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Wind and gravity mechanical effects on leaf inclination angles

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HIGHLIGHTS

- A biomechanical model of Leaf Inclination Angle Distribution (LIAD) is proposed.
- Self-weight and wind loading are considered.
- Leaf flexibility impacts strongly Leaf Inclination Angle Distribution.
- A change in leaf flexibility or external loading may change light interception.

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ABSTRACT

In a tree, the distribution of leaf inclination angles plays an important role in photosynthesis and water interception. We investigate here the effect of mechanical deformations of leaves due to wind or their own weight on this distribution. First, the specific role of the geometry of the tree is identified and shown to be weak, using models of idealized tree and tools of statistical mechanics. Then the deformation of individual leaves under gravity or wind is quantified experimentally. New dimensionless parameters are proposed, and used in simple models of these deformations. By combining models of tree geometry and models of leaf deformation, we explore the role of all mechanical parameters on the Leaf Inclination Angle Distributions. These are found to have a significant influence, which is exemplified finally in computations of direct light interception by idealized trees.

1. Introduction

Among leaf geometrical traits, the leaf inclination angle, defined as the leaf orientation with respect to the vertical axis, is of primary importance in plant ecology as it directly drives radiation interception by canopies and thus impacts gas exchanges, photosynthetic activity level and related processes within canopies. The Leaf Inclination Angle Distribution (LIAD) is commonly described in a given tree through a probability distribution function $p(\varphi)$, where φ is the angle between the leaf normal direction and the vertical axis (Falster and Westoby, 2003; Wang et al., 2007). For instance, when the sun is at zenith, the direct light interception by a canopy, I_0, is commonly modeled as (Monsi and Saeki, 2005; Pisek et al., 2013)

$$\ln\left(\frac{I_0}{I_H}\right) = -A\left[1-\int_0^{\pi/2} p(\varphi)\cos\varphi\,\mathrm{d}\varphi\right], \tag{1}$$

where I_H is the light intensity at the top of the canopy and A is a function of the leaf density profile. Clearly the probability density function of the leaf orientation, $p(\varphi)$, has a strong effect on the interception of light by a canopy.

The LIAD may be defined in several ways, considering that a leaf may be curved and even if not curved, tilted across its mid-rib axis. For the sake of simplicity, we shall hereafter use as inclination angle, ϕ, the angle between the vertical axis and the base-tip axis of the lamina (Fig. 1a). Note that ϕ does now vary from 0 to π, contrary to other definitions such as in Eq. (1) where φ varies from 0 to $\pi/2$. The distributions $P(\phi)$ and $p(\varphi)$ are simply linked by $p(\varphi)=P(\varphi)+P(\pi-\varphi)$. In the following, the probability density function $P(\phi)$ will be referred to as the Leaf Inclination Angle Distribution (LIAD). Fig. 1c and e shows a typical LIAD (Falster and Westoby, 2003; Falster, 2012), one among the immense variety that exists in nature. They may differ by the location of the peak, the width of this peak or even by their general shape, see for instance Falster and Westoby (2003) for typical examples.

Observed LIADs are highly variable between species and can change over time along the growing season or according to abiotic and biotic stresses (Pisek et al., 2013; Falster and Westoby, 2003).

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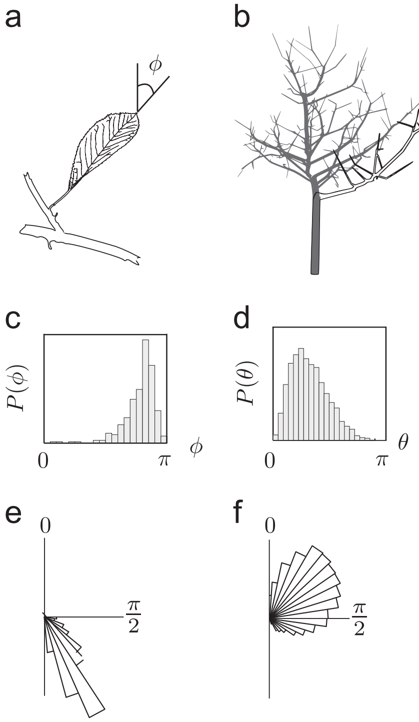

Fig. 1. (a) Definition of the leaf inclination angle, ϕ. (b) Definition of the branch inclination angle, θ. (c) Example of LIAD (data by Falster (2012)), the same LIAD is also plotted in polar representation in (e). (d) Example of BIAD (data by Rodriguez et al. (2012)), the same BIAD is also plotted in polar representation in (f). The distributions are shown with arbitrary amplitudes.

