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SYNTHESIS

Leaf angle as a leaf and canopy trait: Rejuvenating its role in ecology with new technology

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Abstract

Life on Earth depends on the conversion of solar energy to chemical energy by plants through photosynthesis. A fundamental challenge in optimizing photosynthesis is to adjust leaf angles to efficiently use the intercepted sunlight under the constraints of heat stress, water loss and competition. Despite the importance of leaf angle, until recently, we have lacked data and frameworks to describe and predict leaf angle dynamics and their impacts on leaves to the globe. We review the role of leaf angle in studies of ecophysiology, ecosystem ecology and earth system science, and highlight the essential yet understudied role of leaf angle as an ecological strategy to regulate plant carbon–water–energy nexus and to bridge leaf, canopy and earth system processes. Using two models, we show that leaf angle variations have significant impacts on not only canopy-scale photosynthesis, energy balance and water use efficiency but also light competition within the forest canopy. New techniques to measure leaf angles are emerging, opening opportunities to understand the rarely-measured intraspecific, interspecific, seasonal and interannual variations of leaf angles and their implications to plant biology and earth system science. We conclude by proposing three directions for future research.

KEYWORDS
canopy optimization, leaf economics spectrum, light environment, photosynthesis, radiative transfer

OVERVIEW

Leaf angle, the angle between the leaf normal and the zenith (Figure 1, Box 1), is a key leaf trait associated with light interception, photosynthesis, energy balance and competition among individual plants (Anten, 2005; Nilsen & Forseth, 2018; Ross, 1980). These physiological effects of leaf angle are an important component of plant ecological strategy and can scale up to significantly impact land surface properties such as carbon flux, surface temperature and spectral signature (Baldocchi et al., 2002; Myneni et al., 1986; Ollinger, 2011). Interest in leaf angles traces back to the pre-Socratic philosophers Anaxagoras and Empedocles (Whippo & Hangarter, 2006), while modern scientific studies on leaf angles originated in the 19th century by scientists including Darwin and Darwin (1880). Since the mid-20th century, the importance of leaf angle in light interception and photosynthesis has been recognized by pioneering ecological studies (e.g. Monsi & Saeki, 1953; Yin, 1938). Despite these early works, leaf angle has been the green elephant in the ecological room: For example, the acclimation and adaptation of leaf angle in response to environmental and biological drivers represent an important but poorly understood set of plant behaviours (Ehleringer & Forseth, 1980); leaf angle is critical to many ecosystem processes and remote sensing measurements (Figure 2); the role of leaf angle in competition among individuals has rarely been explored (Hikosaka & Hirose, 1997; Pearcy et al., 2004). Meanwhile, leaf angle is often inadequately represented in models and rarely measured in the field, mainly due to the difficulties in measuring leaf angles of complex canopies. With the rapid development of new technologies and algorithms (e.g. Stovall et al., 2021; Vicari et al., 2019), we are on the cusp of understanding this critical dimension in vegetation structure and function.

The importance of leaf angle to physiological processes is hard to overstate: A ten-degree change in the angle of incidence (Figure 1) from 50 to 60 degrees can result in an instantaneous difference in intercepted direct radiation by 22%, which can, in turn, have similar level impacts on photosynthesis, leaf temperature, transpiration and energy balance (Figure 2). Similar rates of changes in light interception at the daily scale have been found in simulations (Pearcy et al., 2005). Leaf angle adjustment can thus be a strategic response to variability in light, heat or water conditions. Studies on short-stature plants (crops, shrubs and grasses) have shown that plants adjust leaf angles to improve light interception or avoid excessive light absorption and damage, with consequent improvements in water use efficiency (King, 1997). Diurnal leaf angle movements in soybean and some desert plants of as much as 60 degrees have been widely observed and viewed as a strategy to adjust light interception and water loss (Ehleringer & Forseth, 1980; Kao & Forseth, 1992b). In general, leaves are more vertical in dry and hot environments while more horizontal in mesic and light-limited environments. However, the range of leaf angle varies significantly even within the same environment and the same individual, indicating additional biological and environmental drivers at play.

The short-term (acclimation) and long-term (adaptation) responses of leaf angle to the changing

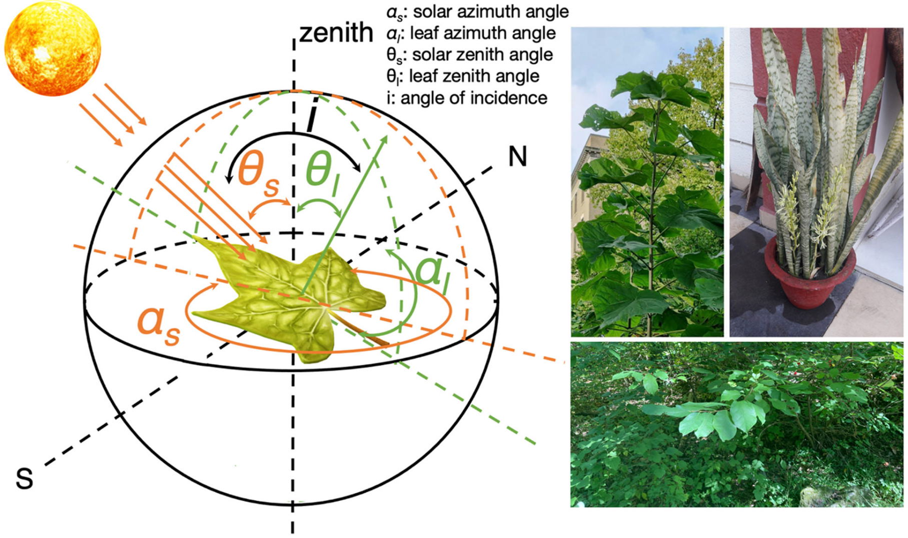

FIGURE 1 Diagram of leaf and solar angles. θ_l is the leaf inclination angle from horizontal, equivalent to the angle between the leaf normal and the zenith (the green arrow is the leaf normal); θ_s is the solar zenith angle; α_s is the solar azimuth angle; α_l is the leaf azimuth angle. The solar plane is denoted as a semi-circle in orange, and the plane that the leaf normal locates is denoted as a green semi-circle. The cosine of the angle of incidence (cos *i*) represents the cosine of the angle between the solar beam and the leaf surface, and it is calculated as $\cos i = \cos\theta_l \cos\theta_s + \sin\theta_l \sin\theta_s \cos(\alpha_s - \alpha_l)$. The right-hand side shows examples of plants with different leaf angle strategies. (Clockwise): Empress tree (*Paulownia tomentosa*) with close-to-horizontal leaves, Snake plant (*Dracaena trifasciata*) with close-to-vertical leaves and Northern Spicebush (*Lindera benzoin*). Credit: Xiangtao Xu, Manuel Lerdau and Wikipedia.

