Tree Age Mediates Plant-Soil Relationships

Subjects: Forestry
Contributor: Talita dos Santos Angélico

The relationships between growth and soil are mediated by plant age. Stem growth and wood anatomy of 9-year-old trees and 2-year-old saplings of *Enterolobium contortisiliquum*, “tamboril” growing in eutrophic and oligotrophic soils were compared. Soil conditions have influenced the growth and variations in wood anatomical features.

Keywords: Enterolobium contortisiliquum ; eutrophic ; oligotrophic ; ontogeny

1. Introduction

Environmental conditions influence the biological processes involved in plant development, thus affecting the final growth. Variations in secondary growth of woody plants can be an answer to gradients in resource availability. Identifying the influence of environmental conditions in wood structure and function of trees growing under different conditions is of particular interest because environment directly affects xylem cell differentiation, i.e. enlargement and secondary wall thickening, and, consequently, the efficiency of water and nutrient transport from roots to leaves [1][2][3].

Studies of plant-soil relationships can gain more insights when comparing individuals of different ages since structure and function of the conducting system in plants change during ontogeny. The nutrient acquisition depends on the age and size of the individuals [4][5]. Thus, investigations of anatomical traits of the xylem could explain why trees of different ages develop different strategies for nutrient acquisition [6][7].

Enterolobium contortisiliquum (Vell.) Morong (Fabaceae), known as *tamboril*, *timboúva*, *orelha-de-negro,* and *pacará earpod tree*, is a tree species spreading in various regions of Brazil [8][9], such as Caatinga, Cerrado, and Atlantic Forest, and exhibits a good adaptation to different conditions. Because of its fast growth, this species can be used to facilitate the natural regeneration of woody shrubs in reforestation and for phytoremediation of oil-contaminated soils [10][11]. Previous observations have detected that tamboril trees growing in eutrophic and clay soil reached a larger stem diameter than those in oligotrophic and sandy soil (personal communication V. L. Engel). Due to the importance of this species for the recovery of degraded areas and abandoned agricultural lands, it is necessary to understand its biological strategies in response to soil restrictions.

In this study, we analyzed stem growth and wood anatomy of tamboril by comparing 9-year-old trees and 2-year-old saplings (Figure 1), growing in eutrophic and oligotrophic soils from areas of semi-deciduous seasonal forest, nearby Botucatu (22°52’32” S and 48°26’46” W), São Paulo State, Brazil. These areas belong to a geographic region of the Cerrado Domain [12]. We expected that the influence of soil type on tree growth reflects changes in wood anatomical features.

Taking all into consideration, this review presents the relationships between growth and soil in tamboril. Also, it summarizes the wood anatomical variations in response to soil conditions where the plant grew. In addition, we discussed how the responses to soil type are mediated by tree age.

Figure 1: Studied 9-year-old trees (A,B) and 2-year-old saplings (C,D) of *Enterolobium contortisiliquum*. (A–C) Plants in eutrophic soil. (B–D) Plants in oligotrophic soil. Note the saplings are taller in eutrophic soil (C) than in oligotrophic soil (D). Blue vertical bar = 35 cm in C.

2. The effects of soil types on plant growth

Trees growing in eutrophic soil had larger stem diameters and heights compared to those growing in oligotrophic soil (Table 1). The same response was observed for 2-year-old saplings (Table 1). Soil type produced significant differences in growth ($p < 0.001$; Table 2), and age influenced the stem's diameter and height as well ($p < 0.001$, Table 2). The interaction age x soil was significant ($p < 0.01$ for diameter and $p < 0.001$ for height), indicating that plants at different ages responded differently to soil type.

Table 1: Studied trees and saplings of *Enterolobium contortisilliquum*. DBH = diameter at breast height; H = height; CD = collar diameter.

Site/ Soil	Trees			Saplings	
	Individual	DBH(cm)	H(m)	CD(cm)	H(cm)
Eutrophic	1	29.6	11	2.73	75.5
	2	25.5	10	2.59	82.7
	3	28.7	16	2.76	90
	4	29	13	2.46	65
	5	43	15	2.71	74
Oligotrophic	1	16.9	3.75	3.30	99.7
	2	22	5.75	1.96	50
	3	14.9	4.5	2.55	55.9
	4	14.6	7.5	2.53	65.6
	5	19.7	7	1.47	41

Table 2: Two-way ANOVA testing for the effect of age and soil on size of *Enterolobium contortisiliquum* trees and saplings.

