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## **Remote sensing of plant-water relations: An overview and future perspectives**

Damm, Alexander ; Paul-Limoges, Eugénie ; Haghighi, Erfan ; Simmer, Clemens ; Morsdorf, Felix ; Schneider, Fabian D ; van der Tol, Christiaan ; Migliavacca, Mirco ; Rascher, Uwe

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## Remote sensing of plant-water relations: An overview and future perspectives

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### ABSTRACT

Vegetation is a highly dynamic component of the Earth surface and substantially alters the water cycle. Particularly the process of oxygenic plant photosynthesis determines vegetation connecting the water and carbon cycle and causing various interactions and feedbacks across Earth spheres. While vegetation impacts the water cycle, it reacts to changing water availability via functional, biochemical and structural responses. Unravelling the resulting complex feedbacks and interactions between the plant-water system and environmental change is essential for any modelling approaches and predictions, but still insufficiently understood due to currently missing observations. We hypothesize that an appropriate cross-scale monitoring of plant-water relations can be achieved by combined observational and modelling approaches. This paper reviews suitable remote sensing approaches to assess plant-water relations ranging from pure observational to combined observational-modelling approaches. We use a combined energy balance and radiative transfer model to assess the explanatory power of pure observational approaches focussing on plant parameters to estimate plant-water relations, followed by an outline for a more effective use of remote sensing by their integration into soil-plant-atmosphere continuum (SPAC) models. We apply a mechanistic model simulating water movement in the SPAC to reveal insight into the complexity of relations between soil, plant and atmospheric parameters, and thus plant-water relations. We conclude that future research should focus on strategies combining observations and mechanistic modelling to advance our knowledge on the interplay between the plant-water system and environmental change, e.g. through plant transpiration.

### 1. Introduction

The soil, plants and atmosphere are connected via flows of energy and matter including water and carbon (Baldocchi et al., 2001). Plant photosynthesis and a complex set of supporting physiological processes are the driving forces of these exchange processes, including the uptake of atmospheric carbon and storage in ecosystems and the extraction of water from the soil and its release into the atmosphere (Lambers et al., 2008). Therefore, vegetation is an important and highly dynamic component of the carbon and water cycle (Reichstein et al., 2013).

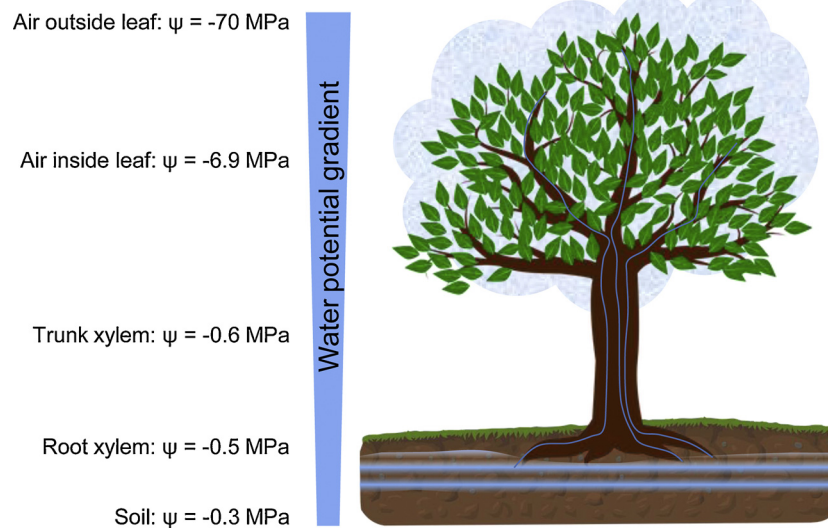
Driven by soil water availability and atmospheric water demand, water is in continuous flow in the soil-plant-atmosphere continuum

(SPAC) (Asbjørnsen et al., 2011). However, only approximately 1% of the water extracted by plants from the soil during the growing season is actually used for plant growth; the rest is released as water vapour to the atmosphere through plant transpiration, an unavoidable by-product of carbon exchange via stomata openings (Green et al., 2017; Nobel, 2009; Reichstein et al., 2013). Evapotranspiration summarizes the water fluxes from terrestrial ecosystems to the atmosphere, and combines plant transpiration and evaporation of water from the soil and plant surfaces. In vegetated ecosystems, transpiration is, with a contribution of up to 90%, the largest component of evapotranspiration (Jasechko et al., 2013). Besides its role in water cycle dynamics, vegetation also responds to changing water availability: water is

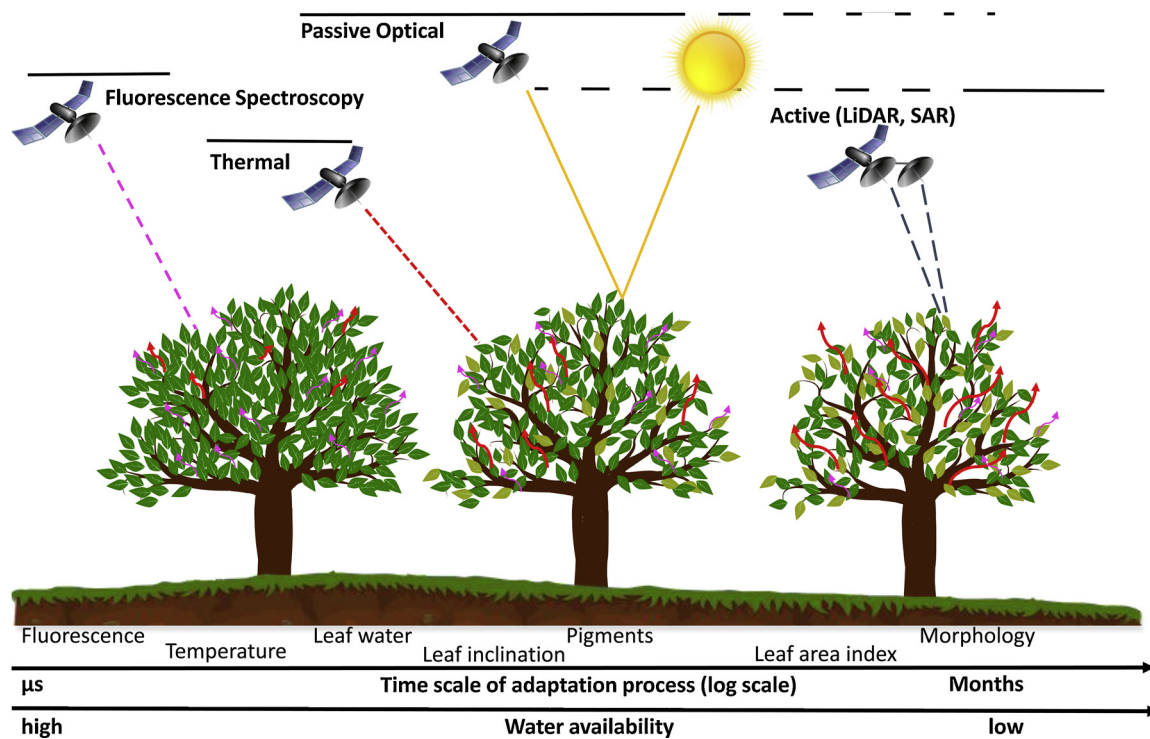
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**Fig. 1.** Schematic drawing of water flow across the SPAC (right) including the gradient of the water potential  $\psi$  (left). Indicated water potentials represent typical values for several species according to Nobel (2009). Water potentials vary with environmental factors and might substantially differ in extreme cases.

