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Research Article

Leaf Vein Density of Tree Saplings Composing Lower Canopy in Tropical Forest Reflects Their Ecophysiological Characteristics

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ABSTRACT
One factor affecting the survival of a species in a tropical ecosystem is its ability to respond to environmental conditions, which depend on their ecophysiological performances. Plants ability to transport water as a major environmental factor would determine their survival. The anatomy of xylem inside leaves and stem as water conductive tissue will dictate the rate of water transport through the plant stem and leaves. Leaf vein, which contains xylem vessels, dictates water transport through leaves and plant's ability to control water loss through stomata. This research found that tree saplings composing a lower canopy of tropical forests have different ecophysiological attributes. Pioneer species, such as *Cinnamomum* sp., *Diospyros macrophylla*, *Castanopsis costata*, *Elateriospermum tapos,* and *Ziziphus* sp., have higher leaf vein density than primary species, such as a member of genus *Garcinia*, *Shorea*, *Dipterocarpus,* and *Syzigium*. It implies that pioneer species might have higher rates of water transport and consequently, higher rates of photosynthesis. If forest vegetation was more opened, then pioneer species may dominate the area as they are more tolerant of light. The Composition of forest vegetation with different ecophysiological characteristics may affect the forest dynamics and hydrological cycle.

Keywords: Ecophysiology, leaf vein density, tropical forest ecosystem, water transport

INTRODUCTION

The efficiency of water to be transported in plants from the soil to the stem and then leaves partly affects plants ability to survive in their environments. This efficiency is driven by several aspects, i.e. the capacity of roots to absorb water from the ground, the rate of water movement in the xylem to the canopy, and the effectiveness of plants to control transpirational water loss from the stomata (Atwell *et al.,* 1999). The structural design of xylem, which is the water conductive tissue, will dictate how water is transported through the stem (Tyree & Zimmerman, 2002). Therefore it will drive water transport efficiency (Tyree & Ewers, 1996). The design of xylem includes dimensions of the vessels, hydraulic conductivity, and vulnerability to the formation of embolism. Hydraulic conductivity is the rate at which water can be transported through xylem at a given pressure (Tyree & Ewers, 1996). As the structural design of xylem may affect the flow of water from the root to the stem and finally to the leaf, it may consequently dictate stomatal conductance, leaf gas exchange, and water potential.

Variation in hydraulic architecture of plants may partially affect the height that can be attained by the plant and their distributions along environmental gradients and (Tyree & Ewers, 1996). Plants with different growth forms, such as epiphytes, vines, and trees have different hydraulic architecture characteristics that result in different ecological and physiological adaptations. Hydraulic architecture of woody plants, such as lianas, primary hemi-epiphytes, shrubs, and trees have been extensively studied (Drake & Franks, 2003; Ewers *et al.,* 1991; Patiño *et al.,* 1995; Tng *et al.,* 2018; Tyree & Ewers, 1996; Tyree & Zimmerman, 2002). Studies on hydraulic architecture of non-woody plants,

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especially climbing plants, have also been conducted (Ganthaler *et al.,* 2019). These studies include observation of vessel size and density and hydraulic capacity of species of climbing rattans (Fisher *et al.,* 2002; Tomlinson *et al.,* 2001), climbing aroids *Monstera acuminata* (Lopez-Portillo *et al.,* 2000), and invasive climbing species *Merremia peltata (Yansen et al., 2015). E*mbolism in palm xylem *Rhapis excelsa* (Sperry, 1986) and the vine *Rhipidocladum racemiflorum* (Cochard *et al.,* 1994) due to drought condition has also been observed.

However, published researches so far on plant hydraulic architecture were more focused on the individuals and species/group of species levels or growth forms. The contribution of plant hydraulic variations on spatial vegetation dynamics has not been widely discussed. As the hydraulic efficiency could affect plants ability to survive and to regulate water loss from the leaf, information on spatial distribution of hydraulic characteristics of plants composing tropical forests can be used to predict future vegetation dynamics and perhaps its effect on the hydrological cycle.