Size	F-value			p		
	Age	Soil	Age x soil	Age	Soil	Age x soil
Diameter of stem	161.1	16.78	15.41	<0.0001	0.0008	0.0012
Height	164.4	30.48	28.08	<0.0001	<0.0001	<0.0001

3. The effects of soil types on wood anatomy

Significant differences were observed in following wood anatomical features (Table 3): fiber wall thickness (4.38–8.04 µm in trees and 2.00–3.22 µm in saplings, minimum and maximum, respectively) and intervessel pit diameter (6.85–9.03 µm in trees and 5.03–6.80 µm in saplings, minimum and maximum, respectively) varied significantly between soil types ($p < 0.05$ for intervessel pit diameter and $p < 0.001$ for fiber wall thickness).

Table 3: Two-way ANOVA testing for the effect of age and soil on wood anatomy of *Enterolobium contortisiliquum* trees and saplings.

Feature	**Age**		**Soil**		**Age × soil**	
	F-Value	***p***	**F-Value**	***p***	**F-Value**	***p***
Vessel density	42.95	<0.0001	0.1789	0.6779	0.2677	0.612
Vessel grouping	36.32	<0.0001	0.7258	0.4068	0.5581	0.4658
Vessel element diameter	158.9	<0.0001	2.638	0.1238	3.284	0.0888
Vessel element length	28.95	<0.0001	0.804	0.3832	0.6581	0.4291
Intervessel pit diameter	43.05	<0.0001	7.074	0.01713	1.988	0.1777
Vessel-ray pit diameter	76.32	<0.0001	0.1881	0.6703	1.172	0.295
Fiber length	266	<0.0001	1.166	0.2963	0.0196	0.8905
Fiber diameter	18.52	0.0005	0.8778	0.3627	1.329	0.2659
Fiber wall thickness	97.95	<0.0001	17.89	0.0006	11.3	0.0039
Rays height	13.59	0.002	0.1753	0.6811	0.9354	0.3479
Rays density	47.14	<0.0001	0.1752	0.6826	1.482	0.2412
Vessels fraction	3.472	0.0809	1.716	0.2087	5.31	0.0349
Fibers fraction	3.618	0.0753	1.643	0.2182	0.0439	0.8366

Parenchyma fraction	66.49	<0.0001	0.5505	0.4689	8.365	0.0106
Rays fraction	60.21	<0.0001	0.6911	0.418	6.047	0.0257

From a qualitative point of view, wood anatomy was similar in eutrophic and oligotrophic soil, except for storage compound contents (Figure 2). Trees growing in eutrophic soil had storage compounds in the reserve cells that were not observed in the oligotrophic soil. Moreover, these storage compounds mostly occurred in the parenchyma cells associated with the vessels. In saplings, the storage compounds spread throughout the axial parenchyma cells.