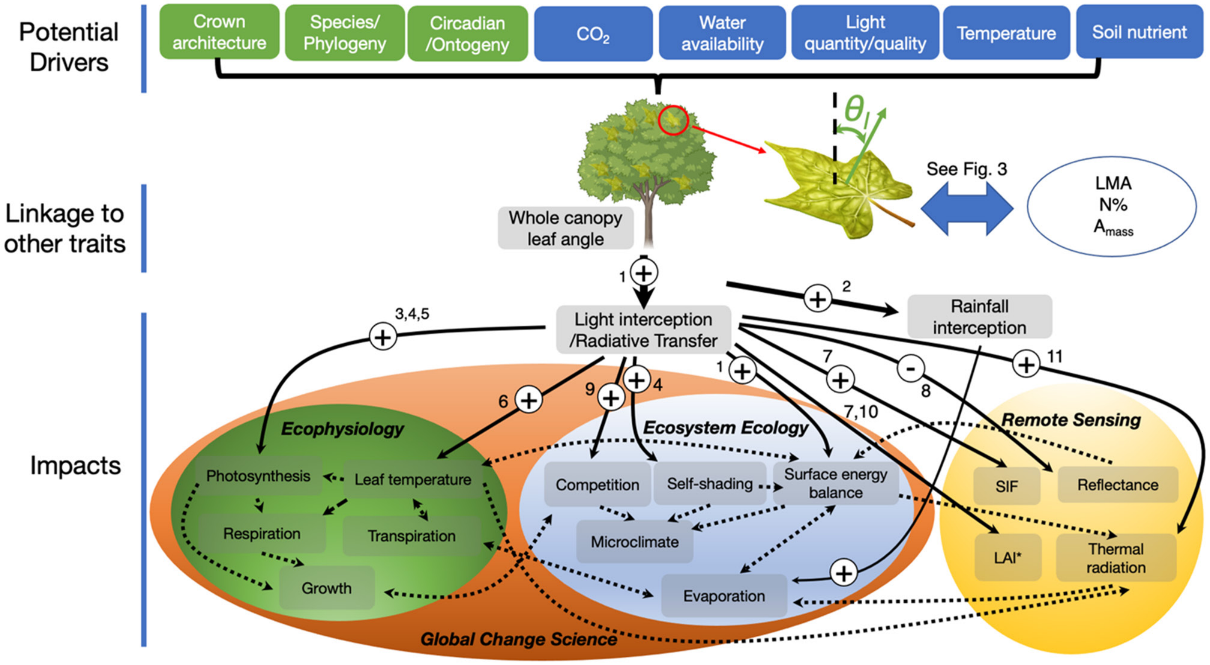

FIGURE 2 Conceptual framework to understand the drivers of leaf angle and the ecological processes associated with leaf angle. The leaf inclination angle (θ_l) is depicted in the center. From top to bottom are the potential drivers of leaf angle, the linkage between leaf angle and other leaf traits, and the impacts of leaf angle on ecophysiological processes, ecosystem processes, global change science and remote sensing metrics. The drivers of leaf angle variations are divided into biotic (green) and environmental (blue) factors. Leaf traits that may be related to leaf angle include Leaf Mass per Area (LMA), leaf nitrogen content (N%) and mass-based leaf photosynthesis (A_{mass}). See Figure 3 for details. Leaf angle's impacts on light and rainfall interception have cascading effects on the processes down the road. The direct impacts on processes via light or rainfall interception are marked as solid lines. The indirect impacts on other ecosystem processes are marked as dashed lines. Positive or negative relationships between leaf angle and ecosystem processes are marked as + or −. We limited these markers to solid lines only. References: 1. Baldocchi et al., 1985; 2. Aston, 1979; 3. Anten, 2016; 4. Pearcy et al., 2005; 5. Monsi & Saeki, 1953; 6. Gates and Tantraporn 1952; 7. Stovall et al., 2021; 8. Ollinger, 2011; 9. Hikosaka & Hirose, 1997; 10. Jonckheere et al., 2004; 11. Guillevic et al., 2003. Note that LAI* means that the estimation of LAI with optical approaches are based on certain assumptions of leaf angle distribution. In addition, the boundaries between ecophysiology, global change science and ecosystem ecology are not always as clear as this graph indicates.

environment can be understood within the framework of the Eco-Evolutionary Optimality (EEO) theory (Harrison et al., 2021; MacArthur & Pianka, 1966; Mooney, 1972). Leaf angle plays a similar role as stomates at the leaf level: By adjusting stomatal conductance, a balance between carbon gain and water loss is achieved; by adjusting leaf angle, the plant canopy can achieve optimized carbon gain while reducing heat stress and water loss. Since leaf angle is tightly related to light interception and leaf energy balance, we expect a close relationship between leaf angle and other important leaf traits in the Leaf Economics Spectrum (LES), such as leaf nitrogen content, leaf mass per area (LMA) and maximum photosynthetic rate (Wright et al., 2004).

Leaf angle also plays a vital role in ecosystem ecology and earth system science. One of the longstanding challenges in ecosystem science is scaling leaf-level processes from the organism level to the global scale (Monson & Baldocchi, 2014; Ollinger, 2011). Fundamental processes such as light absorption, energy balance and photosynthesis are well characterized at the leaf level. Still, the upscaling of these processes to the canopy scale has remained relatively intractable. One main obstacle has been accurately characterizing canopy structures and leaf angle profiles. Modelling studies have shown that leaf angle is an essential parameter to drive simulations of carbon flux, energy flux and remote sensing signals (Baldocchi et al., 2002; Verrelst et al., 2015). Yet, in almost all cases, the leaf angles used in these models are based on a few hypothetical Leaf Angle Distribution types (LADs) (Box 1) and not actual measurements from field studies (e.g. Baldocchi et al., 1985; Oker-Blom & Kellomäki, 1982). These oversimplifications have resulted from a lack of a coherent perspective to develop predictive models of leaf angles and, just as importantly, an absence of empirical data regarding leaf angles in large plants such as trees.

We provide a conceptual framework to understand the drivers of leaf angle and the implications of leaf angle for environmental physiology, ecosystem ecology, global change science and remote sensing (Figure 2). We also discuss technological breakthroughs that allow leaf angle measurements at scales relevant to earth system science. The following sections develop this framework by (i) summarizing the underlying ecophysiological controls over leaf angles and the impacts of adjusting leaf angles on canopy fluxes and temperatures. (ii) synthesizing the relationship between leaf

BOX 1 Definitions of leaf angle.

Here we provide a summary of multiple definitions related to leaf angle. We then present an argument for moving beyond using the statistical distribution of leaf angle for the entire canopy, emphasizing the spatial distribution of leaf angle within a canopy, particularly the vertical distribution of leaf angle. It should be noted that there are other angles that also can be important for plants, including the rotational angle of the leaf blade around the petiole (e.g. Farque et al., 2001), the angle of the petiole itself and, for needle leaves, the shoot angle. These terms are not covered in this box.

Leaf inclination angle: ('leaf angle (LA)' in this study, denoted as θ_L): the angle between the leaf plane and the horizontal plane.

Leaf zenith angle: the angle between the leaf normal and the zenith (vertical direction). Mathematically, it is the same as the leaf inclination angle.

Leaf azimuth angle (α_L): the azimuth angle of the leaf normal relative to the north.

Mean leaf angle (MLA): the average leaf angle of the entire plant canopy. Mathematically, it is $\int_0^{\pi/2} \theta_L f(\theta_L) d\theta_L$. $f(\theta_L)$ is the leaf angle probability density function.

The angle of incidence (*i in* Figure 1): the incidence angle of the direct solar beam on the leaf surface, affecting the amount of intercepted radiation.

Leaf angle distribution (LAD) and the G-function: LAD is the statistical distribution of the fraction of leaf area at any given leaf angle. The probability density function of leaf angle ($f(\theta_L)$) is often fitted with a two-parameter Beta distribution (de Wit, 1965) or similar variants (Campbell, 1990), or a function that is based on trigonometry (Verhoef, 1984). Six types of LADs are widely used by modellers, including planophile (most leaves are flat), plagiophile (most leaves are oblique), erectophile (most leaves are vertical), extremophile (most leaves are either vertical or horizontal), uniform (equal number of leaves with every zenith angle) and spherical (imagine that leaves cover the entire surface of a sphere, the LAD is spherical). While LAD is often assumed to be spherical (Baldocchi et al., 2002), LAD is highly variable across species, and many common species have nonspherical LAD (Pisek et al., 2013; Ross, 1980).

