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Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems

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ABSTRACT

Large areas in the tropics and at mid-latitudes experience pronounced seasonality and inter-annual variability in rainfall and hence water availability. Despite the importance of these seasonally dry ecosystems (SDEs) for the global carbon cycling and in providing ecosystem services, a unifying ecohydrological framework to interpret the effects of climatic variability on SDEs is still lacking. A synthesis of existing data about plant functional adaptations in SDEs, covering some 400 species, shows that leaf phenological variations, rather than physiological traits, provide the dominant control on plant-water-carbon interactions. Motivated by this result, the combined implications of leaf phenology and climatic variability on plant water use strategies are here explored with a minimalist model of the coupled soil water and plant carbon balances. The analyses are extended to five locations with different hydroclimatic forcing, spanning seasonally dry tropical climates (without temperature seasonality) and Mediterranean climates (exhibiting out of phase seasonal patterns of rainfall and temperature). The most beneficial leaf phenology in terms of carbon uptake depends on the climatic regime: evergreen species are favoured by short dry seasons or access to persistent water stores, whereas high inter-annual variability of rainy season duration favours the coexistence of multiple drought-deciduous phenological strategies. We conclude that drought-deciduousness may provide a competitive advantage in face of predicted declines in rainfall totals, while reduced seasonality and access to deep water stores may favour evergreen species. This article has been contributed to by US Government employees and their work is in the public domain in the USA.

KEY WORDS seasonally dry ecosystem; Mediterranean climate; savanna; tropical dry forest; water stress; rainfall variability; soil moisture; carbon balance

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INTRODUCTION

Vast areas in the tropics and mid-latitudes experience seasonally dry climates (Figure 1 top). These climates are characterized by a marked seasonality in rainfall occurrence, with one or two wet seasons, during which most of the annual precipitation occurs, followed by extended dry

periods. Rainfall in these seasonally dry ecosystems (SDEs) is typified by large inter-annual variation in precipitation timing and amount (Rao *et al.*, 1993; Joffre *et al.*, 1999; Fatichi *et al.*, 2012; Feng *et al.*, 2013), which is likely to be exacerbated by climate change (Solomon *et al.*, 2007; Garcia-Ruiz *et al.*, 2011; Dominguez *et al.*, 2012). Despite these commonalities, seasonally dry climates – including Mediterranean climates, tropical monsoon climates, and tropical savannas with dry summers or winters – have rarely been considered as a group. This may be because the meteorological drivers of these

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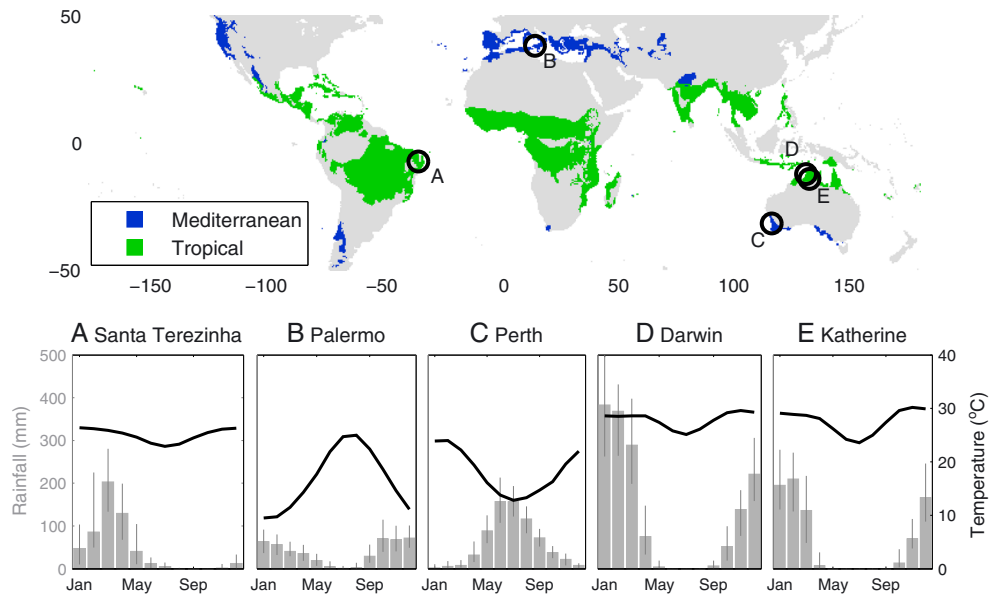


Figure 1. Top: Global distribution of seasonally dry climates: Mediterranean ecosystems correspond to warm temperate climates with dry summer (*Cs* in Köppen-Geiger classification; see Kottek *et al.*, 2006); tropical seasonally dry ecosystems include Equatorial monsoon and Equatorial savannas with dry summer or winter (*Am*, *Aw*, and *As* in the Köppen-Geiger classification). Bottom: seasonal patterns of median monthly rainfall (bars; whiskers indicate 25 and 75 percentiles) and mean monthly air temperature (lines) in the five selected sites (identified with symbols on the map; main features summarized in Table I). Data sources: monthly rainfall data from Osservatorio Astronomico di Palermo Giuseppe S. Vaiana, Australian Government Bureau of Meteorology, and SUDENE; monthly average temperature data after Legates and Willmott (1989).

climates differ or because of differences in the timing of the wet season – variable in tropical regions, but always occurring during the winter in Mediterranean climates (Figure 1, bottom). The implications of large swings between periods of high water availability and extreme water deficit, however, suggest that seasonally dry climates should be treated as a group for ecohydrological studies.

In tropical SDEs, the natural vegetation ranges from closed-canopy forests (e.g. *caatinga*, *cerrado* and *chaco* in South and Central America, and bushland thickets in Africa), to open forests (e.g. *campo cerrado* and *campo sujo* in South America; *forêt claire* and *miombo* in Africa), to savannas (e.g. *campo limpo* in South America; Menaut *et al.* (1995); Sampaio (1995); Blasco *et al.* (2000); Lock (2006)). Mediterranean vegetation is often characterized by shrubland (e.g. *maquis* in Europe, *chaparral* and oak savannas in California, *matorral* in Chile), while open eucalyptus woodland is common in Australia (Cody and Mooney, 1978). These varied ecosystem types support crucial biodiversity hotspots (Miles *et al.*, 2006; Klausmeyer and Shaw, 2009) and help sustain local populations by providing food, fibre, and other essential ecosystem services. Nevertheless, the highly variable rainfall in SDEs impacts the reliability of these services (Ellis and Galvin, 1994; Maass *et al.*, 2005). At the same time, SDEs are subject to multiple anthropogenic threats, including soil erosion, deforestation, and increased exploitation of water resources for agricultural and urban use (Miles *et al.*, 2006; Underwood *et al.*, 2009).

Most SDEs experience periods of high water availability during the wet season, eliciting bursts of ecosystem productivity. The subsequent transition to a dry period of unpredictable length, almost always coupled with high temperatures and high vapour pressure deficits (VPD), creates the potential for significant stress and physiological damage to vegetation. These stresses include reduced photosynthesis due to low leaf water potential, stomatal closure, and metabolic limitations (Xu and Baldocchi, 2003; Galmes *et al.*, 2007; Vico and Porporato, 2008; Lawlor and Tezara, 2009; Peguero-Pina *et al.*, 2009); impairment of water transport in xylem due to cavitation (e.g. Tyree and Ewers, 1991); increased respiratory demand due to higher tissue temperatures (Farquhar and Sharkey, 1982); increased susceptibility to herbivores and diseases (McDowell *et al.*, 2011), and risk of tissue damage and mortality (Adams *et al.*, 2009; Allen *et al.*, 2010).

The pronounced seasonal and inter-annual climatic variation in SDEs has produced a bewildering diversity of physiological and phenological strategies in vegetation to cope with the dramatic changes in water availability (Murphy and Lugo, 1986; Bowman and Prior, 2005; Lock, 2006; Lehmann *et al.*, 2009). Plants either try to (i) avoid these stresses by limiting plant physiological activity during dry periods (for example, drought-deciduous species shed their leaves); or (ii) to endure droughts without experiencing stress by developing physiological adaptations that maximize water storage and photosynthetic activity, minimize water loss, and maintain sufficient carbon (C) stores to allow plant survival

during the dry season (e.g. evergreen species; see Eamus and Prior, 2001). Among drought-deciduous species, two strategies determine the timing at which new leaves are grown (leaf flushing). In ‘opportunistic species’, leaf flushing occurs as water becomes available, while in ‘scheduled species’, leaf flushing occurs in response to photoperiod or temperature. Within each of these strategies, plant behaviour can be further categorized as conservative or aggressive based on the time of flushing with respect to rainfall. Conservative plants avoid water stress by flushing leaves late in the wet season (or by dropping them early), which may however result in lost opportunities for C fixation and growth. By flushing leaves before the wet season or after episodic rain events, aggressive plants may keep leaves longer, but may risk undergoing water stress if drought follows the leaf flush. In comparison to deciduous species, drought endurers such as evergreen species may transpire for longer periods of time but must rely on water and C stored from the wet season; in some cases, these supplies may be insufficient to sustain plant water use and respiration over the dry season (Gartner *et al.*, 1990). Therefore, given the unpredictability of rainfall, each strategy poses its own set of risks to plants (Hoffman and Walker, 1980; Machado *et al.*, 1997; Jolly and Running, 2004; Singh and Kushwaha, 2005a; Hasselquist *et al.*, 2010; Valdez-Hernandez *et al.*, 2010; Markesteijn *et al.*, 2011; Pringle *et al.*, 2011). The presence of inherent risks and ecophysiological tradeoffs in each of these strategies makes the outcome of species competition and selection difficult to predict. This lack of clear advantages of one strategy over the others likely favours coexistence and nuanced variations in the predominant ecohydrological behaviour across climates.

The aim of this study is to provide insight into the relationship between rainfall regimes (including its inter-annual variability) and the most effective plant strategies, with a focus on perennial woody vegetation. We expect the leaf phenology and the functional traits associated with water availability to be the primary driver of plant adaptive strategies in SDEs. While a complete understanding of the species and strategy diversity of SDEs requires consideration of evolutionary constraints, ecological dynamics, disturbance, and succession regimes, here we focus on annual net C gain as a proxy of plant fitness. On this basis, a theoretical framework is proposed for analysis of the C and water balances at the plant level to assess the benefits of adaptation strategies in a variety of SDEs.

