Proceedings of the 7th International Conference on Functional-Structural Plant Models, Saariselkä, Finland, 9 - 14 June 2013. Eds. Risto Sievänen, Eero Nikinmaa, Christophe Godin, Anna Lintunen & Pekka Nygren. http://www.metla.fi/fspm2013/proceedings. ISBN 978-951-651-408-9.

How petiole flexibility changes light interception at the tree scale.

Loïc Tadrist[1,2,]*, Emmanuel de Langre[1] and Marc Saudreau[2]

[1]Department of Mechanics, *LadHyX, École Polytechnique, CNRS, 91128 Palaiseau, France*

[2]*INRA, UMR 547 PIAF, 63100 Clermont-Ferrand, France*

**correspondence:* loic.tadrist@ladhyx.polytechnique.fr

Highlights: Leaf inclination angle plays a key role for light interception of a tree. However existing models for this quantity are empirical, not predictive and do not take into account the fact that leaves are flexible. Based on a petiole deformation model and a multi-scale approach we propose a model of leaf inclination angle distribution. As an example, we quantify how much leaf flexibility may change light interception of a tree.

Keywords: light interception, leaf mechanics, leaf inclination angle distribution

INTRODUCTION

Light transmission within a canopy is commonly described by a Beer-Lambert like law (Chartier, 1966). The transmission coefficient of the Beer-Lambert law mainly depends on two parameters: the leaf area local density and the leaf inclination angle distribution (LIAD). LIAD corresponds to the probability that a leaf taken randomly on the tree has a certain inclination angle, ϕ defined as the angle between the leaf midrib and the vertical axis. Usually, these distributions are measured experimentally and fitted with spherical or ellipsoidal functions (Campbell, 1986) without taking explicitly into account neither the mechanical behavior of the leaves nor the tree structure. However leaves are known to be flexible objects which bend under their own weight or because of wind. Such flexibility can vary among species and with time, affecting LIAD, and thus affecting the direct light interception and plant functions (Parveaud et al., 2008).

LIADs commonly used in functional-structural plant models (FSPM) remain purely empirical and do not account for physiological, structural or mechanical properties of the plant and for abiotic interactions with its environment. The main objective of this work is to build up a model of LIAD of a plant by coupling a single mechanistic model of the system compounded of a flexible simple leaf model with a tree structure model.

For simplicity, we do not take into account growth history, phototropism, gravitropism. The analysis is focused on the effect of petiole flexibility on LIAD. After introducing the model and comparing simulated LIAD with observed LIAD, we quantify the direct effect of leaf flexibility on light transmission within a canopy. To emphasize the necessity of a leaf flexibility model in FSPMs, we also expose a case where the leaf flexibility changes according to the tree physiology: the protective gain of flexibility of anisohydric tree leaves during drought period in summer. At last we conclude giving other applications of our model concerning possible calculation of wind drag, water retention or leaf temperature.

LEAF INCLINATION ANGLE DISTRIBUTION MODELIZATION

The mechanical behavior of a single leaf has been investigated and some models have been already proposed (Niklas, 1999). But for plants, and especially for trees, interesting physiological traits are integrated values at the plant scale such as photosynthesis, global transpiration, or wind drag. Thus beyond the leaf flexibility modeling, the challenge is also to be able to account for the two different scales: leaf scale and whole foliage. As the number of leaves on a tree is large (up to 10^5), we propose to link these two scales through a statistical analysis of the tree structure which holds the leaves.

Leaf mechanics

Leaf mechanical description is based on the model of Niklas (1999) in which we take into account geometrical non-linearities. For the sake of simplicity we describe only simple leaves, not compounded leaves nor sessile leaves. The leaves we consider have only one flexible petiole and one rigid lamina. The petiole is considered to be an elastic beam without mass whereas the lamina is a weighting and rigid plate. Let us consider the deformation of the petiole due to the weight of the lamina. In the non-dimensional equation the number of gravity *G* appears:

$$G = \frac{mgL^2}{EI}$$

where m is the mass of the lamina, L the length of the petiole and EI the bending modulus of the petiole. This number defines two regimes of deformation. If G << 1, the mass of the leaf is not important enough to bend the petiole, this is the rigid regime. If G > 1, the petiole bend and the inclination angle of the leaf changes because of the weight of the lamina, this is the flexible regime.