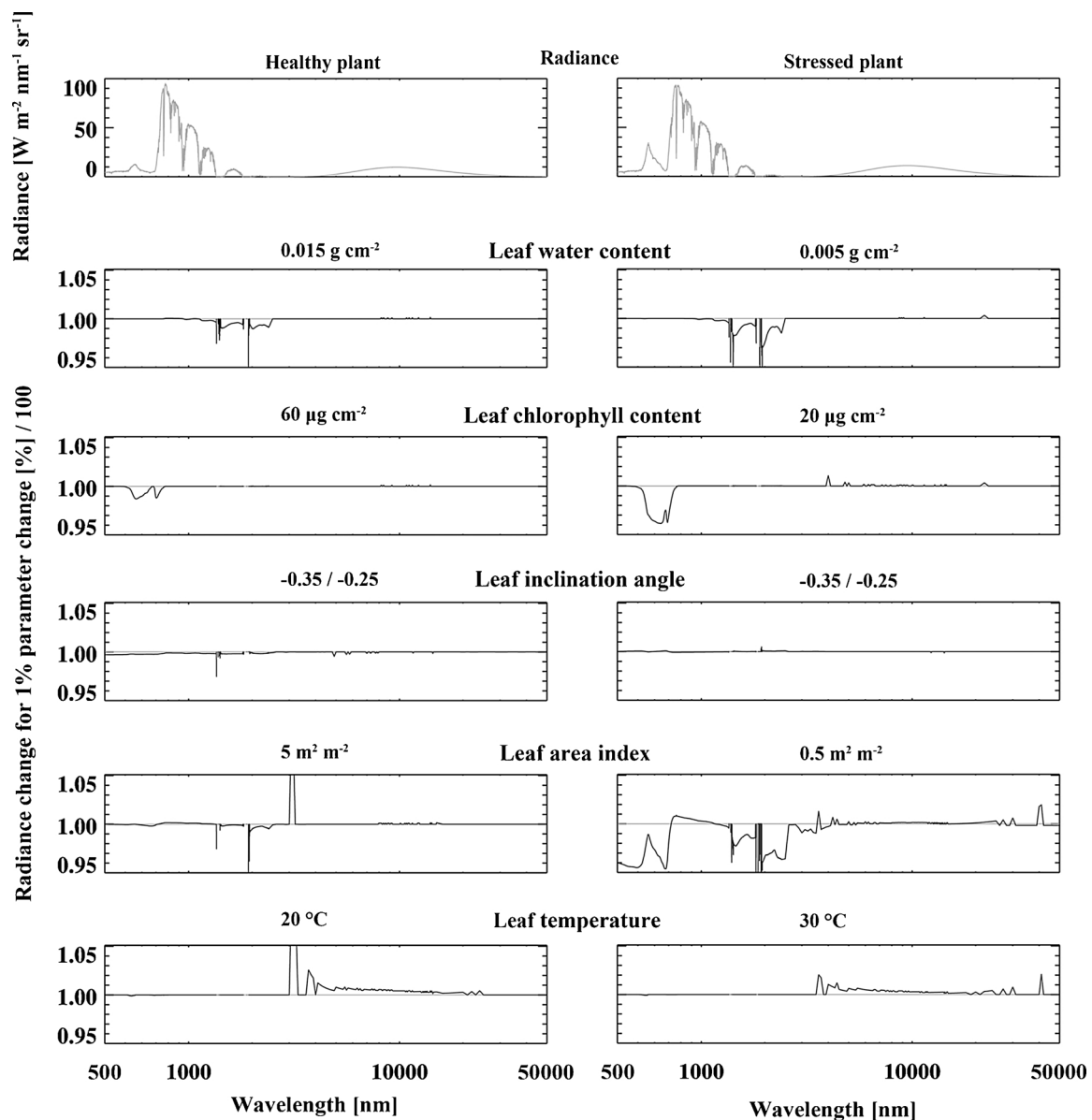


**Fig. 2.** Conceptual overview on the impact of plant water availability on physiological, biochemical, and structural adaptation mechanisms, and remote sensing technology sensitive to such plant adaptation mechanisms. Purple arrows indicate fluorescence radiation emitted by plants, red arrows relate to thermal radiation emission. Bold lines indicate the application spectrum of remote sensing technology, dashed lines indicate limited applicability.

embedded in cells, transports nutrients, provides structural support (turgor), supports plant movements, and stabilizes temperature. Small variations in water availability may lead to functional responses of plants (Nobel, 2009). The double role of vegetation in driving water cycle dynamics and responding to it determines vegetation ecosystems to cause several interactions and feedbacks across Earth spheres (Richardson et al., 2013; Seneviratne et al., 2010; Suni et al., 2015).

Gradients of water potentials across the SPAC provide the physical force for the uptake of soil water by the root system, the transport of water through the plant xylem to the leaves, and the release of water into the atmosphere through stomatal pores (Norman and Anderson, 2005). As a result, plant-water relations (i.e. storage and flow of water

in plants) highly depend on soil water content and atmospheric water vapour deficit. Plant-water relations are thus expected to vary with environmental change (i.e. varying pattern of temperature and precipitation, increasing aerosol emissions, and atmospheric  $CO_2$  concentrations) via complex feedback mechanisms. Increasing atmospheric  $CO_2$  concentrations, for example, fertilize plant photosynthesis and will likely alter carbon and water exchange in vegetated ecosystems (Nobel, 2009). Observed reductions in stomata density of C3 plants with increasing  $CO_2$  concentrations possibly lead to a decrease in transpiration rates (Lammertsma et al., 2011). Such developments could also impact plant diversity of ecosystems due to plant adaptation or shifts towards species communities more resistant to changing environmental



**Fig. 3.** Wavelength dependent change of surface reflected and emitted radiation as a function of biochemical, structural and physiological vegetation traits. Only parameters describing plant processes and properties were assessed. Results were obtained from the SCOPE model considering a healthy vegetation canopy without water stress (left) and a water stressed canopy (right). All parameters were changed by 1% of their theoretical parameter range (cf. [Appendix D](#) for details).

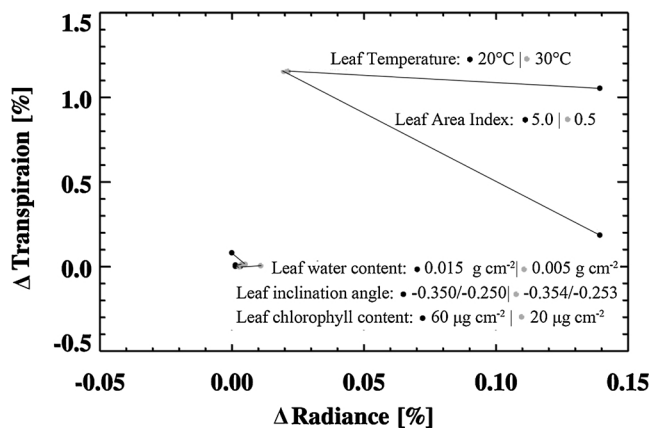
conditions, while the fundamental relationship between plant diversity and ecosystem functioning determines a strong feedback on biogeochemical cycling ([Hooper et al., 2012](#); [Hooper et al., 2005](#)). Although future trajectories of plant development are still unknown, they will likely exert a physiological feedback on hydrology ([Lammertsma et al., 2011](#)).

When unravelling the complex feedbacks and interactions of plant-water relations and environmental change, both the impact of vegetation on the water cycle and its dependencies on water availability must be better understood. [Nobel \(2009\)](#) points to the wealth of interacting and sometimes compensating factors. All of them must be considered, despite our still limited understanding of plants and ecosystems, to advance our understanding of plant-water relations. Thus, strategies to assess plant-water relations across scales ideally comprise the use of models and observations. Models, however, are always simplifications of reality and might be biased due to parameterizations calibrated with site observations ([Waring and Landsberg, 2011](#)). Useful observations of plant-water relations are always local and expensive; large scale

observations are emerging but have not yet sufficiently matured. [Penuelas et al. \(1996\)](#) noted that our assessments of the plant-water status are still based upon measurements of relative water content, water potential, or transpiration, and that accurate measurements can only be done at the leaf level; their upscaling to ecosystem levels remains highly challenging. Even matured techniques such as the eddy covariance technique ([Baldocchi, 2003](#)) yield large uncertainties when partitioning measured evapotranspiration into its component processes evaporation and transpiration ([Villegas et al., 2014](#)).

We hypothesize that advanced cross-scale monitoring of plant-water relations can be achieved by combined observational and modelling approaches. This paper reviews suitable remote sensing approaches to assess plant-water relations ranging from pure observational to combined observational-modelling approaches. Based upon this insight, we use the combined energy balance and radiative transfer model SCOPE ([van der Tol et al., 2009](#)) to assess the explanatory power of pure observational approaches focussing on plant parameters for estimating plant-water relations. We outline and discuss a more effective use of





**Fig. 4.** Simulated sensitivity of reflected radiance and transpiration of a vegetation canopy for changing vegetation parameters. Individual parameters were changed by 1% within a typical value range of them. Two canopy and environmental conditions were simulated: a healthy canopy under moderate environmental conditions (black dots) and a stressed canopy under harsh environmental conditions (grey dots). Grey lines connect corresponding simulations. As an example for interpretation: A 1% change of air temperature at 20° yields a 0.15% change in radiance and a 1.0% change in transpiration. For higher air temperature (30°), a 1% temperature change results in a reduced radiance change (0.02%) while the change in transpiration remains the same. Results are based on simulations with the SCOPE model (van der Tol et al., 2009). Details of the analysis are described in Appendix D.

remote sensing information by its integration into SPAC models. A mechanistic model simulating water movement in SPAC reveals insight into complex relations between soil, plant, and atmospheric parameters for simulating the flow of water in the SPAC and indicates the need for combining remote sensing with SPAC models. We finally discuss strategies to advance the assessment of plant-water relations in view of future observational capability.