The G-function, a widely used term in radiative transfer modelling, is the ratio of the leaf area projected on the plane perpendicular to the incoming solar beam and the actual leaf area (Ross, 1980). G-function is a critical canopy structural parameter that varies with solar zenith angle and LADs. Moreover, leaf clumping is also associated with leaf angle and has been shown to have vertical variations (Béland & Baldocchi, 2021; Pearcy et al., 2005). For the entire canopy, the probability of light transmission, gap fraction (P_{gap}), is estimated with G-function multiplied by LAI and the leaf clumping coefficient (Ω) divided by the cosine of viewing zenith angle ($cos\theta_v$. Equation 1; Monson & Baldocchi, 2014; Cescatti & Niinemets, 2004). We can measure the probability of light transmission.

$$P_{gap} = \exp\left(\frac{-\Omega \times \mathrm{G} \times \mathrm{LAI}}{cos\theta_V}\right) \tag{1}$$

LADs have been efficient in radiative transfer models and land surface models as it only requires one or two parameters (Table 1). Yet, the LAD of a canopy does not provide any information about the vertical variations of leaf angle within a canopy, which is important for modelling the canopy profiles of light and temperature. For example, consider extreme cases of a spherical canopy in which more leaves are vertical than horizontal. Comparing a scenario in which most vertical leaves are at the top canopy with another scenario in which most flat leaves are at the top canopy, the former would likely have a lower canopy temperature at the top and a warmer understory during mid-day. Here, we provide four examples with different leaf angle distributions and profiles. One notable example is *Cecropia schreberiana*, an early successional species in neotropical forests. This is a typical example of a canopy with planophile leaf angle distribution (Figure 3a), which is rarely observed in canopy tree species. The example with *Quercus alba* represents a typical temperate tree species, which has higher leaf angles at the top and lower leaf angles at the bottom. However, we also see significant variations in the vertical profiles for co-occurring species: The black walnut (*Juglans nigra*) individual here has a vertical profile with minimal variations in leaf angle, whereas the American beech example (*Fagus grandifolia*) shows ~20-degree decline in MLA in the top canopy (Figure 3).

TABLE 1 Leaf angle parameter and its variability within models

Model	Leaf angle parameter	Variability	Scale	Notes
CLM	χ_L—the departure of leaf angles from a spherical distribution and equals +1 for horizontal leaves, 0 for spherical leaves (spherical LAD) and −1 for vertical leaves.	Varies among PFTs with predefined values but fixed temporally; multilayer possible but no vertical profiles of leaf angle have been considered yet.	Global (land component of CESM)	$\mathrm{Cos(theta)} = (1 + \chi_L)/2$, theta is the mean leaf angle of the canopy (Lawrence et al., 2019)
LPJ-GUESS	None	None	Global	Smith, 2001
ORCHIDEE	None	Assumed spherical	Global	Pinty et al., 2006
CABLE	Same as CLM	Varies among PFTs with predefined values but fixed temporally		Wang & Leuning, 1998
SEIB	None	None	Plot to global (land component of MIROC-ESM)	Sato et al., 2007
ED2	Same as CLM	Varies among PFTs with predefined values	Plot to global (land component of Regional Atmospheric Modelling System)	Longo et al., 2019
FATES	Same as CLM	Varies among PFTs with predefined values	Plot to global (terrestrial ecosystem component of E3SM)	Koven et al., 2020
LM3-PPA	None	Assumed spherical	Plot to global	Farrior et al., 2013
SCOPE	LIDFa, LIDFb—two parameters of the fit to the LAD	Model input, default is spherical but can be changed by user	Plot	van der Tol et al., 2009
DART	Leaf angle distribution function	Not fixed. Predefined or determined based on imported 3D object (TLS point clouds for example)	Individual to plot	Gastellu-Etchegorry et al., 2017
FLiES	Leaf angle distribution function	Fixed and spherical leaf angle distribution (G = 0.5)	Individual to plot	Kobayashi & Iwabuchi, 2008
Y-PLANT	Realistically represented with measurements, rather than as a parameter(s)	Realistic	Individual; not applicable to larger scales due to computational requirements	Pearcy & Yang, 1996

angle and other leaf traits, (iii) examining the implications of leaf angle for ecosystem processes, (iv) highlighting the new technological development in leaf angle measurements with terrestrial laser scanning (TLS) and (v) reviewing leaf angle in models. We argue that with new technological developments to measure leaf angle (e.g. TLS or digital cameras), we are entering a new era in studying vegetation's structural and functional responses to the environment. Finally, we offer a roadmap to better integrate leaf angle across plant biology, ecology and earth system science.

UNDERSTANDING THE ENVIRONMENTAL AND BIOLOGICAL DRIVERS OF LEAF ANGLE VARIATIONS

Plants adjust to the environment by acclimation on shorter time scales (hours to months—ecophysiological changes) and adaptation on longer time scales (years—genetic adjustments). Leaf angle is no exception—changes in leaf angle serve to maximize carbon gain and reduce stresses (Kao & Forseth, 1992b). The variations in leaf angle are oftentimes coordinated with other physiological and structural traits. A useful framework to understand the changes in leaf angle and its relationship with other traits is the evolutionarily based optimality theory (MacArthur & Pianka, 1966; recently renamed Eco-Evolutionary Optimality [EEO] by Harrison et al., 2021). The EEO theory assumes that noncompetitive trait combinations are eliminated during evolution, and thus, there are only a few predictable sets of coordinated trait combinations in different ecophysiological processes and parts of a plant. In this section, we summarize studies to answer the following questions: (1) What is the extent of leaf angle variability among species? (2) What are the physiological mechanisms by which leaves adjust their angles? (3) How do environmental drivers affect leaf angles? We then present a framework based on the EEO to understand the variations in leaf angle and the relationship between leaf angle and other traits.

Leaf angle has significant interspecific, vertical, latitudinal and seasonal variations. Falster and

Westoby (2003) found the MLA varied by 40–60 degrees in 26 shrub species in Australia. Similarly, temperate broadleaf trees have shown significant interspecific differences in leaf angle (with the MLA varying from 16 to 60 degrees, Pisek et al., 2022). Leaves are more vertical in the top canopy (MLA = 43 degrees) than in the lower canopies (MLA = 17 degrees) in a tropical forest (Hollinger, 1989)—a strategy to enhance whole canopy photosynthesis. A similar pattern of vertical leaf angle variation has been observed by many, including Hutchison et al. (1986) in a temperate forest. Leaf angle varies on a latitudinal gradient—using a common garden approach, Hopkins et al. (2008) showed that the MLA of *Arabidopsis thaliana* grown at different latitudes (37–61 degrees N) varied by ~15 degrees. Leaf angle also varies seasonally, particularly for forest understory species (Stovall et al., 2018).

Plants utilize two types of physiological mechanisms to adjust leaf angles (Nilsen & Forseth, 2018; van Zanten et al., 2010): turgor adjustment using a specialized part at the base of the leaf called the pulvinus or differential cell growth at the abaxial and adaxial side of the petiole. Using these mechanisms, plants adjust leaf angle over the short- or long-term in response to environmental and biological drivers (Figure 2). Some of these drivers are well documented, including light, temperature, gravity, circadian rhythm and water, whereas other factors such as CO_2 (Jayawardena et al., 2019), nutrient availability and phylogeny are less studied. In addition, different parts of a leaf can change their angles at different rates—an extreme case is the curling of a leaf during water stress. In this case, a single leaf angle value cannot fully capture the complex changes.

Both environmental and biological drivers control the variations in leaf angles. A seminal study by Ehleringer and Forseth (1980) showed that desert species change leaf angles according to solar position—leaves that are perpendicular to direct solar beams have a higher photosynthetic capacity; leaves that are parallel to the solar beams lose less water and are cooler. Early work by Mooney et al. (1974) along an environmental gradient in California has shown that shrubs tend to have leaves with lower leaf angles (more horizontal) in the foggy, humid areas in Northern California. Water availability is also one of the major drivers of leaf angle variations because the maintenance of optimal leaf orientation is supported by leaf turgor (Nilsen, 1987). The adjustment in leaf angles may ease the need for leaves to make other physiological or biochemical changes in the face of stresses (Lovelock & Clough, 1992; Pastenes et al., 2005). Nutrient availability is another environmental driver of leaf angle variations. In a controlled experiment on wheat, individuals in high N plots have leaves with lower leaf angles compared with those in low N plots, indicating high N in leaves allows for higher processing capacity for incoming radiation (e.g. higher V_{cmax} or $J_{\max}$), enabling leaves to intercept more radiation per unit area by adjusting leaf angle more horizontally (Brooks et al., 2000).