Leaf vein architecture as part of plant hydraulic has been studied for the last two decades. It has received more attention as it is linked to the physiology, ecology, and evolution of terrestrial plants (Price *et al.,* 2014; Sack & Holbrook, 2006). Leaf vein architecture, including vein size and density, and hydraulic conductivity, might play as the main constraint in water transport for photosynthesis and transpiration. If this architecture could restrict water transport, then the evolutionary strategy to form more adaptive leaf vein architecture for certain environmental conditions may dictate the fitness of certain species (Boyce *et al.,* 2009; Tabassum *et al.,* 2016). Leaf hydraulic capacity is very much related to the ability of species to utilize water and to exchange carbon in different habitat and vegetational zones (Sack *et al.,* 2005; Bodribb *et al.,* 2007; Pagano & Storchi, 2015). Therefore, leaf hydraulic architecture is crucial information in observing forest vegetation dynamics, as well as predicting the response of vegetation to environmental changes. This research aimed to observe leaf vein characteristics of tree saplings composing a lower canopy of tropical forests. Those characteristics were then related to their ecophysiological characteristics, such as light-demanding pioneer species and shade-tolerant primary species (Goodale *et al.,* 2012; Whitmore, 1998).

MATERIALS AND METHODS

This research was conducted in the protected forest of Boven Lais Kemumu, North Bengkulu, Bengkulu Province, Indonesia, which is located between 102° 11'50" - 102°25'40" E (east longitude) and 3°15'24" - 3°33'15" S (south latitude). This forest has a high biodiversity of plants with different characteristics. Twenty plots of 10 x 10 m were placed systematically from the forest edge into the intact area. These 20 plots were put on four lines; hence one line consisted of five plots with 40 m distance between plots.

All tree saplings in every plot were recorded and tagged. Tree saplings are categorized as to have < 10 cm dbh (diameter of breast height), and > 3 m tall. Sapling diameter and height were measured. Tree saplings were chosen as the object of this research since it is assumed that saplings are on their optimum growth and they will dominate the ecosystem in the future. Ten fully expanded leaves of each sapling were taken as samples to be analysed their leaf vein characteristics.

Leaf samples were stored in a container containing alcohol. Those leaves were then cleaned with NaOH and water. Fractions of leaves were placed under a microscope (Olympus) and photos were taken. Leaf vein characteristics were observed using ImageJ software (National Health Institute, USA). Observed leaf vein characteristics include leaf vein level, and leaf vein density per area (mm/mm^2). Environmental conditions were also monitored, including humidity, temperature, and light intensity under the canopy.

RESULTS AND DISCUSSION

The location of the research had relatively dense canopy cover with varied vegetational strata from seedlings to trees. The measurement of environmental conditions shows that observed tree saplings grow under a canopy with high humidity, mild temperature, and low light intensity. No differences in humidity, light intensity, and temperature between forest edge and intact vegetation (Figure 1).

Twenty fives species (13 families) of tree saplings were found on the location (Table 1). *Garcinia* and *Cinnamomum* were two commonly genus found on the location. Tree saplings compose the lower stratum of the forest. The range of the diameter of observed saplings was 4 cm to 9 cm and the range of height was 4 m to 8 m.

Tree saplings were distributed from the forest edge into a more intact canopy. Species such as *Cinnamomum* sp., *Garcinia* sp., *Dipetrocarpus gracilis,* and *Exoecaria bantamensis* were found from forest edge into intact canopy area (Table 2). As explained before, no differences in humidity, light intensity, and temperature between forest edge and intact vegetation (Figure 1). Many factors may affect the

Table 1. Species and number of saplings per species found at study plots in the protected forest of Boven Lais Kemumu.

