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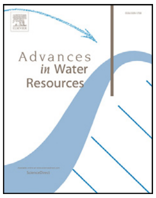

Contrasting leaf phenological strategies optimize carbon gain under droughts of different duration

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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

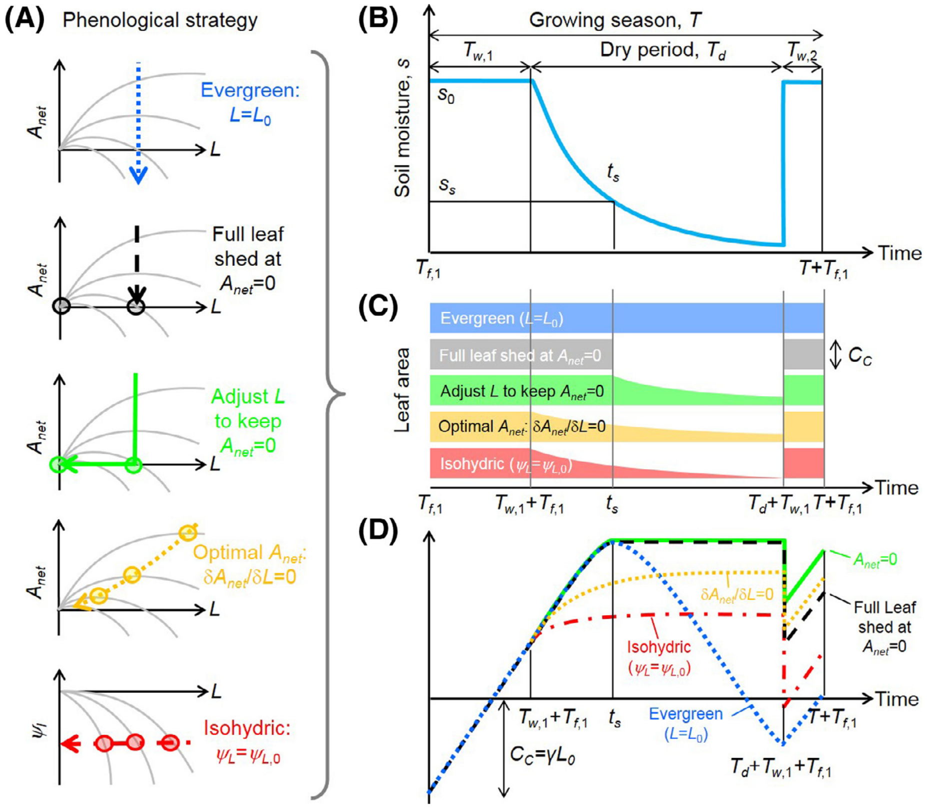

Fig. 1. Schematic representations of: (A) phenological strategies, (B) relative volumetric soil moisture (s, see Eq. (20)), (C) leaf area changes, and (D) cumulative carbon gain (G, see Eq. (4)), as a function of time (T_d may vary in our framework between a few weeks and several months). Panel B defines the symbols used to identify the different periods in the growing season (subscripts 0, w, d, f, and s respectively refer to the initial states, the wet and dry conditions, the times at which leaves are flushed, and at which A_{net}=0); panels C and D also show the amount of C invested in a whole-canopy leaf flush ($C_C = \gamma L_0$, see Eq. (19)). Note that the curves depicted here are illustrative only; the actual shape depends on the specific plant traits and environmental conditions, as described in the text and shown in Fig. 4. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Table 1
Definitions of biochemical and hydraulic parameters and their baseline values, chosen as representative of a cerrado ecosystem.

Symbol	Definition	Value	Units	Notes
a	Ratio of the diffusivities of water vapor and CO_2	1.6	dimensionless	
b	Exponent of the water retention curve	5	dimensionless	[77]
c	Exponent approximating the soil hydraulic conductivity–soil water potential relation	2	dimensionless	[48]
c_a	Atmospheric CO_2 concentration	400	μmol mol^{-1}	
D	Vapor pressure deficit	0.015	mol mol^{-1}	[13]
$g_{sr,sat}$	Soil-to-root conductance in saturated conditions	14×10^3	m MPa^{-1} d^{-1}	Assuming root area index = 10 m^2 m^{-2}
f_C	Leaf C fraction	0.4	g g^{-1}	
$g_{s,max}$	Maximum stomatal conductance per unit leaf area	0.4	mol m^{-2} s^{-1}	[13]
g_x	Xylem conductance	5.2×10^{-3}	m MPa^{-1} d^{-1}	Based on [56] and SAI = 0.002 m^2 m^{-2}
k	Carboxylation efficiency	0.04	mol m^{-2} s^{-1}	Chosen value
L_0	Leaf area index in well-watered conditions	2	m^2 m^{-2}	[47]
LMA	Leaf mass per area ratio	50	g m^{-2}	[21]
n	Soil porosity	0.45	m^3 m^{-3}	[77]
n_f	Number of (partial or complete) leaf flushings	1, 2	dimensionless	
r	Respiration per unit leaf area	5.3	μmol m^{-2} s^{-1}	r combines day respiration and compensation point
R_P	Plant respiration rate	3	g m^{-2} d^{-1}	~half of ecosystem respiration [78]
SAI	Sapwood area index	0.002	m^2 m^{-2}	Based on [13] and L_0 = 2 m^2 m^{-2}
Y	Yield of leaf construction	0.42	g g^{-1}	[18]
Z_r	Rooting depth	0.5	m	Chosen value
ν	Unit conversion factor	0.78	s m^3 d^{-1} mol^{-1}	
$\psi_{s,\,sat}$	Water potential at soil saturation	−0.001	MPa	[77]
$\psi_{50,\,s}$	Leaf water potential at 50% stomatal closure	−1.5	MPa	[59]

a deciduous species during a single whole-canopy flush. With these assumptions, the rate of C investment for evergreen species is given by:

$$\Gamma(L) = \frac{C_c(L)}{T}. \qquad (3)$$

When interpreting Eq. (3), note that the leaf area index, L, is constant through time, but the proportion of old and new leaves changes throughout the growing season.

For all strategies, we use the cumulative C gain (G) as an index of plant fitness, thus facilitating the comparison across phenological strategies (Fig. 1). The likelihood that a given C gain is actually achieved is assessed based on observed drought duration lengths (Section 2.5). Based on Eq. (1) and dropping the functional dependence on L for notational simplicity, G can be written as:

$$G(t) = \int_{T_{f,1}}^{t} (A_{net} - \Gamma - R_P) dt', \tag{4}$$

where t' is an integration dummy variable and $T_{f,1}$ is the time of the first flush. Assuming that R_P is a constant and using Eqs. (2) and (3), we can compute G at the end of the growing season ($t = T_{f,1} + T$). For species with marked leaf flush (i.e., winter- and drought-deciduous species), the cumulative growing season C gain is

$$G(T) = \int_{T_{f,1}}^{T_{f,1}+T} A_{net} dt' - R_P T - \sum_{i=1}^{n_f} C_c \Theta(T + T_{f,1} - T_{f,i}), \tag{5}$$

where $\Theta(\cdot)$ is the unit step function. For leaf-exchanging evergreen species, the growing-season C gain is computed as

$$G(T) = \int_{T_{f,1}}^{T_{f,1}+T} A_{net} dt' - R_P T - C_c. \tag{6}$$

If $n_f = 1$ and all other parameters are held constant, Eqs. (5) and (6) give the same result, although the timing of the C investment is different. Therefore, the C gain at the end of the season is the same for evergreen species and winter deciduous species that do not shed their leaves in response to drought, although the timing of such gain over the season varies. If $n_f = 2$, $G(T)$ is predicted to be lower in drought deciduous species due to the multiple investments in new leaves, provided that all other parameters are equal. Because most terms in Eqs. (4)–(6) depend on leaf area, the different leaf phenological strategies directly impact the plant C gain (Section 2.2).

While the equations described above are general, they are employed here for the case of mature canopies that are assumed to be in equilibrium in terms of carbon investment and allocation. A detailed analysis at ontogenetic time scales is beyond the scope of this contribution. All C and water fluxes are computed at the daily time scale, allowing diurnal water storage in stems or variations in stomatal conductance and photosynthetic rate due to insolation to be neglected. By focusing on leaf area as the variable adjusted by the plant to maximize G, other traits that could also be modified to achieve an optimal behavior are either assumed constant through time (e.g., rooting depth or nutrient allocation to photosynthetic machinery), or to adjust as a function of soil and leaf water status (stomatal conductance), without formally optimizing their values. Sensitivity analyses are thus performed to assess how the optimal phenological strategies vary across a spectrum of these trait values under different climatic scenarios (Section 2.4).