A crucial question regarding the control over leaf angle is 'To what extent are the observed leaf angle variations driven by genetics?' Several genes and quantitative trait loci (QTL) for leaf angle have been identified in crops and utilized to enhance light absorption. Several genes regulate the hormone brassinosteroid (BR), which serve as the primary control of leaf angle in crops (Mantilla-Perez & Salas Fernandez, 2017). Moreover, the diel variation of leaf angles responds to inheritable biological rhythms that are fundamental for protecting from photoinhibition and are also responsible for 15–25% daytime variation in photosynthesis (Resco de Dios & Gessler, 2018). There are still significant knowledge gaps to fill, and similar studies on trees are scant (van Zanten et al., 2010).

The importance of genetics in regulating leaf angles implies that evolutionary history and phylogenetics must also be considered when examining the environmental regulation of leaf angles and the distribution of leaf angles within and among taxa (Owen et al., 2021). The importance of taxonomic identity has been recognized in the study of plant architecture (Hallé et al., 1978), although leaf angle has received less attention. There are two major reasons for considering phylogeny when trying to understand leaf angle. First, the absolute value and variability of leaf angle may be regulated by phylogeny. To our knowledge, the phylogenetic signals in leaf angle distributions have not been formally studied. Second, architecture at the scale of branching patterns shows a strong relationship to phylogeny. Since the branching pattern is directly linked to the leaf angle, there is at least an indirect signal of phylogeny on the leaf angle.

The relationship between leaf angle and other leaf traits has been documented in many studies, but they are often presented in intellectual silos. We use the EEO framework to understand the short and long-term variations in leaf angle (Figure 4). Over the long-term, leaf angles vary along the 'fast-slow' leaf economics spectrum (Wright et al., 2004): Plants with lower LMA, higher N%, higher maximum photosynthetic rate ($A_{\max}$) and lower leaf lifespan (LL) would have lower leaf angles and vice versa. Resource availability may affect leaf angle as strongly as other traits well understood within the LES framework (Ollinger, 2011). The hypothesized relationships between leaf angle and other traits should be viewed as the convergent and coordinated behaviour of leaf traits driven by environmental and biological drivers rather than treating leaf angle as the driver per se. Indeed, experiments on crop species have demonstrated that individuals in plots with high nutrient availability (N or P) have leaves with lower leaf angles compared with those in the controlled plots (Brooks et al., 2000; Kao & Forseth, 1992a). Posada et al. (2009) documented a negative relationship between light intensity and leaf angle in a tropical rainforest. Due to a positive and hyperbolic relationship between maximum photosynthesis ($A_{\max}$) and light intensity, it can be deduced that the relationship

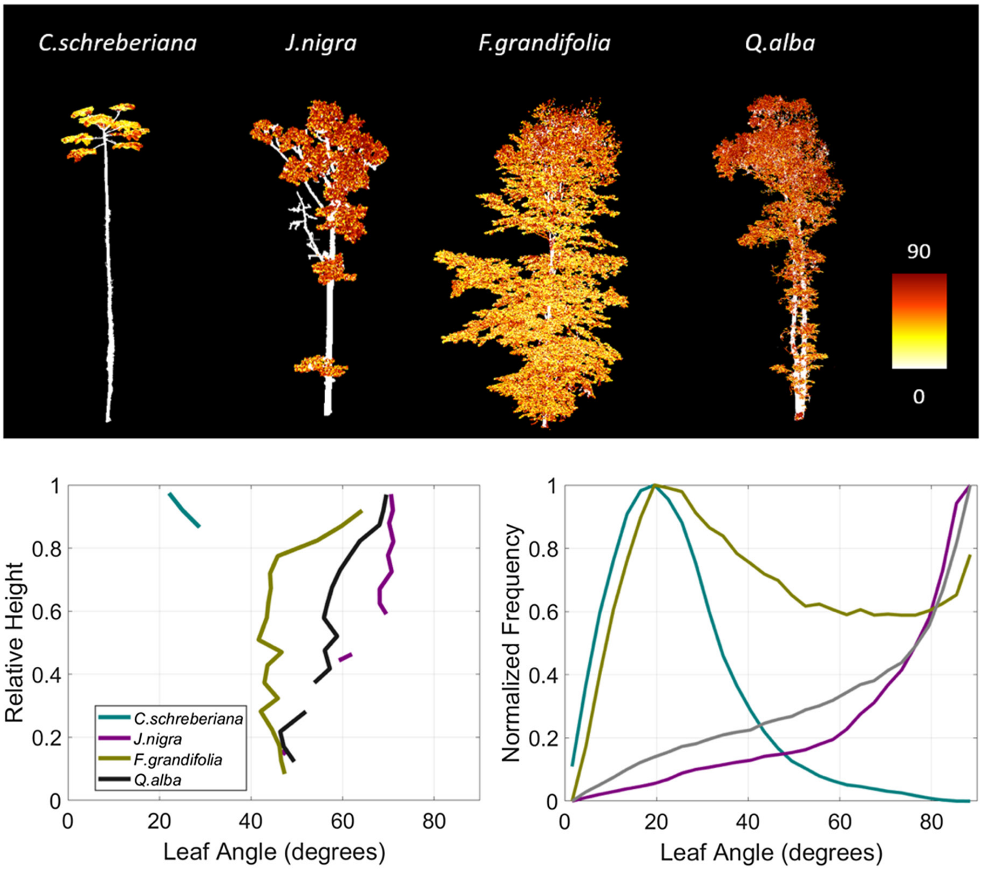

FIGURE 3 Examples of leaf angle strategies from four individuals, including *Cecropia schreberiana*, *Juglans nigra*, *Fagus grandifolia* and *Quercus alba*. For the method to extract the leaf angle of individual trees, see Stovall et al., 2021. The top panel shows 3D visualizations of the surface angles of four individuals. The lower left panel shows the vertical profiles of four individuals. Height values were normalized relative to the highest point of each tree. The lower right panel shows the frequency distribution of the leaf angle values.

between Amax and leaf angle is negative. A steeper leaf angle means less radiation absorbed when solar radiation is the strongest and less need for absorbing and processing the absorbed solar radiation. Therefore, the negative correlation between N% and LMA would result in a positive correlation between leaf angle and LMA. The relationship between the optimum photosynthetic temperature (T_{opt}) and leaf angle comes from two aspects: carbon gain (the relationship to N% and LMA) and leaf energy balance (Michaletz et al., 2016). We hypothesize that leaves with a steeper leaf angle have lower optimum photosynthetic temperature values because of the observed negative correlation between LMA and $\mathrm{T}_{\mathrm{opt}}$. The link between leaf angle and other traits based on the EEO could provide an opportunity for a more parsimonious land surface modelling in that canopy structural traits could be constrained by other leaf traits and vice versa. Leaf angle is also related to the optical properties of canopies—a steeper leaf angle may result in a lower reflectance in the near-infrared region, making it possible to use optical remote sensing to estimate leaf angle (Ollinger, 2011). Over the short-term, leaf angle may respond to environmental stresses such as drought or high temperature. Several crop experiments have shown that leaf angles are related to leaf water potential during drought (Kao & Forseth, 1992a; Pastenes et al., 2005). The relationship between leaf angle and leaf water potential has been observed in shrubs and forests (Comstock & Mahall, 1985). Thus, along the 'high-low' stress spectrum, leaves with a higher water potential should have a lower leaf angle, so that the irradiance at the leaf surface is often at the breakpoint of the light response curve, the point at which photosynthesis is co-limited by ribulose bisphosphate regeneration and carboxylation (Nilsen & Forseth, 2018), or at the point that the light use efficiency is highest (Posada et al., 2012). A reduction in leaf water potential and a loss of turgor may cause a change in leaf angle to more vertical positions, reducing the level of radiation and the need to cool down the leaf.