No	Species	Family	Number of individuals
1	*Artocarpus heterophyllus*	Moraceae	1
2	*Azadirachta* sp.	Meliaceae	6
3	*Castanopsis costata*	Fagaceae	4
4	*Cinnamomum obtusifolium*	Lauraceae	4
5	*Cinnamomum* sp. 1	Lauraceae	13
6	*Cinnamomum* sp. 2	Lauraceae	2
7	*Diospyros macrophylla*	Ebenaceae	4
8	*Dipterocarpus gracilis*	Dipterocarpaceae	5
9	*Elateriospermum tapos*	Euphorbiaceae	2
10	*Elmerillia tsiampacca*	Magnoliaceae	2
11	*Excoecaria bantamensis*	Euphorbiaceae	8
12	*Fragraea racemosa*	Loganaceae	3
13	*Garcinia* sp. 1	Clusiaceae	10
14	*Garcinia* sp. 2	Clusiaceae	2
15	*Lannea coromandelica*	Anarcadiaceae	1
16	*Litsea* sp.	Lauraceae	2
17	*Macaranga gigantea*	Euphorbiaceae	2
18	*Shorea leprosula*	Dipterocarpaceae	1
19	*Shorea multiflora*	Dipterocarpaceae	1
20	*Shorea siamensis*	Dipterocarpaceae	4
21	*Syzigium oides*	Myrtaceae	3
22	*Syzigium* sp.	Myrtaceae	5
25	*Ziziphus* sp.	Rhamnaceae	1

development of vegetation in a tropical forest, e.g. intra and inter-specific competition, predation, *niche* differentiation, disturbances, and stochastic recruitment (Brokaw & Busing, 2000; Goodale *et al.,* 2012; Nathan *et al.,* 2008; Silvestrini & dos Santos, 2015). With relatively similar environmental conditions in most of the studied forest ecosystem, every species would have similar opportunities to grow both on the edge or more to the middle part of the forest.

The level of leaf vein of observed tree saplings ranges between 3 to 5 levels (Figure 2). Saplings with more leaf vein levels usually have more complex vein arrangement (Figure 3a-c), although they do not necessarily have more dense veins. On the other hand, some other species have a simple leaf vein arrangement (Figure 3d). The range of leaf vein density of observed saplings was 0.02 to > 0.3 mm/mm^2 (Figure 2). Leaf vein density of 0.3 mm/mm^2 means that 30% of the leaf area consists of veins. In this research, species found to have high leaf vein density include *Cinnamomum* sp., *Diospyros macrophylla*, *Castanopsis costata*, *Elateriospermum tapos,* and *Ziziphus* sp. On the other hand, *Garcinia*, *Shorea*, *Dipterocarpus,* and *Syzigium* tend to have low vein density.

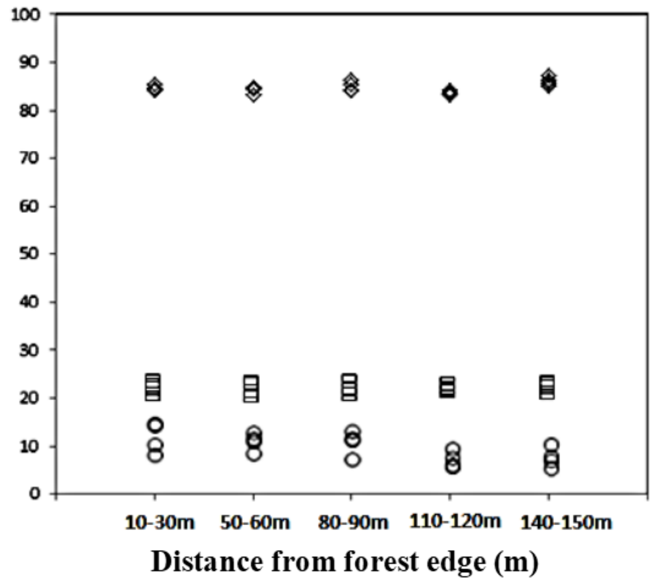

Figure 1. Humidity (◊) (%), temperature (□) (°C), and light intensity (○) (Watt/m^2) of research site with different distances from the forest edge.

Based on their ecophysiological characters, tree sapling species occurring on the studied area can be categorized as pioneer and primary species, following characterization by Whitmore (1998).

Table 2. The distribution of species based on their distance from the forest edge.