## 2. Plant-water relations

Plant-water relations describe the water budget dynamics of plants, i.e. the transport of water through the plants and its storage in cells. One percent of water is effectively used for metabolism during the growing season thus the largest proportion (i.e. approximately 99%) is eventually released into the atmosphere by transpiration (Nobel, 2009). Plant-induced water flow consists of the extraction of water by roots, its transport from the roots through the xylem to the leaves, its storage in the plant via plant metabolism, and the transpiration loss by leaves and sometimes also stems driven by the atmospheric demand (Passioura, 2001) (Fig. 1). Water transport in plants can be explained by the

cohesion-tension theory going back to the work by Dixon and Joly (1894), while the driving force of water uptake and transpiration is the gradient of water potential ( $\psi$ ) from soil to the root and xylem, to leaves, and finally to the atmosphere. Although individual water potentials strongly depend on environmental and plant specific factors, representative values are  $-0.3$  MPa for soil,  $-0.5$  MPa for roots,  $-0.6$  MPa for xylem,  $-6.9$  MPa for the air inside stomata, and  $-70.0$  MPa for the air outside of the stomata at 60% relative humidity (Nobel, 2009).

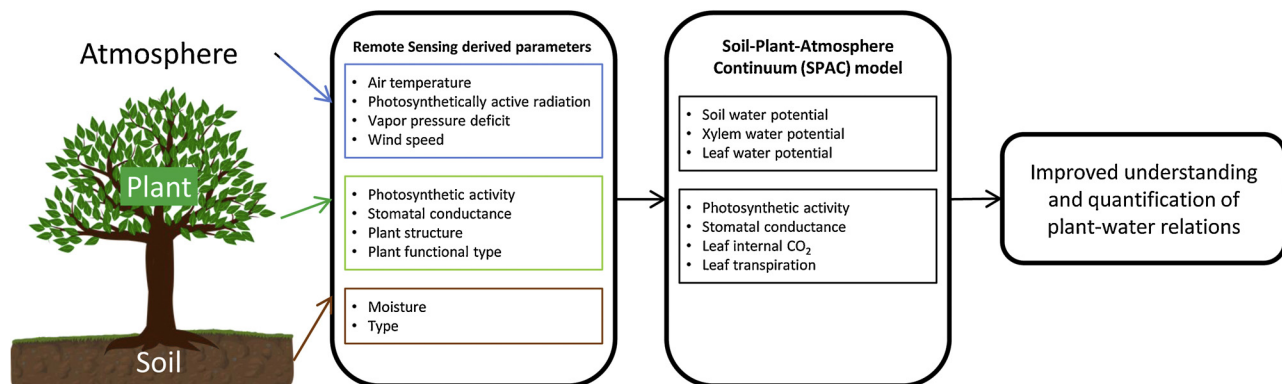
Dynamics in plant-water transport reflect the health of plants and respond to environmental changes. Plants can experience stress or even die due to hydraulic failure, when the atmospheric water demand for water exceeds the supply by the soil (Farooq et al., 2009; Tuzet et al., 2003). The importance of water flow for plants in combination with the dominance of water flow over water storage makes the concept of plant-water relations highly interesting for assessing environmental change impacts on vegetation and ecosystem functioning.

Plant-water relations in the SPAC are highly complex. While Landsberg and Waring (2017) conclude that the research of tree water relations is matured in a sense that theory and understanding of processes are consolidated, the modelling of such processes to scale from individual to ecosystem level is still evolving, and updates for SPAC models are frequently published. The complexity of plant-water relations and the substantially varying environmental conditions and plant properties in space and time explains why studies still point to uncertainties in plant-water relationships across species, locations, and environmental conditions (Landsberg and Waring, 2017).

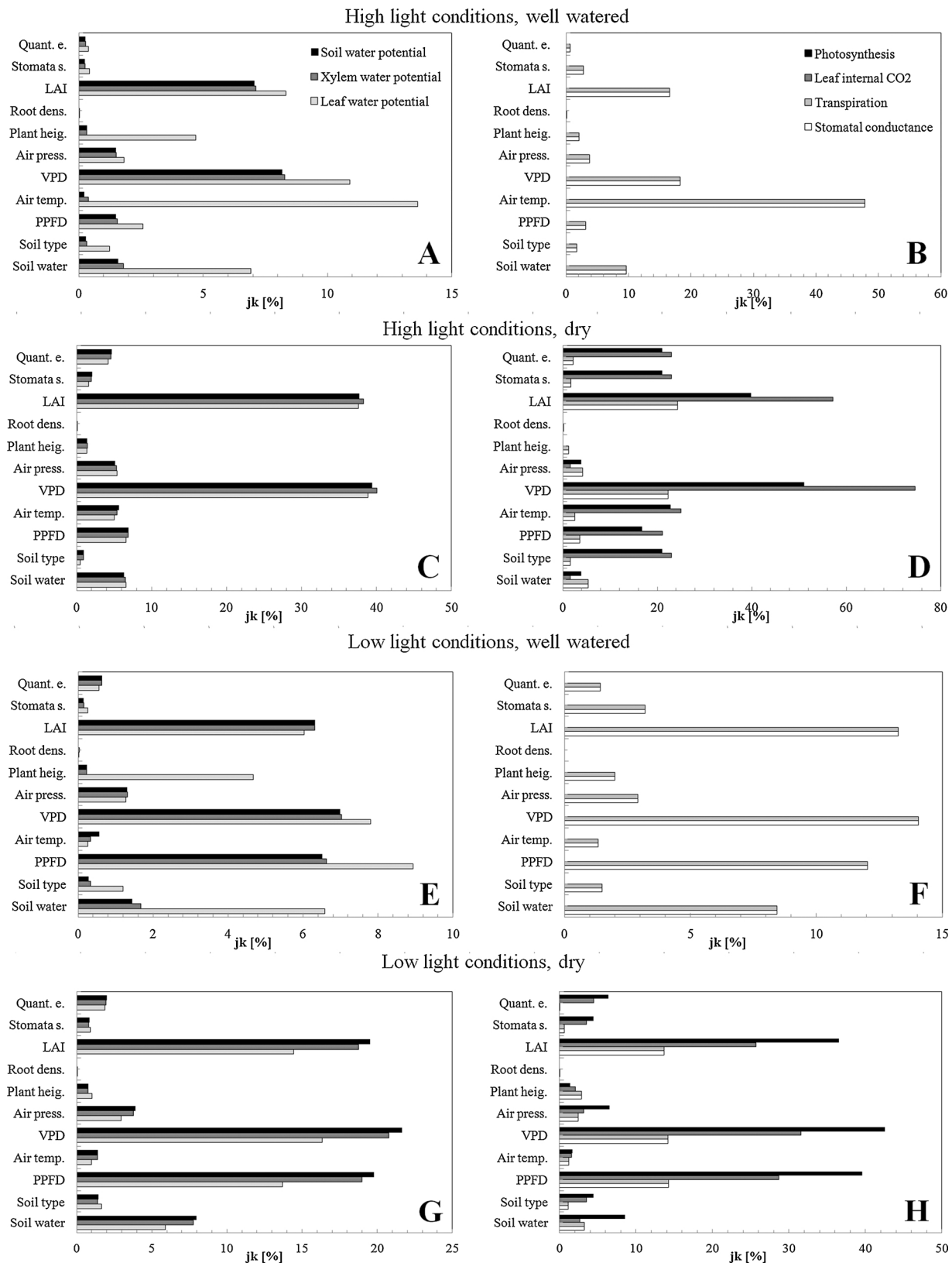
## 3. Remote sensing of plant-water relations

### 3.1. Strategic involvement of remote sensing

The appropriate use of remote sensing to assess plant-water relations requires an in-depth understanding of the radiative transfer in the soil-plant-atmosphere system. Only phenomena that cause radiation changes by absorption or scattering in this system, such as changes in structure or composition, can be detected and potentially quantified from remote sensing data. Other phenomena of interest can only be approached by remote sensing when relations with detectable phenomena (proxies) exist. Most processes related to plant-water relations are not directly observable by remote sensing. For example, root water uptake and water flow in the xylem do not directly influence radiation and are thus per se not visible to remote sensing sensors. Transpired water vapour during that process would have distinct absorption features compared to liquid water within plants and soil (Green et al., 2006), but disentangling transpired water vapour from ambient atmospheric water vapour is highly challenging and only possible in rare cases (Rodriguez et al., 2011).



**Fig. 5.** Conceptual framework to link remote sensing observation of atmospheric, plant, and soil parameters with a process-based SPAC model to advance our understanding of plant-water relations (see text for discussion).



**Fig. 6.** Sensitivity of water potentials (left) and plant functional parameters (right) on varying atmospheric, plant, and soil parameters. jk indicates the percentage impact of a 1% parameter change (y axis) on the evolution of the respective water potentials and plant functional parameters on two consecutive days. A/B: Light intensity represents typical conditions for satellite data acquisitions (i.e. photosynthetic photon flux density (PPFD) of  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and plants are well watered. C/D: As before but plants suffer from drought. E/F: Light intensity represents overcast conditions (i.e. PPFD of  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and plants are well watered. G/H: The same as in E/F but for plants suffering from drought. A description of the various parameters is given in [Appendix C](#). Note the different ranges of x-axis in different panels.