2.2. Leaf phenological strategies

Different criteria have been proposed to describe adaptive changes in leaf area in response to drought. Each criterion has effects on the plant water losses (including feedbacks on the soil water balance) and C uptake, thus ultimately affecting plant fitness. As described below, we consider four criteria to predict the timing and rate of leaf shedding: three optimality criteria based on C uptake rate and a hydraulic criterion based on isohydric behavior. The former three criteria are grounded on the hypothesis that plants maximize their C uptake rate (regardless of the subsequent allocation of assimilates), whereas the latter criterion is based on the hypothesis that plants prevent water stress by reducing leaf area and thus maintaining a stable leaf water potential. As a term of comparison, we include summer-evergreen species that do not shed leaves in response to drought. These strategies are summarized in Fig. 1. For all strategies, we focus on a single period without rain, during which soil moisture declines at a rate proportional to the transpiration rate. Thus, different phenological strategies may affect soil moisture by impacting transpiration, generating a feedback loop that increases water stress if leaves are retained and transpiration is sustained. These criteria drive the daily plant operation, but do not necessarily maximize the cumulative carbon gain G over the period T. Whether a criterion is optimal in terms of total C gain depends also on the occurrence of a second leaf flush after the dry period and on the subsequent C uptake. Flushing a second time allows the favorable post-drought conditions to be exploited, but at the cost of growing new leaves. To evaluate the role of this second flush, Eqs. (5) and (6) are employed to assess a posteriori the implications of each criterion on the total C gain, $G(T)$, and specifically whether the dry period is sufficiently long to justify shedding leaves and then flushing new leaves upon rewetting. The phenological strategies presented here are expressed in general terms, whereas the mechanistic descriptions of the C and water balances are presented in Section 2.3.

2.2.1. Species that do not shed their leaves during droughts

As a baseline for comparison among leaf phenological strategies, we consider summer evergreen species. This strategy includes truly evergreen species, which exchange leaves continuously, and winter deciduous species that do not respond to drought with leaf shedding. In both habits, a constant leaf area (denoted by L_0) is maintained through time. In leaf-exchanging evergreen species, C costs for leaf construction are distributed over the whole growing season, following Eq. (3), while costs of leaf flushing for winter deciduous species is represented by Eq. (2), with $n_f = 1$. Plants adopting this strategy incur significant C losses through respiration when photosynthesis is inhibited at low soil moisture (blue dotted curves in Fig. 1). However, when droughts are relatively short compared to duration of the wet season, this strategy can be advantageous [18].

2.2.2. Maximization of time-integrated net carbon uptake

Plants are often hypothesized to maximize their total C uptake over a given period by changing the value of some control parameter, for example stomatal conductance [39,40] or leaf area [19]. Following this maximization hypothesis, the goal becomes finding the time of leaf shedding that maximizes C gain over a specific period, regardless of subsequent flushes. This optimal shed time is found by differentiating the net C gain, i.e., the first term of Eq. (4), with respect to t and by setting this derivative to zero. The condition for maximization of net C uptake is thus found as (black dashed and solid green curves in Fig. 1):

$$\frac{dG(t)}{dt} = 0 \rightarrow A_{net} = 0, \tag{7}$$

that is, leaf shedding is initiated when the leaf-level C balance turns negative. We denote this instant in time as t_S (Fig. 1). Eq. (7) can also be derived from other independent optimization approaches: (i) as a result of a leaf expansion and shedding optimization model, when declines in photosynthetic capacity during the growing season and leaf loss due to herbivory are neglected [19], or (ii) by maximizing the shoot-level marginal C gain by optimizing leaf number, rather than by selecting the ‘best’ time of shedding [32]. Moreover, the criterion in Eq. (7) is the same employed in a dynamic vegetation model to describe leaf flushing (but not shedding) as a function of environmental conditions [34]. Note, however, that Eq. (7) does not consider C investment in subsequent leaf re-growth, and therefore does not constitute an optimization criterion for G at the growing season time scale.

Once t_S is reached (corresponding to Eq. (7)), two leaf shedding strategies can be defined. Plants could lose their leaves rapidly (solid green curves in Fig. 1), or gradually (dashed black curves) so that the condition of Eq. (7) is maintained through time. The former strategy is less realistic since it implies a total canopy loss, but it represents the end member of a suite of leaf loss strategies, and therefore it is considered here as an extreme case. Mathematically, losing all the leaves at the same time corresponds to the trivial solution of Eq. (7), while losing leaves gradually corresponds to the non-trivial case of equal gross photosynthesis and leaf respiration, for each value of soil moisture during the dry-down.

2.2.3. *Maximization of instantaneous carbon uptake*

An inherent tradeoff occurs between leaf area and C uptake. Increasing leaf area is advantageous as long as the increase in canopy photosynthesis overcomes the increase in respiration. During dry periods, photosynthesis decreases mainly due to reductions in stomatal conductance, while respiration continues unabated, switching leaves from CO_2 sinks to sources. Maintaining a large L lowers the leaf water potential that can be sustained by water supplied from any given root system, further inhibiting gas exchange (Section 2.3). Self-shading can also contribute to lower A_{net} at high L, but this effect is neglected here, where the focus is on open canopies. Due to these tradeoffs, an intermediate leaf area allows instantaneous C uptake to be maximized. The optimal leaf area is found by differentiating A_{net} with respect to L, and setting the derivative to zero (dotted orange curves in Fig. 1),

$$\frac{\partial A_{net}(L)}{\partial L} = 0. \tag{8}$$

This solution, which maximizes instantaneous photosynthesis, does not necessarily maximize the seasonal cumulative C uptake and does not account for carbon costs associated with a second flushing.

2.2.4. *Isohydric behavior*

The optimization approaches described above maximize C gain during the period when leaves are present, but allow plant water potentials to decrease significantly, possibly resulting in hydraulic damage. Alternatively, plants might adjust leaf area and stomatal conductance to preserve a stable leaf water potential [13,41,42]. Such an isohydric strategy allows for a more conservative use of water, at the expense of reducing gas exchange rates and therefore leading to reduced C uptake in the long term [4,9]). Since leaf water potential is related to leaf area through the equations describing water flow through the plant (Section 2.3), the condition to promote isohydric behavior by regulation of leaf area can be expressed as (dot-dashed red curves in Fig. 1):

$$\psi_l(L) = \psi_{l,0}. \tag{9}$$

Unlike the other criteria for leaf shedding explored in this study, the isohydric constraint is purely hydraulic and does not necessarily maximize the plant instantaneous or time-integrated C uptake.

2.3. *Coupled plant gas exchange-hydraulic model*

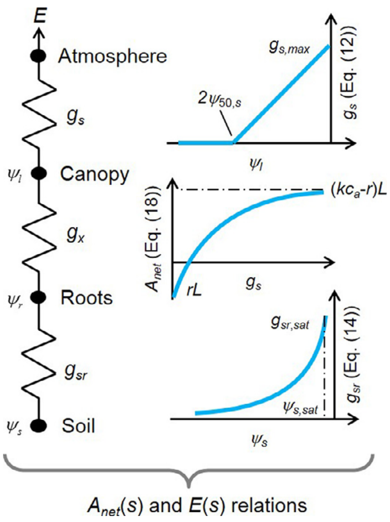

Fig. 2. Schematic representations of the coupled carbon-hydraulic model that links canopy-scale photosynthesis (A_{net}) and transpiration (E) through stomatal regulation (g_s) and describes water transport from the soil (at water potential ψ_s and relative volumetric soil moisture s) to the leaf (ψ_l).

A simplified plant hydraulic model to be interpreted at the daily time scale is employed to link the leaf gas exchange rates to soil water status and other environmental conditions. The ‘big leaf’ approximation is employed for simplicity and the canopy is assumed to be well-coupled to the atmosphere, so that canopy resistance is the most limiting factor to transpiration from the leaves. As in previous work [41,43–46], transpiration is described as a water transport process driven by gradients of decreasing water potential – from the soil (ψ_s) to the leaves (ψ_l) and the atmosphere. At daily time scales, it is reasonable to assume that the water potentials are in equilibrium with the water fluxes feeding and depleting each plant compartment (i.e., it is assumed there is no net storage of water within the plant). The canopy hydrologic balance can thus be written as

$$C_l \frac{d\psi_l}{dt} = E_s - E = 0, \tag{10}$$

where E and E_s are respectively the transpiration rate from the leaves and the rate of water supply to the leaves from the soil, and C_l is the canopy hydraulic capacitance, here set to zero.

The transpiration rate from the canopy can be modeled as:

$$E = \nu a g_s L D, \tag{11}$$

where g_s is the stomatal conductance to CO_2 per unit leaf area, L is the leaf area index, D is the vapor pressure deficit, $a = 1.6$ is the ratio of the diffusivities of water vapor and CO_2, and the coefficient ν converts the transpiration units from [mol m^{-2} ground s^{-1}] to [m^3 m^{-2} ground d^{-1}]. This approximation holds for canopies that are well-coupled to the atmosphere (as in the cerrado woodland considered here as a case study [47]), but is expected to overestimate the transpiration rate of dense canopies. For simplicity, we assume that the stomatal conductance responds linearly to changes in leaf water potential:

$$g_s(\psi_l) = \max\left[0, g_{s,max}\left(1 - \frac{\psi_l}{2\psi_{50,s}}\right)\right], \tag{12}$$

where the stomatal conductance under well-hydrated conditions is denoted by $g_{s,\,max}$ and the water potential at 50% stomatal closure is denoted by $\psi_{50,\,s}$ [48]. Because ψ_l becomes more negative with decreasing soil water potential during a dry period, Eq. (12) describes stomatal closure and the corresponding reduction in transpiration rate as soil moisture declines. In addition to stomatal closure, also leaf shed reduces transpiration – either directly (Eq. (11)) or indirectly via changes in ψ_l, which in turn alter stomatal conductance. All these effects are implemented through the coupled equations for transpiration (Eq. (11)), stomatal conductance (Eq. (12)), and leaf water potential, as described next.