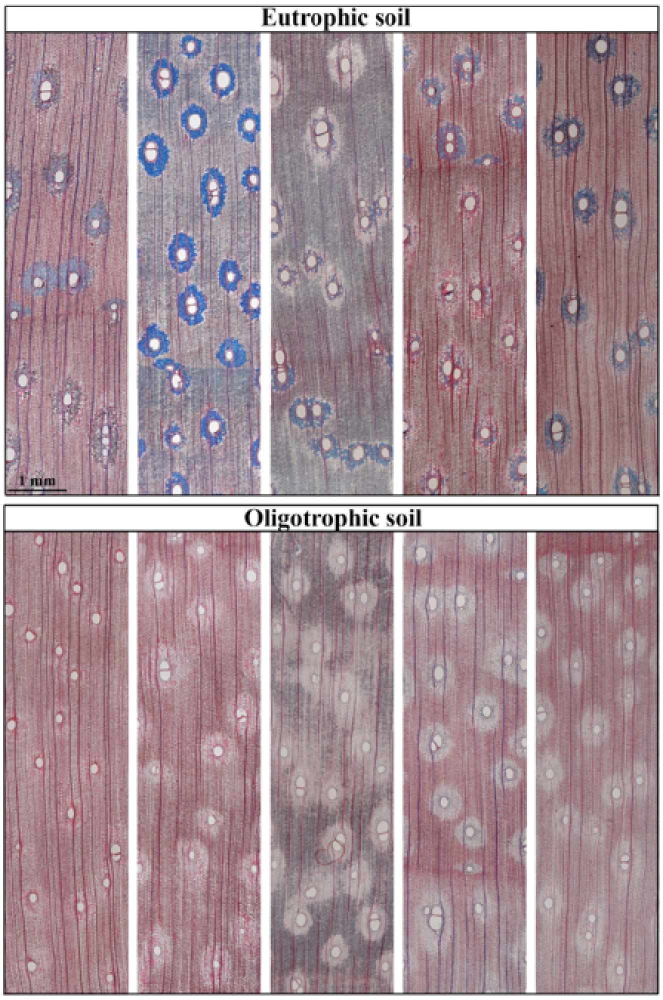

Figure 2: Cross-sections of *Enterolobium contortisiliquum* 9-year-old trees in eutrophic soil and oligotrophic soil.

4. The effects of age on wood anatomy

All measurements varied in function of age, except for the fraction of vessels and fibers (Table 3). The interaction age × soil influenced fiber wall thickness ($p < 0.01$), axial parenchyma fraction ($p < 0.05$), and ray fraction ($p < 0.05$).

Compared to the trees, saplings had more multiple vessels, more parenchymatous cells, and predominantly uniseriate rays. Sapling had high values of vessel grouping index (1.87–2.37 in trees and 3.04–6.78 in saplings – minimum and maximum), vessel density (2.47–3.82/mm^2 in trees and 8.33–26.47/mm^2 in saplings – minimum and maximum), and ray density (4.67–5.67/mm^2 in trees and 6.10–7.60/mm^2 in saplings – minimum and maximum) than trees. Trees produced more resistant tissues (63% of them were fibers), regardless of the soil type (Figure 3). Saplings had prioritized the formation of storage tissue (64% axial parenchyma and ray cells), specifically in eutrophic soil. These differences among trees and saplings were due to the cambium age, considering that young plants may change considerably in their xylem structural and functional features as a tree grows and matures [7].

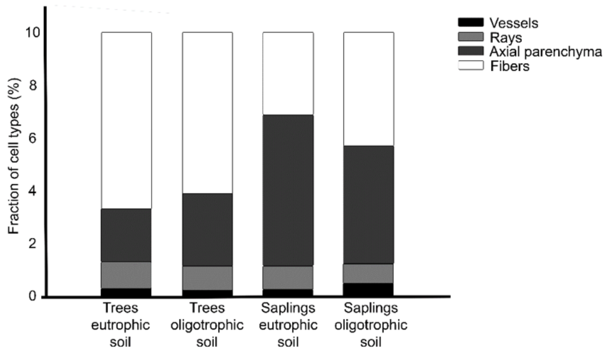

Figure 3: Fraction of cell types (%) of *Enterolobium contortisiliquum* 9-year-old trees and 2-year-old saplings in eutrophic and oligotrophic soil. Bars: black = vessels fraction; white = fibers fraction; dark grey = parenchyma fraction; light grey = rays fraction.

5. How soil effects on wood anatomy were mediated by plant age

Given the difference in age between saplings and trees, different responses to soil conditions were expected [13]. We detected differences in fiber wall thickening, intervessel pit diameter, storage tissues, and storage compound contents in the secondary xylem of trees in response to soil types. In opposition, no significant response to soil type occurred in saplings, thus demonstrating that the relationship between soil type and wood growth is mediated by tree age.

In addition, saplings might have different nutrient demands than trees. Therefore, it is necessary to consider their ability to allocate mineral nutrients that are essential for physiological events that lead to wood formation and differentiation.

