Journal of Theoretical Biology 396 (2016) 125–131

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Are leaves optimally designed for self-support? An investigation on giant monocots

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HIGHLIGHTS

- Large leaves are optimally designed to self-support and intercept light efficiently contrary to small leaves.
- The optimal design of leaf with constraints on biomass and mechanics is theoretically inspected.
- Measurements on palms have been conducted.
- Leaf design for light interception is discussed.

ARTICLE INFO

Article history:
Received 8 October 2015
Received in revised form
4 February 2016
Accepted 12 February 2016
Available online 23 February 2016

Keywords:
Palms
Optimality
Biomechanics
Biomass allocation
Self-support

ABSTRACT

Leaves are the organs that intercept light and create photosynthesis. Efficient light interception is provided by leaves oriented orthogonal to most of the sun rays. Except in the polar regions, this means orthogonal to the direction of acceleration due to gravity, or simply horizontal. The leaves of almost all terrestrial plants grow in a gravity field that tends to bend them downward and therefore may counteract light interception. Plants thus allocate biomass for self-support in order to maintain their leaves horizontal. To compete with other species (inter-species competition), as well as other individuals within the same species (intra-species competition), self-support must be achieved with the least biomass produced. This study examines to what extent leaves are designed to self-support. We show here that a basic mechanical model provides the optimal dimensions of a leaf for light interception and self-support. These results are compared to measurements made on leaves of various giant monocot species, especially palm trees and banana trees. The comparison between experiments and model predictions shows that the longer palms are optimally designed for self-support whereas shorter leaves are shaped predominantly by other parameters of selection.

1. Introduction

Leaves are responsible for intercepting light and creating sugars from photosynthesis (Vogel, 2012). The ability of a plant to produce biomass, to grow and reproduce (in other words to compete for survival) depends on the efficiency of photosynthesis. Photosynthesis yield depends on various parameters, mainly gas exchange, leaf temperature and light interception (Farquhar et al., 1980). Different factors may have a role on those key parameters: leaf perspiration, stomata aperture and ability to flutter may alter heat and gas exchange at the level of the leaf (Roden and Pearcy, 1993; Roden, 2003).

Leaf orientation towards the sun's rays plays a key role for light interception (Tadrist et al., 2014) and different strategies have been adopted by the vegetal kingdom. In the first strategy, leaf orientation has no preferred direction to collect diffuse light that comes from every direction. In the second strategy, leaves have to be properly oriented to collect direct sun light. More complex strategies to improve the rate of photosynthesis also exist, giving rise to rather dynamical plant behaviour depending on environmental parameters. One example is the time-dependent orientation of leaves to follow the sun's position in the sky, but they can be even more complex. For instance, during a drought period, the inability to access water from the soil prevents the plant from perspiring. The leaf-refreshing effect of transpiration is cancelled, leaf temperature increases and the rate of photosynthesis drop to zero. To

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http://dx.doi.org/10.1016/j.jtbi.2016.02.018

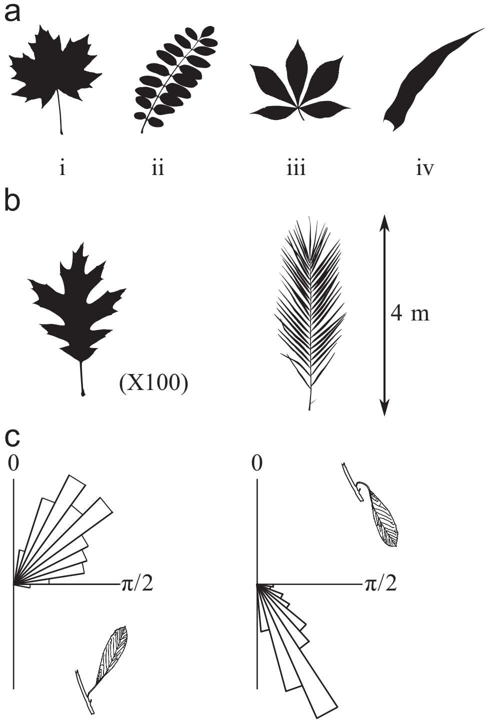

Fig. 1. (a) Variety of shapes of leaves: (i) simple leaf, (ii) palmate leaf, (iii) pinnate leaf, and (iv) sessile leaf, without petiole. (b) Variety of sizes: the first leaf is an oak leaf which has typical dimensions on the order of few centimetres, compared with phoenix palm that has a typical dimension of a few meters. In proportion, the oak leaf size has been magnified by a factor 100. The largest leaf was measured on *Raphia regalis* with a length of 25.11 m Hallé (2005). (c) Variety of leaf orientations in terms of leaf inclination angle distribution. The first distribution depicts erected leaves whereas for the second one (*Trema aspera*) most of the leaves are hanging down.

avoid such dramatic loss, leaves' orientations are changed to intercept less light, reduce leaf temperature and keep leaves active for photosynthesis, (Vogel, 2012; Gonzalez-Rodriguez et al., 2015).