Strategies to assess plant-water relations can be based on observations or the combined use of observations and models. Pure observational approaches typically build upon measurements of plant properties or processes affected by changing plant-water flows, e.g. surface temperature, plant water content, changing biochemistry, and plant structure. Combined observation-modelling approaches rely on process models, e.g. for photosynthesis or for the complete process chain in the SPAC, and use observations to partly constrain model parameters. This includes measurements of plant parameters and processes (e.g. photosynthesis, stomatal conductance) and of environmental parameters describing the atmosphere and the soil (e.g. air temperature, vapour pressure deficit (VPD), irradiance, soil properties). The following sections and [Appendix A](#), [Appendix B](#) provide an overview of remote sensing approaches that facilitate either observational or observation-model strategies to assess plant-water relations in the SPAC.

### 3.2. Observational approaches to assess plant information

This section describes remote sensing approaches to assess plant properties or processes that allow plants to cope with changing soil water availability and atmospheric demand for water. Various processes acting at different time scales evolved to protect plants from water stress ([Fig. 2](#)). The most important plant properties and processes that can be assessed with remote sensing techniques, and are thus intensively studied, include changes in physiology (e.g. photochemical and non-photochemical quenching (NPQ)), leaf temperature changes due to stomatal conductance regulation ([Farooq et al., 2009](#); [Gerhards et al., 2016](#)), biochemistry (e.g. plant water content, altered pigment composition), and canopy structure (e.g. leaf area index (LAI), leaf size, leaf orientation). At the community level, distance between individual plants or plant morphology (i.e. plant height) could be impacted, but such effects are not in the scope of our investigation. [Fig. 2](#) provides an overview of remote sensing technology to assess such plant processes and indicates time scales of plant reactions to changing soil water availability (i.e. inversely proportional to water stress).

#### 3.2.1. Stomatal conductance and photosynthetic activity

Photosynthesis is a key determinant of water flow in plants. The photosynthetic process puts a demand on leaf internal CO<sub>2</sub> to be provided through leaf stomata openings. Open stomata in combination with VPD lead to an unavoidable loss of water due to transpiration. Depending on the plants homeohydric strategy, stomatal conductance shows a fast (isohydric) or delayed (anisohydric) response to decreasing water availability ([Konings et al., 2017](#)). Stomatal closure allows plants to control their water loss, but also causes a down-regulation of plant photosynthesis and invokes protection mechanisms (e.g. NPQ, chlorophyll fluorescence) to avoid cellular damages due to excessive light not useable for photosynthesis ([Porcar-Castell et al., 2014](#)). Transpirational water loss can be mechanistically quantified by stomatal conductance, photosynthetic activity, and other non-stomatal limitations. The latter factors are important since stomatal conductance and photosynthetic activity can be decoupled when non-stomatal limitations reduce photosynthesis ([Drake et al., 2017](#)).

Stomatal conductance or canopy conductance (i.e. leaf stomatal conductance scaled with LAI) can hardly be measured directly. A wealth of empirical and mechanistic models exists to estimate stomatal conductance at leaf and canopy level. Such models typically incorporate environmental, hydraulic, and photosynthetic gain parameters ([Buckley and Mott, 2013](#); [Damour et al., 2010](#); [Sperry et al., 2017](#)) that can partly be assessed with remote sensing (cf. next chapters). Purely observational approaches range from simple empirical relationships between remote sensing information and stomatal conductance to the use of surrogates (i.e. proxies used to infer the phenomena). Empirical relationships are typically established between vegetation indices and the conductance term of Penman Monteith's equation. [Yebra et al. \(2013\)](#), for example, found several vegetation

indices to yield good results, including the Normalized Difference Vegetation Index (NDVI), the Normalized Difference Water Index (NDWI), or the Enhanced Vegetation Index (EVI). Another approach combines green vegetation biomass estimates (i.e. NDVI) and canopy temperature to empirically reveal changes of stomatal conductance ([Sandholt et al., 2002](#)). [Waring and Landsberg \(2011\)](#) indicate that photosynthetic capacity (i.e. actual or potential) can be used as surrogate of stomatal conductance or as a variable to predict it.

Plant photosynthetic activity is difficult to assess, but approaches building upon remote sensing techniques substantially increased in recent years. Common remote sensing approaches approximate photosynthetic activity with gross primary productivity (GPP), assuming a constant rate ratio between photosynthesis and GPP, and the validity of the resource balancing paradigm (i.e. plant growth can be estimated by assessing only one growth limiting factor and its use (i.e. light), cf. [Field et al. \(1995\)](#)). Estimates of GPP are available for local ([Damm et al., 2010](#)), regional ([Damm et al., 2015a](#); [Wieneke et al., 2016](#)), and global scales ([Frankenberg et al., 2012](#); [Guanter et al., 2014](#)). The determination of photosynthetic activity, however, remains an open research field since the relation between GPP and photosynthetic activity changes with species and environmental conditions. Few studies building upon measurements of sun-induced chlorophyll fluorescence (SIF) show a sensitivity of SIF to track photosynthetic regulation ([Green et al., 2017](#); [Pinto et al., 2016](#); [Rossini et al., 2015](#)) but mechanistic models fed by remote sensing data to predict actual photosynthetic rates are still missing. Further, subtle protection mechanisms related to the process of photosynthesis need to be better constrained. One example is the process of NPQ and the associated decomposition of xanthophyll pigments. It is suggested that the NPQ can be assessed with remote sensing proxies such as the Photochemical Reflectance Index (PRI) ([Gamon and Berry, 2012](#); [Hilker et al., 2011](#); [Hilker et al., 2009](#)). Although recent remote sensing techniques offer high spectral resolution and signal quality to assess such protection mechanisms, the retrieval of these signals and its association with underlying physiological processes remains challenging. The PRI, for example, is known to show additional sensitivities to canopy structure and illumination conditions ([Barton and North, 2001](#); [Damm et al., 2015b](#); [Garbulsky et al., 2011](#)). Also fluorescence retrievals are challenged by the effects of canopy structure, atmospheric conditions, and instrumental properties ([Damm et al., 2015a](#); [Köhler et al., 2017](#)).

#### 3.2.2. Leaf temperature

Leaf transpiration extracts heat from the leaf due to the energy required for the phase change from liquid water to water vapour and thus results in leaf cooling (i.e. evaporative cooling effect). Stomatal regulation due to limited water availability impacts transpiration rates and causes a change of leaf surface temperature ([Inoue et al., 1990](#)). Many approaches use this dependency and incorporate differences between the measured air and leaf temperatures or between a non-stressed baseline temperature and the actual leaf temperature ([Berni et al., 2009](#); [Cohen et al., 2005](#); [Gerhards et al., 2016](#); [Leinonen et al., 2006](#)). Other approaches build on the combined use of optical (plant greenness) and thermal observations (leaf temperature) to estimate plant transpiration and thus plant-water status ([Leinonen et al., 2006](#); [Leinonen and Jones, 2004](#); [Sandholt et al., 2002](#)). Investigating leaf temperatures and their spatio-temporal changes provides a rather sensitive measure of plant-water relations, as leaf skin temperature is strongly coupled with stomatal conductance and related to transpiration rates. The reliability of leaf temperature estimates retrieved from remote sensing, however, remains critical since confounded by atmospheric effects ([Li et al., 2013](#)) (cf. [Appendix A](#)).

#### 3.2.3. Plant water content

The most intuitive approach to assess plant-water relations is to focus on the leaf water content itself. An increasing gradient between water supply in the soil and demand by the atmosphere causes an

increasing loss of water through leaf stomata, resulting in reduced leaf turgor, and eventually a reduction in stomatal conductance associated with reduced transpiration rates. This regulatory mechanism, referred to as isohydric behaviour, facilitates maintaining a sufficiently high leaf water potential to allow leaf functioning (Konings and Gentine, 2017; Manzoni et al., 2013a,b). Numerous studies follow this logic and exploit changes in reflected radiation between 800 nm and 2500 nm caused by varying leaf water content (Penuelas et al., 1993; Zarco-Tejada et al., 2003). Proposed spectral indices facilitate the development of empirical models that show good performances although only representative for specific plant types, environmental conditions, and observational scales (Rodriguez et al., 2011). Usually much more computer-intensive model inversion techniques could be successfully applied (Colombo et al., 2008), which allow for compensating sensitivities of spectral indices to factors that eventually confound relationships between radiance measurements at canopy or ecosystem scale and leaf water content (Rodriguez et al., 2011). Besides the use of optical remote sensing systems for leaf water content retrievals, also active and passive microwave systems are used. Such approaches are based on the sensitivity of backscattered or emitted microwave radiation on, e.g. vegetation optical depth (Konings and Gentine, 2017; Konings et al., 2017; Momen et al., 2017) and/or leaf dielectric properties (Pampaloni and Paloscia, 1986; van Emmerik et al., 2017) that are directly proportional to aboveground vegetation/leaf water content.