Tree structure

The tree structure is simply rendered by an iterative model for a sympodial tree (Rodriguez, 2008). The iteration starts from a vertical trunk. At each iteration, a mother branch gives two daughter branches. These two branches are separated from the mother axis by a branching angle, θ_0. For trees, typical number of iteration is 8 up to 10. We compute the distribution of shoots bearing leaves for a tridimensional tree. Results show that the distribution is a normal distribution which depends only on the branching angle. Expressions of the mean, μ, and the standard deviation, σ, are:

$$\mu = \frac{\pi}{2}\sin\frac{3\theta_0}{2} \qquad \sigma = \frac{\pi}{4}\sin\frac{3\theta_0}{2}$$

Tree structure model was assessed on a digitized walnut tree (fig.2. a,b). Petiole deformation model has proved efficiency on idealized leaves and real leaves (Apricot tree, cherry tree, apple tree and ficus, data not show).

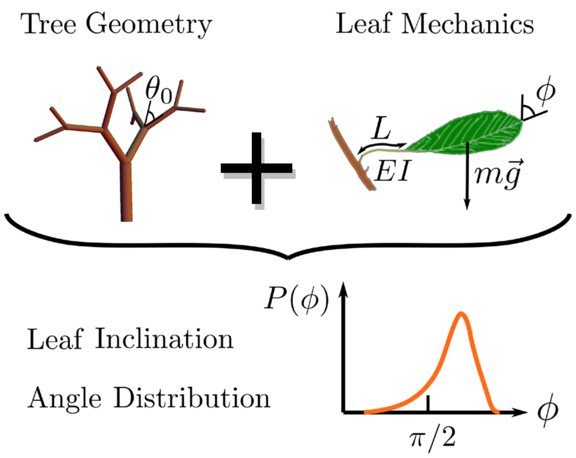

Fig. 1. Schematic view of the methodology used for obtaining leaf inclination angle distribution. Definition of the geometrical and mechanical parameters.

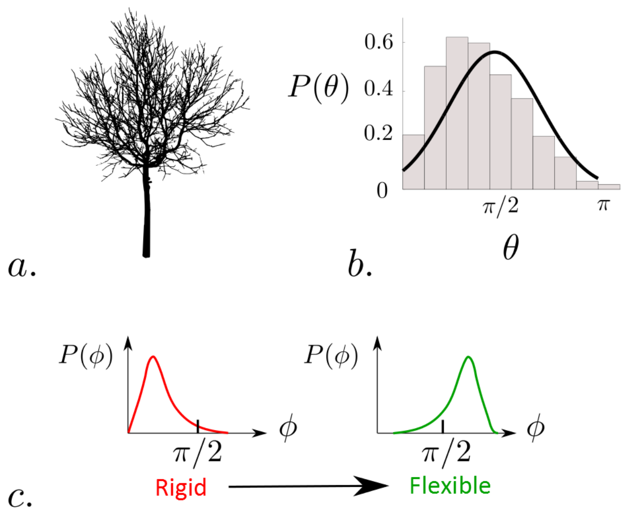

Fig. 2. (a) Digitalized walnut of which the branch inclination angle is plotted in (b). (c) Example of two different leaf inclination angle distribution (red correspond to rigid leaves and green to flexible ones).

Leaf inclination angle distribution

Leaf inclination angle distribution is computed from the branch inclination angle assuming that leaves grow with a branching angle θ_0 with the holding branch and that the leaf can bend because of gravity (fig.1). In this manner, we obtain an analytical expression of the peak of the LIAD taking into account both tree structure and leaf mechanics. We show in figure 2.c the evolution of LIADs between the rigid case and the flexible case. The model predictions compare well several LIADs measured on different trees (apple tree) give satisfactory tendencies.

RESULTS AND DISCUSSION

Effect of flexibility on light interception

Since we know explicitly the dependence of the LIAD on the leaf flexibility, we can predict the position of the mean value, the peak of the distribution and its width. If the leaves are rigid, the peak position is only due to the tree structure. Contrary, when leaves are flexible, the peak is shifted towards π, meaning that the leaves bend down, (fig.2 c, fig.4 insets a,b).

With this LIAD expression, we compare light interception ($I(G)$) for different leaf rigidity. For a sun at zenith, direct light interception calculation was done numerically thanks to the Beer-Lambert law:

$$\frac{I(G)}{I(0)} = \frac{1 - e^{-A \int P_G(\varphi) \cos\varphi \, d\varphi}}{1 - e^{-A \int P_0(\varphi) \cos\varphi \, d\varphi}}$$

where A is a constant depending on the leaf foliage density, P_G the LIAD at a given G and P_0 the LIAD when the petioles are completely rigid.

