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Contrasting leaf phenological strategies optimize carbon gain under droughts of different duration

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ABSTRACT

In most ecosystems, plants face periods with limited water availability, during which stomatal conductance is reduced to maintain hydration. However, prolonged dry spells might require more drastic strategies to conserve water, such as drought-deciduousness. If drought-related changes in leaf area are adaptive, it can be hypothesized that leaf area is optimized to maximize the growing-season carbon (C) gain. Different phenological strategies during drought have been proposed: (i) leaf area index (L) declines when net photosynthetic rates (A_{net}) reach zero to maintain a non-negative A_{net}; (ii) L adjusts to avoid water potentials with negative impacts on $A_{net;}$ (iii) a constant leaf water potential is maintained (isohydric behavior); and (iv) leaf area remains unaltered (i.e., summer-evergreen leaf habit). However, whether these strategies are optimal in terms of growing season C gains has not been assessed. Here we consider these theories in a unified framework using the same set of equations to describe gas exchanges and water transport in the soil–plant–atmosphere continuum, and quantify the effect of the leaf phenological strategy on plant C gain over the entire growing season in different climates. Longer dry periods tend to favor drought-deciduous rather than summer-evergreen habit. Deciduous plants that allow leaf water potential to fluctuate (anisohydric) while preventing negative A_{net} assimilate more carbon than deciduous plants with fixed leaf water potentials (isohydric). Increased rooting depth allows evergreens to more effectively compete with drought-deciduous species. Moreover, increasing leaf nitrogen concentrations and thus photosynthetic capacity can be an effective acclimation strategy when dry periods are relatively short.

1. Introduction

In most ecosystems, plants experience periods of dry conditions forcing them to reduce photosynthetic activity and possibly inducing physiological damage. Limited water availability primarily reduces leaf gas exchange due to stomatal closure [1], but as the soil dries the plant hydraulic system may be damaged due to increasing cavitation and limited refilling [2,3]. Both hydraulic damage and depletion of carbon (C) stores after prolonged inhibition of gas exchange may cause temporary shed of root tips and leaves, permanent loss of terminal branches and eventually plant death [4–7]. When widespread, this damage might affect hydrologic fluxes not only at the plant level, but also at the watershed scale due to vegetation changes.

To reduce the risk of damage, perennial plants have evolved a suite of adaptations to either tolerate or avoid drought effects [8,9]. In seasonally-dry ecosystems (under both Mediterranean and tropical climates), prolonged dry periods occur predictably during the growing season, forcing plants to develop strategies that allow CO_2 uptake to be maintained when conditions are favorable, while avoiding excessive water stress during the dry season [10–14]. In mesic climates, summer dry periods are more unpredictable and plants are less well adapted to cope with water restrictions. The consequences of exceptional drought in mesic climates are thus potentially long-lasting [2,15]. Although stomatal closure provides a rapid response to lowered water availability, in the long-term it might not be sufficient to preserve plant water status: non-stomatal water losses continue [e.g., through the leaf cuticle, 16] and the net carbon balance of the leaves eventually turns negative due to reduced CO_2 uptake. Therefore, shedding leaves may become a more effective strategy to avoid water stress and the associated carbon costs [9,17–21]. Indeed, drought-deciduous species are widespread in tropical dry ecosystems with extended dry seasons [13,22–24] and some degree of drought-related reduction in leaf area is frequently observed in Mediterranean ecosystems as well [25]. Occasional summer droughts also trigger leaf

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loss in mesic tropical [26] and temperate climates [27–29]. Notably, the timing and rate of leaf shed (or dieback) during dry periods varies significantly across species [5,7,23,24], suggesting that different leaf area regulation strategies may be adopted.

Although shedding leaves allows plants to avoid extreme water stress, this strategy also inhibits opportunities for future carbon uptake should conditions become favorable after the dry spell. An alternative strategy, in which no leaf shed occurs during dry periods, is common in some tropically dry and Mediterranean ecosystems (summer evergreen species). This strategy facilitates the exploitation of even small increases in soil moisture because leaves are poised to exchange gases as soon as stomata re-open. However, to maintain leaves hydrated and functional in dry periods, a larger belowground carbon allocation is required to reach deep soil water reserves [30]. We might thus expect that the triggers for leaf shedding depend not only on the current conditions (e.g., soil water potential), but also on the long-term mean climatic conditions to which the plants' growth schedule is adapted.