The third spectrum is the light competition spectrum, along which leaf angles vary with other canopy structural traits (Anten, 2016). Considering that leaf angle is an important strategy for plants to compete for light, we expect lower leaf angles under a lower level of competition and vice versa. However, the scientific community has conflicting views on the ideal leaf angle strategy when plants compete for light, and some studies have suggested that lower leaf angles are a strategy

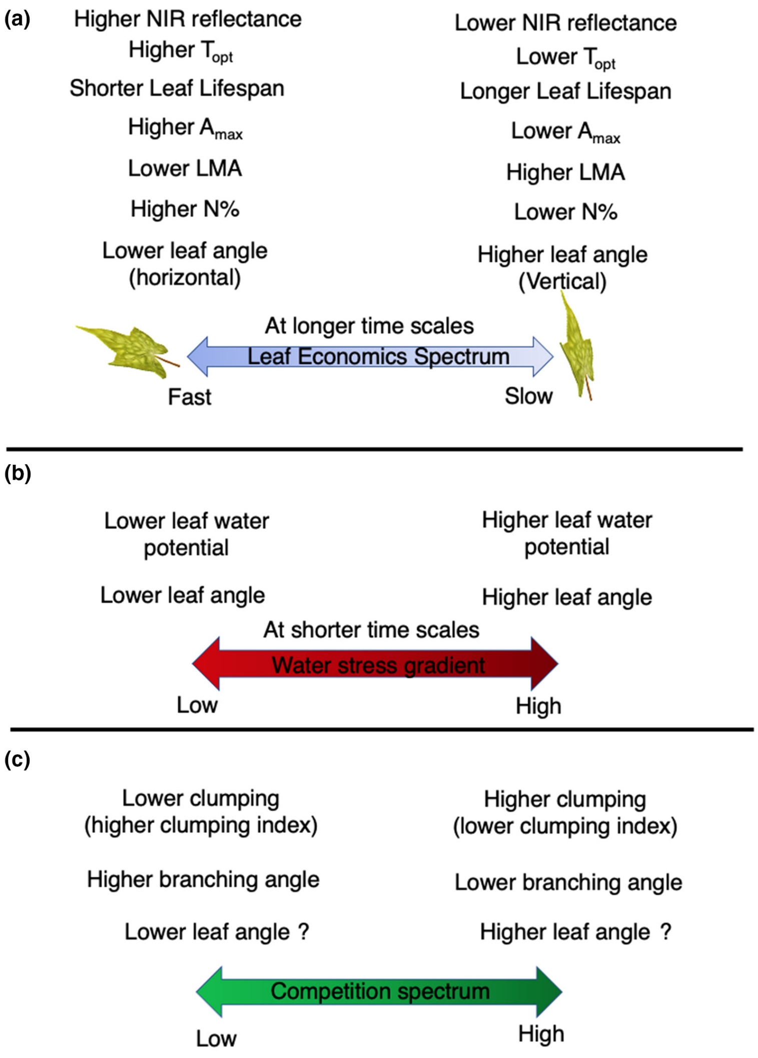

FIGURE 4 Hypothesized relationship between leaf angle and other plant traits under (a) LES, (b) water stress at shorter time scales and (c) under different levels of competition for light. The hypothesis is for canopy species. See text for details. Question marks indicate that there are contrasting views.

to compete for light and shade neighbours (Hikosaka & Hirose, 1997; Tremmel & Bazzaz, 1993), and it is still unclear whether the findings on short-stature species are applicable to canopy trees. LAI, as an important factor of light interception, plays a major role in modulating leaf angle variations within the canopy. The relationship between LAI and leaf angle can be clearly seen in the early modelling study by Monsi and Saeki (1953) and also in more recent studies (Posada et al., 2012; Terashima et al., 2005). In these studies, higher LAI usually resulted in more vertical leaves. Several other canopy structural traits should be positively correlated with leaf angle, including leaf clumping, branching angles and possibly plant height. For example, leaf clumping and vertical leaf angle can be used in tandem to reduce the potential damage of photoinhibition under high light conditions for understory species (Pearcy et al., 2005). A significant vertical variation in branch angle at different heights (more vertical branches at the top), similar to the vertical variations in leaf angle, was observed in a tropical forest (Osada & Takeda, 2003, Figure 3). The relationship between branching pattern and leaf angle also has been noted in Kull et al. (1999), in which the bifurcation ratio of branches declines with light intensity, the opposite of leaf angle.

LEAF ANGLE MEASUREMENTS

Understanding the regulation of leaf angle variations requires the measurements of hundreds to thousands of leaves in a short period of time, but making measurements at these scales has been, until recently, logistically impossible. In this section, we review the three categories of approaches to measure leaf angle and present the pros and cons of each approach. We emphasize a new technique that can revolutionize our ability to collect leaf angle data.

Traditionally, leaf angle was measured by hand (Norman & Campbell, 1989; Ross, 1980). This category of measurement technique has a few variants. The simplest version is using a hand-held inclinometer or protractor. A more sophisticated version is the Spatial Coordinate Apparatus (SCA, Lang, 1973), which measures the coordinates of the apices of triangles that form the surface of the leaf. Leaf inclination angle can be derived from the measurements in the 3D space. A more recent and advanced version of this approach is the 3D digitizer (Falster & Westoby, 2003). The leaf angle of narrow leaves (e.g. needleleaf or grass) is harder to measure than broadleaf species. One method to address this difficulty is to use quadrats at several inclination angles. Using the number of contacts per unit length at different inclination angles, the average leaf angle of a grass stand can be estimated (Wilson, 1959). The approaches used in this category are time-consuming, and it is an impossible task if the goal is to measure more than a few leaves in a plant canopy. Another caveat is that these measurements are often limited to plants with short stature.

A set of less labor-intensive approaches is based on the use of upward hemispherical photography, plant canopy analyser or horizontal digital cameras (Lerdau et al., 1992; Ryu et al., 2010; Welles & Norman, 1991). The first two approaches derive the MLA of the stand by measuring G-functions at various viewing angles. These two approaches assume that all the leaves on a canopy are oriented at the same zenith angle and have a uniform azimuthal angle distribution. The third approach uses horizontally mounted digital cameras to take pictures of tree canopies. The angle of a selected group of leaves is estimated using image software by a trained person. This approach is relatively cheap, but it only analyzes leaves that are parallel to the camera's viewing direction, limiting the number of leaves used. Leaf angle is manually estimated in image software, which can be subjective and time-consuming. Recent advances in high-throughput image processing have enabled using digital cameras to characterize the leaf angle of crops in a fast manner (Müller-Linow et al., 2015).

Terrestrial Laser Scanning is a new approach that has the potential to provide a fast and accurate way to measure the leaf angle of the entire forest canopy, alongside other important canopy structural parameters including leaf clumping index, plant area index and branching angles (Calders et al., 2020; Stovall et al., 2021). In essence, the leaf angle is estimated by calculating the normal of TLS point clouds (Stovall et al., 2021). Oftentimes, multiple leaf angle values can be estimated from a single leaf, providing a way to capture the fine-scale leaf angle variations even within a leaf. TLS overcomes many of the limitations of earlier methods: It is *R*apid (~1–3 min scanning time that covers an area of 30 to 50 meters radius that includes hundreds of thousands of leaves), *R*obust (validated in studies such as Stovall et al., 2021) and *R*epeatable (fully automated data collection and processing with minimal human interference). This approach allows the characterization of leaf angles' spatial distributions (vertical and horizontal), providing the true leaf angle distribution without subsampling a tiny set of leaves. Scans from different angles can provide a comprehensive view of individual trees, which addresses the issue of occlusion (Wilkes et al., 2017). Compared with the digital camera approach, TLS is more accurate in retrieving leaf angles from beech trees (Liu et al., 2019). The major disadvantage of this approach is that TLS instruments are still relatively expensive. However, the price of TLS will drop as the market grows with the increasing uses of LiDAR in other fields (e.g. autonomous driving, surveying and construction). TLS is not, however, a panacea. As with the abovementioned approaches, TLS scans do not resolve fine needle leaves far away from the instrument. Another disadvantage is that processing TLS data is time-consuming and requires extensive expert knowledge. However, many free algorithms have been developed to process the data (e.g. Hackenberg et al., 2021).