The supply of water to the leaves can be modeled as a mass transport process controlled by two conductances in series (soil–root and xylem conductances, see Fig. 2) and driven by the soil-to-leaf water potential difference [41],

$$E_s = \frac{g_x g_{sr}(\psi_s)}{g_x + g_{sr}(\psi_s)}(\psi_s - \psi_l), \tag{13}$$

where g_{sr} and g_x are the soil–root and xylem conductances, respectively. Here for simplicity we consider constant xylem conductivity and neglect the effects of xylem cavitation. This approximation is justified as long as no catastrophic cavitation events occur, as is the case in normal operating conditions when plants tend to be hydraulically 'safe' [49]. Adding xylem cavitation would alter the shape of the transpiration–leaf water potential relation without qualitatively changing the dynamics of the soil-plant system. The soil–root conductance is expressed for all phenological strategies as a function of soil water potential,

$$g_{sr}(\psi_s) = g_{sr,sat}\left(\frac{\psi_{s,sat}}{\psi_s}\right)^c, \tag{14}$$

where subscript *sat* indicates saturated conditions and $c = 2$ approximates the exponent of the soil hydraulic conductivity–soil water potential relation when root extension at low soil moisture is also accounted for [48,50]. By reducing the sensitivity of the soil-to-root conductance to declining moisture, this model implicitly accounts for shifting allocation to roots during dry periods [51,52].

Combining Eqs. (10)–(14), the leaf water potential can be found as:

$$\psi_l = \frac{g_{sl}\psi_s - E_{max}}{g_{sl} - E_{max}/(2\psi_{50,s})}, \tag{15}$$

where $E_{max} = \nu a g_{s,max} LD$, with $g_{s,\,max}$ being the maximum stomatal conductance, and $g_{sl} = g_{sr}g_x/(g_{sr} + g_x)$ is the total soil-to-leaf conductance. In well-watered conditions (i.e., $g_{sl} \approx g_x$ and $\psi_s \approx 0$), Eq. (15) simplifies to $\psi_l = \psi_{l,0} = [1/(2\psi_{50,s}) - g_x/E_{max}]^{-1}$. This value of water potential is the least negative attainable leaf water potential, which is also imposed in Eq. (9) to describe the isohydric behavior. In this case, leaf area is changed so that ψ_l in Eq. (15) remains equal to its maximum value, $\psi_{l,\,0}$.

The canopy-scale net C uptake is approximated by linear kinetics with respect to internal CO$_2$ concentration [40,53,54]:

$$A_{net} = (kc_i - r)L, \tag{16}$$

where k is the carboxylation capacity per unit leaf area (temporal changes of k due to leaf aging are neglected), c_i is the CO$_2$ concentration inside the stomatal cavity, and r is the leaf respiration rate per unit leaf area. Coupling Eq. (16) with the rate of CO$_2$ diffusion from the atmosphere (c_a) through the stomata

$$A_{net} = g_s(c_a - c_i)L, \tag{17}$$

the expression linking net C uptake and stomatal conductance is found as

$$A_{net} = \left(\frac{kg_sc_a}{k + g_s} - r\right)L. \tag{18}$$

Through Eqs. (12) and (15), the net C uptake is also linked to leaf area and soil moisture temporal evolution. In well-watered conditions, larger leaf area improves photosynthesis. However, larger leaf area also increases water losses for a given water supply from the soil. As a consequence, larger L decreases ψ_l and therefore may reduce C uptake when soil moisture becomes limiting. Due to these two contrasting effects, the function $A_{net}(L)$ is concave downward, admitting an optimum at intermediate (and moisture-dependent) values of leaf area (Eq. (8); Fig. 1A).

Eqs. (11) and (15) lead to an analytical relation between transpiration and leaf area, for given soil water potential. Combining Eqs. (14), (15), and (18) yields a second relation between net C uptake and leaf area (also for a given ψ_s). Using these relations and imposing the constraints on leaf area dictated by the optimization and hydraulic criteria (Section 2.2), closed-form formulas for leaf area as a function of ψ_s and other environmental and plant parameters are found for the different phenological strategies (Table 3). Specifically, for species maximizing time-integrated net C uptake, leaves are dropped instantaneously or gradually as soon as the soil water potential decreases to the point that $A_{net}(L) = 0$ (Eq. (7); second and third rows in Table 3). Conversely, the maximization of instantaneous A_{net} is imposed through Eq. (8) (fourth row in Table 3). Finally, isohydric species adjust leaf area to maintain $\psi_l = \psi_{l,0}$ (Eq. (15) and last row in Table 3), where $\psi_{l,\,0}$ is defined as the leaf water potential under well-watered conditions.

2.4. Model parameterization and sensitivity analysis

The coupled C-water model was parameterized based on published observations from a cerrado (tropical dry forest) ecosystem, where different degrees of drought-deciduousness occur (parameter values and their sources are reported in Table 1). This parameterization is not intended to give a detailed description of this particular ecosystem, but rather to offer a set of baseline parameters to explore the role of the different phenological strategies in a plausible region of the parameter space. Using these parameter values, predictions are expected to be representative of tropical dry and Mediterranean woodlands and forests with relatively open canopies that can be assumed well-coupled to the atmosphere and not limited by light availability. For the sake of simplicity, we also kept (or implicitly assumed) some environmental parameters as constant (VPD and temperature), although seasonal trends are often observed.

Soil parameters refer to a loam with rooting depth $Z_r = 0.5$ m. Since the rooting depth may vary between deciduous and evergreen species, the role of Z_r is assessed in a sensitivity analysis. The soil-to-root conductance in saturated conditions $g_{sr,sat}$ is modeled based on dimensional analysis as the ratio of the soil hydraulic conductivity and a characteristic distance between root surface and bulk soil [50,55]. The characteristic distance is in turn a function of the ratio of root area index and rooting depth. A higher root area index and shallower roots increase the root surface area per unit soil volume, thus decreasing the root-bulk soil distance. Xylem conductance (g_x) is modeled as the product of sapwood area-specific conductivity (here 0.6 kg m^{-1} s^{-1} MPa^{-1}; [56]) and sapwood area index (SAI), divided by the canopy height (here assumed to be 10 m; [41,55]). Thus, the size of the conductive area (SAI) and the hydraulic path length (height) are both accounted for in the numerical definition of g_x.

Leaf construction costs C_c per unit leaf area are modeled as a linear function of leaf area to be constructed at the end of the dry period, $L_0 - L$, as

$$C_c = \gamma(L_0 - L), \quad \gamma = \frac{\mathrm{LMA}f_C}{Y}, \tag{19}$$

where LMA is the leaf mass to area ratio, f_C is the leaf C fraction ($f_C = 0.4$) and Y is the yield of leaf construction, equivalent to a C use efficiency ($Y = 0.42$, following Givnish [18]).

A range of sensitivity analyses was performed to quantify the interactions between trait values and phenology. Different values of k and r (Eq. (16)) are considered in sensitivity analyses to simulate species with varying leaf nitrogen concentrations [57, 58]. Plant respiration (R_P) is assumed to be constant through time, but it is varied in sensitivity analyses together with k and r, on the grounds that changing plant nitrogen status alters consistently photosynthetic capacity and respiration rates from all organs [57]. We also tested the effect of plant architecture on C gain by altering the sapwood area index (SAI), for a given leaf area index (L) in well-watered conditions. Lower SAI reduces xylem conductance and therefore constraints transpiration; a similar effect would be obtained by altering the xylem hydraulic conductivity or increasing the canopy height. A trade-off between stomatal conductance and water potential at 50% stomatal closure has been noted [59; T. Klein, personal communication]. We tested the role of this trade-off by simultaneously increasing $g_{s,\,max}$ and shifting $\psi_{50,\,s}$ to less negative values (Eq. (12)).

2.5. Soil moisture dynamics and durations of dry periods

We focus on a prototypical moisture regime, encompassing two wet periods, of durations $T_{w,1}$ and $T_{w,2}$, interrupted by a dry period T_d (all symbols used to characterize the moisture regimes are illustrated in Fig. 1B). This simplified representation may capture different climatic conditions: a temperate climate with an episodic summer drought (i.e., the dry period is embedded within an otherwise wet growing season); a Mediterranean climate with the growing season coinciding with the dry season (i.e., the initial wet period within the growing season is shorter than the dry one); or a tropical dry climate if the second wet period does not occur (i.e., the thermal growing season extends to the whole year and encompasses one wet and one dry season).

For simplicity, we assume that the soil remains well-watered for a duration $T_{w,1}$, until the beginning of a dry period of duration T_D. During the dry period, limited rainfall occurrences do not significantly alter the moisture balance, which can then be expressed as,

$$nZ_r \frac{ds}{dt} = -E, \tag{20}$$

where s is the relative volumetric soil moisture (or saturation), n is the soil porosity, Z_r is the mean rooting depth (nZ_r is the soil water storage capacity over the rooting zone), and E is the transpiration rate. Leakage losses and evaporation from the soil surface are neglected. The end of the dry period is characterized by a rapid replenishment of the soil moisture pool, modeled for simplicity as an instantaneous event. Well-watered conditions last for a duration $T_{w,2}$, before the growing season comes to an end (i.e., $T = T_{w,1} + T_d + T_{w,2}$). Soil water potential used in the equations for water transport and gas exchange is converted to volumetric soil moisture through a water retention curve, $\psi_s = \psi_{s,sat} s^{-b}$ [60].