Distance from forest edge (m)				
10 - 30 m	50 - 60 m	80 - 90 m	110 - 120 m	140 - 150 m
Castanopsis costata	*Castanopsis costata*	*Artocarpus heterophyllus*	*Azadirachta* sp.	*Azadirachta* sp.
Castanopsis costata	*Cinnamomum obtusifolium*	*Azadirachta* sp.	*Azadirachta* sp.	*Azadirachta* sp.
Castanopsis costata	*Cinnamomum obtusifolium*	*Cinnamomum obtusifolium*	*Cinnamomum* sp. 1	*Azadirachta* sp.
Cinnamomum sp. 1	*Cinnamomum obtusifolium*	*Cinnamomum* sp. 1	*Cinnamomum* sp. 1	*Dipterocarpus gracilis*
Dipterocarpus gracilis	*Cinnamomum* sp. 1	*Cinnamomum* sp. 1	*Cinnamomum* sp. 1	*Dipterocarpus gracilis*
Dipterocarpus gracilis	*Cinnamomum* sp. 1	*Cinnamomum* sp. 1	*Cinnamomum* sp. 1	*Elateriospermum tapos*
Elateriospermum tapos	*Cinnamomum* sp. 1	*Cinnamomum* sp. 2	*Cinnamomum* sp. 2	*Excoecaria bantamensis*
Elateriospermum tapos	*Cinnamomum* sp. 1	*Cinnamomum* sp. 2	*Cinnamomum* sp. 2	*Garcinia* sp. 1
Fragraea racemosa	*Cinnamomum* sp. 1	*Dipterocarpus gracilis*	*Diospyros macrophylla*	*Garcinia* sp. 1
Litsea sp.	*Cinnamomum* sp. 1	*Dipterocarpus gracilis*	*Diospyros macrophylla*	*Garcinia* sp. 1
Macaranga gigantea	*Elmerillia tsiampacca*	*Dipterocarpus gracilis*	*Diospyros macrophylla*	*Garcinia* sp. 1
Syzigium sp.	*Excoecaria bantamensis*	*Elmerillia tsiampacca*	*Diospyros macrophylla*	*Garcinia* sp. 1
Syzigium sp.	*Excoecaria bantamensis*	*Excoecaria bantamensis*	*Garcinia* sp. 1	*Shorea leprosula*
Syzigium sp.	*Excoecaria bantamensis*	*Excoecaria bantamensis*	*Garcinia* sp. 1	
Unknown species 1	*Excoecaria bantamensis*	*Litsea* sp.	*Garcinia* sp. 1	
Unknown species 2	*Excoecaria bantamensis*	*Macaranga gigantea*	*Garcinia* sp. 1	
Unknown species 2	*Fragraea racemosa*	*Shorea multiflora*	*Garcinia* sp. 1	
	Fragraea racemosa	*Shorea siamensis*	*Garcinia* sp. 1	
	Shorea siamensis	*Shorea siamensis*	*Garcinia* sp. 1	
	Shorea siamensis	*Syzigium oides*	*Garcinia* sp. 2	
	Syzigium oides	*Syzigium oides*	*Lannea coromandelica*	
	Syzigium sp.	Unknown species 2	Unknown species 1	
	Syzigium sp.	Unknown species 2	Unknown species 2	
	Unknown species 2	*Ziziphus* sp.		

Pioneers are light-demanding and fast-growing species. Their seeds germinate when the environmental conditions favour and the seedlings then quickly grow (Goodale *et al.,* 2012; Silvestrini & dos Santos, 2015). On the other hand, primary species are shade tolerant (Franklin, 2003). In this research, some species can be categorized as pioneer species, including *Cinnamomum* sp., *Diospyros macrophylla*, *Castanopsis costata*, *Elateriospermum tapos,* and *Ziziphus* sp. Primary species found in the research site include genus *Garcinia*, *Shorea*, *Dipterocarpus,* and *Syzigium*.

The responses of plants to genotype, age, ontogeny, and environmental heterogeneity result in differences in the ecophysiological performance by the plants (Goodale *et al.,* 2012; Zotz, 2000; Zotz *et al.,* 2001). Light intensity, CO_2 uptake, variation in temperature, and humidity, soil fertility and nutrient cycling are prominent environmental entities that affect the dynamics of individuals, as well as the population of plants. The interactions between these environmental factors result in a certain micro-climate for the plants to live in. As the environment may vary seasonally and spatially, plants must respond continually and consequently adapt to the change in environmental conditions (Dickison, 2000). Genetic properties and environmental factors will dictate the nature of responses by the plants.