Leaf angle measurements can improve the estimation of the Leaf Area Index (LAI). A widely used assumption for estimating LAI from hemispherical photography or light sensors is that the LAD is spherical and homogenous across azimuth angles (Jonckheere et al., 2004). However, ample evidence suggests that this assumption is invalid. In a recent study where leaf angle is measured with TLS, estimates based on realistic leaf angle measurements could be 25% higher than the Plant Area Index values with the assumption of spherical and homogenous distribution (Stovall et al., 2021).

MODELLING WITH LEAF ANGLE

The oversimplification of leaf angle distribution discussed above has enormous implications for Earth System Models. These models treat leaf angle as a fixed parameter for each plant functional type (PFT) (Table 1). Leaf angle parameters affect light interception by a considerable amount. For example, in the Community Land Model version 5 (CLM5) (Lawrence et al., 2019), each PFT in CLM5 has one fixed χ_L—the departure of canopy leaf angle distribution from spherical—temperate deciduous forests have an χ_L of 0.25 (51.3 degrees), while C3 crops have an χ_L of −0.30 (69.5 degrees). Everything else being equal, the relative difference in the direct solar radiation intercepted by these two PFTs is 37%.[1] More realistic representations of leaf angle can be found in models focusing on a small set of individuals, for example, Y-plant and DART (Gastellu-Etchegorry et al., 2017; Pearcy & Yang, 1996).

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[1] (cos(51.3 × 3.14/180)—cos(69.5 × 3.14/180))/cos(69.5 × 3.14/180) = −0.374; Note that this calculation does not consider the impact on the intercepted diffuse radiation.

The large impacts of leaf angle occur because it is one of the most sensitive parameters in the simulation of optical signals (canopy reflectance and solar-induced chlorophyll fluorescence) and carbon, water and energy fluxes (Widlowski et al., 2007; Widlowski et al., 2011; Verrelst et al., 2015, but see Wang & Jarvis, 1990, which shows a secondary role of leaf angle). Leaf angle directly affects canopy radiative transfer and the simulations of carbon and water fluxes by its control on the surface area to intercept and scatter sunlight—simulations from a radiative transfer model have shown that variations in LADs can cause a change as significant as four-fold in the rate of net carbon uptake and ~20% in sensible and latent heat fluxes (Baldocchi et al., 2002). Leaf angle also indirectly affects the processes above by influencing LAI estimation, which can vary by up to ~25% between scenarios with and without the correct leaf angle measurements (Stovall et al., 2021).

As far as we know, no current land surface model considers the vertical distribution of leaf angle (Bonan et al., 2021). While there is always the caution against 'indiscriminate model elaboration' (Box, 1979), due to leaf angle's importance in modelling canopy fluxes and microclimate and the potential increasing data availability in the coming years, it is worth considering the inclusion of the seasonal and vertical variations of leaf angle in models. Considering the vertical variations of leaf angle and the related changes in leaf area would have a significant impact on canopy photosynthesis and their vertical variations (Stovall et al., 2021). With the increasing amount of leaf angle measurements from various platforms, especially TLS, more data on the vertical leaf angle profiles will be available for modellers.

MODEL SIMULATIONS OF THE IMPACT OF CHANGING LEAF ANGLES ON CANOPY FLUXES AND ENERGY BALANCE

We used a radiative transfer and surface energy balance model, SCOPE 2.1 (Yang et al., 2021) and a terrestrial biosphere model, ED2.2-hydro (Xu et al., 2021), to demonstrate the impact of leaf angle on canopy processes (Figure S1).

SCOPE simulations

We tested the impact of changing MLA from 10 to 80 degrees on the diurnal variations of net photosynthetic rate (A), latent and sensible heat (LE and H), canopy temperature (T_c) and intrinsic water use efficiency (iWUE) at different canopy layers (a total of 90 layers) and the whole canopy under five different scenarios (Sunny day; Overcast day; lower LAI (LAI = 1 instead of LAI = 5 in other cases); Higher temperature (daily mean temperature of 32°C); Lower temperature (daily mean temperature of 17°C). See supplementary materials for more details).

In general, increasing MLA of the canopy leads to a higher photosynthetic rate for the majority of the canopy, except that there were no significant changes in the layers close to the top (layers 70–80; Figure 5; Figure S2). At high MLA, the top layers have lower T_c-T_a, whereas the bottom layers have higher T_c-T_a, indicating that the canopy temperature profile becomes more homogeneous. iWUE of the top canopy does not change much due to concurrent increases in A and g_s, while there is a significant increase in iWUE of the lower canopies.

MLA has a considerable impact on canopy fluxes on clear days (Figure 6) and a smaller one on overcast days. The impacts are higher than noon values compared with the daily mean. With a dense canopy ($LAI = 5\,m^2\,m^{-2}$), the change in MLA could result in large impacts on LE and A (11–24% for daily fluxes and 22–44% for noon fluxes) and moderate impact on APAR and H (3–8% for daily fluxes and 9–17% for noon fluxes).

ED2.2-Hydro simulations

The strong impacts of leaf angle configuration on ecosystem functioning hold when we use ED2.2-hydro, a model that includes individual-level plant ecophysiology, microenvironment and competition, over tropical moist forests. ED2.2-Hydro has more explicit and realistic representation of canopy vertical heterogeneity and more detailed canopy biophysical and ecophysiological processes (Figure S1). We simulated three scenarios (Figure 7): a standard one Plant Functional Type (PFT) scenario where MLA of cohorts at different heights change from 40 to 80 degrees; a 'canopy-only' scenario in which only the canopy cohort (individuals >10 m) changes MLA from 40 to 80 degrees while the understory holds at 50 degrees; an 'understory-only' scenario in which individuals <10 m change MLA from 40 to 80 degrees, while canopy MLA holds at 50 degrees. We limited our simulations to 40–80 degrees because low leaf angle values resulted in a failure in leaf energy balance.

Like SCOPE 2.1, ED 2.2-Hydro simulations suggest that increasing MLA in both canopy and understory from 40 degrees to 80 degrees increases canopy photosynthesis, reduces the differences in T_c-T_a (note for ED2.2-Hydro, Ta is the average canopy air temperature) and increases the iWUE of understory more significantly than the canopy.

