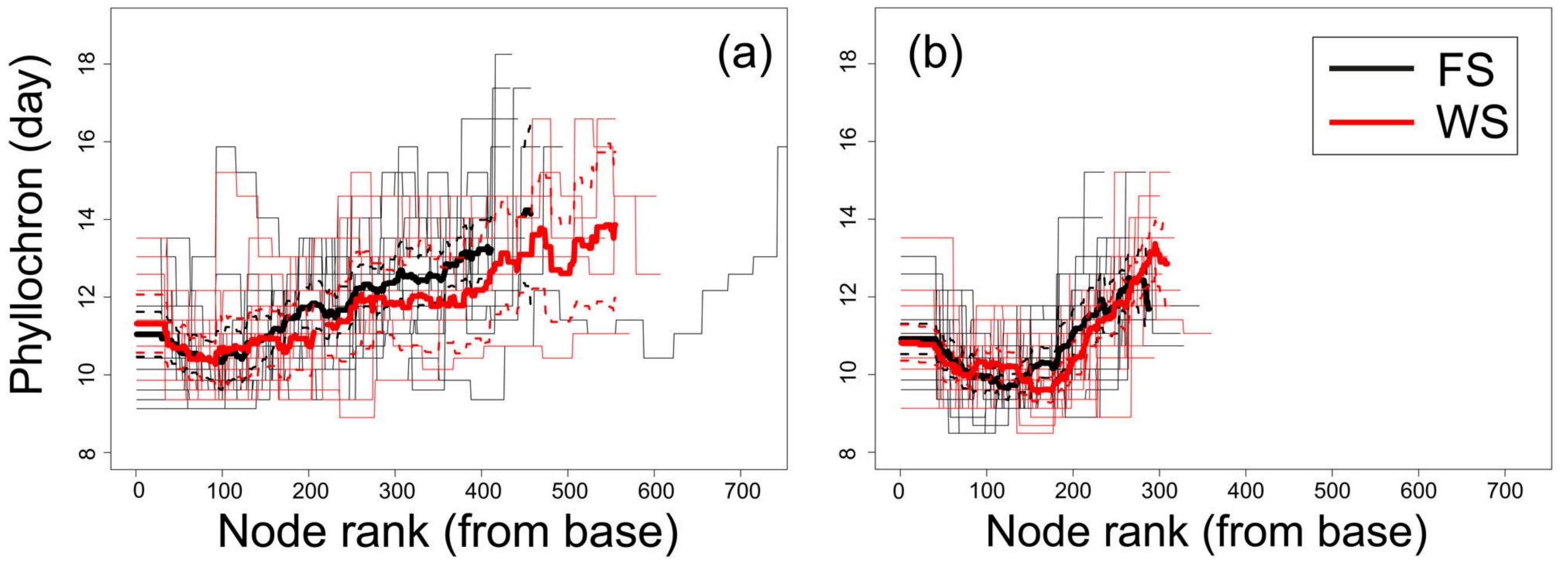**Appendix S3.** Materials and methods: measurement of leaf and trunk functional traits.

Fig. S1. Morphological features of *Cecropia obtusa* Trécul (Urticaceae). (a) Focus on an apex, ca: calyptra; pe: petiole; if: inflorescence. (b) Focus on a branch tier, br: branch; in: internode, axis as the trunk are made of a linear succession of internodes; ins: inflorescence scars, these are twice just above the axillary leaf; les: leaf scar. (c) Focus on an internode, in: internode; ins: inflorescence scars; les: leaf scar; no: a node marled by the calyptra scar, allowing for the delineation of internodes along an axis as the trunk.