It could be hypothesized that the soil and plant hydrologic balances control leaf hydration and that leaf shedding represents a strategy to avoid excessive dehydration and optimization of canopy C uptake over the whole growing season. The same optimization principle could apply to both prolonged dry seasons (lasting a few to several months) and shorter droughts within an otherwise favorable growing season (lasting a few to several weeks). Based on this optimality principle, several conceptual [31] and mathematical [17–19,32–36] models have been developed to predict the timing of leaf shed and leaf habit under unfavorable climatic conditions or due to self-shading. Some are also implemented in global dynamic vegetation models [34–36]. These models distinguish between favorable and unfavorable growing conditions and predict leaf habit based on the durations of these seasons or the availability of soil moisture. However, most models neglect plant hydraulic features and the linkage between C economy and hydraulic regulation, which represent the mechanistic connection among environmental conditions, plant water status, and phenology during dry periods. Including these mechanisms would improve the mechanistic representation of leaf phenology in ecosystem models. Improved representation of leaf area regulation would facilitate better modeling of land-atmosphere water exchange, due to the effects of changing leaf area on transpiration rates. In particular, since leaf re-growth is slower than variations in stomatal opening, capturing the drivers of leaf phenology may be important for understanding ecosystem and hydrological responses to pulses of water availability following drought.

This study develops a suite of coupled plant C-hydraulic models that link soil moisture availability to plant water status and gas exchange. We start from the premise that leaves are retained or shed based on C uptake or hydraulic constraints, resulting in four different phenological strategies. The environmental conditions for drought-related leaf shedding are quantified as a function of plant hydraulic and biochemical traits as well as climatic parameters. We investigate both seasonal and shorter occasional droughts, described as dry intervals of a given duration occurring between relatively wetter periods. Using this framework we address two main questions: i) how do different strategies differ in terms of the timing of leaf shedding and the resulting net C gain? and ii) which phenological strategy provides the best compromise between avoidance of water stress and maintenance of high net C uptake capacity, as a function of rainfall seasonality or drought duration? To address these questions, the article is structured as follows:

1. A mathematical framework is proposed to describe contrasting phenological strategies, including as a term of comparison evergreen species relying on a continuous leaf exchange or winter-deciduous species that do not respond to drought with leaf shedding (Sections 2.1 and 2.2).
2. The leaf phenological strategies are implemented in a coupled plant hydraulic-C uptake model (Section 2.3), which is used to predict growing-season C gain for each strategy.
3. Growing-season C gains are compared across strategies under a range of idealized (Sections 3.1 and 3.2) and realistic climatic scenarios (Section 3.4).
4. Sensitivity analyses are performed to assess how varying plant functional traits alters the C gains of each phenological strategy (Section 3.3).

2. Theory

Section 2.1 presents the coupled mass balances for plant-available carbon and soil moisture, which are used in the following sections to link phenological strategies to environmental conditions. Section 2.2 outlines the different criteria governing leaf area adjustments during dry periods, which are expressed mathematically as constraints on the C fluxes or the canopy water balance, as described by a coupled plant hydraulic- C uptake model (Sections 2.3 and 2.4). The soil moisture balance and rainfall data used to characterize the duration of dry periods for different sites are presented in Section 2.5. The symbols are defined in Fig. 1 and Table 1.

2.1. Plant carbon balance equation

The mass balance for plant-available assimilated carbon (C_P) can be written as a function of leaf area index (L):

$$\frac{dC_P}{dt} = A_{net}(L) - \Gamma(L) - R_P, \tag{1}$$

where A_{net} is the net C uptake, which includes the C costs of leaf maintenance; and Γ is the leaf construction cost in C units, defined as the amount of C spent to grow a leaf area L to full maturity (including C in leaf biomass and C respired to produce that biomass). The term R_P represents the respiration rate associated with sustaining metabolic activity in the plants' stem and root system and is therefore modeled as independent of leaf area (leaf respiration is already accounted for in the net photosynthesis; Eq. (16)). To retain analytical tractability, this approach neglects the details of how assimilated C is used. C investment for defense [37] would be partly coupled to leaf area (thereby affecting leaf-level respiration, Section 2.3) and partly decoupled (and conceptually included in R_P). The model also neglects whether C stored from previous years is used for growth in the current growing season [38], because different hydrologic years are considered as independent. The leaf construction cost is parameterized differently between species with whole-canopy flushing events (e.g., drought and winter deciduous species) vs. species that undergo continuous leaf exchange (e.g., several evergreen species). In the former, leaf flushing is modeled as an instantaneous event occurring at time $T_{f,i}$, where subscript i refers to the ith (complete or partial) leaf flush,

$$\Gamma(L) = \sum_{i=1}^{n_f} C_c(L)\delta(t - T_{f,i}), \tag{2}$$

where C_c is the C investment for new leaves at each flushing (i.e., it accounts for residual leaf area at rewetting; Eq. (19)), n_f is the number of flushing events over the growing season of duration T, and $\delta(\cdot)$ is the Dirac delta function. In the following we will consider for simplicity only the case $n_f = 1$ or 2, i.e., we account for the costs associated to a first flush at the beginning of the growing season and at most for the cost of a second flush after the dry period. This second flush may be incomplete if a fraction of leaf area was still available upon rewetting. Evergreen leaf-exchanging species are assumed to invest C at a constant rate, so that over the course of a single growing season of duration T they grow an equivalent leaf area to the one produced by