Clearly, flexibility changes the light interception capacity of trees. The graph below shows the variation of the light interception at noon for a tree of branching angle, $\theta_0 = \pi/3$ (fig.3) when varying G.

When the flexibility is increasing, light interception of the tree decreases. Accordingly, light interception is higher when flexibility is low. This result is not general and may change depending on the latitude and the day of year.

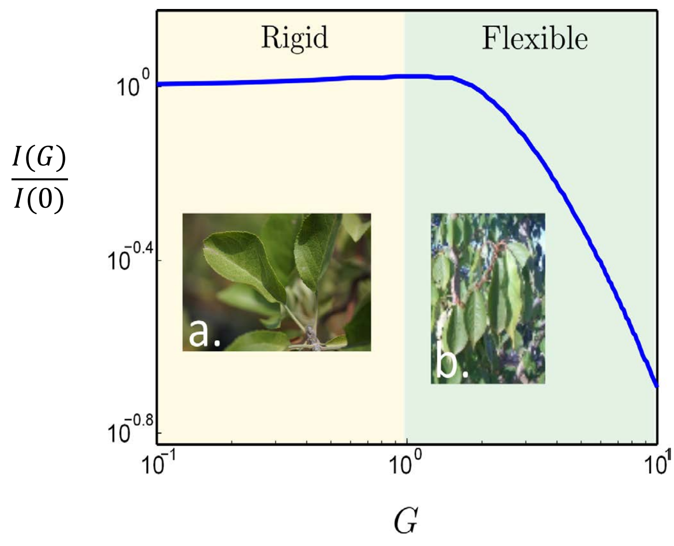

Fig. 3. Evolution of light interception in function of flexibility. G=1 separates the yellow domain where leaves are rigid (b) from the green domain where leaves are flexible (a). Light interception is lower for flexible leaves.

An example of excess radiation protection varying flexibility

As an example of change of leaf flexibility, some anisohydric trees can change their flexibility during the day thanks to a change in their turgor pressure, Faisal et al. (2010). This phenomenon appears when the tree is in water stress, mainly in summer. It decreases its internal turgor pressure in order to close its stomata and avoid evaporating to much water. Without stomata sweating, the leaf temperature is given by the balance of light radiation and air convection. If the leaf stops sweating but receives as much radiation energy as before, its temperature will increase. This can result on photo-inhibition and even leaf necrosis. For this kind of trees, increase of flexibility make them sure not to intercept as much light as before and favor air convection, thus protecting their leaves without sweating. Our model allows to understand and to quantify this physical phenomenon taking into account the loss of rigidity of the petiole due to a decrease of turgor pressure onto the LIAD

CONCLUSION

We developed a simple model of leaf inclination angle distribution in order to understand the effect of leaf flexibility on light interception on a tree. This model is based on a multiscale approach, from the mechanics of a single leaf to the entire foliage properties through the tree structure. This work shows that: (i) the LIAD changes strongly due to leaf flexibility; and (ii) the direct light interception depends highly on flexibility of leaves. Our approach of tree foliage properties remains general. It proved to be an efficient model to understand the effect of leaf flexibility on light interception. However, much more can be deduced from such a model like leaves temperature, wind drag due to leaves on a tree or water/snow retention.

LITERATURE CITED

Chartier P. 1966. Étude du microclimat lumineux dans la végétation, *Annales d'agronomie* **17**, 571–602.

Campbell G. 1986. Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination angle distribution, *Agricultural and forest meteorology* **36**, 317–321.

Niklas K. 1999. A mechanical perspective on foliage leaf form and function. *New phytologist* **143**, 19–31.

Parvaud C-E, Chopard J, Dauzat J, Courbaud B, Auclair D. 2007. Modelling foliage characteristics in 3D tree crowns: influence on light interception and leaf irradiance. *Trees* **22,** 87-104.

Rodriguez M, de Langre E, Moulia B, 2008. A scaling law for the effects of architecture and allometry on tree vibration modes suggests a biological tuning to modal compartmentalization. *American Journal of Botany,* **95**, 1523–1537.

Faisal T, Abad E K, Hristozov N, Pasini D. 2010. The Impact of Tissue Morphology, Cross-Section and Turgor Pressure on the Mechanical Properties of the Leaf Petiole in Plants. *Journal of Bionic Engineering* **7 Suppl.**, S11 – S23.