To provide realistic climatic scenarios for the theoretical analyses, we selected long climatic time series from five locations to represent the diversity of SDEs, in terms of both climate and the most common plant strategy (Table I, Figure 1). In Section on Precipitation Forcing, the rainfall patterns and their variability in three of these locations are analysed. Section on Vegetation Adaptation Strategies reviews physiological and phenological traits of woody vegetation in SDEs. The findings of this synthesis are used

Table I. Summary of the case study sites (Figure 1).

Location	Climate	Seasonality	Mean annual rainfall (mm) (period of observation)	Vegetation
Palermo, Southern Italy (38.11°N, 13.22°E)	Dry Mediterranean	Moderate/predictable	549 (1797–1999)	Evergreen sclerophyllous woodland/forest
Perth, South-Western Australia (31.93°S, 115.98°E)	Moist Mediterranean	Moderate/predictable	771 (1944–2011)	Evergreen sclerophyllous woodland/forest
Katherine, Northern Australia (14.46°S, 132.26°E)	Moist monsoonal	Strong/predictable	945 (1890–1996)	Evergreen overstorey; scarce drought-deciduous understorey
Darwin, Northern Australia (12.42°S, 130.89°E)	Moist monsoonal	Strong/predictable	1722 (1941–2011)	Evergreen overstorey; drought-deciduous understorey
Santa Terezinha, North-Eastern Brazil (7.11°S, 37.45°W)	Tropical dry	Strong/unpredictable	722 (1925–2008)	Drought-deciduous (<i>caatinga</i>)

The ‘strength’ of seasonality refers to the magnitude of the difference in mean rainfall between the wet season and the dry season, the ‘predictability’ to the degree of inter-annual variability in rainfall amounts and timing of the wet season (see also Section on Precipitation Forcing).

to guide the parameterization of a minimalist water and C economy model (Section on Modelling Framework). The results of the analyses are discussed in Section on Quantitative Assessment of Phenological Strategies with reference to observations. Additional disturbances as drivers of phenological strategy are briefly discussed in Sections on Non-Ecohydrological Drivers of Leaf Phenology.

PRECIPITATION FORCING

Seasonally dry climates (Figure 1) share a strong seasonality and a high degree of inter-annual variability in rainfall, even though they are outcomes of very different physical drivers of the global climate – for instance, the movement of the inter-tropical convergence zone or the dynamics of the West African, Asian-Australian, and North American monsoons. To illustrate commonalities and differences across seasonally dry climates, we analysed the rainfall regime of three representative locations: Santa Terezinha (tropical dry climate), Katherine (moist, tropical monsoon climate) and Palermo (Mediterranean climate; Table I).

Figure 1 (bottom) illustrates the seasonality and inter-annual variability in monthly rainfall and temperature, while examples of intra-annual variability in rainfall are reported in Figure 2A–C. Synoptic and planetary patterns modulate rainfall variability across a wider range of temporal scales, spanning from few months to decades. The scale-by-scale contributions can be resolved through the use of signal filtering techniques such as the continuous wavelet transform. This spectral technique decomposes the total variability of a signal (e.g. daily rainfall) in terms of both time and characteristic scale of the fluctuations (Torrence and Compo, 1998; Molini *et al.*, 2010). Figure 2D–F shows the average wavelet spectra for the three locations, thus offering an integrated picture of the time scales of rainfall variability. The seasonal variation in rainfall (i.e. the annual cycle) is the dominant peak in all three spectra and is therefore the most important source of variation. The difference in the power of the annual peaks across locations corresponds to the difference in mean rainfall in the dry season and the wet season and represents the strength of rainfall seasonality: stronger in the tropical moist climate (Katherine; Figure 2D) and weaker in the Mediterranean climate (Palermo; Figure 2F). Katherine and Santa Terezinha (Figure 2D and E) also exhibit a smaller peak in spectral energy at sub-annual time scales – the result of secondary, ‘minor’, wet and dry seasons, which are common in tropical climates but become less important away from the equator (Murphy and Lugo, 1986). Although none of these peaks are statistically significant (see, e.g. Torrence and Compo, 1998 for details on the significance test adopted here), lower magnitude peaks in the power spectra are suggestive of a degree of coupling with synoptic circulation and slowly oscillating climatic patterns, such as El Niño-Southern Oscillation, the Indian

Ocean Dipole, and the Pacific Decadal Oscillation (Kane, 1997; Mason and Goddard, 2001; Kayano and Andreoli, 2006; Rodrigues *et al.*, 2011).

Wavelet analysis also allows the exploration of non-stationarity by means of scale-time decomposition diagrams (Figure 2G–I). In these plots, the spectral power (ranging from low in green to high in dark red in Figure 2G–I) measures how important the variability on a particular time scale is (vertical axis), at a given moment in time (horizontal axis). For example, the annual signal for the three sites is easily identified as the dark horizontal band, with regions of significant power contoured in white. At Katherine (Figure 2G), this signal is continuous in time, appearing with similar intensity every year. At Santa Terezinha (Figure 2H), this signal becomes intermittent: the very weak annual signals correspond to major droughts and strong El Niño-Southern Oscillation events. At Palermo, the annual power decreases from the 1960s onward, as apparent from the almost total absence of white contoured areas after 1960 in Figure 2I): this pattern corresponds to a known drying trend over the Mediterranean region (Knippertz *et al.*, 2003; Brunetti *et al.*, 2004; Kostopoulou and Jones, 2005; Rodrigo and Trigo, 2007; Alpert *et al.*, 2008). Similar drying trends have been noticed in Western Africa, but not in other tropical SDEs (Feng *et al.*, 2013).

In summary, differences in rainfall patterns across SDEs include the strength of the seasonality (with strongest seasonality in the wet tropics); extent of inter-annual variability in annual rainfall amounts (greatest in the dry tropics); and differences in the degree of inter-annual variability of the timing of the wet season (greatest in the dry tropics). Despite these differences, all the selected sites share a strong seasonality in rainfall occurrence, with well-defined wet and dry seasons, and often a high degree of inter-annual variability in rainfall timing and amounts. These shared characteristics justify their common identification as seasonally dry climates for the purposes of ecohydrological analyses. In the following, the effects of these rainfall regimes on plant water availability and hence plant activity will be characterized.

VEGETATION ADAPTATION STRATEGIES

This section reviews and synthesizes the range of phenological strategies and physiological traits observed in a variety of species and SDEs.

Leaf phenological strategies

Leaf habit varies significantly across woody species in SDEs. The mechanisms that induce leaf flushing or abscission may be complex and the relative roles of endogenous and exogenous

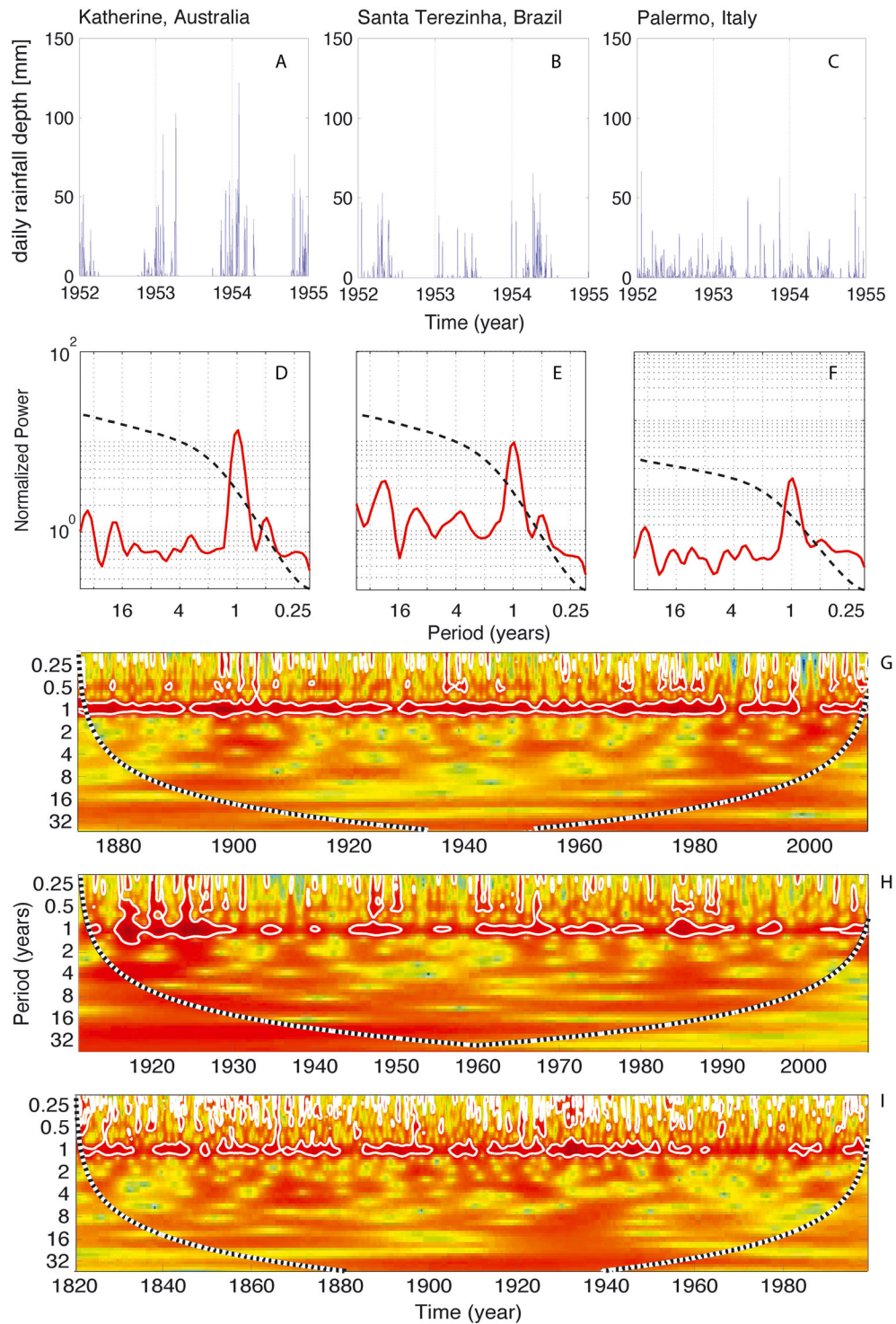


Figure 2. Multi-scale variability of rainfall at (A,D,G) Katherine (Northern Australia, moist tropical SDE), (B,E,H) Santa Terezinha (NE Brazil, dry tropical SDE) and (C,F,I) Palermo (Southern Italy, Mediterranean SDE). In (A–C), examples of 3-year subsamples extracted from daily rainfall time series. Panels (D–F) show the corresponding spectral densities averaged over the complete time series (dashed lines indicate the 95% significance level for the average power when tested against a Monte Carlo simulated ‘red noise’ process (Fraedrich and Larnder, 1993; Torrence and Compo, 1998). Panels (G–I) show the scale-time decomposition of rainfall variability via wavelet analysis applied to monthly data (colours indicate the total normalized power, ranging from green for low power to dark red for high power; black and white dashed lines show the cone of influence for the wavelet total power – i.e. the 95% confidence limits for the local spectrum – while white thin contours highlight regions of significant power).

factors in driving leaf phenology in individual species are not always well known (Borchert and Rivera, 2001; Brodribb *et al.*, 2002; Choat *et al.*, 2006; Ishida *et al.*, 2010). Nevertheless, following the approach of Borchert (1994); Eamus and Prior (2001); Singh and Kushwaha (2005a), and Elliott *et al.* (2006), we distinguish three main leaf phenological strategies (Table II): (i) opportunistic drought-deciduous species (Section on Opportunistic Drought-Deciduous Species); (ii) scheduled drought-deciduous species (Section on Scheduled Drought-Deciduous Species); and (iii) evergreen species (Section on Evergreen Species). It should be noted, however, that not all species conform to this classification.