Ample evidence underpins the reliability of leaf water content estimates for mild to severe leaf water stress conditions, but show limited sensitivity at high leaf water content when light absorption saturates and small changes are difficult to detect (Penuelas et al., 1996). Thus, the investigation of plant-water relations based on leaf water content only is hardly possible when leaves are healthy, contain a large amount of water, and show diurnal variations in stomatal conductance and transpiration (Farooq et al., 2009). Since leaf water content estimates exploit water absorption, dew drops on leaves can also confound retrieved values.

### 3.2.4. Pigment composition

Leaf pigments and their composition are another set of biochemical tracers to estimate plant-water relations. If water as a resource is limited, plants avoid water loss through stomatal conductance control according to their homeohydric strategy (Nobel, 2009). Closed stomata reduce the CO<sub>2</sub> uptake and photosystems become increasingly deactivated (Foyer, 1993). At the same time, several pigments continue absorbing light to provide energy for photosynthesis but the energy cannot be fully used when photosystems are partly closed. Only the existence of protection mechanisms (e.g. NPQ, chloroplast movement, both acting in minutes to hours) and other adaptation mechanisms (i.e. the degradation of pigments within days to weeks) avoid a damage of the photosynthetic machinery (Gamon and Berry, 2012; Porcar-Castell et al., 2014). This implies that estimates of pigments acting at different time scales are indirectly indicative for plant-water relations.

Short term pigment changes, such as the conversion of xanthophylls associated with NPQ, impact the reflectance properties in the visible wavelength domain and can be quantified with, for example, the PRI (Gamon et al., 1990). The PRI was indeed suggested as a proxy for plant-water stress (Suarez et al., 2008; Zarco-Tejada et al., 2012). More severe and sustained water stress leads to a degradation of chlorophyll content over the course of days to weeks. Chlorophyll content can be estimated with spectral indices (e.g. the Chlorophyll Absorption Reflectance Index (CARI) (Kim et al., 1994), the Optimized Soil Adjusted Vegetation Index (OSAVI) (Rondeaux et al., 1996), three-band indices (Gitelson et al., 2006)) or model inversion approaches (Jacquemoud et al., 2009; Verrelst et al., 2015a). Several studies successfully use estimates of leaf chlorophyll content as a proxy for prolonged plant-water stress (Gago et al., 2015; Govender et al., 2009).

Pigment changes are sensitive proxies to track water loss in plants and detect plant-water stress. However, it must be noted that the time

delay in pigment changes following a reduction in available water and the fact that a certain severity of water stress is required to detect a change limits the sensitivity of pigment estimates to track short term or partial stomatal closure and related variations in water flow through plants.

### 3.2.5. Plant structure

Plant architecture substantially impacts the flow of water in plants. Leaf area and plant height, for example, are of relevance in determining the number of leaking water stomata in a canopy and the distance water has to be transported from the roots to the leaves. Particularly the leaf area determines the water use (Waring and Landsberg, 2011), as scaling the number of leaf stomata also allows determining canopy conductance (Yebara et al., 2013). Further, leaf area in combination with leaf shape, orientation and distribution (e.g. clumping) defines the roughness of the canopy and, consequently, the coupling between the atmosphere and canopy (Beerling et al., 2001). Plant height determines the gravitational hydrostatic gradient limiting maximum plant height (Nobel, 2009). In contrary, plant architecture can also be indicative for changes in leaf water content: a change in cell turgor can impact leaf orientation and on the long term morphology and architecture due to loss of leaves (Save et al., 1993).

Active remote sensing systems such as LiDAR and SAR are best suited to assess and quantify structural or volumetric vegetation properties. Active systems illuminate the Earth surface with laser or radar pulses (i.e. with different frequencies leading to very different scattering processes) and provide structural information in the form of the backscattered and altered pulse. This signal, in the case of SAR in combination with a-priori information of ground elevation, allows estimating vegetation height and other biophysical vegetation parameters. Full-waveform LiDAR systems retrieve a vertical profile representing the distribution of canopy elements by recording the backscattered signal over time (Lefsky et al., 1999; Morsdorf et al., 2009; Wagner, 2010). High-density 3D point clouds obtained with airborne or terrestrial laser scanning (ALS and TLS) systems also allow estimates of leaf area index (Kükenbrink et al., 2017; Moeser et al., 2014; Morsdorf et al., 2006). ALS and recent high-resolution SAR techniques can be used for the detection of single trees, including the derivation of parameters such as tree height, crown diameter or crown volume (Magnard et al., 2016; Morsdorf et al., 2004), and forest tomography (Frey and Meier, 2011), providing volumetric backscatter information.

Estimates of structural and volumetric vegetation information with optical remote sensing systems are only partly possible (Fatehi et al., 2015; Zarco-Tejada et al., 2014). In particular, optical signals saturate quickly with increasing leaf area and are typically not sensitive for LAI values greater than four. Since leaf orientation substantially impacts optical signals (Jacquemoud, 1993; Verrelst et al., 2015b), model inversion techniques hold the potential to retrieve such information, although the ill-posedness of inversion problems substantially limits reliability and success of such approaches (Koetz et al., 2007; Laurent et al., 2013). Plant height cannot be directly retrieved from single-angle optical data. However, photogrammetric approaches relying on multi-angle observation were frequently used in the past to analyse aerial photographs (Næsset, 2002) and nowadays face a revival with the advent of unmanned aerial vehicle (UAV) systems (Zarco-Tejada et al., 2014).

Vegetation clumping can be assessed with angular measurements or from images obtained with a wide field of view. The backward scattering behaviour of vegetation causes the so-called canopy hot spot, characterized by an increasing proportion of sun-lit leaves observed when measuring in the direction of incoming solar radiation. The structure of this hot spot (i.e. intensity and width) (Simmer and Gerstl, 1985) is indicative for canopy clumping (for detail cf. Hapke et al., 1996). A dark spot is observed in the forward scattering direction, and the difference between hot and dark spot can be exploited for an



improved characterization of vegetation structure (Lacaze et al., 2002).

### 3.2.6. Plant functional type

Photosynthetic pathway, pigment composition, and canopy structural properties among others determine the capacity of individual plants to adapt to environmental changes. The above sections described the main plant processes and properties impacting the water flow in plants. Additional plant specific parameters are relevant for determining water fluxes in the SPAC, e.g. root density or photosynthesis type. Further, models can only account for a reduced level of detail, as they are developed on few species only, but there is substantial progress in model development and models are frequently updated to more universally account for different plant types and species (Deng et al., 2017), a tendency also observed in the development of land surface modules of atmospheric models (Sulis et al., 2015). Considering more plant characteristics in models would require the capability to differentiate plant functional types as well as their changes over time.

Measuring plant functional types using remote sensing techniques offers several advantages. Large areas can be measured continuously in space and plant functional types can be mapped consistently on local to global scales. Moreover, measurements can be repeated in time for monitoring subtle changes to range shifts due to climate change or anthropogenic influence. By linking plant functional types with field measurements of plant specific information including below ground components, among them root structural information, a major limitation of remote sensing can be overcome, i.e. its focus on plant components in the upper canopy. Many possibilities exist to differentiate plant functional types via remote sensing (Schweiger et al., 2017; Ustin and Gamon, 2010). Approaches range from classification approaches using spectral information only to complex classification and stratification approaches building upon derived plant functional traits including biochemical, structural or phenological plant characteristics. Advanced approaches based on functional traits allow to group functionally similar plants at the desired level of detail of a given model, which exceeds a mere simplification of taxonomic information. In species-rich environments, such as tropical rainforests, some species might be redundant with regards to their functional traits and ecosystem functioning; thus not every species needs to be mapped and resolved in a model. Asner et al. (2017), for example, characterize the tropical forest and its functional diversity by grouping plant functional traits measured using airborne imaging spectroscopy, resulting in 36 forest functional classes and six associated functional groups. In other ecosystems, there might be considerable functional differences within species, as for example in species-poor temperate forests. Plant functional types might then go beyond species-level and can be grouped directly from functional traits. Schneider et al. (2017) show the capability of the combined usage of airborne laser scanning and imaging spectroscopy to map morphological and physiological traits and trait diversity in a temperate mixed forest, independently of any predefined taxonomy or vegetation units, and therefore allows to group plant functional types at any desired spatial scale, only limited by the original resolution of the data. Detailed measurements of plant characteristics have been limited to airborne remote sensing, but the developed methodologies can be applied to larger scales once corresponding spaceborne technology is in place (Jetz et al., 2016).