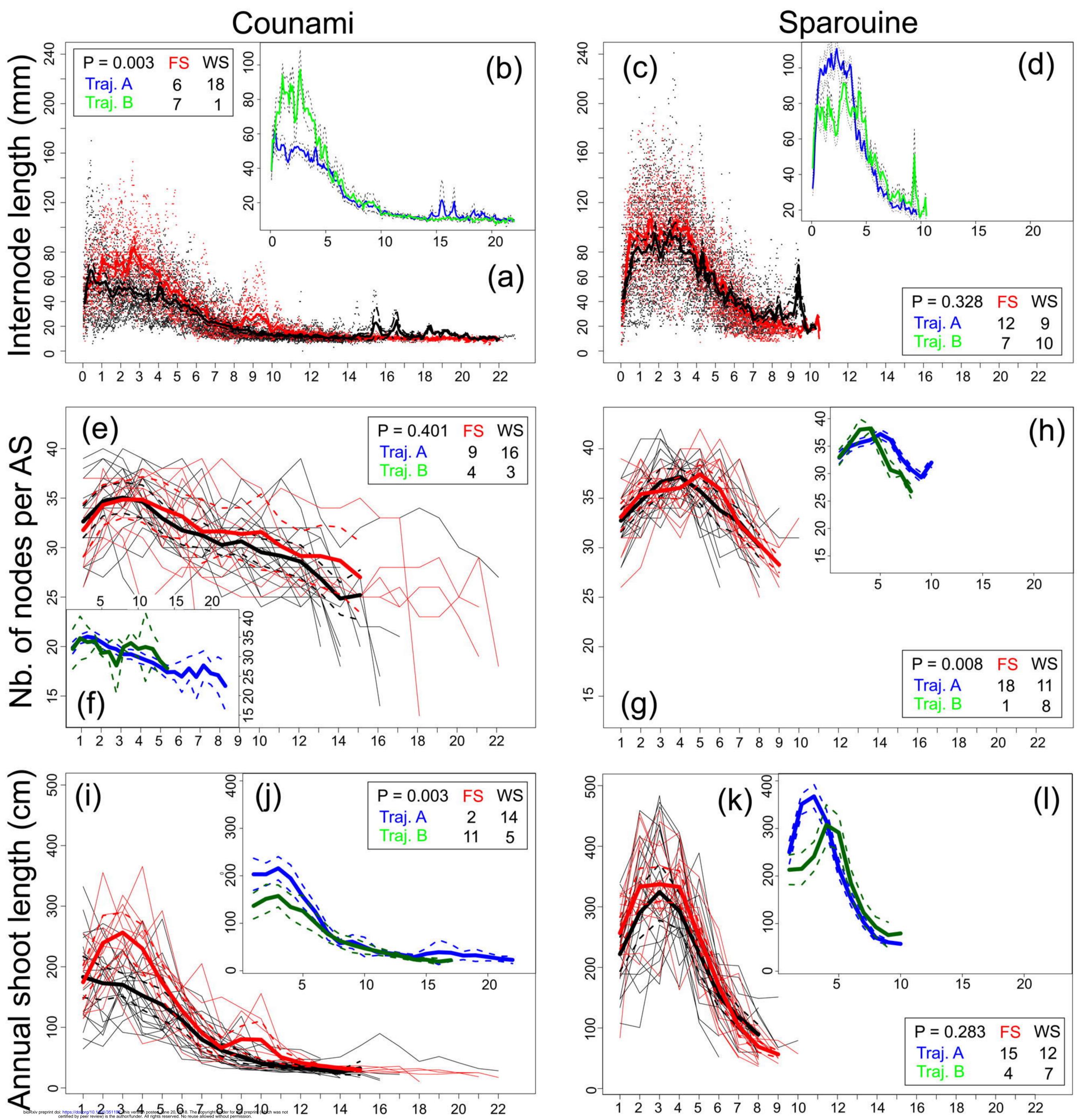**Fig. S2**. Box plots of mean annual rainfall (mm) from 1980 to 2016. (a) Counami, (b) Sparouine.