Pioneer species were found to have higher leaf vein density than primary species. High leaf vein density may provide these pioneer species with a higher capacity to transport water (Boyce *et al.,* 2009; Price *et al.,* 2014; Sack *et al.,* 2005; Sack & Holbrook, 2006). Consequently, pioneer species may have higher rates of photosynthesis and growth. Vegetation is an important part of the hydrological cycle. Forest plants take water up from the ground to the forest canopy. Most of the water then transpires into the air. The amount of water regulated by the vegetation transportation and

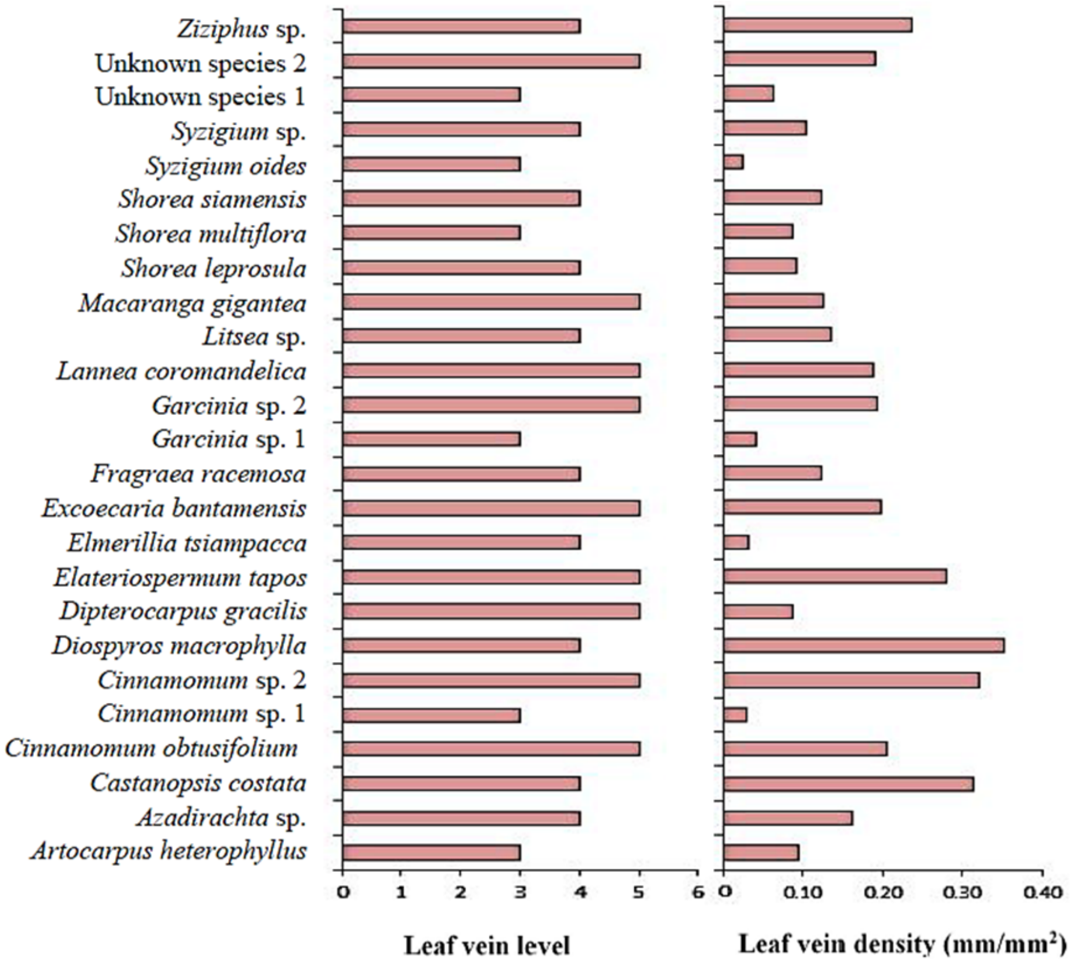

Figure 2. Leaf vein level and density of tree saplings composing lower canopy at the protected forest of Boven Lais Kemumu.