### 3.3. Observational approaches to assess atmospheric and soil information

Atmospheric parameters including air temperature, humidity, wind speed, and radiation components, as well as soil information including soil volumetric water content and soil type were found to be essential in determining water fluxes in vegetated canopies (cf. Section 2 and

Appendix C). A detailed review of the state-of-the-art approaches are provided in Appendix A and Appendix B.

## 4. Towards an advanced use of remote sensing to study plant-water relations

### 4.1. Sensitivity of observational approaches for plant-water relations

Remote sensing approaches building upon the measurement of plant properties and plant processes impacted by changing plant-water flow are diverse, well consolidated, and provide valuable information on the interplay between vegetation and water. However, proposed approaches often rely on assumptions (cf. Section 3.1), while the complexity of underlying processes requires a full consideration of causality between remote sensing proxies and plant-water relations. Indeed, a sensitivity analysis based on the combined energy balance and radiative transfer model SCOPE (van der Tol et al., 2009) suggests that the causality between plant information retrieved from remote sensing observations and the flow of water in the SPAC is in some cases quite indirect. We used this model and varied plant information typically used in studies of plant-water relations (cf. Section 3.1) to assess i) the impact of changing plant information on reflected and emitted canopy radiance, and ii) the sensitivity of measured radiance changes (as a function of vegetation parameters) for plant-water relations. Hereby, we assumed that transpiration is the most direct process related to water movement through plants (cf. Appendix D).

Results of this sensitivity analysis indicate that all investigated parameters caused a change in either reflected or emitted (i.e. thermal) radiation (Fig. 3). This dependency is the foundation of many approaches documented for an empirical assessment of plant-water relations. However, results also show that the strength of observed sensitivities varies across remote sensing proxies and depends on the initial state of the variable, a well-known and documented effect (Damm et al., 2014; Verrelst et al., 2015b) (Fig. 3).

Our sensitivity analysis also indicates that only few suggested vegetation parameters accessible with remote sensing techniques (i.e. leaf area index and canopy temperature) show a substantial causal relationship to plant water flow (i.e. a 1% change of the vegetation parameter causes a substantial sensitivity in both radiance and transpiration (Fig. 4)). Other vegetation parameters (i.e. leaf water and leaf chlorophyll content, leaf inclination angle) only moderately impact reflected radiance signals ( $\Delta$ Radiance) and only barely transpiration ( $\Delta$ Transpiration) (Fig. 4).

Results imply that depending on the gradient between water supply in the root zone and the water demand by leaves due to transpirational water loss, only few remote sensing parameters show large sensitivity to plant-water relations. The limited sensitivity of several parameters (e.g. leaf water content, pigment composition, or leaf inclination angle) can be partly explained by the fact that the SCOPE model lacks an explicit link between these parameters and stomatal aperture. Stomatal aperture is modelled as a function of the photosynthesis rate, the carbon dioxide concentration in the air, and the relative humidity (Ball et al., 1987). SCOPE only includes some indirect effects of pigments, leaf water and leaf inclinations on transpiration through their effects on the radiance interception and APAR. Other indirect effects via leaf turgor pressure and the relationship between the abundance of stomata and leaf pigments are not included because they are not universal and depend on the tolerance of species age (Egea et al., 2011; Farooq et al., 2009), requiring frequent re-parameterization for monitoring purposes. Nevertheless, our results indicate that documented sensitivities between plant-water relations and less sensitive remote sensing proxies (i.e. leaf water and chlorophyll content) (cf. Section 3.1) are partially

caused by a covariance with other processes such as wilting or senescence acting at different time scales. In fact, certain studies indicate that for isohydric species stomatal conductance is more affected by drought than leaf water content (Farooq et al., 2009). Yet other studies indicate that leaf water content is in several cases indicative for drought effects depending on the tolerance of species (Farooq et al., 2009). This suggests that such approaches can be well applicable locally but would require frequent re-parameterization for large-scale monitoring purposes to reflect the heterogeneity of vegetation and contrasting effects of environmental conditions.

#### 4.2. Combined observational-modelling approaches to assess plant-water relations

Combined observational and modelling approaches provide another strategy to investigate plant-water relations (Fig. 5), while particularly SPAC models are frequently used (Garcia-Tejera et al., 2017; Haghighi and Kirchner, 2017; Tuzet et al., 2003). The complexity of plant-water relations mandate many model parameters that, at the same time, limit the operational use of such models. Further, several model parameters relate to environmental conditions and plant properties that can substantially vary in space and time but are kept rather constant. This explains why studies still point to uncertainties in variations of plant-water relationships across species, locations, and environmental conditions (Landsberg and Waring, 2017). The combination of SPAC models with observational approaches would open new perspectives to assess plant-water relations: Remote sensing observations can be used to constrain e.g. the most sensitive model parameters and thus replace assumptions or static model parameterizations (Fig. 5).

Ample evidence in the literature (Garcia-Tejera et al., 2017; Tuzet et al., 2003; Williams et al., 1996) indicates complex interactions of atmospheric, plant, and soil parameters with water potential and plant functional parameters (e.g. photosynthesis, transpiration) in dependency on environmental conditions (e.g. PPFD, soil water availability). Results of a local sensitivity analysis (LSA) using the SPAC model developed by Garcia-Tejera et al. (2017) confirm this complexity (cf. Appendix C and Appendix D for details on the SPAC model and the LSA). Atmospheric, plant and soil parameters were systematically varied and the evolution of water potentials and plant functional parameters within two consecutive days was evaluated considering two levels of irradiance intensity and soil water availability (Fig. 6).

The LSA reveals different and complex connections of a fully coupled SPAC, for example, the connection of atmospheric parameters (i.e. VPD, air temperature, PPFD) with soil water potential. Further the impact of SPAC model parameters on leaf, xylem, and soil water potentials as well as plant functional parameters substantially varies. For the investigated setting, LAI, VPD, PPFD, and soil water content were found as the key factors determining the water flow in the SPAC. The results also demonstrate positive and negative effects of certain model parameters that additionally change the relative impact across model parameters with varying environmental conditions (Fig. 6).

It must be noted that the presented LSA provides only a very limited insight into the complexity of parameter interactions and the effects of environmental factors on water movements in plants. Further, it is not clear which homeohydric strategy is implemented in the underlying model. More elaborated and systematic analyses considering isohydric (fast stomatal regulation) and anisohydric (delayed stomatal regulation) plants are essential to further advance understanding. Nevertheless, results underline that modelling and predicting plant-water relations under the force of environmental change must simultaneously consider a variety of model parameters and consider their spatio-temporal variability.

The combination of remote sensing and SPAC-models provides a way forward to scale plant water-relations to entire landscapes (Waring and Landsberg, 2011). Their combined use can overcome the limited sensitivity of pure observational approaches as discussed in the previous section and address the need for more representative parameterization of dynamic SPAC model parameters. Thereby, direct parameterization of models (Waring and Landsberg, 2011) with observations is one strategy to advance model predictions. Besides, Scholze et al. (2017) provide a comprehensive assessment of how remote sensing can be combined with process-based models (in their example to facilitate carbon cycle research). Discussed strategies include benchmarking (i.e. an evaluation of models based on a comparison of model outputs (ensemble) with observations) and data assimilation to evaluate intermediate model results with observations. Such strategies provide interesting avenues towards improved process understanding and advanced capabilities to model and observe processes (Scholze et al., 2017).

#### 4.3. Available and upcoming observational capabilities

Research of plant-water relations using remote sensing requires observations of critical plant, soil, and atmospheric parameters across scales from single leaves and plants, to canopies and small fields, to ecosystems, and to the entire globe. A diversity of in situ employable instrumentation exists to measure parameters relevant to facilitate SPAC modelling activities. The market for field instrumentation is vibrant and an up-to-date overview of instruments and their properties is thus difficult or even impossible. Thus, we refer to review papers that investigate existing in situ instrumentation to measure plant optical properties (Balzarolo et al., 2011; Julitta et al., 2016), emission of thermal radiation (Schlerf et al. 2012), and canopy structure using terrestrial laser scanning systems (Morsdorf et al., 2018).

Available airborne instrumentation is diverse as well. Optical imaging spectrometers used to assess vegetation biochemistry and structural parameters include, for example, the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) (Green et al., 1998), the Airborne Prism Experiment (APEX) (Schaeppman et al., 2015), HyMap (Cocks et al., 1998), and the Compact Airborne Spectrographic Imager (CASI). For fluorescence spectroscopy, only few instrumentation exists so far, for example, the HyPlant imaging spectrometer (Rascher et al., 2015). For airborne based thermal instruments, we refer to the review provided by Schlerf et al. (2012). Airborne laser scanning is operationally used at the regional and national level, often in a general forestry context or driven by the need for accurate terrain models. A good overview of technologies and implementations of laser scanning in general is provided by Vosselman and Maas (2010) and for forestry applications in particular by Naesset (2014).