Because of these reasons, one may think that leaf orientation, leaf shape and leaf size would be parameters subjected to strong pressure of selection because of their role in light interception. The design of the leaf (thickness, length, width, petiole, midvein, secondary veins, etc.) must be optimal to obtain the larger rates of photosynthesis without threatening the plant's life. The highest photosynthetic rates of plants can reach up to 30% with a mean rate around 3% (Raven et al., 2003). In this context, it is surprising to observe such a variability in leaf shape, sizes and orientations (see Fig. 1). Discussions about plant mechanical optimality make a long story. The first authors to introduce the concept of plant design constrained by mechanics were McMahon and Kronauer (1976), who proposed that tree height and tree width are bound features. A few discussions of plant optimality concern branches (Wei et al., 2012) and leaves (Niklas, 1992, 1993; Niklas and Spatz, 2012), and Jensen and Zwieniecki (2013) have shown that leaf size is limited by optimal sap flow in tall trees.

Simple calculation of light interception with geometrical arguments shows that the optimal position to collect direct sun light is orthogonal to the local gravity field; see Appendix A and Tadrist et al. (2014). On terrestrial plants, leaves grow on branches and must support their own weight in order not to hang down. Some bio-material used to make the leaf must be dedicated to create surface area for light interception, but the rest of the bio-material should be used for mechanical self-support. On the one hand, if too little bio-material is used for self-support, the leaf will hang down and despite the large amount of bio-material used to create surface area, it will not intercept much light. On the other hand, if too much bio-material is used for self-support, the leaf will be properly oriented to intercept light but will have no surface area to collect light. An optimal mass allocation trade-off exists between those two extrema. What would be the shape of a leaf that has optimally allocated biomass? Note that when no self-support is needed, all the biomass would be used to create surface area for light interception. This is the case for water lilies that occupy the interface between air and water.

Answering questions considering optimality in nature is not easy because of the large number of functions performed by an organ and because of the still larger number of environmental parameters to take into account. Those functions may naturally encourage antagonistic shapes; for instance, the optimal leaf would be thin enough to have a large surface area-to-volume ratio to enhance gas and heat exchange, but also thick enough for efficient transport of water and sap in xylem and phloem. Abiotic and biotic stresses are also shaping factors for the leaf. For example, a leaf may be designed to flutter to increase photosynthesis rate (Roden, 2003), to expel water drops and prevent fungus attacks or simply to remove hervibory insects (Yamazaki, 2011). Leaves have also developed mechanical tricks to be stiffer for the same amount of bio-material and thus to reduce the amount of biomass needed to support their own weight. Those tricks are (i) the inhomogeneity of the leaf tissues (Xylem and phloem vessels are much more lignified – and thus stiffer – tissues than mesenchymatous cells), (ii) the anisotropic placement of the tissues and (iii) the shape of the leaf itself. For instance, the shape of the leaf could lead to a stiffer U-shaped petiole (Ennos et al., 2000) or stiffer lamina through curvature-induced rigidity (Barois et al., 2014).

In this paper, we focus on the trade-off between self-support and creation of surface area for light interception. Our approach is based on a basic mechanical modelling of the leaf which neglects the different stresses or parameters of selection that apply on leaves, nor on the complex mechanical tricks developed to enhance leaf rigidity while minimizing biomass use.

Optimal leaf shape is examined for the giant monocots leaves, especially palms of palm trees and banana trees. Palm trees belong to the large family of *Arecaceae* (more than 2600 species) within the monocots clade. In this family, plants exhibit leaves of different sizes and different shapes. We choose here to study plants with consistent, simple leaf geometry: one short petiole and one long lamina with one major vein. In the first part of this paper we take advantage of this simple geometry to describe theoretically what would be the optimal leaf of a palm tree. In the second part of this paper, we describe the measurements done on actual palm trees and banana trees. Finally, we compare the theoretical results with the measurements on monocot trees. We show that the shape of larger leaves is close to the predicted optimal shape whereas the smallest palm shapes differ strongly from prediction. We predict a minimal size for which our model applies. For smaller leaves, self-support does not appear to be the strongest factor of selection.

2. Model

We aim at modelling what would be the optimal shape of a leaf under mechanical self-support constraints. We develop here a simple model based on mechanical considerations. For the sake of clarity, mechanical and geometrical assumptions are made for the considered leaf.

2.1. Model assumptions

We detail the assumptions as follow: first, the geometry of the considered leaf is chosen as the geometry of a palm of *Phoenix*