6. Conclusions

Our study provides evidence that the influence of soil conditions on growth of tamboril reflects variations in wood anatomical features. The difference of age between trees and saplings could explain the different responses to the soil conditions. Therefore, assessing soil-plant relationships is necessary to explain the anatomical strategies of tropical species in response to the edaphic conditions. These strategies would be crucial for plant survival under degraded conditions where soil restrictions may occur in the future.

References

1. Carlo Sorce; Alessio Giovannelli; Luca Sebastiani; Tommaso Anfodillo; Hormonal signals involved in the regulation of cambial activity, xylogenesis and vessel patterning in trees. *Plant Cell Reports* **2013**, *32*, 885-898, 10.1007/s00299-013-1431-4.
2. Susanne Spannl; Jürgen Homeier; Achim Bräuning; Nutrient-Induced Modifications of Wood Anatomical Traits of Alchornea lojaensis (Euphorbiaceae). *Frontiers in Earth Science* **2016**, *4*, 885-898, 10.3389/feart.2016.00050.
3. Valentina Buttò; Philippe Rozenberg; Annie Deslauriers; Sergio Rossi; Hubert Morin; Environmental and developmental factors driving xylem anatomy and micro-density in black spruce. *New Phytologist* **2021**, *230*, 957-971, 10.1111/nph.17223.
4. Louis S. Santiago; Nutrient limitation of eco-physiological processes in tropical trees. *Trees* **2015**, *29*, 1291-1300, 10.1007/s00468-015-1260-x.
5. Jennifer L. Soong; Ivan A. Janssens; Oriol Grau; Olga Margalef; Clément Stahl; Leandro Van Langenhove; Ifigenia Urbina; Jerome Chave; Aurélie Dourdain; Bruno Ferry; et al. Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. *Scientific Reports* **2020**, *10*, 1-13, 10.1038/s41598-020-58913-8.
6. Kazumichi Fujii; Makoto Shibata; Kaoru Kitajima; Tomoaki Ichie; Kanehiro Kitayama; Benjamin Turner; Plant–soil interactions maintain biodiversity and functions of tropical forest ecosystems. *Ecological Research* **2017**, *33*, 149-160, 10.1007/s11284-017-1511-y.
7. Rodriguez-Zaccaro, F.D.; Valdovinos-Ayala, J.; Percolla, M.I.; Venturas, M.D.; Pratt, R.B.; Jacobsen, A.L. Wood structure and function change with maturity: Age of the vascular cambium is associated with xylem changes in current-year growth. Plant Cell Environ. 2019, 42, 1816–1831.
8. Enterolobium contortisiliquum . Flora do Brasil 2020. Retrieved 2021-8-27

9. Anne Ranielly Monteiro Luz; Lamarck Rocha; Luciano Paganucci De Queiroz; Élvia Rodrigues De Souza; Flora da Bahia: Leguminosae – Enterolobium (Clado Mimosoide: Ingeae). *SITIENTIBUS série Ciências Biológicas* **2021**, *21*, 1-9, 10.13102/scb6160.
10. Vera Lex Engel; John A Parrotta; An evaluation of direct seeding for reforestation of degraded lands in central São Paulo state, Brazil. *Forest Ecology and Management* **2001**, *152*, 169-181, 10.1016/s0378-1127(00)00600-9.
11. De Oliveira Gonçalves, P.J.R.; Vieira, L.C.; Nogueira, A.V.; Corseuil, H.X.; Mezzari, M.P.; Tolerance of Tree Reforestation Species (Schizolobium parahyba, Mimosa scabrella and Enterolobium contortisiliquum) to Gasoline and Diesel Phytotoxicity Assays. *Journal of Bioremediation & Biodegradation* **2010**, *s7*, 1-9, 10.4172/2155-6199.S7-004.
12. Marcelo Leandro Bueno; Kyle G. Dexter; Toby Pennington; Vanessa Pontara; Danilo Neves; James Alexander Ratter; Ary Teixeira De Oliveira-Filho; The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas. *Journal of Ecology* **2018**, *106*, 2109-2120, 10.1111/1365-2745.12969.
13. Dickison, W.. Integrative Plant Anatomy; Academic Press: San Diego, CA, USA, 2000; pp. 161.