To test the role of hydro-climatic variability on optimal phenological strategies, measured rainfall time series were selected from three locations with contrasting climates (Table 2). For the temperate locations, T_d was identified as the longest period in each growing season with less than 0.3 mm of rain per day on average. For the tropical location, wet and dry seasons were identified using the following procedure. First, the cumulative daily rainfall records in each year were calculated, starting from the beginning of the driest month. Second, the cumulative rainfall was fitted through nonlinear regression using a piece-wise linear function, where the first and second break points represent the beginning and the end of the wet season, respectively. Finally, the obtained set of $T_{w,1}$, T_d, and $T_{w,2}$ values was used to drive the C gain model. Considering several years, a representative ensemble of C gain values for each site was obtained.

3. Results

Solutions for the time trajectories of leaf area and soil moisture for the different phenological strategies are reported first for a dry down of given duration (Section 3.1). Second, we assess which strategy is most suited as the proportion of dry and wet periods during the growing season is altered (Section 3.2). Last, the optimality of phenological strategies is assessed considering observed combinations of wet/dry periods (Section 3.3).

3.1. Gas exchange and leaf area changes across phenological strategies

Fig. 3 shows leaf area changes, transpiration rate, leaf water potential, and instantaneous net C uptake, as a function of soil water potential during an extended dry period, for the different phenological strategies. Perfectly isohydric species have the most conservative phenological strategy, losing leaves at the beginning of the dry period to maintain a stable and relatively high water potential (dot-dashed red curves in Fig. 3A and C). This early loss of leaves

Table 2
Parameter definitions and their baseline values. Data distributions are shown in insets of Fig. 7.

Location	Coordinates	Climate	Mean annual rainfall (mm)	Period of observation	$T_{f,1}$ (DOY)	T (days)	$T_{w,1}$ (mean in days)	T_d (mean in days)	Source	Notes
Durham, NC (USA)	36.05°N; 78.97°W	Warm temperate	1218	1910–2005	92	200	92	25	NOAA (Station ID: 312515)	Second flush possible; $T = T_{w,1} + T_d + T_{w,2}$
Hallettesville, TX (USA)	29.47°N; 95.07°W	Warm temperate	968	1893–2006	92	200	92	39	NOAA (Station ID: 413873)	Second flush possible; $T = T_{w,1} + T_d + T_{w,2}$
Santa Terezinha	7.11°S; 37.45°W	Seasonally-dry tropical	722	1925–2008	0	365	169	196	SUDENE	No second flush; $T = T_{w,1} + T_d$

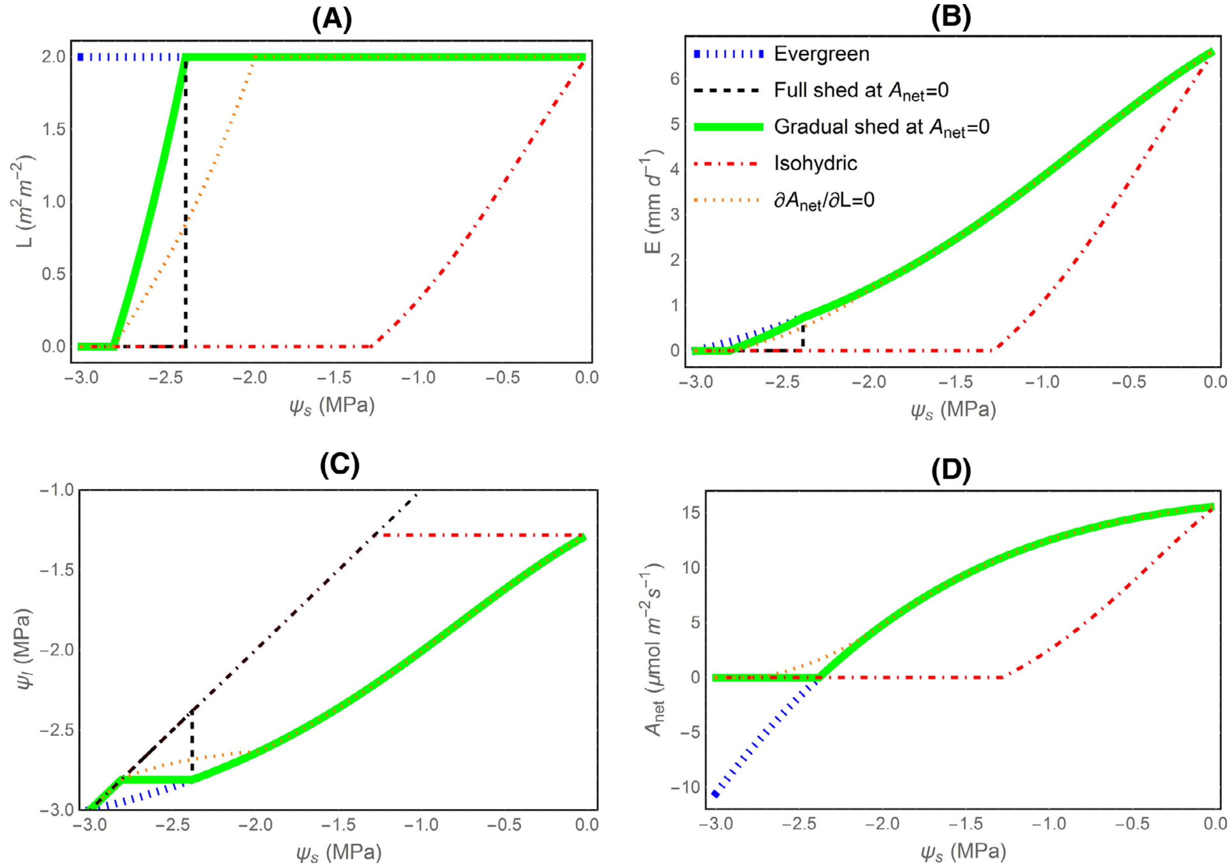

Fig. 3. Predicted changes in (A) leaf area index (L), (B) transpiration (E), (C) leaf water potential (ψ_l), and (D) net C uptake (A_{net}), as a function of soil water potential (ψ_s) for different leaf phenological strategies (line styles as in Fig. 1; the black dot-dashed line in panel C is the 1:1 line). In panel C, the increase in ψ_l for plants shedding leaves rapidly (dashed black line) indicates re-equilibration with ψ_s. Analytical expressions for the relations shown in panel A are reported in Table 3. Solid green and dashed black curves in D overlap. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

corresponds to a faster decline of transpiration and photosynthesis compared to strategies where leaves are retained until $A_{net} = 0$ (Fig. 3B and D). Controlling leaf area to maximize the instantaneous photosynthesis (dotted orange curves) leads to earlier leaf loss compared to imposing $A_{net} = 0$ (solid green and dashed black curves). On one hand, earlier leaf loss reduces transpiration (Fig. 3B); on the other hand, lowered leaf area reduces leaf respiration (for a given basal respiration R_P), thereby preventing the C losses sustained by summer-evergreen species (Fig. 3D). Losing leaves rapidly as soon as instantaneous net photosynthesis drops to zero (dashed black curves in Fig. 3) allows respiratory costs to be avoided during the driest period, similar to the gradual leaf loss strategy, but transpiration is reduced faster. Summer-evergreen species that do not shed their leaves in response to drought maintain their leaf area, thus reducing the leaf water potential more than other strategies (dotted blue curve in Fig. 3C). As a result, transpiration rates are higher and the net C uptake more negative (due to leaf respiration) in dry conditions (Fig. 3B and D).

When the transpiration rate for each strategy is coupled to the soil moisture balance (Eq. (20)), the temporal evolution of soil moisture and the associated gas exchange rates and leaf area are found. For simplicity, changes in VPD or temperature during the dry down (as well as seasonal changes) have been neglected. However, the role of these environmental variations on the relative differences between phenological strategies is limited (not shown). As shown in Fig. 4A–C the time trajectories over the dry period mirror the gas exchange patterns illustrated in Fig. 3. Based on these temporal trajectories, the cumulative C gain is also calculated following Eq. (4) (Fig. 4D). As a result of lower leaf area and C uptake, the cumulative C gain of isohydric species is lower than for other strategies, followed by species that maintain $A_{net} = 0$ and that maximize instantaneous C uptake (Fig. 4D). Evergreen species that continuously exchange leaves (dotted blue curves in Fig. 4) invest C gradually, therefore starting with a less negative C balance at the beginning of the growing season (not shown) and reaching the beginning of the dry season with an advantage over the deciduous species. However, due to this gradual C investment, their C gain increases less through time than in other strategies during wet periods, while during prolonged dry periods the presence of leaves drives the cumulative C gain downwards (Fig. 4D). For winter deciduous species that do not shed their leaves in response to drought, a different time trajectory of G would be obtained, although the cumulative G would be the same for evergreens with continuous exchange of leaves (not shown). Moreover, increasing the initial leaf area (for a given sapwood area) would only increase the rates of water transport and the steepness of the soil moisture dry-down, without altering the relative differences among phenological strategies (not shown). When the net C gain of evergreen species becomes lower than the C gain for a drought-deciduous plant, deciduousness becomes advantageous. In the example shown in Fig. 4, this transition point occurs around a month after the beginning of the dry period.