Opportunistic drought-deciduous species. The leaf phenology of opportunistic drought-deciduous species is mainly driven by water availability. Leaf flush occurs following the first significant rainfall event in the wet season, with events of 20–30 mm or relative volumetric soil water content exceeding $0.13\text{--}0.18\text{ m}^3\text{ water m}^{-3}$ soil pore space typically needed to induce flushing (Yoshifuji *et al.*, 2011). Flushing is generally synchronous among conspecific trees, although spatial variability in rainfall, infiltration, and soil moisture stores may lead to spatial variations in flushing dates (e.g. Penuelas *et al.*, 2004; Singh and Kushwaha, 2005b). Leaf flush can also be triggered by environmental cues that precede the wet season, such as decreased atmospheric water demand in association with small rainfall events during the dry season (Borchert, 1994; Williams *et al.*, 1997). Opportunistic flushing is typical in tropical species, but it has also been observed in warm Mediterranean ecosystems, where a second flush of leaf growth may be triggered by autumn rainfall (Penuelas *et al.*, 2004).

Among species that display opportunistic flushing, two different patterns of leaf abscission occur. (i) Softwood species tend to shed their leaves early in the dry season. Leaf abscission begins shortly after the rains stop, in response to the first signs of soil water shortage (Reich and Borchert, 1984; Borchert, 1994; Machado *et al.*, 1997; Singh and Kushwaha, 2005a; Fallas-Cedeno *et al.*, 2010; Lima and Rodal, 2010). The plants enter a dormant state but maintain a relatively high stem water potential (Borchert and Rivera, 2001). (ii) Conversely, hardwood species generally shed their leaves later in the dry season, often 2–3 months after the last rain event. Leaf abscission in these trees appears to occur in response to declining leaf or stem water potential. Irrigation or groundwater sources may delay the onset or slow the rate of leaf abscission (Myerscough and Murray, 1992; Valdez-Hernandez *et al.*, 2010). However, plants can lose leaves even when soil moisture remains high, suggesting that the leaf drop may also respond to increased VPD at the end of the wet season (Reich and Borchert, 1984; Wright and Comejo, 1990; Myerscough and Murray, 1992; Williams *et al.*, 1997).

Table II. Leaf phenological strategies employed in the model scenarios.

	Phenology	Growing season	LAI range	Trigger for leaf flush		Trigger for leaf abscission	
				Environmental cue	Model	Environmental cue	Model
Tropical species	Opportunistic	Wet season	$0\text{--}LAI_{\max}$	Soil moisture, rainfall	$s_{\text{plant}} > s^*$ (conservative) or $s_{\text{plant}} > 1.2s_w$ (aggressive)	Soil moisture (softwoods) or leaf/stem water potential (hardwoods)	$s_{\text{plant}} < s_w$ (softwoods only)
	Scheduled	Wet season	$0\text{--}LAI_{\max}$	Photoperiod, temperature	First of scheduled time and $s_{\text{plant}} > s_w$. Scheduled time: $-20, 0, +20$ days from the normal start of wet season	Soil moisture (softwoods) or leaf/stem water potential (hardwoods)	$s_{\text{plant}} < s_w$ (softwoods only)
Mediterranean species	Evergreen Scheduled (spring/summer growth)	Whole year Dry season	LAI_{\max} $0\text{--}LAI_{\max}$	Photoperiod, temperature	Set date: $-40, -20, 0, +20$ days from the spring equinox	Soil moisture (softwoods) or leaf/stem water potential (hardwoods)	$s_{\text{plant}} < s_w$ (softwoods only)
	Evergreen	Dry season	LAI_{\max}	—	—	—	—

Brevi-deciduous and leaf-exchanging species can also be considered opportunistic, because the timing of leaf flushing seems to depend on local water availability. These species tend to occupy wet niches, with year-round access to rainfall-independent water stores. Leaf abscission occurs early in the dry season, in response to lowered hydraulic and photosynthetic efficiency and increased water stress in older leaves and is often followed by an increase in stem water potential, consistent with water uptake from deep soil stores (Jackson *et al.*, 1995). Although the exact timing varies with local water availability, leaf flushing typically occurs less than a month after abscission, so that brevi-deciduous and leaf-exchanging species are to all effects near-evergreen.

Scheduled drought-deciduous species. Scheduled drought-deciduous species share similar leaf abscission cues with opportunistic species, but their leaf flushing behaviour is largely independent of rainfall or water status, as also evidenced by lack of response to irrigation. Instead, these species flush their leaves in response to predictable environmental cues such as photoperiod, temperature, insolation (Wright and Cornejo, 1990; Myerscough and Murray, 1992) or the decrease in VPD associated with the 'build up' before the Northern Australian summer monsoon (Duff *et al.*, 1997; Do *et al.*, 2005). Scheduled flushing occurs in both tropical and Mediterranean climates (Penuelas *et al.*, 2002; Rivera *et al.*, 2002). Ecosystems dominated by scheduled flushing species exhibit a higher degree of interspecific synchrony and a lower inter-annual variability in flushing dates than those dominated by opportunistic species.

Many scheduled species have access to additional, persistent water stores (e.g. groundwater) or rely on the combination of multiple flushing cues to reduce the risks associated with the unpredictable timing of the wet season onset. For example, in an Asian monsoon forest with deep soils, most large (and presumably deep-rooted) trees exhibited photoperiod-driven flushing (Elliott *et al.*, 2006). Some Mediterranean species schedule leaf flushing based on both winter rainfall totals and spring temperature (Penuelas *et al.*, 2004). Also, a second, opportunistic flush following the onset of the rainy season may occur – a strategy that may limit the negative effects of herbivory (see Section on Non-Ecohydrological Drivers of Leaf Phenology).

Evergreen species. Evergreen species shed and regrow their leaves asynchronously throughout the year, so that no substantial seasonality is apparent in their leaf area index (LAI). Although evergreen species need to endure periods of water shortage, the extent to which they display physiological adaptations to minimize water loss is unclear (Borchert, 1994; Nepstad *et al.*, 1994; Lima and Rodal, 2010; Markesteijn *et al.*, 2011), as discussed in the next section.

Ecophysiological adaptations

The extent to which climatic variability impacts plant transpiration and photosynthesis is mediated by plant ecophysiological traits. A set of coordinated functional traits (xylem and stomatal conductances and water potential thresholds; photosynthetic capacity) and plant morphological characteristics (root, sapwood, and LAI) control water transport and transpiration (Tyree and Ewers, 1991; Manzoni *et al.*, 2013). In this section, on the basis of a synthesis of published studies on ~400 species, we assess if these traits, and therefore transpiration rate and its relation to soil moisture, covary with the phenological strategies (see Figure 3 and the Supplementary material for details).

Root systems. Laterally extensive and deep root systems exploit soil water efficiently. Compared with drought-deciduous species, evergreen species might require deeper roots to sustain water uptake during the dry season (Sobrado, 1986; Canadell *et al.*, 1996; Eamus and Prior, 2001). Indeed, there are also some indications that rooting architecture depends on leaf phenology: tap roots tend to be more prevalent in evergreen species, whereas more distributed rooting systems are typical of deciduous trees (Scholz *et al.*, 2008). However, rooting depth does not always follow leaf phenology (Franco *et al.*, 2005; Miranda *et al.*, 2010) and some evergreen species have been shown to utilize water from shallower soils than deciduous species (Jackson *et al.*, 1999; Goldstein *et al.*, 2008).

Plant hydraulic traits and regulation of transpiration. The maximum measured stomatal conductance, $g_{s,max}$, is a proxy of the transpiration rate per unit leaf area under favourable VPD and water availability. Observed $g_{s,max}$ values tend to be lower in evergreen species than in drought-deciduous ones in both tropical and Mediterranean SDEs (Figure 3A). The rate of transpiration in well-watered conditions follows a similar pattern across leaf habits for a given VPD and LAI.

As soil moisture decreases, stomatal conductance and hence transpiration per unit leaf area are reduced. The timing of stomatal closure depends on the balance of water supply to the leaves through the soil-plant system and water evaporation from the leaves. As soil dries, the water supply decreases because of reductions in both soil-root and plant xylem conductances; therefore, stomata conductance needs to decrease to avoid excessively negative leaf water potentials. Two stomatal strategies bound the spectrum of observed strategies: (i) an early stomatal closure during the dry period, so that high leaf water potential values can be maintained and the plant avoids water stress at the expense of lower C uptake; and (ii) a late stomatal closure, which results in more negative xylem and leaf water potentials that may lead to cavitation and metabolic limitations to photosynthesis. Different hydraulic traits correspond to these stomatal regulation strategies (e.g. Manzoni *et al.*, 2014).