Fig. S3. Tree heights (m) according to diameters at breast height (cm). Red: ferralitic soils; black: white-sand soils. Cross: Sparouine; square: Counami.
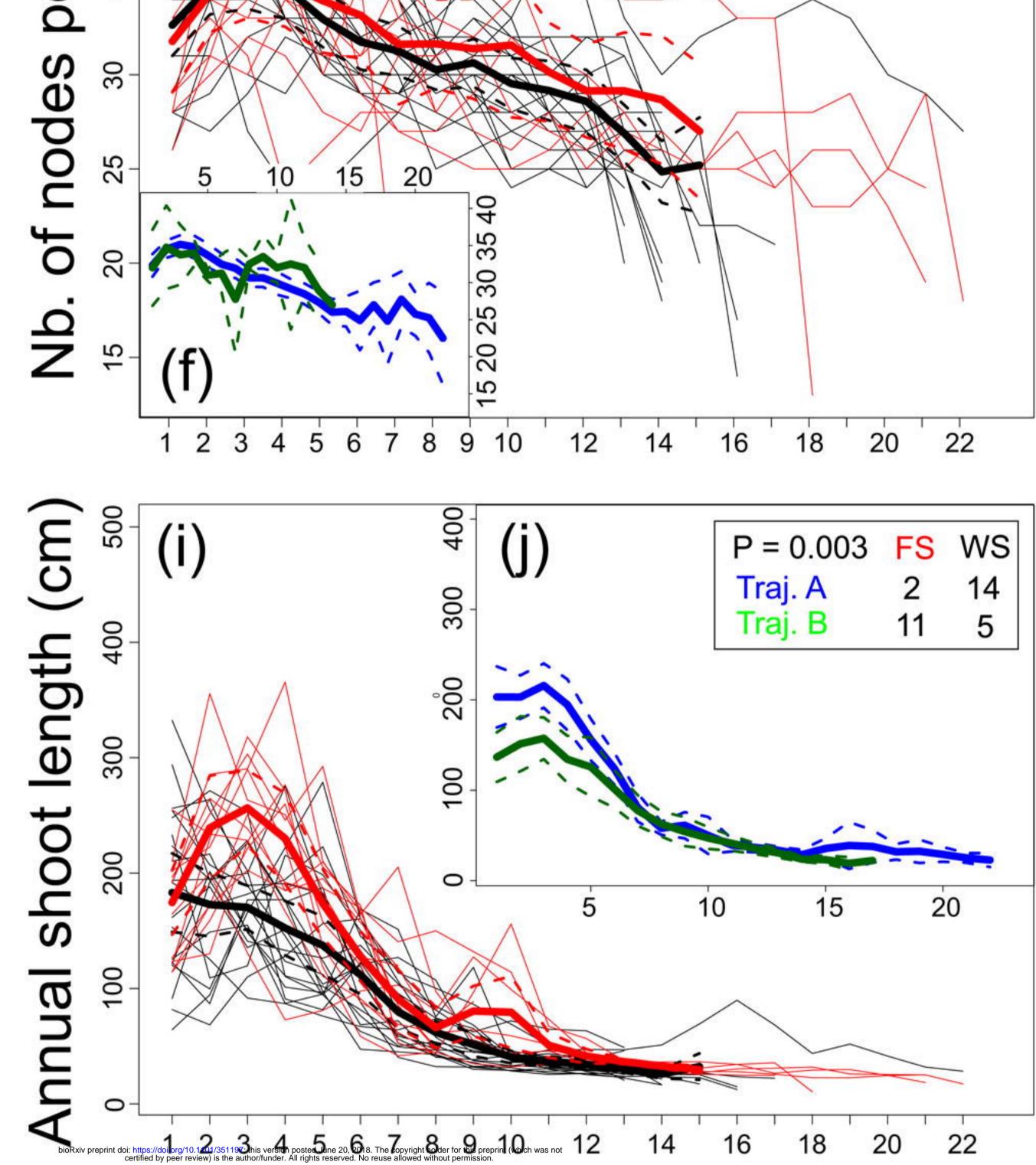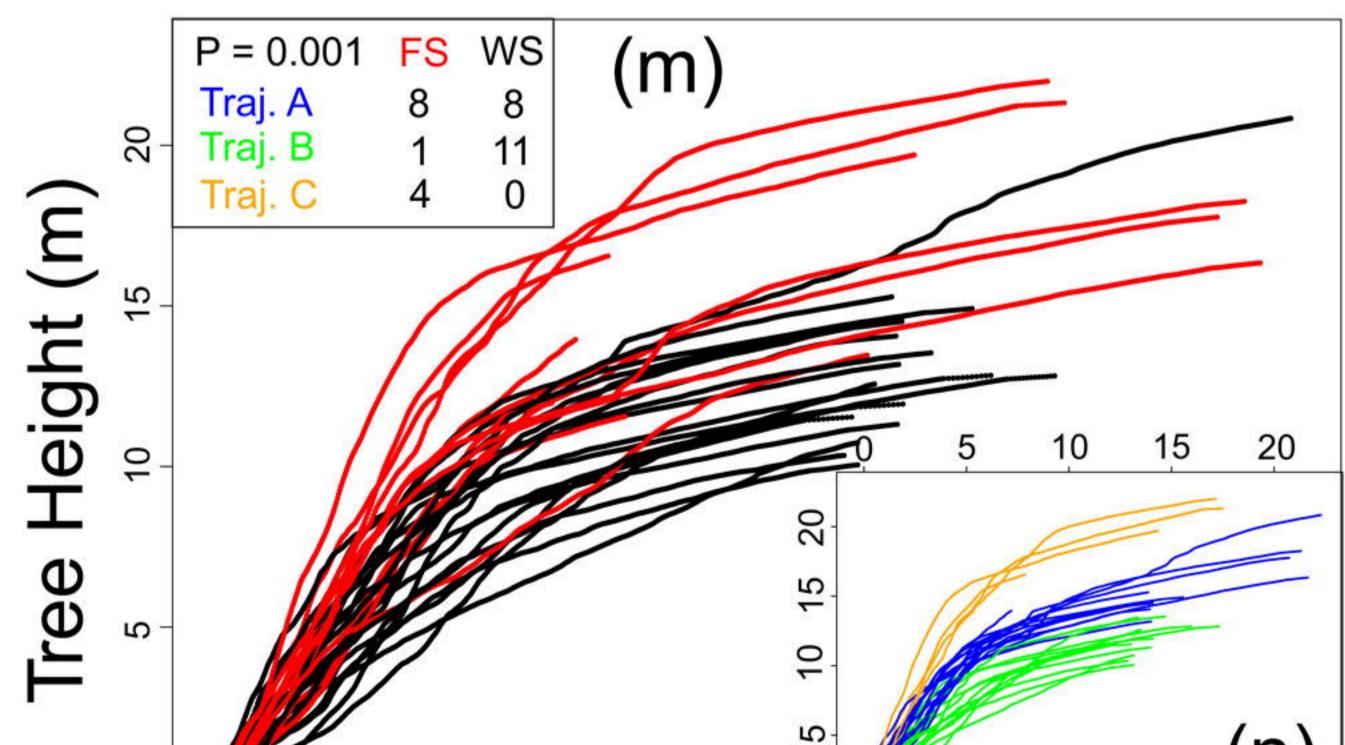
Counami (a)

Sparouine (b)

FS
WS

Counami

Sparouine

(b) P = 0.003 FS WS
Traj. A 6 18
Traj. B 7 1

(a)

(c)

(d) P = 0.328 FS WS
Traj. A 12 9
Traj. B 7 10

Internode length (mm)

(e) P = 0.401 FS WS
Traj. A 9 16
Traj. B 4 3

(f)

(h)

(g) P = 0.008 FS WS
Traj. A 18 11
Traj. B 1 8

Nb. of nodes per AS

(i) **(j)** P = 0.003 FS WS
Traj. A 2 14
Traj. B 11 5

(k) **(l)**

P = 0.283 FS WS
Traj. A 15 12
Traj. B 4 7

Annual shoot length (cm)

(m) P = 0.001 FS WS
Traj. A 8 8
Traj. B 1 11
Traj. C 4 0

(n)

(o) P = 0.011 FS WS
Traj. A 13 6
Traj. B 6 7
Traj. C 0 6

(p)

Tree Height (m)

Age (year, from germination)

Age (year, from germination)