3.2. Optimal phenological strategy under deterministic conditions

As the proportion of periods in well-watered and dry conditions varies, e.g., along a climatic gradient, phenological strategies are expected to perform differently, because of their different durations of

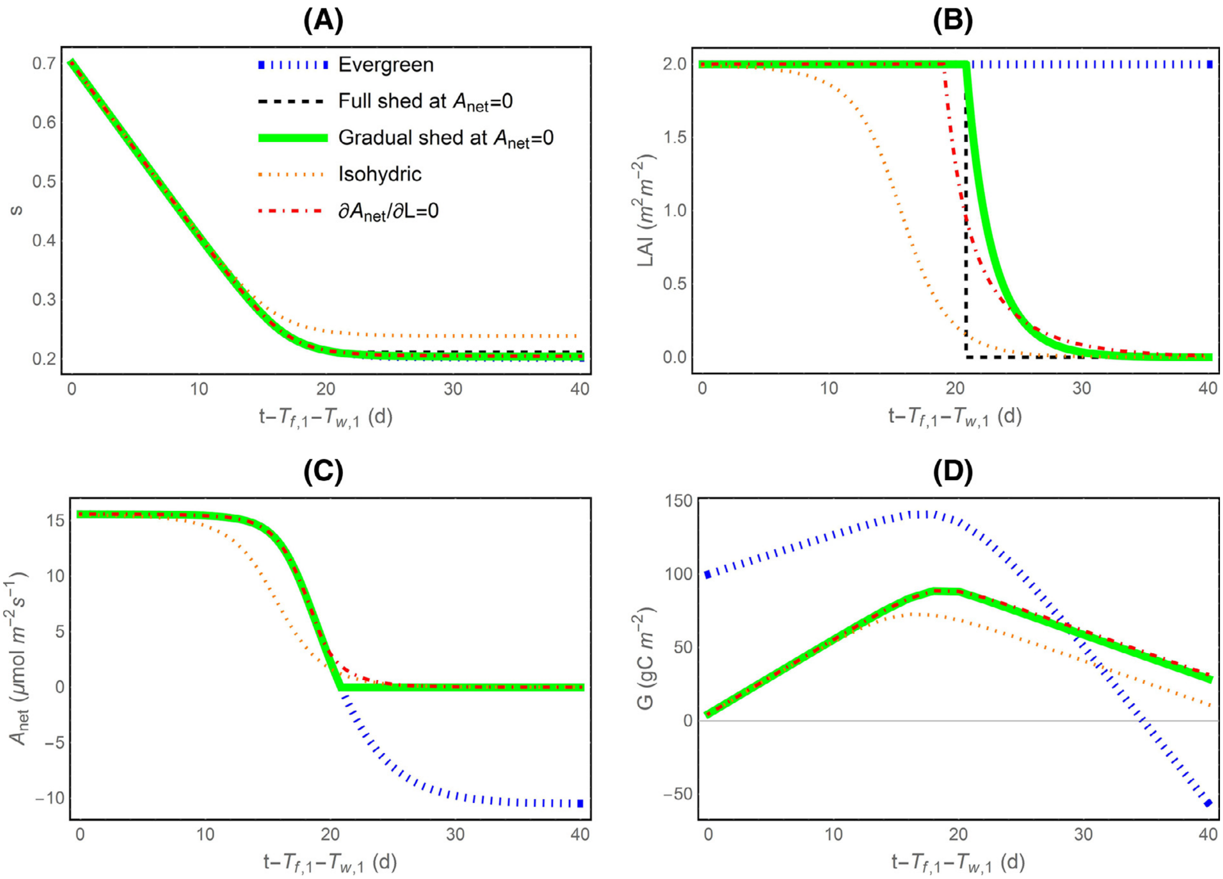

Fig. 4. Predicted changes in (A) soil moisture (s), (B) leaf area index (L), (C) net C uptake (A_{net}), and (D) cumulative C gain (G) as a function of time since the beginning of a dry period ($t - T_{w,1} - T_{f,1}$), for different leaf phenological strategies (line styles as in Fig. 1). The G for all deciduous strategies stabilizes when leaf shedding is initiated, whereas the decrease in G for the evergreen strategy is due to the continuous leaf construction costs. For illustration, a C gain of 100 gC m^{-2} before the dry period (minus leaf flushing costs for deciduous plants) was arbitrarily set for all strategies. Solid green and dashed black curves in C and D are overlapped. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Table 3
Summary of leaf shedding strategies during extended dry periods.

Phenological strategy	Criterion	Condition	Time of initial leaf loss	$L(\psi_s)$ (Fig. 3)
Summer evergreen	Continuous leaf exchange	No leaf loss during drought	No leaf loss	L_0
Rapid leaf loss	Maximize G	$A_{net} = 0$ at T_s	T_s	$L_0\Theta(s_s - s)$[a]
Gradual leaf loss	Maximize G	$A_{net} = 0$ after T_s	T_s	$\frac{g_{s,\max}\left(\frac{c_a}{r}-\frac{1}{k}\right)(\psi_s-2\psi_{50,s})+2\nu\psi_{50,s}}{E_{\max,l}\left[\frac{1}{g_{sr,sat}}\left(\frac{\psi_s}{\psi_{s,sat}}\right)^2+\frac{1}{g_{x,\max}}\right]}$[b]
Isohydric behavior	Maintain stable ψ_l	$\psi_l = \psi_{l,0}$	Continuous adjustment	$\frac{2\nu(\psi_{l,0}-\psi_s)}{E_{max,l}\left(\frac{\psi_{l,0}}{\psi_s}\right)\left[\frac{1}{g_{sr,sat}}\left(\frac{\psi_s}{\psi_{s,sat}}\right)^2+\frac{1}{g_{x,max}}\right]}$
Gradual leaf loss	Maximize A_{net}	$\frac{\partial A_{net}}{\partial L} = 0$	Continuous adjustment	$\frac{g_{s,\max}(2\psi_{50,s}-\psi_s)+2\nu k\psi_{50,s}+\sqrt{\frac{c_a g_{s,\max}k}{r}(2\psi_{50,s}-\psi_s)[(2\psi_{50,s}-\psi_s)g_{s,\max}+2\nu k\psi_{50,s}]}}{E_{\max,l}k\left[\frac{1}{g_{sr,sat}}\left(\frac{\psi_s}{\psi_{s,sat}}\right)^2+\frac{1}{g_{x,\max}}\right]}$

[a] Θ indicates the Heaviside function.

[b] $E_{max,\,l}$ is the leaf-area specific maximum transpiration rate.

C uptake, but also due to the varying C costs associated with flushing leaves vs. maintaining them. Fig. 5 illustrates these effects as the duration of the dry period (T_d) is increased while the duration of the initial wet period ($T_{w,1}$) is maintained constant. Thus, conditions change on the abscissa of Fig. 5 from moist ($T_d \sim 0$, $T_{w,1} + T_{w,2} = T$) to dry climates without a second wet period ($T_{w,2} = 0$, $T_{w,1} + T_d = T$). Two scenarios are considered in Fig. 5: i) new leaves are flushed after the dry period to re-establish the initial leaf area (Fig. 5A) or ii) leaves are not renewed and the plant takes up C with the sole aid of the remaining leaves (Fig. 5B). In other words, the first scenario assumes that plants will have a full canopy during the wet period following the drought event, at the cost of reconstructing the lost leaf biomass. In contrast, the second scenario assumes that in the wet period after the drought plants take up C with the remaining leaves, and the plant will replenish the canopy only in the following growing season.

As the dry period lengthens, the C gain decreases for all phenological strategies, as expected. The rate of decrease, however, differs among strategies. When considering species that undergo a second leaf flush, leaf loss is limited as long as T_d is short (except for isohydric species, dot-dashed red curve in Fig. 5A), so that costs for re-establishing a full canopy upon rewetting are also small. As T_d lengthens, a larger fraction of leaf area needs to be produced upon rewetting, increasing C costs and decreasing G. This effect is evident in the abrupt steepening of the decline of the G vs. T_d relation at