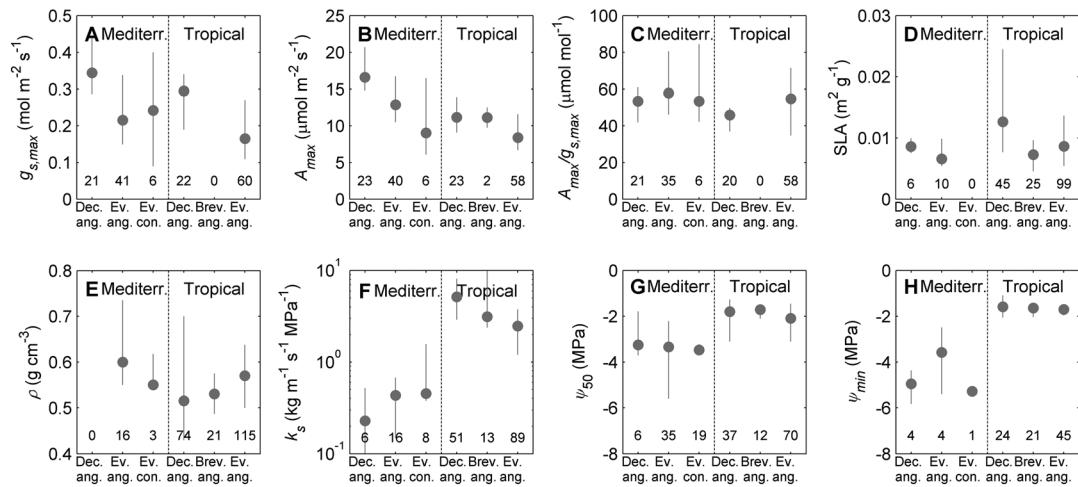


Figure 3. Relationship between ecophysiological traits and leaf phenological strategy in woody species from SDEs: (A) maximum stomatal conductance to water vapour (as measured at moderate vapour pressure deficits and moisture deficit); (B) light-saturated photosynthesis under well-watered conditions; (C) ratio between maximum photosynthesis and stomatal conductance, a proxy of leaf-level water use efficiency; (D) specific leaf area; (E) wood density; (F) sapwood-specific saturated hydraulic conductivity of the stem or branches; (G) water potential at 50% cavitation; and (H) minimum leaf water potential measured in dry conditions, for deciduous, brevi-deciduous and evergreen ('Dec', 'Brev', and 'Ev' for brevity), angiosperms ('ang'), and conifers ('con'). Circles and bars indicate median values and first and third quartiles, respectively; the number of data points used is also reported for each group; data relative to Mediterranean deciduous species include both winter and summer deciduous leaf habits; data have been collected from several published sources (see Supplementary Materials for details).

Early stomatal closure, drought avoidance, and nearly constant leaf water potential (i.e. an isohydric behaviour) are associated to higher water transport efficiency (low wood density, ρ , and high saturated xylem conductivity, k_s ; Figure 3E and F). These hydraulic features allow a smaller water potential gradient between the soil and the leaves for a given stomatal conductance and thus a less negative leaf water potential (Figure 3H), despite the fact that k_s is often negatively correlated with resistance to cavitation (water potential at 50% loss of conductivity, ψ_{50} ; Figure 3G). Early stomatal closure is often observed in tropical SDEs (Meinzer *et al.*, 1999; Bucci *et al.*, 2004; Bucci *et al.*, 2005; Goldstein *et al.*, 2008). In contrast, most Mediterranean species have low hydraulic efficiency and maintain relatively high stomatal conductance during the dry season, providing higher potential CO₂ uptake at the expense of lowered leaf water potentials (i.e. anisohydric behaviour; Figure 3G and H) (Sobrado, 1993b; Eamus and Prior, 2001; Franks *et al.*, 2007; Miranda *et al.*, 2010; Quero *et al.*, 2011). Under such conditions, substantial cavitation and metabolic limitations to photosynthesis may occur (Xu and Baldocchi, 2003; Galmes *et al.*, 2007). Mediterranean species may be forced to adopt this strategy (together with strong drought resistance) because their growing season, as defined by adequate temperature and solar radiation, often coincides with the dry season.

As apparent in Figure 3, these patterns across climates appear stronger than the pattern across leaf habits within a single climatic zone. Drought-deciduous species in tropical SDEs tend to maximize transport efficiency during the wet season (avoiding cavitation by dropping their leaves),

while evergreen species are more conservative in their water use, with low conductance and high wood density (Sobrado, 1993a; Eamus and Prior, 2001; Chen *et al.*, 2009; Miranda *et al.*, 2010; Fu *et al.*, 2012). However, leaf phenological strategy does not map closely to hydraulic traits; rather, water use strategies, xylem conductivities, resistance to cavitation, and minimum leaf water potentials overlap substantially across leaf habits (Figure 3F–H) (Borchert, 1994; Brodribb *et al.*, 2002; Bucci *et al.*, 2004; Santiago *et al.*, 2004; Goldstein *et al.*, 2008; Meinzer *et al.*, 2008; Ishida *et al.*, 2010; Markesteijn *et al.*, 2011). A similar lack of consistent variation across phenological strategies is apparent in Mediterranean climates.

Photosynthetic rate, water use efficiency, and specific leaf area. Evergreen species are known to have lower photosynthetic rates on a per leaf mass basis (Eamus and Prichard, 1998; Eamus and Prior, 2001; Wright *et al.*, 2004; Franco *et al.*, 2005). Contrasting with previous reports (Eamus and Prior, 2001; Cianciaruso *et al.*, 2013), we found the same pattern both in Mediterranean and tropical SDE also when expressing photosynthetic rates on a leaf area basis (Figure 3B). Nevertheless, because of a similar pattern in maximum stomatal conductance across leaf habits, the intrinsic water use efficiency ($A_{\max}/g_{s,\max}$) depends only weakly on leaf phenology (Figure 3C).

Finally, the specific leaf area (leaf area per unit leaf dry weight, SLA; Figure 3D) is generally higher in drought-deciduous than evergreen species, in agreement with most previous observations (Sobrado, 1986; Franco *et al.*, 2005; but see also Brodribb and Holbrook, 2005).

MODELLING FRAMEWORK

The joint effects of physiological and phenological strategies ultimately define transpiration and C gain, thus linking the climatic variability to plant fitness and determining the suitability of different strategies to a given climate. A minimalist model describing the coupled soil water and plant C balance is employed here to describe these linkages. Climate and plant parameters are based on the previous analysis of climatic regimes (Section on Precipitation Forcing) and synthesis of ecophysiological traits (Section on Vegetation Adaptation Strategies). Although this framework undoubtedly simplifies both plant responses to environmental conditions and soil and plant water dynamics, it preserves the key interactions between climate, soils, and vegetation while requiring few physically based parameters. Our aim with this modelling analysis is to assess which phenological strategies are most effective in a given climate. Additional factors potentially influencing phenological strategies, but not included in the model, are discussed in Section on Non-Ecohydrological Drivers of Leaf Phenology.

Soil moisture balance

In the absence of parenchymatic storage, plant-available water is mainly driven by the dynamics of soil water within the rooting zone. Plant roots span both shallow soil layers and deeper, more persistent water stores that may be partially decoupled from seasonal variations in rainfall (e.g. groundwater) and that could sustain plant activity in rainless periods. At daily time scales, the total plant-available soil water per unit ground area can thus be described by two coupled mass balances, representing the temporal evolution of the soil moisture $s_1(t)$ averaged over the top layer of depth $Z_{r,1}$, and the soil moisture $s_2(t)$ within an additional water store of depth $Z_{r,2}$ (as e.g. in Yu and D'Odorico, 2014):

$$\begin{cases} nZ_{r,1} \frac{ds_1(t)}{dt} = R(t) - T_1(s_1, s_2) - E(s_1) - L_1(s_1) \\ nZ_{r,2} \frac{ds_2(t)}{dt} = L_1(s_1) + I(t) - T_2(s_1, s_2) - L_2(s_2) \end{cases} \quad (1)$$

Soil in both water stores is assumed to have porosity n . Rainfall $R(t)$ represents the main input to the system, enhancing soil moisture in the top layer. Losses from the shallow layer occur via plant water uptake, $T_1(s_1, s_2)$, soil water evaporation, $E(s_1)$, and deep percolation, $L_1(s_1)$. The latter term represents the main input to the deep store, possibly complemented by a rainfall-independent deep recharge $I(t)$. Losses from the deep water store occur through plant water uptake $T_2(s_1, s_2)$ and deep percolation $L_2(s_2)$. In both layers, percolation is assumed to occur instantaneously whenever the soil moisture of the corresponding layer exceeds a threshold s_{\max} around the field capacity (Milly, 2001; Porporato *et al.*, 2004; Vico and Porporato, 2010). Soil water evaporation is a piecewise

linear function of $s_1(t)$, with maximum soil water evaporation E_{\max} when $s_1 \geq s_w$, $E_{\max} s_1 s_w^{-1}$ otherwise. We note that averaging soil moisture over a water store implicitly accounts for the hydraulic redistribution within that soil volume – a phenomenon observed in some SDE species (Kurz-Besson *et al.*, 2006; Scholz *et al.*, 2008; Prieto *et al.*, 2010; Neumann and Cardon, 2012). However, hydraulic redistribution between the two soil water stores is neglected.

Total plant water uptake from both stores is determined by plant transpiration demand, a function of atmospheric VPD, D , plant size (as described by LAI, $LAI(t)$), and stomatal conductance to water vapour, $g_s(t)$,

$$T_{\text{tot}} = g_s(t)D(t)LAI(t). \quad (2)$$

To capture the separate effects of VPD and soil moisture, stomatal conductance is described as $g_s(t) = g_{ww}(D)f_s(s_{\text{plant}})$, where $g_{ww}(D)$ is the stomatal conductance under well-watered conditions and the function $f_s(s_{\text{plant}})$ accounts for the effect of ‘plant-sensed’ soil water in reducing the effective stomatal conductance from its well-watered level, by lumping plant hydraulic traits in a single ‘effective’ function (see Buckley (2005) for a review of more mechanistic approaches). The plant-sensed soil moisture s_{plant} is defined as $s_{\text{plant}} = \max[s_1, s_2]$, assuming that leaf-level activity is driven by the highest soil moisture between the two compartments. This assumption is supported by the observation of high stomatal conductance during the dry season in trees that have access to deep water stores (David *et al.*, 2007; Miller *et al.*, 2010) as well as by localized irrigation experiments (Green *et al.*, 1997; Kang *et al.*, 2003; Guswa, 2012). The stomatal conductance under well-watered conditions is assumed to depend on D as $g_{ww}(D) = g_{s,\max}(1 - m \ln D)$, with $g_{s,\max}$ corresponding to a reference stomatal conductance at $D = 1$ kPa (Oren *et al.*, 1999), here approximated by the maximum measured stomatal conductance (Figure 3A). As a first approximation, the effect of soil moisture can be summarized by considering that, for given D , transpiration proceeds unhampered when the available plant-sensed soil moisture, s_{plant} , is above a threshold s^* , and is linearly reduced when water is in scarcer supply,

$$f_s(s_{\text{plant}}) = \begin{cases} \frac{s_{\text{plant}}}{s^*} & s_{\text{plant}} < s^* \\ 1 & s_{\text{plant}} \geq s^* \end{cases} \quad (3)$$

The threshold s^* is the soil moisture availability corresponding to incipient stomatal closure and captures the response of stomatal conductance (and hence transpiration per unit leaf area) to reduced soil water availability, thus lumping the effect of changes in soil water content on leaf-level activity as mediated by plant hydraulics. On the basis of the synthesis of the physiological traits (Section on Plant Hydraulic Traits and Regulation of Transpiration), a single function, $f_s(s_{\text{plant}})$, and threshold, s^* , common to all functional types, is employed.