In addition, the three scenarios allow us to separate the direct ecophysiological effects and indirect competitive effects of leaf angle. The canopy-only scenario has higher understory photosynthesis compared with the standard scenario, suggesting that if carbon gain is the only metric for competitiveness, a canopy would have vertical leaves on the top and horizontal leaves at the bottom. Indeed, this pattern was widely observed

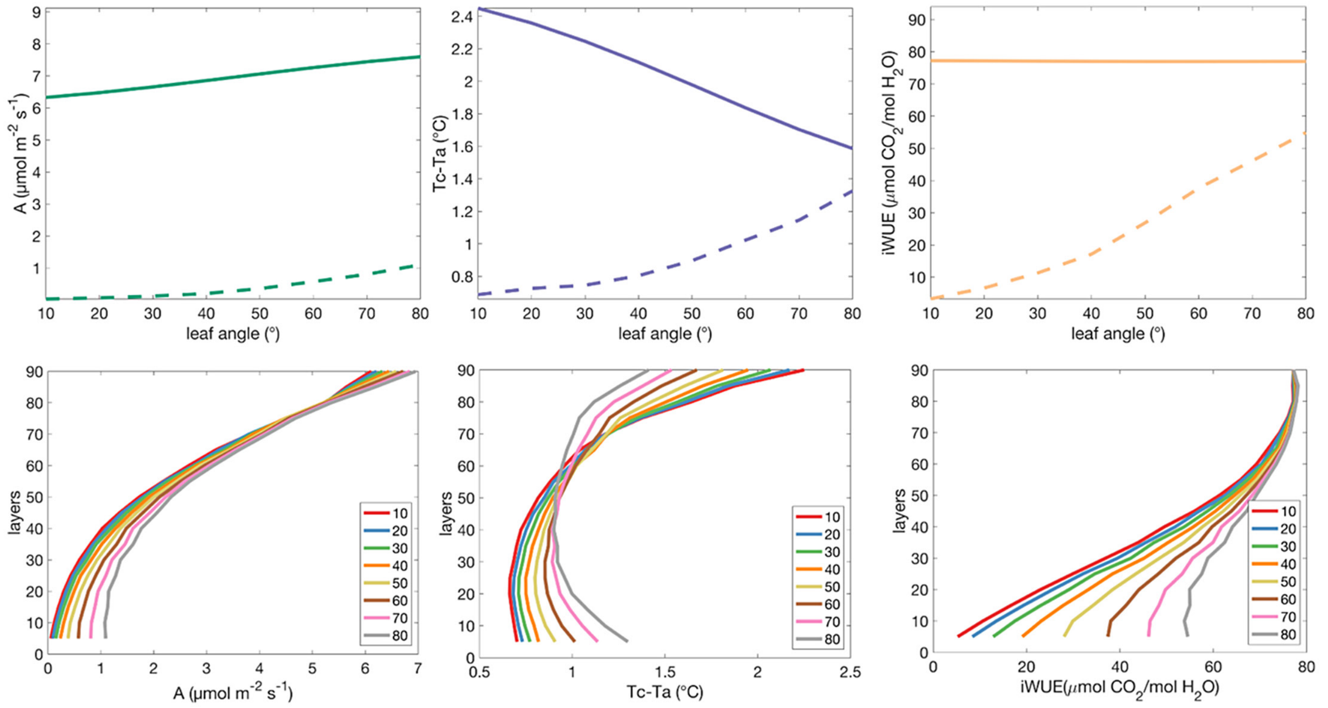

FIGURE 5 The impact of mean leaf angle of the canopy on net photosynthesis (A), the difference between canopy temperature and air temperature (T_c-T_a), and the intrinsic water use efficiency (iWUE). Top panels: solid lines are for top canopy; dashed lines are for the bottom canopy. Bottom panels: vertical profiles of A, T_c-T_a and iWUE from different MLA scenarios. Colours indicate MLA (degrees). Similar figures for latent heat, sensible heat and stomatal conductance can be found in the supplementary materials.

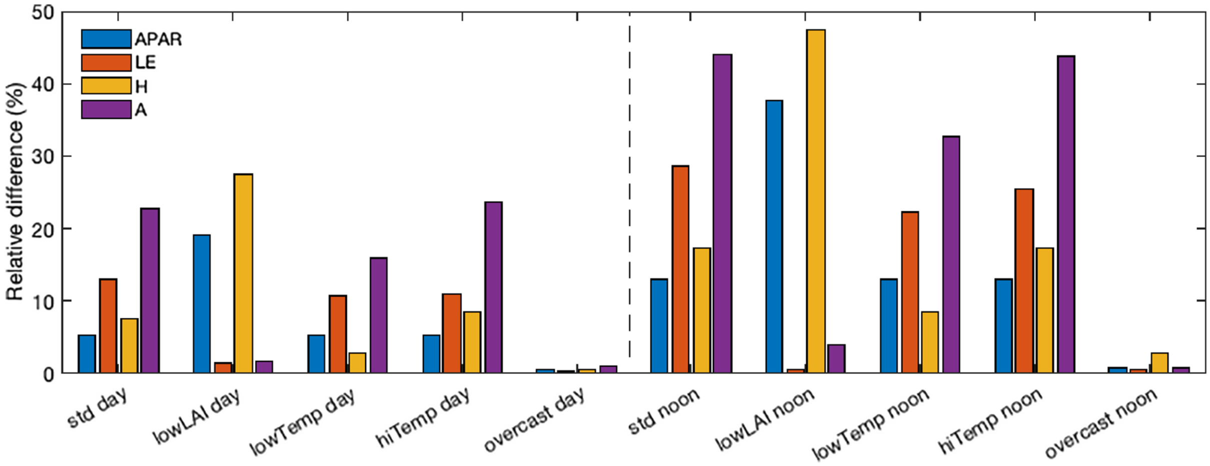

FIGURE 6 The relative difference between fluxes (Absorped Photosynthetically Active Radiation—APAR, Latent Heat—LE, Sensible Heat—H and Photosynthesis—A) simulated with MLA varying from 10 degrees to 80 degrees. Relative difference calculated by abs[(maximum–minimum)/mean]. Results from daily mean values are listed on the left, separated from the results from noon values on the right. std—clear day; lowLAI—low LAI; lowTemp—low temperature; hiTemp—high temperature; overcast—overcast day. For a comparison between MLA at 30 to 70 degrees, see Figure S3.

in nature, yet there are abundant cases that do not follow this pattern (Figure 3), suggesting other important factors at play. The magnitude of the competitive effect is comparable to the direct ecophysiological effect, suggesting the potentially pivotal role of leaf angle in within-canopy light competition.

Leaf angle's impact on photosynthesis is similar to one of the most important parameters in ecosystem models, V_{cmax}, the maximum carboxylation rate (Figure S4). We ran SCOPE and ED2.2-Hydro with varying V_{cmax} values (30–70 μmol m^{-2} s^{-1}) and leaf angle (30–70 degrees). The changes in net photosynthesis along the leaf angle