Spaceborne capability to constraint plant-water relations is diverse. Guanter et al. (2015b) provide an extensive overview of existing spaceborne imaging spectrometers to assess vegetation biochemistry and structure. For physiological vegetation information several missions already provide first insights into vegetation activity, e.g. the atmospheric missions GOME-2, GOSAT, SCIAMACHY, and OCO-2 (Guanter et al., 2015a). New missions are upcoming in the next years, e.g. ESA's Sentinel-5p or Fluorescence Explorer (FLEX) (Drusch et al., 2017). Schlerf et al. (2012) provide an overview on thermal satellite missions to assess air and surface temperatures (e.g. TERRA-AQUA/MODIS, TERRA/ASTER, Landsat/TM-ETM+). Microwave missions for soil moisture retrievals include, for example SMAP (Entekhabi et al., 2010) and SMOS (Kerr et al., 2010). Regarding structural measurements from space, SAR has the longest tradition with missions such as ALOS PALSAR (Rosenqvist et al., 2007) and TerraSAR X (Krieger et al.,

2007). In addition, the upcoming BIOMASS mission (Le Toan et al., 2011) will provide near-global biomass estimates. Regarding LiDAR, the unfortunately short-lived ICESat GLAS (Zwally et al., 2002) instrument provided the first structural waveforms of vegetation from space, albeit for the very large footprints less suited for vegetation. The upcoming GEDI instrument on ISS (Stavros et al., 2017) will be another test-case for a vegetation-focused LiDAR in space. All current space-borne LiDARs, however, provide point sampling only and will need upscaling with other sensors to provide near-global coverage.

This brief summary of observational capabilities indicates that instrumentation is not the limiting factor to advance our understanding of plant-water relations. The challenge is to ensure data continuity over larger time spans to possibly assess trends and interactions of plant-water relations under changing environmental conditions. The Sentinel program by ESA and the European Commission do a substantial step in this direction and ensure data availability over at least the next 30 years; also NASA's Landsat program is essential for this purpose.

## 5. Conclusions

Plant-water relations are an important source of information to understand vegetation functioning and its impact on water cycle under the force of global environmental change. Both remote sensing

observations and mechanistic modelling of the SPAC are advanced approaches to understand water flow and storage in plants. However, our analyses indicate limitations of both approaches when applied operationally across space and time. Particularly more in depth knowledge of remote sensing information and their causality to processes related to plant-water relations are required.

We conclude that assessments of the highly variable flow and storage of water in plants across spatial and temporal scales require sophisticated approaches based on either simply relating process models and remote sensing observations or using complex data assimilation schemes. Such endeavours would substantially gain our predictive capabilities to assess plant-water relations and eventually the role of vegetation in the water cycle by disentangling the complex interplay of plants impacting water cycle dynamics and being responsive to such dynamics.

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## Appendix A. Observational approaches to assess atmospheric information

Atmospheric parameters, in particular air temperature, air humidity and wind, but also radiation components, were found to be essential in determining water fluxes in vegetated canopies (cf. Section 2 and Appendix A). Imaging near-surface parameters of the atmosphere using e.g. observations from satellites are plagued with fundamental problems (cf. below), besides the problem that most near-surface state variables are inaccessible during cloudy conditions. This obstructs the path of information-bearing radiation from the surface to the satellite. Driven by the need to provide quantitative predictions especially of the near-surface state of the atmosphere, the atmospheric science community has turned among other reasons to so-called analyses. Analyses (or re-analyses when past time periods are re-analysed with the same setup, e.g. Bollmeyer et al. (2015)) are the output of numerical atmospheric models and are prepared by most national weather service's on daily to hourly time intervals. Results of analysis are for example used for weather predictions fed by all available observations using data assimilation. In this process the numerical model is used as an intelligent interpolation tool, generating complete and physically consistent states of the atmosphere (and the land surface) and, at the same time, reproduce within their errors any observation used in this process without – in the ideal case – involving any retrieval step. Such data must, however, be used with care since numerical atmospheric models use their own land surface schemes, which might bias near-surface atmospheric states accordingly. Thus, a detailed evaluation of these quasi-observations is advisable before their use as forcing data. In the next sub-sections, we will restrict ourselves to pure observational data on near-surface atmospheric state variables and concentrate on state-of-the-art remote sensing approaches to assess the most important ones.

### Air temperature

Air temperature is the driving force of many biological and chemical reactions and substantially impacts, for example, photosynthetic rates of plants e.g. Collatz et al. (1991). Furthermore, air temperature drives the heat energy exchange (sensible heat flux) in the soil-plant-atmosphere system, which competes with evapotranspiration in the exploitation of the net radiation flux. Since air temperature substantially varies in space and time, accurate estimates of air temperature are essential to understand and quantify water movement in ecosystems. The temperature of the air within and directly above the plant canopy – as for any layer of the atmosphere – cannot be estimated directly by remote sensing from space. This can be explained by the weighting functions in the thermal infrared and the microwave spectral ranges that quantify the relative contributions of atmospheric layers to the measured signal for single wavelengths at a distant sensor extend over kilometres (Rodgers, 1976). Most times, however, the surface temperature of leaves (cf. Li et al. (2013) for a comprehensive overview on remote sensing of leaf temperature) is close to air temperature, although significant differences may occur over the course of a day (e.g. Dong et al. (2017)).

The signal observed at the satellite consists of the thermal emissions of the surface and thus correspond to skin temperatures of measured objects (leaves). This signal is typically superimposed by atmospheric disturbances that need to be corrected (Li et al., 2013). The retrieval accuracy for surface temperature further relies on the capability to accurately estimate the surface emissivity per pixel. Past approaches in the thermal infrared (TIR) simply assumed constant values per land cover type. More sophisticated approaches use multi-spectral observations (or multi-channel methods) to increase the retrieval accuracy of land surface temperature (Atitar and Sobrino, 2009; Wan and Dozier, 1996). These approaches apply normalization to correct emission anisotropy effects (Li et al., 1999) or temporal variability caused by changing solar illumination (Jiang et al., 2006; Li et al., 2013). Since clouds completely obstruct the surface from the satellite view in the TIR range, microwave observations are also used since clouds are semi-transparent in that spectral range (Duan et al., 2017). The main drawback of passive microwaves is the much higher variability of the soil moisture dependent surface emissivity in that spectral range and the much lower achievable spatial resolution. Duan et al. (2017) estimate the retrieval errors of a combined TIR-MW algorithm to 2 K under cloud-free conditions and 4 K under cloudy conditions.

### *Incident photosynthetic active radiation*

Incident photosynthetic active radiation (PAR), the integrated sun-emission between 400 and 700 nm reaching the Earth surface, is a key driver of photosynthesis and thus substantially impacts water movements in plants and vegetation ecosystems.

Providing spatio-temporal measurements of incident PAR using satellites is challenging although radiation is the physical quantity optical remote sensing measures. The difficulty becomes clear when looking at the radiative transfer: PAR is estimated from measured radiation that twice travelled through and interacted with the atmosphere and was reflected by the surface. Surface reflection in turn largely depends on the surface properties (e.g. vegetation state) and the sun and view angle. Accurate estimates of PAR, hence, require compensation for absorption and scattering effects in measured radiation stemming from interactions with the atmosphere and the surface. Most available approaches to estimate PAR combine a-priori knowledge of top-of-canopy solar irradiance, radiance measurements, and atmospheric radiative-transfer models to calculate atmospheric transfer functions such as down- and up-welling transmittance, spherical albedo, path radiance, and thus forward modelled PAR (Liang et al., 2006; Olofsson et al., 2007). Radiance measurements are used to obtain the atmospheric conditions (e.g. aerosol load, water vapour content, cloud coverage) and surface albedo particularly determining the diffuse irradiance component at a pixel base (Damm et al., 2015b). Other approaches like in Shi et al. (2017) assimilate top-of-atmosphere radiance observations at different spectral channels into coupled soil-vegetation-atmosphere transfer models. Such approaches yield most reliable estimates of the state of the coupled system including the radiation components reaching the surface, like PAR and its absorbed fraction (FAPAR).

### *Vapour pressure deficit*

Vapour pressure deficit (VPD) is the difference between actual and saturated vapour pressure at a given temperature (Choudhury, 1998). It poses an atmospheric water demand and, thus, substantially impacts the leaf water potential and water movement from the plant to the atmosphere (Asbjornsen et al., 2011; Waring and Landsberg, 2011).