Assuming that the water stored in plant tissues is in equilibrium (i.e. neglecting water stored in plant parenchyma),

the water uptake from the soil, the flux through the stem, and the plant level transpiration are all equal. Hence, the water uptake demand set in Equation (2) must be met by total plant water uptake from the two water stores, $T_1(s_1, s_2)$ and $T_2(s_1, s_2)$. The two water stores are assumed to contribute to meet plant water demand proportionally to their own soil water content and the fraction of roots located in each one,

$$\begin{aligned} T_1(s_1, s_2) &= T_{tot} \frac{\alpha s_1}{\alpha s_1 + (1 - \alpha) s_2} \\ T_2(s_1, s_2) &= T_{tot}(s_1, s_2) - T_1(s_1, s_2), \end{aligned} \quad (4)$$

where α is the fraction of total root biomass located in the top compartment. It follows that, for set root distribution, the plant depletes faster the compartment with higher water availability. Should roots be completely located in the shallower layer (i.e. $\alpha=1$), plant transpiration would be driven by the soil moisture on the top layer only (i.e. $s_{\text{plant}}=s_1$) and all the water uptake would occur from the top layer ($T_1(s_1, s_2)=T_{tot}$). Water uptake by nearby competing vegetation (non-beneficial losses at the individual plant level) are neglected: these additional losses would not significantly alter the results as they would act in similar ways under all climates.

Carbon economy

When assessing the long-term C economy of evergreen and deciduous leaf habit, several factors should be considered: (i) the higher photosynthetic rate in deciduous species leaves is counterbalanced by their shorter lifespan (Wright *et al.*, 2004; Mediavilla *et al.*, 2008; van Ommen Kloeke *et al.*, 2012); (ii) the leaf construction costs are lower in deciduous species due to their larger SLA; (iii) leaf respiration during the dry, unfavourable season negatively affects only the evergreen species; and (iv) although rooting morphology appears to only partially map onto leaf habit (see Section on Root Systems), root-associated costs are generally assumed higher for the evergreen species because they need to maintain leaf hydration throughout the year (Givnish, 2002). Here, we consider factors i–iii based on leaf habit-specific data from Figure 3 and other sources, whereas root allocation and depth are varied independently of leaf habit.

To proceed quantitatively, a minimalist C balance is employed, representing the annual C gain per unit ground area, G , with input from C fixation via photosynthesis, G_{gross} , and losses occurring via maintenance respiration, R_m , and leaf construction costs, c :

$$\begin{aligned} G &= G_{\text{gross}} - R_m - c \\ &= \int_{\text{year}} \eta_A A(t) LAI(t) dt - \int_{\text{year}} r LAI(t) dt - f_{\text{flush}} f_C \frac{LAI_{\text{max}}}{SLA}. \end{aligned} \quad (5)$$

In (5), $A(t)$ and r are the leaf-level photosynthetic and maintenance respiration rates, expressed on a per unit leaf area basis, $LAI(t)$ is the LAI (which changes in time between 0 and LAI_{max} , see Section on Representation of Phenological Strategies), η_A accounts for the carbon use efficiency and the reduced light availability early in the morning and late in the day, f_{flush} is the frequency of leaf flushing (i.e. the number of flushing occurring over the year), f_C is the fraction of C per unit leaf mass, and SLA is the specific leaf area. Using a linearized photosynthesis model and neglecting the CO_2 compensation point, the leaf-level photosynthetic rate can be estimated as (Hari *et al.*, 1986; Manzoni *et al.*, 2011)

$$A(t) = \frac{k(T) c_a g_s(t)}{g_s(t) + a k(T)}, \quad (6)$$

where c_a is the atmospheric CO_2 concentration, $g_s(t)$ is the stomatal conductance to water vapour, $a=1.6$ is the ratio between the diffusivities of water vapour and CO_2 in air, $k(T)$ is a macroscopic kinetic constant, accounting for the metabolic capacity and how it is affected by temperature T and light availability. Neglecting light limitations, it can be shown that $k(T) \cong V_{c\text{max}}(T) [r_C c_a + K_c(T) (1 + o_a K_o(T)^{-1})]^{-1}$, where $V_{c\text{max}}$ is the maximum carboxylation rate, r_C is the long-term average ratio between stomatal and atmospheric CO_2 concentrations, K_c and K_o are the Michaelis–Menten constants for CO_2 fixation and oxygen inhibition, and o_a is the oxygen concentration in the air. Employing the temperature dependences of Bernacchi *et al.* (2001), $k(T)$ increases linearly with temperature in the temperature range typical of the considered sites and can be modelled as $k(T) \cong k_{25} (0.03 T + 0.25)$, where k_{25} is the macroscopic kinetic constant at 25°C – the only kinetic parameter to be estimated. When stomatal conductance is high, assimilation rate is not limited by CO_2 availability and $A \cong k c_a$, so that k_{25} can be estimated as $k_{25} = A_{\text{max}} c_a^{-1}$ (implicitly assuming that the assimilation rates where collect at about 25°C and ambient c_a). The obtained photosynthetic rate is further reduced to account for daily changes in light availability. In contrast, the decline in photosynthetic efficiency with leaf age is neglected, potentially overestimating total C fixation, particularly in evergreen species.

The C loss terms in Equation (5) are estimated as follows. Maintenance respiration rate per unit leaf area is assumed to be equal to a fraction f_{resp} of the maximum C assimilation rate, A_{max} , i.e. $r = f_{\text{resp}} A_{\text{max}}$ (Givnish, 2002), thus resulting in a higher respiration rate per unit leaf area in deciduous species. Leaf construction costs per leaf mass are independent of leaf habit (Eamus and Prichard, 1998), but construction cost per unit ground area vary with leaf phenology. Evergreen species have lower SLA than deciduous species (Figure 3D), resulting in higher construction costs for a given LAI_{max} . However, evergreen leaves may have lifespans extending beyond 12 months, so

that the frequency of leaf flushing, f_{flush} , is lower than in drought-deciduous species. Potential additional costs stemming from water shortage (e.g. xylem refilling after cavitation; osmolyte production to maintain leaf turgor) are neglected.

Model parameterization

Plant functional type impacts water and C balances primarily through two mechanisms: (i) ecophysiological traits that regulate water losses and C uptake at the leaf level and (ii) changes in LAI that affect the timing and rates of transpiration and C exchanges at the whole plant level. Here, the representation of these mechanisms in the model and the necessary climatic data are discussed.

Representation of phenological strategies. Phenological variations are coupled to the soil water and plant C balances framework by allowing changes in time of the LAI. We treat evergreen species as having a constant LAI, equal to a preset LAI_{max} , regardless of water availability. Conversely, the time variation of LAI for drought-deciduous species is idealized as a step increase from zero to LAI_{max} at leaf flushing, whereas leaf abscission is assumed to occur more gradually, with a rate depending on soil water availability. The dates of leaf flushing are determined differently for tropical and Mediterranean SDEs, while leaf abscission is modelled in the same way in both ecosystems and for both opportunistic and scheduled species, as detailed next and summarized in Table II. Treating leaf flushing as an instantaneous process may overestimate transpiration for species that complete leaf extension gradually (e.g. Reich, 1995; Lima and Rodal, 2010) but is an effective way to capture the main patterns in water use across SDEs.

Leaf flushing: For tropical opportunistic species, the leaf flush date is assumed to be a function of the plant-sensed soil moisture, s_{plant} (as defined in Section on Soil Moisture Balance). Flushing is triggered by soil water availability crossing the threshold, s_{flush} (*sensu* Yoshifuji *et al.* (2011)). Two soil water availability thresholds triggering leaf flushing are considered (Table II). The more conservative species flush their leaves when the soil is wet enough to allow full stomatal opening, i.e. $s_{\text{flush}} = s^*$. Aggressive species flush their leaves as soon as the soil water availability exceeds a lower threshold, $s_{\text{flush}} = 1.2s_w$, where s_w is the soil moisture at the wilting point and $s_w < s_{\text{flush}} < s^*$.

For tropical scheduled species, leaf flush is idealized as occurring on a set date – as if plants responded to photoperiod only (Table II). Conservative scheduled species flush their leaves *after* the ‘normal’ beginning of the wet season. Aggressive scheduled species flush their leaves *before* the beginning of the wet season. Three leaf flushing dates are explored, ‘early’, ‘normal’, and ‘late’,

referring to species flushing their leaves respectively 20 days before, at, and 20 days after the ‘normal’ beginning of the wet season. The ‘normal’ beginning of the wet season is defined as the average date on which the 20th percentile of annual total rainfall is reached; hydrologic year is treated as starting at the end of the driest month. We allowed for leaf flush in scheduled species to be deferred in abnormally dry years until the soil water content reaches at least s_w but did not consider multiple leaf flushes in a single growing season (e.g. in response to damage inflicted by a delayed wet season onto previously flushed leaves).

In Mediterranean SDEs, spring/summer growing species exploit soil water accumulated during the wet winter and have scheduled leaf flushing in the early spring driven by photoperiod or temperature cues. Here, we focus on photoperiod-driven species and consider different dates for leaf flushing with respect to the spring equinox, thus covering a wide range of dates (from 40 days before the equinox to 20 days after that), following the observations of Penuelas *et al.* (2002) for North-Eastern Spain. Non-woody opportunistic species growing in the wet fall/winter are not included.

Leaf abscission: Regarding leaf abscission, only softwood species are considered in both tropical and Mediterranean SDEs. In these species, leaf abscission is initiated when available soil water declines below an abscission threshold, for simplicity set at the wilting point s_w . In agreement with observations (e.g. Valdez-Hernandez *et al.*, 2010) and earlier models (Arora and Boer, 2005), leaf abscission rate is assumed to accelerate as soil moisture drops below s_w , and to be interrupted when rainfall brings soil moisture back to values above s_w (although the previously lost leaves are not restored), i.e.

$$\frac{dLAI(t)}{dt} = \begin{cases} 0 & s_{\text{plant}} > s_w \\ -LAI(t)\beta_{\text{absc}}[s_w - s_{\text{plant}}(t)] & s_{\text{plant}} \leq s_w \end{cases} \quad (7)$$

where the higher the constant β_{absc} , the faster the decline.