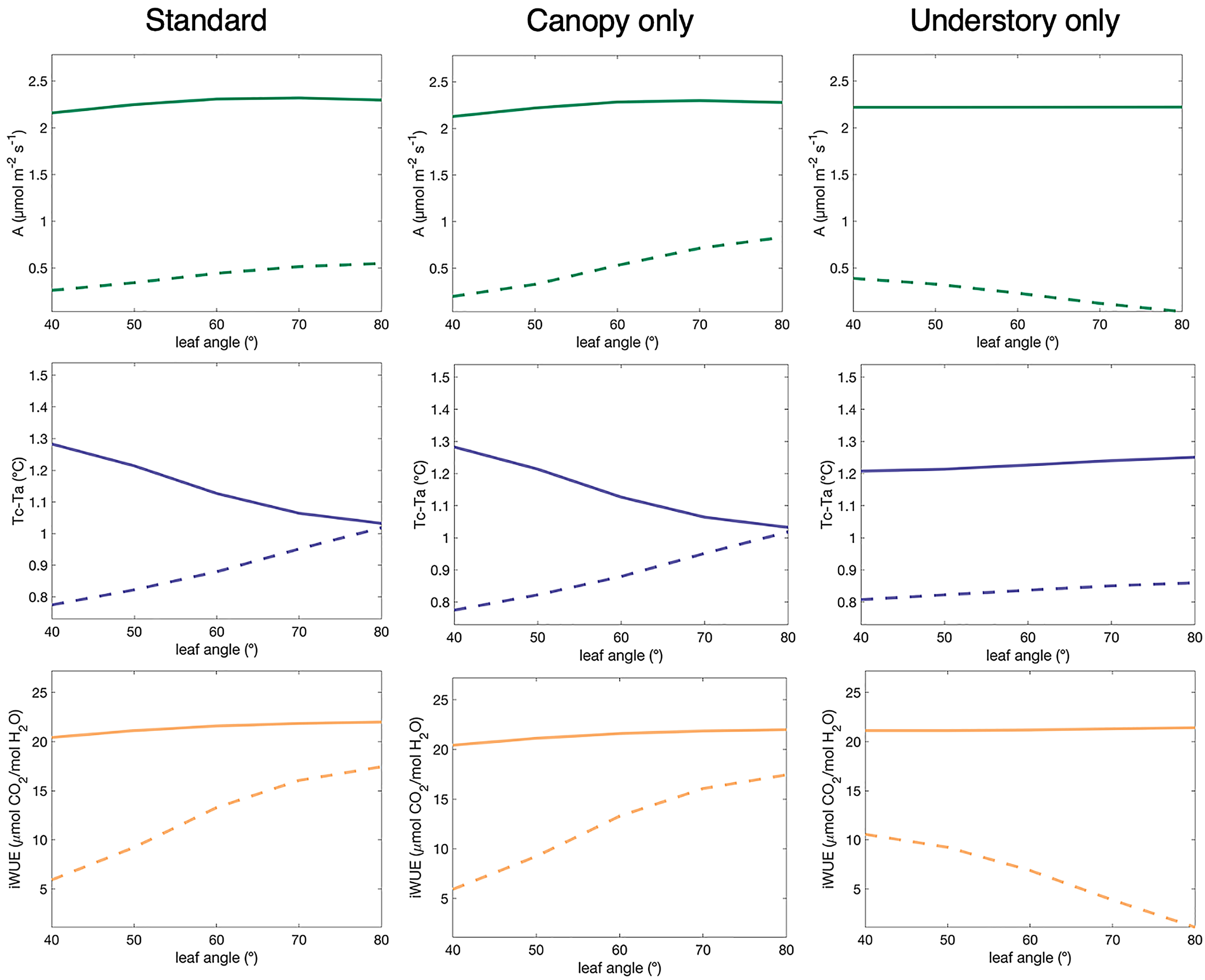

FIGURE 7 The impact of mean leaf angle of the canopy on net photosynthesis (A), the difference between canopy temperature and air temperature (T_c-T_a) and the intrinsic water use efficiency (iWUE) of the three scenarios in ED2.2-Hydro. Solid lines are for top canopy. Dashed lines are for bottom canopy.

gradient are similar to that along the V_{cmax} gradient (Figure S4).

Overall, our simulations have demonstrated the importance of leaf angle parameterization because it can significantly influence the highly coupled processes that determine carbon, energy and water dynamics. The effort is not a comprehensive analysis covering the full range of possible biological and environmental parameters but a demonstration and a stepping stone for future studies.

SUGGESTIONS FOR FUTURE RESEARCH

With the growing use of TLS and algorithms available to process TLS data to acquire leaf angle and other structural information, we are entering a new era to advance our understanding of the relationship between plant structure and function. Using leaf angle as a focal point, we can start to better integrate leaf traits and canopy structural traits in a whole plant framework. We suggest a few key directions to take, including (I) understanding the environmental and biological drivers of leaf angle by quantifying the global variations in leaf angle, (II) exploring the coordinated relationship between leaf angle as a canopy structural trait and other leaf traits, and (III) efficiently incorporating leaf angle in models to improve our simulations of vegetation dynamics and biogeochemical fluxes.

Quantifying global variations in leaf angle

The current paradigm that leaves are more vertical in dry and hot environments while more horizontal in mesic and light-limited environments does not explain the wide range of variations in leaf angle for individuals in the same environment. The first and foremost step is to characterize the variations in leaf angle, particularly its vertical profile, across a wide range of ecosystems, from tropical to boreal ecosystems. Existing data from TRY is limited, mostly to low statue plants and to the mean leaf angle values (Kattge et al., 2011). Leaf angle has strong vertical plasticity, and the extent of variability differs from species to species. This impact on light interception may explain the contrasting patterns of leaf economics spectra from sunlit and shade parts of the canopy (Keenan & Niinemets, 2016). A key question to answer is how much the variations in vertical leaf angle profile are driven by light, and how much they are driven by other factors such as water?

The leaf angle within each individual is highly variable and thus the statistical distribution of critical. Canopies with similar MLA may have quite different statistical distributions and vertical profiles (Figure 3), both of which can significantly affect canopy carbon, water and energy fluxes. TLS makes it possible to sample a large number of individuals at a relatively low cost (in both money and time). Existing TLS data collected for other purposes could be processed with leaf angle algorithms (Stovall et al., 2021; Vicari et al., 2019). Often, due to the challenges of measuring leaf angle, the seasonal, intra- and interspecific, and vertical variations in leaf angle are assumed to be minimal, even though limited evidence suggests otherwise. We recommend research focusing on characterizing the spatiotemporal variations in leaf angle. Measurements at a high temporal frequency (e.g. hourly) across the season and various biomes can help understand the plasticity of leaf angle. Besides leaf angle data, TLS provides estimates on other important canopy parameters, including plant area index, clumping index, branching angle, etc.

Integrating leaf angle and other plant traits in the EEO-based framework

Our proposed framework provides a way to integrate various plant traits in a holistic view. With concurrent measurements of leaf angle and other traits, we will be able to investigate the role of leaf angle in the leaf economics spectrum (LES) and structural economics spectrum (Verbeeck et al., 2019; Wright et al., 2004) and to understand how leaf angle could contribute to the plasticity in the LES (Keenan & Niinemets, 2016). A key question to answer with these measurements is, 'are the observed leaf angle profiles optimal for plants, and what is the role of competition?' Previous modelling work suggests that individuals with horizontal leaves on the top of the canopy have a competitive advantage, yet observations suggest the opposite (Hikosaka & Hirose, 1997; Figure 3). To address this question, the canopy structure of the target individuals and their surrounding environment (other individuals) needs to be characterized, and TLS is suitable for this task.

We recommend leaf angle measurements combined with concurrent measurements of leaf traits, response variables (e.g. carbon and water fluxes from eddy covariance) and other environmental conditions (temperature, light intensity, etc.), which would be helpful for further interpretation of the variations in leaf angle and understand the impact of leaf angle variations on carbon, water and energy fluxes (Figure 2). In addition, canopy structure is often not the variable measured in global change experiments (drought, free air CO_2 enrichment, temperature, etc.); we recommend making measurements of canopy structure with TLS in these experiments.

Incorporate leaf angle plasticity in canopy, ecosystem and land surface models

Light interception is an essential process in vegetation demographic models, radiative transfer models and land surface models. The representation of leaf angle and its role in the light interception in these models vary considerably (Table 1). For models simulating individuals and/or vegetation demography, it is important to represent the vertical variations in leaf angle and leaf area as they affect the competition among individuals. For models at the global scale with a coarser spatial resolution (such as land surface models), incorporating the vertical profiles of leaf traits and angles has a significant impact on canopy fluxes (Bonan et al., 2021). Our results have shown that varying leaf angles have a nontrivial impact on canopy photosynthesis, temperature and water use (Figure 5). In addition, the magnitude and direction of the impacts of leaf angle changes on these processes vary vertically within the canopy.

On a similar note, leaf angle could be a critical parameter in plants' efforts to achieve optimal performance, and the ability to vary leaf angle could be essential for plants to maintain optimality as the environment changes (Harrison et al., 2021). Given the possible coordination and correlation between leaf angle and other leaf traits, it is possible to incorporate this relationship in models to improve leaf and canopy level processes while reducing the number of parameters.

AUTHOR CONTRIBUTIONS

XY conceived the idea and performed the literature review; RL conducted the SCOPE simulations; YM and XX conducted the ED2.2-Hydro simulations; AJ and JK collected the TLS data; JK visualized the TLS data; XY wrote the first draft of the manuscript; and all authors contributed substantially to revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Model simulation results from SCOPE 2.1 to ED2.2-Hydro and leaf angle data are available at https://doi.org/10.5061/dryad.w9ghx3ftk.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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