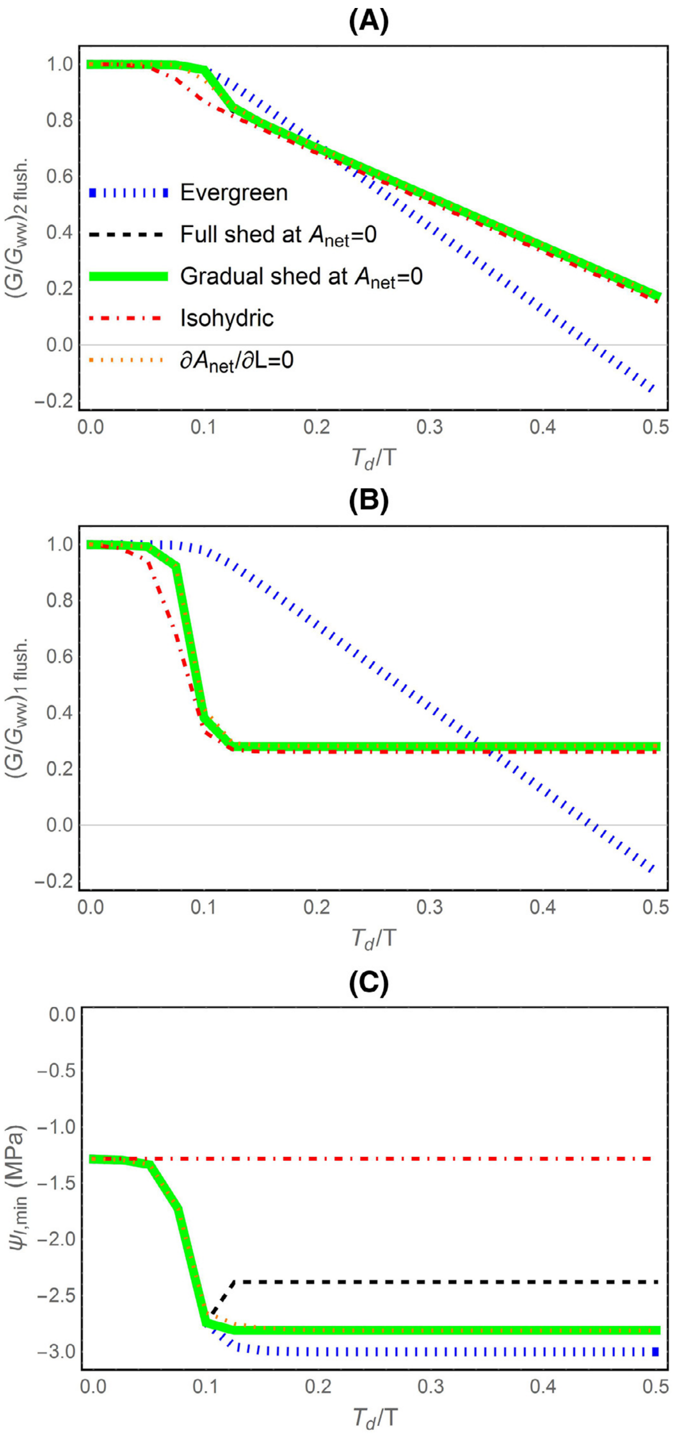

Fig. 5. Effect of dry period length (T_d) on the growing-season C gain (G) for different phenologies and two leaf flushing strategies: (A) a second flushing occurs at the end of the dry period for all deciduous species; (B) no second flushing occurs (when curves in A have higher values than in B, a second flush is advantageous). (C) Minimum leaf water potential at the end of the dry season ($\psi_{l,\,min}$) for the different phenological strategies. Line styles are as in Fig. 1. In all panels $T_{w,1} = 100$ days and $T = 200$ days, and T_d is varied from 0 to 100 days. Dry period duration is normalized to the length of the growing season (T) and total gain is normalized to the gain under constantly well-watered conditions, denoted by $G_{WW} = G(T_d = 0)$. Solid green and dashed black curves in A and B are overlapped. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$T_d \sim 0.1 \times T$. Eventually, the dry period becomes too long for a positive C balance to be achieved. Evergreen species, by exchanging leaves gradually, show a gradual steepening towards longer T_d, as the cost of maintaining leaves becomes increasingly important.

Patterns in G are slightly different when leaves are not flushed a second time after the dry period, except for evergreen species (Fig. 5B). In all deciduous strategies the C gain drops more rapidly at T_d around $0.1 \times T$ than in Fig. 5A, because the second wet period cannot be exploited due to leaf loss. However, as T_d lengthens ($T_d \sim 0.4 \times T$), not flushing leaves a second time becomes advantageous, as the C gains during the second wet period would not compensate for the C investment in new leaves (compare Fig. 5A and B). A further aspect to be considered is the minimum leaf water potential, which may indicate the occurrence of hydraulic damage. Minimum leaf water potential is unaffected by the occurrence of a second flush, but depends markedly on phenological strategy. Except for the isohydric strategy, the leaf water potential at the end of the dry period ($\psi_{l,\,min}$ in Fig. 5C) decreases as T_d lengthens. The lowest $\psi_{l,\,min}$ is achieved when maintaining leaves during the dry period, followed by strategies that maximize photosynthesis in the short term.

3.3. *Interactions between phenological strategy and plant traits*

Figs. 1–5 show results for baseline parameters representing a specific set of plant traits. However, plant traits may vary across species and due to plastic responses to environmental conditions. Fig. 6 explores the effects of changes in four key traits on the C gain-drought duration relations: i) increase in rooting depth (Z_r, but not accounting for costs associated to such an increase); ii) increase in leaf and plant nitrogen (or temperature), as mirrored by a simultaneous increase in carboxylation efficiency (k), leaf respiration (r), and plant respiration (R_P); iii) decrease in sapwood area (SAI) for a given L_0; and iv) simultaneous increase in stomatal conductance under well-watered conditions and stomatal sensitivity to declining ψ_l.

Increasing rooting depth improves water storage, thereby lengthening the interval of plant activity during a dry period. As a consequence, deeper roots improve the growing season C gain and delay the decline in leaf water potential (Fig. 6, left column). The improvement is largest at intermediate dry period durations, while it decreases at high T_d, except for evergreen species. Higher leaf and plant nitrogen concentrations may increase photosynthetic capacity and respiration rates, with feedbacks on the C balance and G. Higher plant nitrogen improves G by increasing photosynthesis more than respiration, but the effect is most evident for short dry periods (Fig. 6, second column from the left). If temperature rather than leaf N were increased, respiration would grow faster than photosynthesis and C gains would be reduced relatively to the baseline conditions. The third column of Fig. 6 shows that decreasing sapwood area decreases C gain throughout the range of dry season durations T_d (except at intermediate T_d for a single flush). Lower SAI increases water stress by lowering xylem conductance and thus leaf water potential (Eq. (15)); this effect causes water stress to start at less negative soil water potential and thus gas exchange to be reduced. Finally, the rightmost column of Fig. 6 illustrates the role of the trade-off between maximum stomatal conductance and leaf water potential at 50% stomatal closure. Species allowing large transpiration in well-watered conditions, while reducing stomatal conductance at a less negative water potential, achieve lower G than under the baseline scenario, except at intermediate T_d for a single flush. Note that the leaf water potential maintained by isohydric species ($\psi_{l,\,0}$) varies in the two right columns of Fig. 6. This change occurs because $\psi_{l,\,0}$ equals the water potential in well-watered conditions, which in turn depends on both SAI and the parameters of the stomatal response function.

The main patterns in Fig. 6 are consistent between plants flushing leaves only once (top panels) and flushing also after the dry period (bottom), except for intermediate dry season durations, at which reducing SAI or increasing $g_{s,\,max}$ can be advantageous only with a single

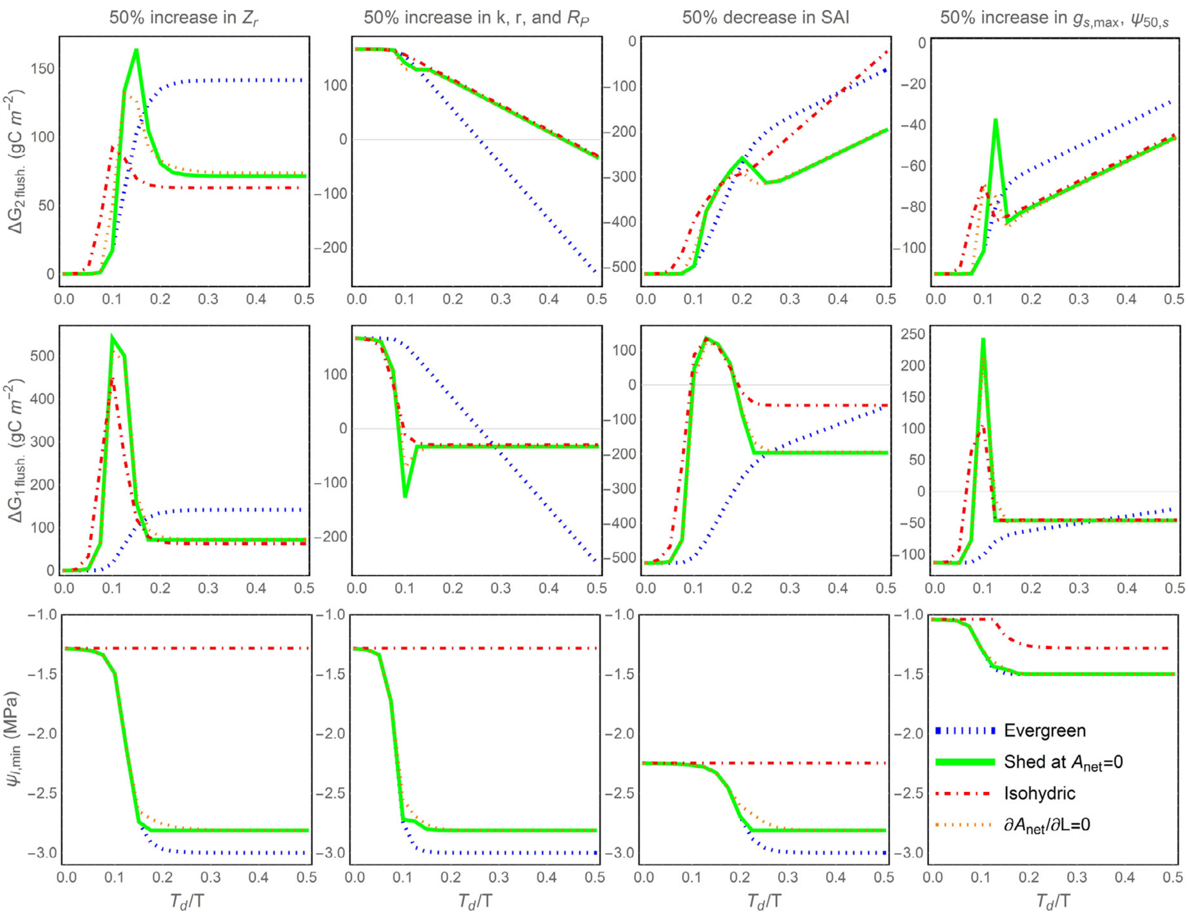

Fig. 6. Role of different trait values on cumulative C gain (G, top and middle panels) and minimum leaf water potential ($\psi_{l,\,min}$, bottom panels) during dry periods of increasing duration (T_d), for different phenological strategies ($T_{w,1} = 100$ days and $T = 200$ days) and two leaf flushing strategies (top panels: second leaf flushing after the dry period; middle: no flushing until the following growing season). Line styles are as in Fig. 1. C gains are expressed as differences compared to the baseline shown in Fig. 5 (the scale on the ordinate varies). First column: baseline rooting depth (Z_r) is increased by 50%; second column: baseline carboxylation efficiency (k), leaf respiration (r), and plant respiration (R_P) are increased by 50%; third column: baseline sapwood area index (SAI) is decreased by 50% (i.e., xylem conductivity is decreased); fourth column: baseline maximum stomatal conductance ($g_{s,\,max}$) and leaf water potential at 50% stomatal closure ($\psi_{50,\,s}$) are increased by 50%.

leaf flush at intermediate T_d. The responses of different phenological strategies are also similar, with the exception of non-leaf shedding plants, which improve their C gain more than the deciduous ones in drier conditions when Z_r is increased or loose less C in drier climates when SAI is decreased and g_s increased.