Describing leaf abscission in hardwood species would require describing the temporal evolution of their stem water storage, which lies beyond the scope of this work. Qualitatively, for a given leaf flushing strategy and water availability, hardwood species will have longer leaf lifespans than softwood ones.

Rooting systems and deep water storage. To elucidate the effects of rooting depth and rainfall-independent ground-water recharge on the optimal leaf strategy, both shallow rooting systems ($\alpha = 1$, $s_{\text{plant}} = s_1$), and plants with access to deep water stores ($\alpha < 1$, $s_{\text{plant}} = \max[s_1, s_2]$) are explored. In the latter case, the effect of groundwater recharge is also considered ($I = 0$ vs $I > 0$). In each scenario, the rooting depths and distribution ($Z_{r,1}$, $Z_{r,2}$, and α) are maintained

constant across plant functional types and sites. We assume that the dry seasons are long enough for water availability in the active rooting zone at beginning of the hydrologic year to be independent of the rainfall occurrence and plant activity during the previous year, so that subsequent years may be considered as independent.

Ecophysiological parameters. Plant water use strategy impacts primarily the maximum stomatal conductance, $g_{s,max}$, and maximum assimilation rate, A_{max} , and, to a lesser extent, specific leaf area, SLA (Figure 3). In the model, these parameters are set equal to the median of the observed values (circles in Figure 3; for evergreen species, only angiosperms are considered). Conversely, the soil moisture threshold for incipient stomatal closure, s^* , is assumed to be invariant with functional type, because of the weak dependence of hydraulic traits on phenological strategy. Moreover, to facilitate the comparison among different climates, the analyses are conducted assuming a ‘prototype’ species, i.e. keeping the peak LAI (LAI_{max}), and the abscission rate coefficient (β_{absc}) constant across functional types and climates.

Climatic forcing. The model is forced with historical rainfall data from the five case study sites (Figure 1; Table I). Because data on air humidity and temperature were not available for all locations, the seasonal evolution of VPD is idealized as a sinusoidal curve, with $D(t)$ reaching its minimum, D_{wet} , during the wettest month, and

its maximum, D_{dry} , 6 months later; the daily temperature was reconstructed by fitting a sinusoidal function to the monthly average temperatures (Figure 1). While using long-term average temperatures does not account for the inter-annual variability, it does incorporate the negative effects of winter conditions on the C assimilation of Mediterranean evergreens.

QUANTITATIVE ASSESSMENT OF PHENOLOGICAL STRATEGIES

For each site and phenological strategy, the model provides the temporal evolution of soil moisture, stomatal conductance, and LAI. It is then possible to determine the flushing date and leaf duration, total seasonal transpiration and C gain, and how they vary from year to year in different climates and for different plant functional types. As such, the model results allow quantifying the effects of the intra-annual and inter-annual variability in rainfall patterns apparent in Figure 2. The following sections present such results for the five study sites and compare them with observations available in the literature.

Temporal evolution of soil moisture, transpiration, and leaf area index

Figure 4 shows an example of the modelled temporal evolution of LAI, water uptake and available soil water, for

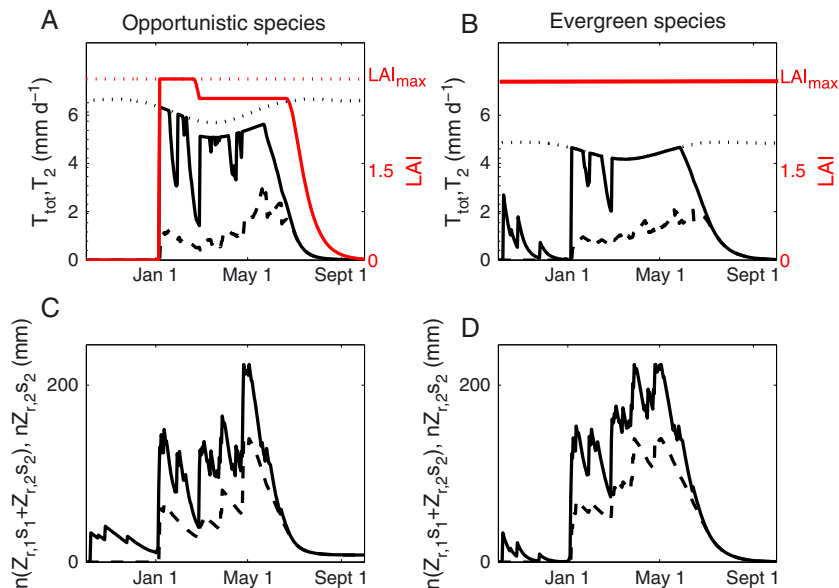


Figure 4. Example of the temporal evolution of (A,B) transpiration and LAI (black and red lines respectively) and (C,D) soil water availability for opportunistic species (left) and evergreen species (right), relative to year 1939–1940 in Santa Terezinha, assuming access to a deep water store of capacity $nZ_{r,2}$. In all panels, black solid lines refer to transpiration and soil water totals and dashed lines to the contribution of the deeper water store (T_2 and $nZ_{r,2}S_2$). In (A,B), the actual transpiration rate T_{tot} (solid black line) is compared with the corresponding transpiration rate under well-watered conditions (dotted black line), the actual LAI (solid red line) to the peak LAI, LAI_{max} (dotted red line). Other parameters are: $Z_{r,1}=0.3$ m, $Z_{r,2}=0.5$ m, $\alpha=0.7$; soil is sandy loam ($n=0.43$, $s_w=0.18$, $s^*=0.46$, $s_{max}=0.65$; Laio *et al.*, 2001), $m=0.6$ (Oren *et al.*, 1999), $D_{wet}=1$ kPa, $D_{dry}=2.2$ kPa, $LAI_{max}=3$, E_{max} is 10% of the total transpiration under well-watered conditions and maximum LAI, and $\beta_{absc}=0.4\ d^{-1}$; $g_{s,max}$ is set at the median of the data collected in Figure 3 (for the evergreens, only angiosperms are considered).

deep-rooted opportunistic and evergreen species for a specific year in Santa Terezinha (Northeastern Brazil). Total soil water content (Figure 4 bottom) is driven by the occurrence of rainfall as well as by losses through transpiration, which in turn are impacted by water availability (Figure 4 top). Moreover, in drought-deciduous species (Figure 4 left), LAI is controlled by the water availability, which drives flushing and shedding dynamics (Figure 4A, red line). Thanks to the permanence of leaves, evergreen species are able to exploit water input regardless of its timing, although isolated events (such as the one occurring at the beginning of the hydrologic year in this example) cannot sustain long periods of high transpiration. This continuous uptake of water by evergreen species reduces peak transpiration rates with respect to drought-deciduous species. At the same time, transpiration rates under well-watered conditions are lower in evergreens, a consequence of their lower $g_{s,max}$ (Figure 3A). When combined, these mechanisms result in less abrupt changes in soil moisture in both compartments in the presence of evergreen species, while soil moisture tends to be accumulated before leaf flushing and then depleted faster in the presence of drought-deciduous species (compare Figure 4C with D).

Rainfall and water use patterns affect the recharge of and contribution from the two water stores. Regardless of vegetation type, deep store recharge occurs only as a consequence of rainfall events that are able to increase soil moisture in the top compartment above field capacity. Hence, with drought-deciduous species, deep store recharge occurs mostly at the beginning of the wet season and after leaf abscission, when the absence of leaves reduces transpiration. Furthermore, the water-richest compartment is exploited first, thus resulting in a faster depletion of its water content until the two moisture levels become similar. The water depletion is always fastest in the top layer, where most roots are located (in the example of Figure 4, $\alpha = 0.7$).

Figure 4 also shows the corresponding temporal evolution of LAI (red solid lines). The modelled LAI qualitatively matches observations in drought-deciduous species, with a sharp increase in leaf area following significant rainfall and a more gradual decline in LAI at the onset of the dry season (e.g. Valdez-Hernandez *et al.*, 2010). This decline is slow at moisture level just below the threshold s_w , accounting for the plant ability to withstand brief periods of water stress, whereas the decline is faster for intermediate LAIs and soil moisture. If a rainfall event increases soil moisture above s_w (e.g. the 1 March event in Figure 4), leaf abscission is temporarily halted, until soil water availability declines again (Equation (7)). Because it is assumed that previously lost leaves are not replaced, the transpiration and photosynthetic rates per unit ground area are reduced accordingly, regardless of any later rainfall occurrence.

Timing of leaf flushing and leaf duration in drought-deciduous species

The potential growing season for evergreen species spans the entire year. Conversely, the growing season of drought-deciduous species is limited to the time in which leaves are present – the result of the combined effects of rainfall amount and timing, leaf phenological strategy, and ecophysiological traits. Here, we define the leaf duration and C fixation season for drought-deciduous species as the time between leaf flushing and leaf abscission (Table II). Because leaf abscission is a gradual process (Equation (7)), here we define abscission date as the day in which LAI is reduced to $LAI_{max}/4$: although LAI may then remain at such level for a prolonged period if rainfall occurs, the water and C fluxes generated by such reduced LAI contribute little to the annual totals.

The high rainfall inter-annual variability in SDEs causes broad and often bimodal distributions of flushing and abscission dates, as illustrated in Figure 5A and B for Santa Terezinha. In scheduled species, the distribution of abscission dates is bimodal (Figure 5A). Flushing before or at the average onset of the main wet season results in extremely short growing periods when the onset of the wet season is delayed. Conversely, the same strategy is beneficial in those years when the wet season begins on its average date, permitting plant activity over a longer period. In opportunistic species, the flushing dates also vary from year to year (dot-dashed lines in Figure 5B), resulting in a unimodal distribution around the typical onset of the wet season (6 February in Santa Terezinha). Abscission dates exhibit a bimodal distribution similar to scheduled species, with a small peak immediately following the average beginning and a larger one following the end of the wet season. The former peak pertains to years in which the wet season is not consistently wet, causing early leaf loss. The patterns in Figure 5 are similar to those observed in other SDEs (Yoshifuji *et al.*, 2011).

Leaf duration is also highly variable from year to year, with a bimodal distribution for all phenological strategies (Figure 5C and D). On average, scheduled normal flushing allows longer leaf durations than scheduled early and opportunistic flushing. In fact, in dry climates such as Santa Terezinha, aggressive strategies ('early' scheduled flushing or opportunistic flushing in response to small increases in soil water availability) are counterproductive, because water stress early in the wet season is likely. More conservative strategies, such as 'normal' scheduled species or opportunistic species with higher soil water thresholds, lead to the greatest leaf durations. With these strategies, the risk of damage if the wet season is delayed is reduced.

