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Understanding and evaluating some allometric relationships useful for functional-structural plant modeling

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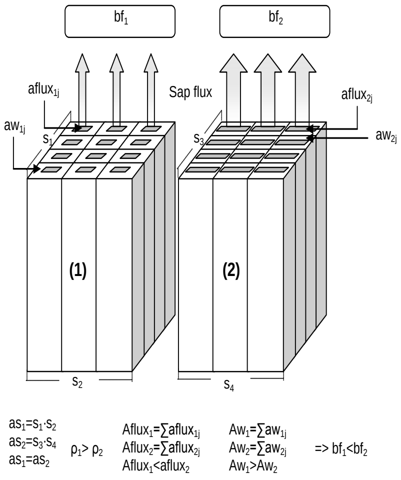
Highlights: The dynamic process of development and growth of *Pinus radiata* trees was studied during an entire growing season and the allometric relationship between foliage biomass and the supporting conductive area of tissues analyzed. Changes in the stem through time of this relationship suggest that the use of a constant and fixed value for modeling purposes leads to wrong results. This subject is discussed and illustrated by means of simulations.

Keywords: Plant allometry; pipe model; foliage development; wood formation.

INTRODUCTION

When new structures are formed two important principles seem to operate: economy and optimization. Economy in the sense of minimal use of energy or material to obtain the goal; optimization, in the sense of optimal configuration in order to achieve multiple goals or attain a balance between physiological and structural demands. As a result we observe an harmonic structure so designed as to maintain those principles throughout the lifespan of the individual. We perceive an optimal equilibrium, even if we do not fully understand the commanding forces behind it, as allometric relationships between organs, tissues, between structure and function, as studied by Niklas (1994) among others.



$$Aflux_t = A_t - Aw_t = \omega_1 Bf_t^{\omega_2} \qquad \rho_t = \frac{Bw_t}{\Delta V_t}$$

Figure 1: Sketch showing the assumption of proportionality between the demanding foliar biomass (bf1 and bf2) and the cross section area characteristics. Aflux corresponds to the truly conductive cross section area (summ of all cell lumens or $aflux_i$). With A_t total area and A_w area of cell wall. We assume that $Aflux_t$ is proportional to foliar biomass ($\omega_1 Bf_t^{\omega 2}$) in a power relation. Therefore it will influence the value of B_w (wood biomass that will be assign to wood cell), and the associated wood density ρ.

If these rules apply to stem building during tree growth it should conduct water and metabolic products as a pipe system but at the same time it will have to withstand the increasing weight and mechanical forces acting on the crown and bole. These goals are to be achieved at a minimal cost and as an optimized solution. Already Shinozaki (1964) and later many other authors like Mäkelä (2002) have analyzed the allometry involved in this pipe system, and Matheck and Kluber (1997), Niklas (1992) among others, the bio-mechanical balance of these at times huge structures.

In functional-structural modeling one of the key factors that concerns us is the way in which growth is allocated. After photosythesis and respiration have been taken care of, surplus material may be sent to new organs or to enlarge existing ones. Particularly, when modeling the stem growth of the trees, key questions are the amount of material that is used to build the new mantle of wood and the kind of structure derived therefrom. Leaves require a continuous supply of water from roots to replace that lost in transpiration. So, a relationship should exist between the amount of foliage (leaf biomass) and the cross section of the trunk or branches that support it in order to satisfy the required flow of water. To solve this matter a common solution in various models is to use an allometric relation between the mass of transpiring foliage and the pipe system that has to be constructed to supply it. Such a relationship has actually been documented for different species (Mäkelä, 2002) and has been used in structural-functioning models. Obviously, it is not only the area of cross sections that are involved in the flow, but also the inherent conducting capacity, which in turn depends on the density of the wood (Santiago

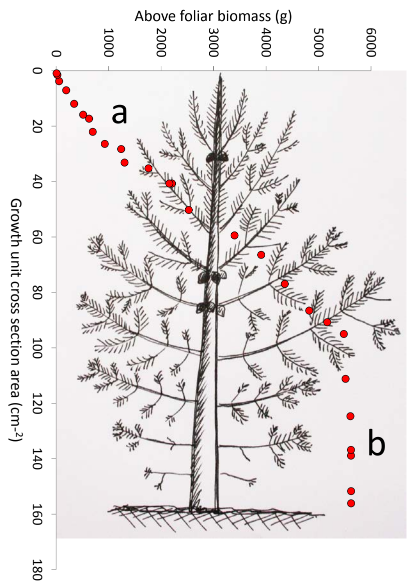
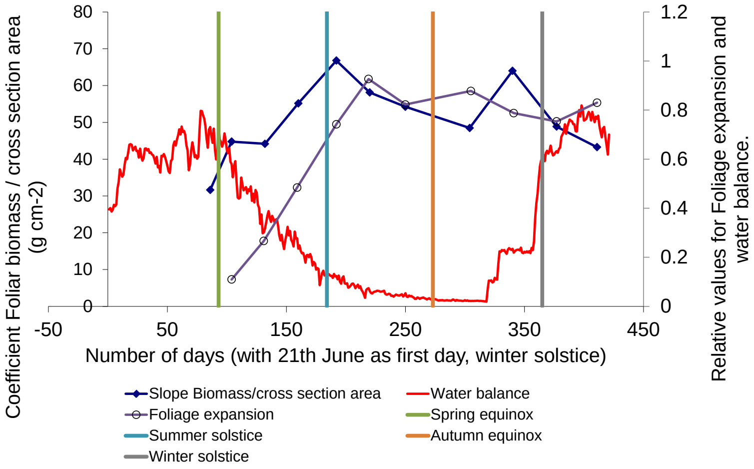