3.4. Optimal phenological strategy under unpredictable conditions

Random variations in wet and dry season lengths affect the distribution of possible C gains G (Fig. 7). In temperate climates (Fig. 7A and B), with relatively short, occasional summer droughts the performance of summer-evergreen and drought-deciduous species is comparable (Fig. 7A and B). Nevertheless, phenological strategies affect the mode of the gains distribution in temperate climates, with lower values of C gain for isohydric species. Under the wetter climate of Durham (NC, USA), productivity is larger than under the comparatively drier climate of Hallettesville (TX, USA) and summer-evergreen species have a higher C gain mode. In contrast, in the seasonally-dry tropical climate of Santa Terezinha (North Eastern Brazil), evergreen species do not have a competitive advantage and the different drought deciduous strategies are roughly equivalent (Fig. 7C). Carbon gains of summer-deciduous and evergreen strategies are compared in Fig. 8 for the two temperate climates (corresponding to Fig. 7A and B). In the most productive years (shorter dry periods), the two groups achieve similar values of G, because leaf shedding is limited and all other traits are the same. In the driest years, summer deciduous strategies are clearly advantaged, whereas in years with dry periods of intermediate duration keeping leaves improves G.

4. Discussion

Drought deciduous species populate forests of both seasonally-dry [22,23] and more mesic climates [27,29,61], suggesting that shedding leaves could be an optimal strategy to cope with prolonged dry periods [18,31]. Employing optimality criteria for the degree of leaf loss and its timing could be useful to improve currently available phenological models, which tend to be less accurate in seasonally-dry areas, where moisture variability and plant hydraulic strategies create complex phenological patterns [62]. In addition, it could help to improve global climate change predictions, because leaf phenology feeds back onto the atmosphere and surface water by changing albedo and transpiration. For example, large scale reductions in leaf area (as experienced in South America during dry seasons [61]) may alter the regional energy balance and ultimately precipitation patterns. Here we synthetized current hypotheses on leaf phenology during drought (four drought-deciduous strategies, Fig. 1) within a common framework and assess which one is optimal with respect to the growing season C gain.

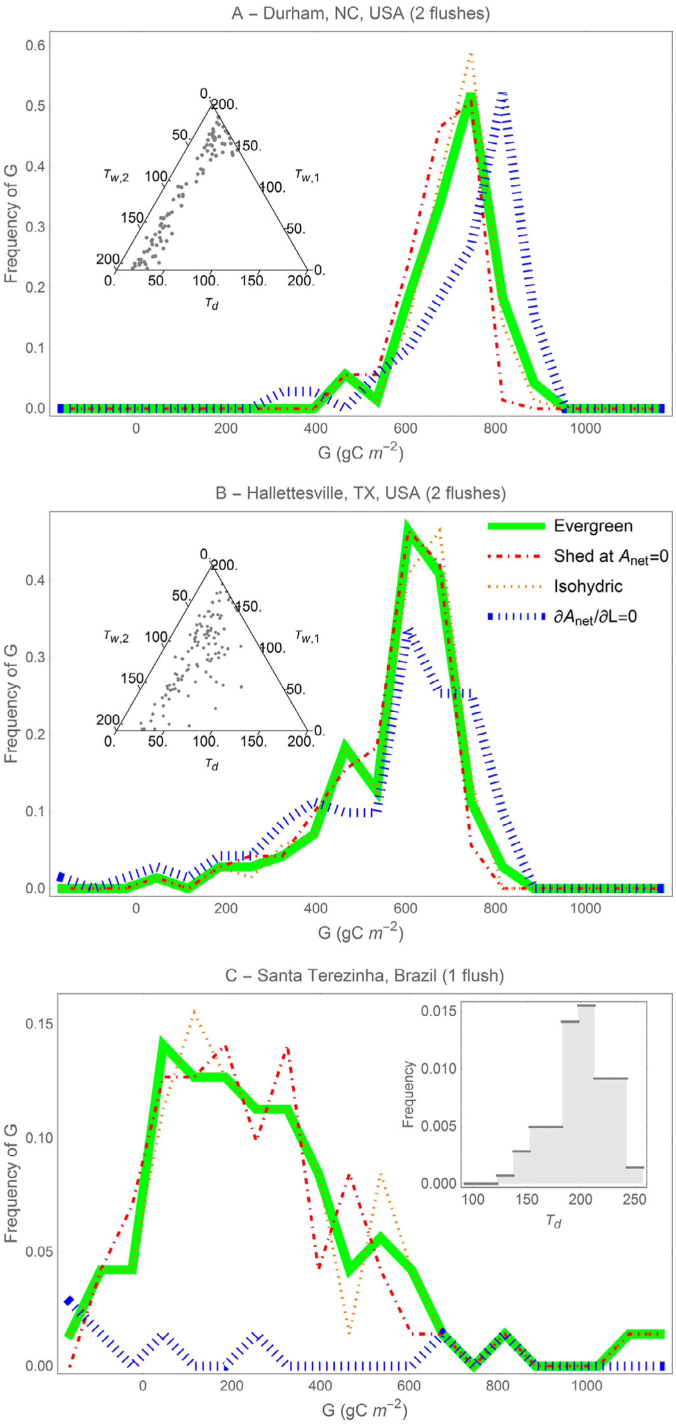

Fig. 7. Frequency plots of growing-season C gain (G) for the different phenological strategies under two temperate climates with summer droughts (A, B) and a seasonally dry tropical climate (C). Line styles are as in Fig. 1. Since under tropical climate temperature is not limiting, results are presented only for plants flushing leaves once. Insets in A and B are ternary plots of the combinations of $T_{w,1}$, T_d, and $T_{w,2}$ obtained from the rainfall time series (Table 2; note that $T_{w,1} + T_d + T_{w,2} = T$); the inset in C is the frequency histogram of T_d (for the tropical site, $T_{w,1} + T_d = T$). In C, evergreen species are predicted to often have a negative C balance (out of plotted range).

4.1. Criteria for drought-induced leaf shed

Previous studies argued that plants need to optimize the average C gain over their whole lifespan, which is equal to maximizing the leaf marginal C gain (gain per unit time). In this case, the plant is assumed to be at steady state and to continuously change its leaves [17,32,33]. Each leaf is thus shed as soon as it marginal C gain reaches its maximum. This approach has been criticized because it implicitly assumes that leaf resources (structural carbohydrates) can be reallocated to younger leaves with a higher marginal C gain, even though that does not seem to occur [18]. To circumvent these limitations, an alternative approach is proposed here, with leaf shedding criteria based on the hypothesis that plant maximizes C gain. Specifically, two criteria are considered: the net C uptake during a dry period is maximized (Eq. (7)) or the instantaneous photosynthesis is maximized (Eq. (8)). These approaches have the further advantage of being more suitable in the highly unsteady conditions imposed by a soil drying and wetting.

The temporal trajectories of gas exchange rates we found are partly different from results based on models optimizing stomatal conductance rather than leaf area during dry periods [40,54,63,64]. In fact, here we prescribe how canopy-level stomata conductance changes as leaf water potential declines (Eq. (12)), so that the instantaneous relation between gas exchange rates and soil moisture is prescribed through the C and water balance equations, whereas changes induced by plastic leaf area emerge from the optimization assumptions. Our results indicate that optimal leaf loss should initiate around a soil water potential of −2 MPa (Fig. 3A). By then, stomatal closure is already well under way (Fig. 3B), suggesting that optimal leaf loss is a later and more drastic measure of water loss regulation than stomatal closure. Based on the hypothesis that plants maximize their fitness, and considering that stomatal closure may interact with leaf loss, it could be argued that stomatal conductance and leaf area should be optimized simultaneously, whereas here we set stomatal response to ψ_l and employed leaf area as the only control parameter.

Two factors make this coupled stomatal-leaf area optimization complex to implement: on the one hand, leaf area and stomatal conductance act in a multiplicative way in the transpiration rate (Eq. (11)), and are weakly decoupled in the photosynthetic rate (Eq. (18)), so that changing either of them allows reaching comparable gas exchange rates. On the other hand, optimizing leaf area requires a longer time perspective than the single dry period, because the occurrence of a second flush needs to be considered and makes a large difference in the obtained C gain values (Figs. 5 and 6). Therefore, the optimization of stomatal conductance during episodic dry periods (for given leaf area) [40] and the optimization of leaf area over the growing-season (for given stomatal behavior) can be seen as the end members of a continuum of optimization approaches at partly overlapping time scales.