This variability is probably due to both physical and biological factors: the tree architecture (through the inclination of branches), the deformation of the petioles, which itself depends on turgor pressure, phototropism, growth history and even instantaneous reactions to stimuli. To account for this huge variability numerous functions such as spherical, ellipsoidal or Beta distributions are commonly used (Campbell, 1986; Wang et al., 2007; Pisek et al., 2011). However these functions do not take into account any of the factors listed above. We expect that including some of these factors into a model can account simply for this variability. We shall focus hereafter on the combined role of the first two of the above list, namely the tree architecture and the elastic deformation of petioles under gravity or wind loading. The first one is mainly geometrical and the second mechanical.

We define at this step the Branch Inclination Angle Distribution (BIAD), which describes the orientation of the shoots supporting the leaves with the vertical axis, Fig. 1b. Fig. 1d and f shows a typical BIAD corresponding to a specific walnut tree (Rodriguez et al., 2012). Modeling the BIAD requires some knowledge of the tree geometry. Successful models, using simple iterating branching laws, have been used for tree vibration (Rodriguez et al., 2012) and for tree fracture (Lopez, 2011; Eloy, 2011). These models are based on a branching angle and allometric laws only.

On the other hand, the elastic deformation of a petiole has been considered by Vogel (1989) and Niklas (1999), using simple beam models. They showed that the static and dynamic deformations of the whole leaf are concentrated in the petiole for most leaves. This idealized model of leaf deformation is not adapted when the lamina is more flexible than the petiole or for complex geometries such as pinnate leaves and sessile leaves. Nevertheless, models considering the lamina as rigid and the petiole as flexible are efficient in most applications (Niklas, 1992; Niinemets and Fleck, 2002).

The aim of the present paper is to combine simple models of branch orientation with models of petiole deformation under external loading, in order to understand and ultimately predict some of the existing features of leaf inclination angle distributions. More precisely we seek to clarify the respective role of these two factors, geometrical or mechanical, affecting LIADs.

Considering the large number of branches and leaves we shall use standard methods of statistical physics to build the probability density functions. In Section 2, the Branch Inclination Angle Distribution is built for idealized two-dimensional and three-dimensional trees. In Section 3, a model is proposed to describe the deformation of a leaf under two types of loads: that induced by gravity and that induced by wind. In Section 4 these results are combined to derive LIADs and their variations with parameters. The possible effects on a global quantity such as the light interception are also discussed.

2. Branch inclination angle

2.1. The two-dimensional tree

We seek to establish first the role of tree geometries on inclination angles of branches which hold leaves. To do so we use a description based on the assumption of an iterative branching process. This is similar in principle to the models used by Rodriguez et al. (2008), Lopez (2011) or Eloy (2011) recently. The simplest model, referred hereafter as the 2D tree model, is illustrated in Fig. 2a. Here, the geometry results from a series of n iterations where the end segments of the tree are prolongated by two daughter branches, emerging with an angle θ_0 from each mother branch. As only inclinations are involved no other information is needed on length or diameter of the branches (see Rodriguez et al., 2008; Lopez, 2011).

As the BIAD describes the inclination angle of the shoots supporting leaves, we focus our analysis on the branches of the ultimate order of the tree, n. Elementary calculus shows that the

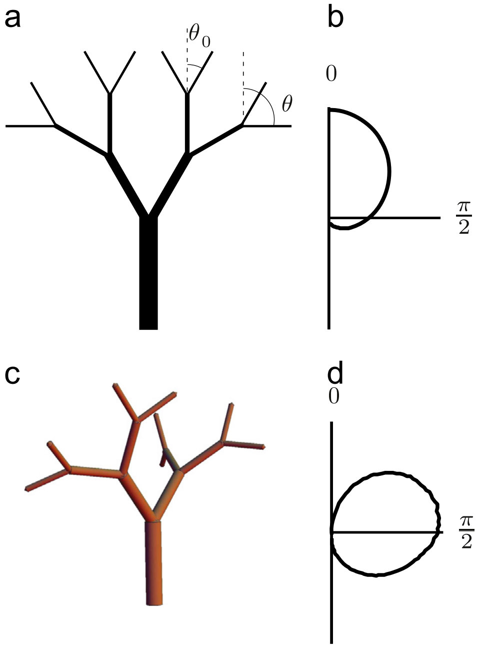

Fig. 2. Iterative idealized branched trees. (a) A two-dimensional tree, (b) the corresponding BIAD, Eq. (3), with the number of iteration n is equal to 4, for a branching angle $\theta_0 = \pi/6$. (c) A three-dimensional tree, (d) the corresponding BIAD obtained by numerical simulation with the same values of n and θ_0 by averaging over 10^5 trees.