The impacts of the phenological strategies on leaf duration depend on climate and rooting depth. Examples of leaf duration distributions for scheduled species with different root depths are presented in Figure 6 for the cases of

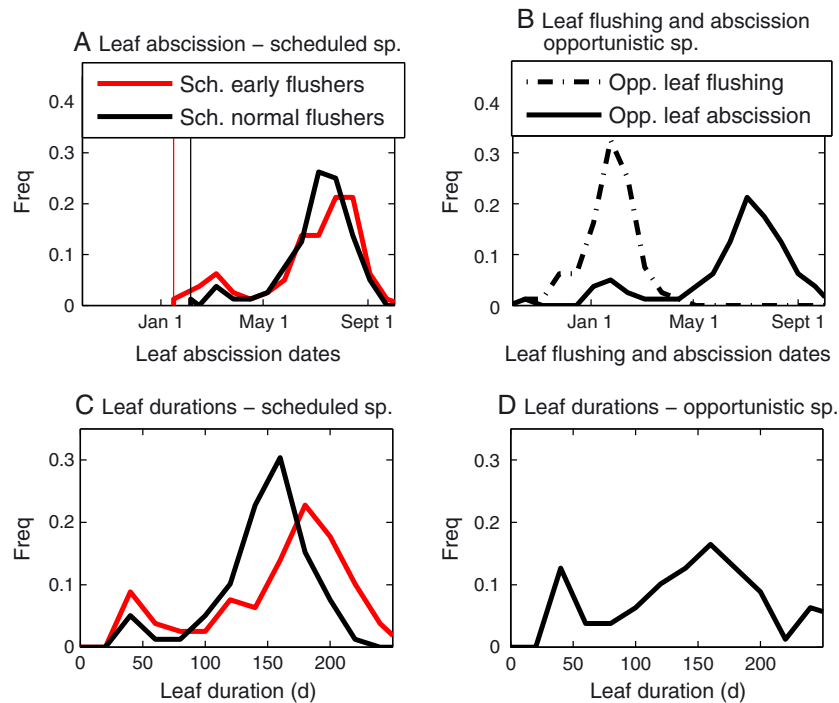


Figure 5. Frequency distributions of (A,B) leaf flushing and abscission date and (C,D) leaf duration, as a function of leaf flushing strategy (scheduled, left; opportunistic, right), for plants that have access to a deep water store of capacity $nZ_{r,2}$. (A,C) refer to scheduled species, flushing their leaves on either 17 January (scheduled early flushers; red lines) or on 6 February (scheduled normal flushers; black lines). (B, D) depict the case of opportunistic species, flushing their leaves at $s_{flush} = s^*$. The vertical lines in A denote the flushing dates for scheduled early and normal flushers (red and black lines, respectively); the dot-dashed line in B represents the frequency distribution of the opportunistic flushing dates. Rainfall data refer to Santa Terezinha. All other parameters are as in Figure 4.

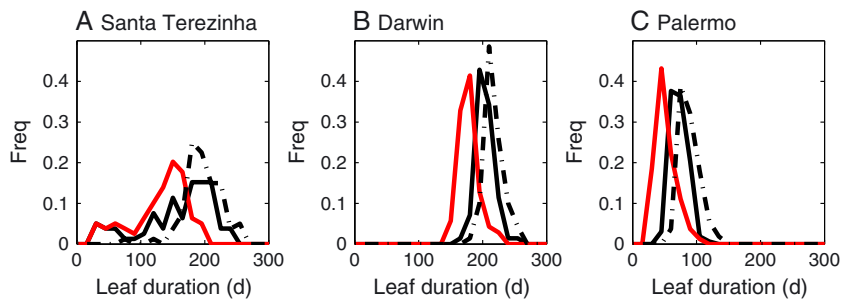


Figure 6. Frequency distributions of leaf durations in (A) Santa Terezinha (dry tropical SDE), (B) Darwin (wet tropical SDE), and (C) Palermo (Mediterranean SDE) for scheduled drought-deciduous species with shallow roots (red lines), and deep roots accessing the water store $nZ_{r,2}$, without and with groundwater input (black solid and dot-dashed lines respectively). Leaf flushing occurs 20 days before the normal beginning of the wet season for tropical SDEs or before spring equinox for Mediterranean SDE. All other parameters are as in Figure 4.

Santa Terezinha, Darwin, and Palermo. In wetter climates like in Darwin, the risk of water shortage early in the wet season is reduced and leaf durations are correspondingly longer (compare Figure 6B with A and C). In tropical SDEs, the effect of rainfall amounts is compounded with inter-annual variability: the extreme variability in the rainfall amount and wet season timing at Santa Terezinha leads to a greater variability in leaf durations than in the Australian sites, characterized by higher rainfalls and smaller inter-annual variability (Figure 6A and B). Inter-annual variability in rainfall timing and amount is less relevant in spring

flushing Mediterranean species. In Palermo, leaf abscission occurs early after the end of the wet season, resulting in a unimodal distribution of durations with low average (Figure 6C), while in Perth leaves may be sustained for longer periods in the wettest years, thus giving rise to a slightly bimodal distribution of leaf durations (not shown). Hardwood species (not considered here) may sustain leaves longer, potentially throughout the dry season, thus becoming winter-deciduous.

Rooting depth further alters the distribution of leaf abscission dates and durations. In general, the risk of water limitation immediately after leaf flushing is partially

mitigated by access to deep water stores (Borchert and Rivera, 2001; Lima and Rodal, 2010), so that leaf durations become longer and more unimodally distributed (compare red with black lines in Figure 6A and B). Similarly, in Mediterranean climates, deep water stores allow larger water accumulation during the winter, yielding longer and slightly more variable leaf durations (Figure 6C).

Effect of leaf strategy on water and carbon economies

While useful when considering the timing of water use, leaf durations *per se* do not allow assessment of the best adapted phenological strategy for a given climate. Conversely, net annual C gain provides a metric by which all the phenological strategies, including evergreen habit, can be compared within a common framework.

Figure 7 summarizes net C gain achieved by each leaf phenological strategy in all case studies, for shallow-rooted plants (top), deep-rooted plants without rainfall-independent groundwater input (center; $I(t)=0$), and deep-rooted plants with groundwater input (bottom; $I(t)>0$). As expected, higher average rainfall input (from black to light grey symbols) enhances C gains for all phenological strategies and rooting depths. In tropical climates, the combined effects of lack of deep water stores and longer and more intense dry seasons, favour deciduous species. Indeed, drought-deciduousness is more common under climates

with strong seasonality or with low rainfall during the dry season and is less related to total annual rainfall (Givnish, 2002; Bowman and Prior, 2005). As a result, in dryer climates, such as Santa Terezinha, drought-deciduousness is always beneficial, while in wetter climates (e.g. Darwin), a deeper rooting system is sufficient to make evergreen species competitive. Conversely, in Mediterranean ecosystems, evergreen habit confers a competitive advantage, thanks to the ability to exploit winter rainfall throughout the seasons, as opposed to just the accumulated water. Consistent with the results of the model, the highly variable South American *caatinga* (Sampaio, 1995) is dominated by drought-deciduous species (Machado *et al.*, 1997; Lima and Rodal, 2010; Cabral *et al.*, 2013), while the less climatically variable Australian tropics are predominantly evergreen (Hutley *et al.*, 2001; Bowman and Prior, 2005; Lehmann *et al.*, 2009). Finally, evergreen woody species are dominant in Mediterranean ecosystems (Cody and Mooney, 1978), despite the out-of-phase patterns in temperature, light, and water availability.

Among tropical drought-deciduous species, median C gain suggests that the most beneficial strategy is scheduled normal flushing in drier sites and where roots are shallow (strategy N in Figure 7 left), while in wetter locations C gain is maximized by opportunistic and early scheduled flushing (strategies s^* and E in Figure 7 left). Indeed experimental observations in the Darwin area showed that 80% of the dominant species flushed leaves during the dry

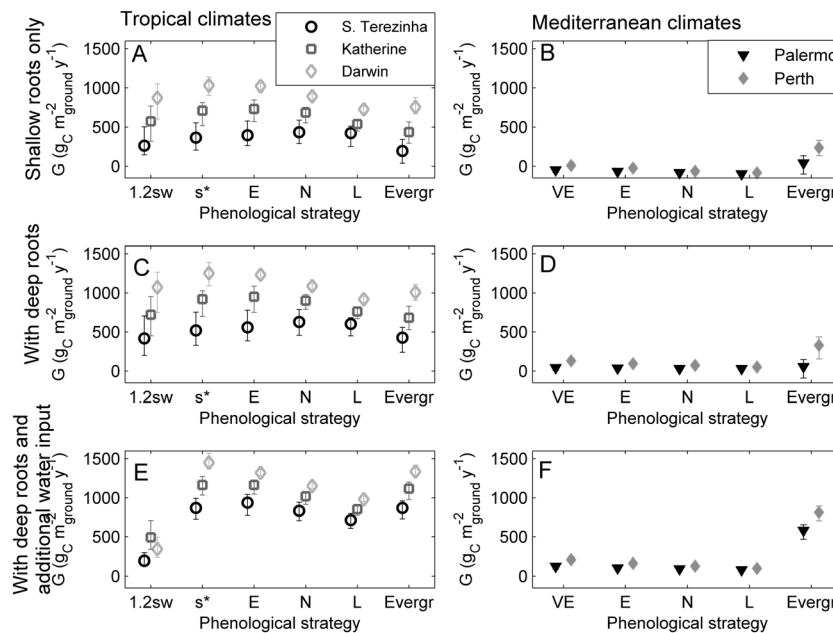


Figure 7. Median (symbols) and 25–75 percentiles (whiskers) of carbon gain G as a function of phenological strategy and access to deep water stores, for (left) three contrasting tropical climates and (right) two Mediterranean climates (Table I, Figure 1). A and B refer to plants with shallow roots ($\alpha=1$). C–F refer to deep-rooted plants accessing the deep water store without ($I=0$; C,D), or with groundwater recharge ($I=0.5 \text{ mm d}^{-1}$; E,F). Opportunistic flushing is triggered at $s_{\text{flush}}=1.2s_w$ and s^* . Scheduled flushing is defined with respect to typical onset of wet season in tropical regions or the spring equinox in Mediterranean climates (VE, 40 days earlier; E, 20 day earlier; N, at the onset of wet season/equinox; L, 20 days after). All the other parameters are as in Figure 4. Additionally, for the carbon balance, $f_{\text{resp}}=0.07$, $f_C=0.45$, $f_{\text{flush}}=1 \text{ y}^{-1}$ for drought-deciduous species and 0.67 y^{-1} for evergreen species, $\eta_A=0.65$, $c_a=380 \mu\text{mol mol}^{-1}$, $a=1.6$, and A_{max} , $g_{s,\text{max}}$, and SLA are the median of the data in Figure 4 (only angiosperms are considered).

season, i.e. ‘early’ (Williams *et al.*, 1997). Indian SDEs, which are affected by the Indian Ocean Monsoon like Northern Australian SDEs, also exhibit early scheduled flushing (1–2 months before the beginning of the wet season; Kushwaha and Singh, 2005) or opportunistic flushing triggered by pre-monsoonal rainfall events despite low soil water contents (Prasad and Hedge, 1986). The model results also show that shifting from opportunistic to normal and late scheduled strategies in Santa Terezinha increases the median leaf duration and C gain. The opposite trend holds in Darwin and Katherine, in particular in the presence of deep roots. These findings are consistent with the general phenological pattern suggested by Rivera *et al.* (2002), with photoperiod-driven leaf flushing often occurring where annual precipitation is above 800 mm (and the dry season lasts 4–6 months) but rarely in the presence of lower annual rainfall (such as in Northeastern Brazil) or shorter dry seasons. In contrast to tropical ecosystems, in Mediterranean SDEs early or very early scheduled flushing (strategy VE and E in Figure 7 right) increases leaf duration and C gain by allowing the exploitation of late winter and early spring rainfall.