We also considered isohydric behavior as a criterion for leaf shedding. Typically, isohydric behavior is identified with stomatal regulation rather than leaf area regulation, but when considering prolonged dry periods, changes in transpiring area can be as or more important to maintain a stable leaf water status than stomatal closure [13]. This criterion is only based on the canopy hydraulic balance, and thus is not related to the C uptake maximization hypothesis employed in the other leaf shedding strategies. However, maintaining stable leaf water can be advantageous to prevent hydraulic damage and metabolic inhibition due to low leaf water potential, at the expense of lowered C gain [65,66]. Therefore, isohydric behavior could be considered an optimal strategy in terms of damage risk minimization, but not C gain maximization. Nevertheless, preventing hydraulic failure can reduce the cost of repairing or re-growing damaged tissues. Leaf water potential has been employed as a constraint in plant hydraulic models at ontogenetic time scales [41,44,46]. At such scales, drier conditions require lower leaf-to-sapwood area ratios – a conceptually similar result to the one presented here at the dry-down scale.

Comparing different models implementing drought-deciduous leaf habit, a marked difference emerges between those developed to address ecological questions and those implemented in global dynamic vegetation models. The former often employ optimization criteria [17–19], whereas the latter link leaf shed to soil moisture availability [34,36], or a combination of declining

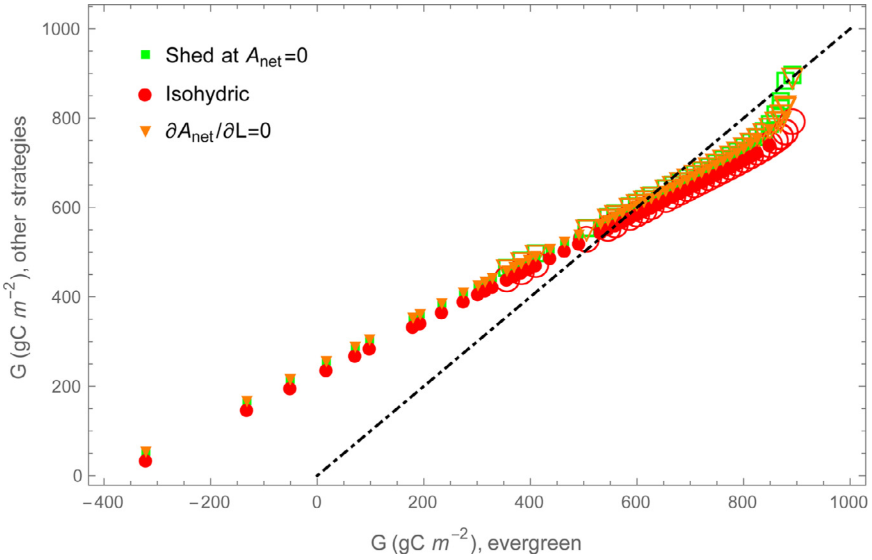

Fig. 8. Scatterplot of growing-season C gain (G) achieved by summer-deciduous species as a function of C gain by evergreen species, under two temperate climates with summer droughts (open symbols, Durham, NC; solid symbols, Hallettesville, TX). Line styles are as in Fig. 1; the black dot-dashed line represents equal G values for evergreen and deciduous strategies.

soil moisture and C gain [35]. The proposed optimization (or hydraulic) criteria could offer an alternative to the current empirical approaches to describe drought-induced leaf loss in dynamic vegetation models. Thanks to their simplicity and reliance on environmental and eco-physiological parameters that are typically employed in such models, their implementation should be feasible without major structural modifications, while also providing tighter links to ecological theories. Moreover, adopting the proposed criteria in more detailed models that also account for trends in VPD and temperature during the dry season could shed more light on the possible interactions between environmental conditions and C gains, which we have not explored here.

4.2. Comparing phenological strategies at the growing season time scale

The different phenological strategies lead to a range of growing season C gains. We argue that the strategy maximizing this C gain is evolutionarily advantageous. However, our results hold for homogeneous vegetation, where all individuals share the same functional traits. Therefore, when contrasting phenological strategies and C gains, we are actually comparing different stands that do not interact with each other. Direct inter- and intra-specific competition could lead to dynamically adapting traits in the long term [67]. Over shorter time scales (weeks to months), competition for the same moisture pool triggers higher transpiration rates to exploit the available water faster than competitors [40]. Therefore, while maximization of C gain alone gives an indication of the viable water use strategies, it does not guarantee that a strategy is evolutionarily stable.

With this caveat in mind, our results suggest that evergreen and non-leaf shedding winter deciduous species are advantaged when the duration of the dry period is moderate, whereas drought-deciduous species may out-compete them in drier conditions (Figs. 5 and 7). This pattern is due to increasing leaf maintenance costs in evergreen species when C uptake is water-limited, as also noted in previous studies [18,21]. In line with these results, in the mixed temperate forest of Durham, NC, species that adjust their leaf area during drought are fewer than summer-evergreen ones [27], whereas the *caatinga* woodland in the seasonally dry tropical site is dominated by drought-deciduous species [68]. As dry periods lengthen, evergreen species can still be competitive, but they require deeper roots to access comparatively larger water stores (Fig. 6), consistent with observations [30]. Root depth depends also on the bedrock and genotypic differences between species [69,70]. Deep root systems are especially advantageous in dry or seasonally-dry ecosystems; e.g., deep roots sustain plant activity in half of the forests in Brazilian Amazonia during the dry season [71]. Growing deep roots, however, also carries an additional cost that was not accounted for here – including such a cost would result in an optimal rooting depth that depends on climatic conditions [72]. Until the plants can tap these deep water reserves, C has to be allocated to the root system, which in turn is dependent on the efficiency of the canopy to assimilate C, especially when droughts occur regularly every year. Thus, well adapted species with an optimized C gain strategy will reach deep water reserves more quickly. As a positive feedback, these species will be able to reduce leaf shed and maintain C gain during dry periods.

Among the drought-deciduous species, differences in C gains were not as large as between evergreen and deciduous habits. Nevertheless, isohydric behavior yields lower C gains compared to other strategies when the dry period duration is short (Fig. 5), because maintaining the leaf water status (i.e., high leaf water potential, see bottom panels in Figs. 5 and 6) significantly impairs photosynthesis [4,66]. Other summer-deciduous strategies and the evergreen strategy in particular imply more negative leaf water potentials, which may expose the plants to greater risks of hydraulic failure. In the current model, however, we assumed that stomatal conductance and reduction of xylem conductivity are coordinated (as typically the case [49,59]), so that stomatal closure in association to leaf area reduction prevents catastrophic cavitation. Moreover, complete stomatal closure is assumed at $\psi_l = 2\psi_{50,s}$ (Eq. (12)) – a threshold effectively setting the lower leaf water potential that the model can predict. Therefore, with the current model setup, it is not possible to predict xylem hydraulic failure, as it might occur in anisohydric species during prolonged drought.

Differences in C gain also arise when comparing species that flush leaves once or twice (Fig. 5). Flushing leaves after a dry period can be advantageous only if the subsequent favorable period is sufficiently long to pay back the leaf construction costs. The second flush might also be incomplete, indicating an acclimation response to the conditions after the dry period – this possibility was not explored, but would lead to C gains intermediate between the values obtained from plants flushing once and twice.

Increased photosynthetic capacity (k) improves growing season C gains, even if respiration also increases (Fig. 6), although longer dry periods reduce the relative advantage of increased k. These results suggest that increasing leaf N concentrations is a viable strategy of acclimation to increased water stress [73,74], but only when the duration of the dry period is short and thus the negative effects of increased respiration are not strong. It is also possible that during multi-year droughts soil water recharge during relatively wet periods is too limited to actually support a full flush. This case has not been considered here (we assumed well-watered conditions except during the period T_d), but requires a suite of further acclimation strategies, such as reduced size of the new leaves, increased LMA, and self-pruning.

Overall, the predicted distribution of evergreen vs. drought-deciduous habits is consistent with observed patterns. Moreover, the productivity values obtained are qualitatively in line with empirical estimates and trends along rainfall gradients [75], lending support to our approach, despite its simplicity. More accurate predictions could be achieved by calibrating the parameters describing plant biochemical and hydraulic traits. In this study we deliberately kept these parameters constant across climates in order to isolate the role of phenological strategies on growing season C gain. Furthermore, implementing these strategies into detailed ecohydrologic models in which daily and seasonal variations of rainfall and atmospheric drivers can be accounted for [e.g., 76] could allow a more rigorous test of long-term optimality, albeit at the expense of higher computational demand.

5. Conclusions

We identified and compared different drought-induced leaf shedding strategies, employing a coupled hydraulic and plant C balance model. Leaf shed strategies are mathematically encoded in a range of optimization and hydraulic criteria (Fig. 1), including drought-deciduous leaf habit based on the maximization of long-term gross C uptake, the maximization of instantaneous photosynthetic rate, or isohydric behavior. Summer-evergreen habit is employed as a reference. Our results indicate that drought-deciduousness is increasingly advantageous as the duration of the dry period lengthens. Only through deep roots can summer-evergreen species reach comparable productivity as drought-deciduous ones in dry climates. Moreover, higher photosynthetic capacity (at the expense of correspondingly higher leaf and plant respiration rates) can be a successful acclimation strategy when dry periods are relatively short, so that the contribution of leaf respiration is still relatively low. Anisohydric species are shown to be superior to hydraulically-safe isohydric species in terms of growing season C gains, but we did not take into account the risk of hydraulic failure and therefore the advantage of anisohydric species could be overestimated.

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