Figure 2: Sketch of a pine tree crown indicating the relationship between the upper foliar biomass and the corresponding supporting cross section area. Section (a) shows a linear relation between both variables in the living crown. Section (b) shows an increase of the cross section area while foliar biomass remains rather constant.

et al., 2004; Bucci *et al*., 2004). In addition, as shown by Santiago *et al.* (2004) and Bucci *et al.* (2004) density is negatively correlated with the water saturation capacity of tissues, with the specific hydraulic conductivity of leaves, with the net assimilation rate of CO_2 , stomatal conductance, specific leaf area and the leaf water potential. It may then be inferred that wood of high density would restrict the productive activity of leaves by reducing flow of water and nutrients in the sapwood. Therefore, we expect that the effective area of water conduction (Aflux, Figure 1) in the xylem should be proportional to the foliar biomass (Mäkela, 2002; Fernández 2008).

MATERIALS AND METHODS

During a growing season (June 2009–August 2010) the development of foliage, main apex, and wood of 38 nine years old *Pinus radiata* trees in an unmanaged stand (Mediterranean Central region of Chile) were monitored. Every 15 days at the beginning of the growing season and every 30 days later on, the development of wood was traced by means of microcores. Simultaneously, we measured the development of the main apex and foliage. In each occasion 3 trees were felled, their whole tree architecture measured and described, and discs from each growth unit collected for further analysis. The discs where stained with a solution of benzidine (Koch and Krieg 1938) in order to detect heartwood. No heartwood was observed in the majority of the discs. The whole foliar biomass was classified according to position and age, collected and weighed. Two pieces of the stem, at the base of the living crown and at the middle of the crown, were analyzed by Magnetic Resonance Imaging that showed the distribution or concentration of water in the wood. Also, an X-ray transversal profile was obtained at the same level the microcores were sampled to analize the wood density. Hourly environmental data (temperature, rainfall, wind speed, solar radiation) were recorded on a nearby automatic weather station . Pertinent soil data was obtained to compute water balance and thermal accumulation (Fernández et al. 2011).



Fgure 3: Evolution of the ratio foliar biomass / cross section area during the growing season, showing marked changes as foliage expands. Water balance is also shown.

RESULTS AND DISCUSSION

For each tree, the relationship between the total cross section area of the growth units and the total leaf biomass over them was analyzed. Figure 2 shows a typical profile. As can be seen foliar biomass is linearly related to the cross section area in the zone of the active crown (Figure 2a). In contrast, in the lower part of the crown (Figure 2, b) the foliar biomass shows a rather constant value while the cross section area steadily increases. These trends are a clear indication that the value of the allometric relation of these parameters depends on what part of the crown we are dealing with. In most trees there were no evidence of heartwood as shown by benzidine staining, but the fact is that the cross section area in the lower part of the crown appears to be active no more.

Figure 3 shows the slope of the relation Y=a*X with Y foliar biomass and X the cross section area of the supporting section. Each dot corresponds to the slope found on the three trees sampled at each date. Time is indicated in days with number 1 as June 21th (winter solstice in the southern hemisphere). The water balance is given as the ratio ET/ET_{max}, with ET as the real evapotranspiration and ET_{max} maximum atmospheric water demand. The close relationship between the slope values and the extent of the foliage is clear. Also, the seasonal pattern of the allometric relation is evident. Both matters have important implications in sampling and modeling.

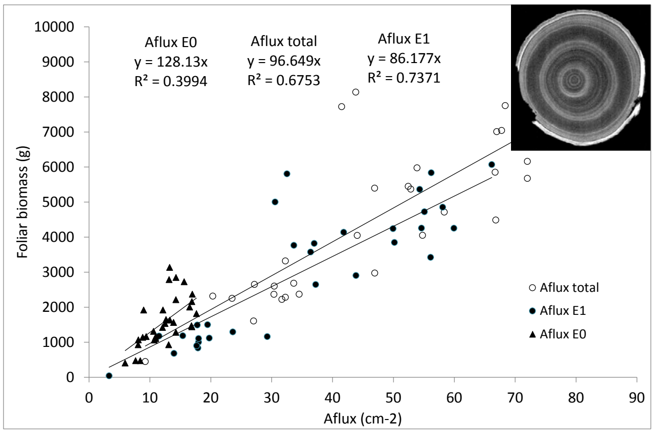


Figure 4: (a) Relationship between real conductive area (Aflux) of the total cross section area, of the developing ring (Aflux E0) and of the previously formed rings (Alfux E1) with the respective foliar biomass (Etotal, E0 and E1). (b) Cross section proton image obtained with Magnetic Resonance Imaging. The different gray values indicate higher or lower concentrations of water in the tissues.

Figure 4 shows the relationship between the leaf biomass and the real or effective conductive cross section area obtained by analysis of MRI images. The data have been divided into (a) the foliar biomass developed during the sampling season (E0) and the corresponding conductive area formed in the new ring (Aflux E0) and (b) the foliar biomass and conductive tissue of the previous years (E1 and Aflux E1). The value of slopes changes in every case showing a larger amount of foliar biomass in relation to cross section in the new ring, in comparison to the previous one. Probably the steady development of wood after the foliage expansion ends (observed also in Figure 3) triggers this change of proportions. Usually, samples are taken at predetermined times, not necessarily in tune with dynamic events of development and growth. In addition, we investigated the strategy of wood deposition along the stem. Results (not shown here) indicated a variable distribution of the wood mantle during the year. These results and the consequences of not taking them into account in the modeling process will be presented and discussed.

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