Within this general framework, the variability of the climatic forcing may cause marked inter-annual variability in C gains (whiskers in Figure 7 represent the 25th and 75th percentiles). The more consistent seasonality in Mediterranean compared with tropical climates (Figure 2) is mirrored by the lower variability in leaf durations and, as a consequence, in C gain. Conversely, in tropical SDEs, the inter-annual variability in C gain within a phenological strategy is comparable with the differences among phenological strategies. It follows that the ‘optimal’ leaf strategy changes from year to year, explaining the coexistence of the different phenologies in many SDEs. For example, the *caatinga* (the most common ecosystem in the Santa Terezinha region) comprises species that flush their leaves before the beginning of the wet season, apparently in response to isolated rainfall events (Machado *et al.*, 1997), and scheduled flushers with higher stem water storage (Lima and Rodal, 2010). Moreover, in Northern Australia, a generally evergreen overstorey coexists with a drought-deciduous understorey (Hutley *et al.*, 2001).

The model results further suggest that access to deeper water stores allows a higher total transpiration and enhance net C gain, by reducing water lost to deep percolation, and by buffering rainfall intermittency. The buffering effect of deep soils is particularly relevant in Mediterranean drought-deciduous scheduled species, for which a deeper storage allows a better exploitation of winter precipitation, as long as such storage is replenished during the wet season (Viola *et al.*, 2008). While these results are consistent with observations (Schenk and Jackson, 2002) and model predictions (Guswa, 2008; Feng *et al.*, 2012) in both tropical and Mediterranean ecosystems, net C gain across

rooting depths should not be compared here, as root construction and maintenance costs have not been included. In general, while deep roots may provide a C benefit if the wet season is characterized by deep but intermittent rainfall events, or for Mediterranean species utilizing stored winter rainfall, their cost may not be balanced by enhanced C uptake in wet climates or when rainfall intermittency in the wet season is low (Guswa, 2008)

Finally, groundwater input to the deeper water store is in most cases beneficial, with the notable exception of opportunistic species (Figure 7 bottom). In fact, the dry season recharge of the deep water store may cause those species to flush their leaves well before the wet season begins, but the little available water is often unable to support plant activity for long periods. The other effect of rainfall-independent groundwater input is buffering against rainfall intermittency, thus generally limiting the inter-annual variability in net C gains.

NON-ECOHYDROLOGICAL DRIVERS OF LEAF PHENOLOGY

The framework discussed here makes it possible to capture the effects of rainfall occurrence on water availability and C dynamics. Nevertheless, there are other ecological and evolutionary factors that may influence the phenological strategies observed in SDEs, such as herbivore-leaf interactions, fire frequency, nutrient availability, and evolutionary legacies.

In many locations, insect herbivory plays a role in defining the most beneficial leaf phenology (van Schaik *et al.*, 1993; Reich, 1995; Eamus and Prior, 2001; Wilf *et al.*, 2001), with implications for many processes that shape and maintain SDE structure (Coley and Barone, 1996). Plants can invest C in chemical and physical defences, reducing palatability, at the expense of photosynthetic capacity, and hence C gain and growth rate (Herms and Mattson, 1992; Pringle *et al.*, 2011). This strategy tends to be associated with evergreen species. Conversely, drought-deciduous species maintain high growth rates (which may require high nitrogen content and lead to palatable, tender leaves; Agrawal and Fishbein, 2006) and optimize leaf flushing time to limit leaf predation of young, more palatable leaves. Depending on resource availability, three leaf flushing strategies can be applied. One option is to flush the leaves during the dry season when insects are less prevalent (Aide, 1988; Aide, 1992; Murali and Sukumar, 1993; Sloan *et al.*, 2007); insect damage during the subsequent wet season then occurs on old leaves with decreased photosynthetic capacity. This strategy is feasible only when dry season water storage levels sustain transpiration prior to the wet season. The second strategy is community synchronization of leaf flushing during the wet season, leading to herbivore satiation (Lieberman and Lieberman, 1984; van Schaik *et al.*, 1993).

A third option is delayed leaf greening, so that leaves become nutritionally appealing only after toughening (Kursar and Coley, 1992).

Fire disturbance may further alter SDE C balance. Fire is a natural event in many Australian, African and Californian SDEs, while it is mainly linked to human presence in South America and in other Mediterranean-type ecosystems (Murphy and Lugo, 1986; Bowman and Prior, 2005), thus resulting in fewer fire-adapted species in the latter SDEs (Lock, 2006). Because fires occur mostly during the dry season, they mainly damage the evergreen species, altering the active leaf lifespan and reducing the benefits of evergreen leaf habit. The frequency of fires may be reduced by the activity of large grazers, which reduce fuel loads (typical of African SDEs).

Nutrient availability may be an additional factor in determining dominant leaf habit. For example, low-fertility Australian soils may favour evergreens (Bowman and Prior, 2005), because their longer lifespan and lower nutrient concentrations enhance nutrient retention in the ecosystem (Aerts, 1995).

Finally, the physiological mechanisms that generate plant responses to phenological cues appear to be highly heritable (Vitasse *et al.*, 2009; Alberto *et al.*, 2011), raising the prospect that observed phenological strategies may not always represent an adaptation to local conditions so much as a legacy of historical climate and species assemblages. For example, although evergreen habit appears to be favourable in Mediterranean climates (Figure 7), evergreen and winter-deciduous species coexist in Mediterranean climates in Europe, the Middle East, and the USA (Blumler, 1991). The origin of this coexistence is hypothesized to lie in Pleistocene climates when cold winters would have eliminated sclerophyllous species and favoured winter-deciduous trees (Wright, 1962; van Zeist, 1967).

SYNTHESIS AND CONCLUSIONS

Despite differences in temperature regimes, tropical seasonally dry and Mediterranean climates share similarities in their rainfall patterns, in terms of both seasonality and inter-annual variability. Thus, a common framework is appropriate to investigate the ecohydrology of SDEs. To cope with the fluctuations in water availability, plants in SDEs have developed a wide array of adaptation strategies. A synthesis of field observations revealed that leaf phenological strategies, rather than plant ecophysiological traits, provided the greatest source of variation in plant level ecohydrology under a given climate. Leaf phenology therefore plays a crucial role in determining C and water fluxes in SDEs, as quantitatively explored here by a minimalist ecohydrological model applied to five case studies with contrasting rainfall regimes. Our results suggest that longer and more intense dry seasons favour

deciduous plants, while the evergreen leaf habit is beneficial in wetter tropical climates, particularly in the presence of deeper water stores, as well as in Mediterranean ecosystems. Among drought-deciduous species, the inter-annual variability in rainfall is likely to support the coexistence of multiple leaf flushing strategies. Nevertheless, more aggressive strategies (early scheduled flushing or flushing in response to small rainfall events) are generally beneficial when the wet season is consistent and in Mediterranean climates where early spring flushing allows the exploitation of the last part of the wet season and winter water stores. These modelling results are supported by phenological observations across SDEs.

Ongoing and predicted changes in global climate are anticipated to alter seasonal rainfall patterns and thus the functioning of SDEs (Feng *et al.*, 2013). Climatic changes are likely to increase dry season duration and decrease soil moisture in tropical SDEs (Hulme and Viner, 1998; Wetherald and Manabe, 2002; Jung *et al.*, 2010). Changes in the Mediterranean Basin include decreases in mean precipitation and increased variability during the dry season (e.g. Giorgi, 2006; Goubanova and Li, 2007; Alpert *et al.*, 2008; Arnone *et al.*, 2013). If these changes continue, they will stretch the adaptive limits of plants and prompt possible shifts in ecosystem composition and geographical range. On the one hand, decreasing rainfall may shift leaf phenology from evergreen to drought-deciduous species, as rainfall may become insufficient to replenish soil water reserves regularly (Borchert, 1998; Enquist and Enquist, 2011). On the other hand, a less marked seasonality may shift species composition toward a higher fraction of evergreens (Givnish, 2002). Superimposed on these patterns, the projected increases in ambient CO₂ concentration may reduce transpiration rates and slow the depletion of soil moisture, further favouring longer leaf lifespans (Reich, 1995) and increasing the total C gain in deciduous species. However, these beneficial effects of CO₂ enrichment might be offset by faster soil water depletion and reduced leaf lifespan caused by the expected increases in temperature and VPD. Shifts in species composition may have significant implications for the long-term water balance of SDEs, with higher abundance of drought-deciduous species resulting in larger fluctuations of soil moisture and an increase in deep percolation and hence groundwater recharge. Also, water availability impacts biogeochemical cycles, so that an increased variability in wet season timing may have deleterious effects on the coordination of nutrient mineralization supply and demand by vegetation (Lodge *et al.*, 1994; Augustine and McNaughton, 2004), and changes in rainfall regimes will likely alter soil C storage (Rohr *et al.*, 2013).

Given the global distribution of SDEs, their ecological complexity and relevance for human activities, and the still limited understanding of ecological fluxes and functioning,

there is a clear need for additional research, made urgent by the rapid and potentially severe climate change projected for these ecosystems.

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