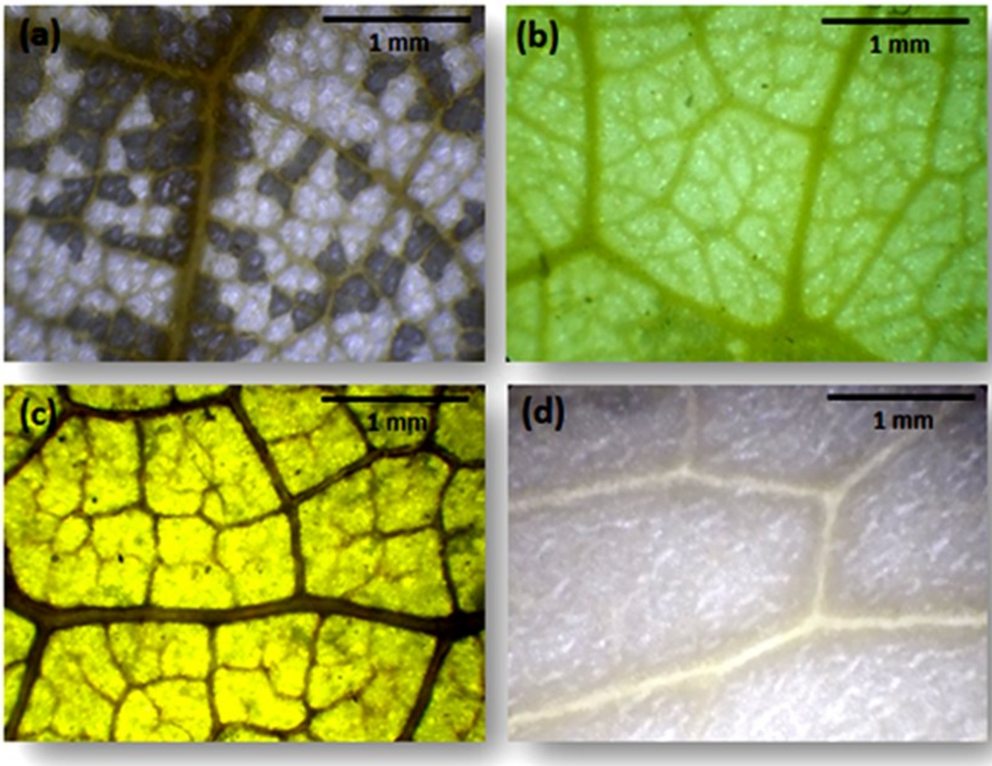

Figure 3. Examples of leaf veins of several tree saplings species found on the protected forest of Boven Lais Kemumu. The species are pioneer species (a) *Cinnamomum obtusifolium* and (b) *Exoecaria bantamensis,* and primary species (c) *Lannea coromandelica* and (d) *Shorea multiflora* .

transpiration process in the soil-plant-atmosphere continuum will affect the hydrological cycle in general. Therefore, different compositions of vegetation with different ability to transport water will contribute differently to the hydrological cycle. If the ecosystem becomes more opened, pioneer species may dominate as they are more light-demanding. As they are physiologically more water demanding to support high rates of photosynthesis, the domination of pioneer species (if happening) will hypothetically affect the hydrological cycle.

CONCLUSION

Tree saplings composing a lower canopy of tropical forest have different ecophysiological attributes and leaf vein characteristics. Pioneer species, such as *Cinnamomum* sp., *Diospyros macrophylla*, *Castanopsis costata*, *Elateriospermum tapos,* and *Ziziphus* sp., have higher leaf vein density than primary species, such as *Garcinia*, *Shorea*, *Dipterocarpus,* and *Syzigium*. As leaf vein density may affect the capacity of plants to transport water, pioneer species might have higher rates of water transport and higher rates of photosynthesis. Consequently, the composition of forest vegetation with different ecophysiological characteristics will affect the forest dynamics and in the long-term hydrological cycle. Future research is directed to measure water conductivity and transpiration rates. Then, total water transport and transpiration will be spatially analysed and the contribution of the vegetation to the hydrological cycle can be simulated.

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