Besides assessing VPD with in-situ measured or extrapolated meteorological values, remote sensing techniques are increasingly used to provide spatial information of VPD and overcome the limited reliability of VPD estimates in regions with sparse meteorological observations (Hashimoto et al., 2008; Zhang et al., 2014). Given a reliable surface temperature estimate that facilitates the computation of the saturation pressure at this temperature, VPD would involve an estimate of the water vapour content of the near surface air. The limitations mentioned earlier concerning the near surface air temperature are even more valid for near surface air moisture; weighting functions are even broader and thus retrievals even less accurate. As a result, it is extremely challenging to estimate VPD from the difference of two inaccurate estimates. Current approaches consequently rely on empirical or semi-empirical relationships between measurable quantities and VPD. A well-known method estimates near surface moisture via regionally and seasonally variable statistical relations from the vertically-integrated or total precipitable water, e.g. Smith (1966), that can be retrieved from satellites with acceptable accuracy based on the split-window technique (e.g. Schroedter-Homscheidt et al. (2008) for an application to METEOSAT-SEVIRI observations). Zhang et al. (2014) provide a recent and comprehensive summary of current progress and indicates that available approaches typically depend on measurements of surface temperature, total precipitable water, and vegetation density. Results show moderate to good success depending on spatio-temporal aggregation scales.

### *Wind speed*

Wind speed is another important environmental forcing that not only contributes to observed variations in atmospheric evaporative demand (McVicar et al., 2012), but also influences leaf boundary layer conductance constraining water vapour, heat and CO<sub>2</sub> exchange rates at the leaf-atmosphere interface (Haghighi and Kirchner, 2017; Schymanski and Or, 2017). Quantifying wind speed effects on plant transpiration rates is of critical importance, given nonlinearities associated with transpiration-wind speed relations under different environmental conditions. Studies have shown that transpiration rate would increase by increasing wind speed under cloudy sky conditions due to the increased water vapour concentration gradient across the leaf boundary layer (Haghighi and Kirchner, 2017; Schymanski and Or, 2016; Schymanski and Or, 2017). Under clear sky conditions, however, increasing wind speed could result in more efficient convective cooling (i.e. upward sensible heat flux from leaf to the atmosphere), thereby reducing leaf surface temperature and suppressing transpiration rates accordingly (Schymanski and Or, 2016). This places significant importance on i) the proper representation of wind speed in plant-water relations prediction models and ii) its quantification as an important input model parameter using advanced monitoring techniques, given the widespread declining trend in mean wind speed across the globe (McVicar et al., 2012) that could adversely affect leaf water use efficiency (Schymanski and Or, 2016).

Remote sensing technology to quantify wind speed is based on Doppler shift Sound Detecting and Ranging (SODAR) or LiDAR. Such systems are installed on ground to determine 3D wind fields for single locations by detecting the time delay of backscatter sound or electromagnetic radiation (Du et al., 2017; Lundquist et al., 2015). The backscatter is caused by small particles and aerosols (Mie scattering) or air molecules (Rayleigh scattering) drifted with the wind (Reitebuch et al., 2009). Vertical profiling for single locations exist also from radiosonde networks, balloons, starting or descending aircrafts, and sounding polar-orbiting satellites (Stoffelen et al., 2005). Airborne systems and geostationary or polar satellites allow single level horizontal profiling (i.e. no vertical information of wind speed) (Stoffelen et al., 2005). Global coverage of 3D wind fields will be provided by ESAs ADM Aeolus mission (Stoffelen et al., 2005) after its launch in 2018. Besides the use of Doppler shift LiDAR and SODAR systems, indirect observations providing quasi spatial and vertical information are based on cloud movement analysis from satellites with multi-angular observation capability (e.g. NASA's MISR mission) (Horvath and Davies, 2001).

## **Appendix B. Observational approaches to assess soil information**

### *Soil volumetric water content*

Soil parameters across relevant spatial and temporal scales are only accessible with remote sensing techniques in the absence of vegetation or



sparse vegetation cover (Mulder et al., 2011; Owe et al., 2008; Srivastava, 2017). One key parameter is soil volumetric water content, being on the supply side of the water transport in the SPAC. Various approaches evolved over time to estimate soil volumetric water content from remote sensing data. Early attempts focused on the use of optical spectroscopy data and exploited water absorption features caused by soil water content (Liu et al., 2002; Lobell and Asner, 2002). Other approaches use thermal and optical data, and relate soil volumetric water content empirically with a combination of derived land surface temperature and indices describing green biomass (i.e. NDVI) (Sandholt et al., 2002). Other confounding factors impacting the radiative transfer in the optical domain and the empirical nature of thermal-optical approaches hinder a wider acceptance of these approaches for global mapping of soil volumetric water content.

Passive and active microwave satellites provide more reliable estimates of soil water content at a global scale (Scholze et al., 2017; Srivastava, 2017) with the two dedicated satellite missions Soil Moisture and Ocean Salinity (SMOS) (Kerr et al., 2010) and Soil Moisture Active Passive (SMAP) (Entekhabi et al., 2010) recently launched by the European Space Agency (ESA) and National Aeronautics and Space Administration (NASA), respectively. Microwave remote sensing builds upon the dielectric properties of soil and its change with increasing water content: passive systems measure the emitted microwave radiance and active systems record the backscattered microwave radiance (Scholze et al., 2017). Several approaches are available and yield soil moisture as a volumetric measure (i.e. model inversion techniques, machine learning approaches, linear regression) or soil moisture as percentage of total saturation (i.e. change detection methods, (Scholze et al., 2017)). Microwave methods are, however, also limited in the presence of dense vegetation like forests; also the very low spatial resolution (e.g. 40 km for SMOS) can be a drawback depending on the application. Finally, it must be kept in mind that only the upper very few centimetres (depending on soil moisture itself) are sensed, and that the highly dynamic profile of soil water content close to the surface must be taken into account, when interpreting or using the signal for data assimilation in land surface models (Wilker et al., 2006).

### Soil type

Soil type is a bulk parameter characterizing the water holding capacity of soil, water transport in soil and soil water potential. Differentiating soil types largely impacts the success of estimating water content since various inherent and dynamic soil properties (i.e. texture, structure, composition) impact the water holding capacity and water flow rates in the soil. Approaches to differentiate soil types (digital soil mapping) are typically based on a combination of soil properties derived from spectral measurements used as primary or secondary data source in geostatistical approaches (Mulder et al., 2011). Such soil properties include soil organic carbons content, soil salinity, soil iron content, clay/sand fraction or its mineralogy (Ben-Dor et al., 2009; Mulder et al., 2013; Stevens et al., 2010).

### Appendix C. Sensitivity of plant water flow and storage on environmental factors

A model describing water flow in the soil-plant-atmosphere continuum (SPAC) developed by Garcia-Tejera et al. (2017) was used for a local sensitivity analysis (LSA) to assess the impact of atmospheric, plant and soil parameters on water potentials at different places across the SPAC. Note that water transport and the capability of plants to store or lose water are determined by water potential and its gradient across the SPAC.

The SPAC model as proposed by Garcia-Tejera et al. (2017) was used to simulate soil ( $\psi_s$ ), xylem ( $\psi_x$ ) and leaf ( $\psi_l$ ) water potential, as well as stomatal conductance ( $g_s$ ), leaf transpiration (T), leaf photosynthesis (A), and leaf internal  $\text{CO}_2$  concentration (Ci). The model sequentially calculates the different parameters in three basic steps:

- 1)  $\psi_s$  is calculated according to Campbell (1985) as a function of soil water content, soil water content at saturation (approximated by soil porosity), and the air entry potential. Further, soil water content can be stratified for different layers vertically and horizontally, while the redistribution of water follows gradients of soil water potential according to Ritchie (1998).
- 2) Soil and root resistance is calculated for subsequent calculations of  $\psi_x$ .
- 3) The third step is an optimization procedure to calculate  $\psi_l$  and stomatal resistance for  $\text{CO}_2$ . The iteration procedure assumes a value of leaf internal  $\text{CO}_2$  and estimates a maximum stomatal conductance for  $\text{CO}_2$  at water unlimited leaf water potential by combining a general diffusion function and Farquhar's approach for biochemical photosynthesis (Farquhar et al., 1980). The derived maximum stomatal conductance for  $\text{CO}_2$  is used to calculate  $\psi_l$ , actual  $g_s$  using the approach by Tuzet et al. (2003) and finally the new value of Ci. After convergence of the initial Ci and the new Ci estimated actual  $g_s$  is used to obtain  $\psi_x$ , T, and A.

We simulated the water transport in the SPAC for two consecutive days and investigated the evolution of the model output within both days for the same time a day (noon). Therefore, we considered four combinations of two environmental conditions, i.e. high and low light intensity as high and low soil water availability. We modified several soil, plant and atmospheric variables and assessed their importance for SPAC modelling with a LSA. Selected parameters determine the demand of water for transpiration (i.e. VPD, PPF, and air temperature), the supply of water for transpiration (i.e. soil moisture content, soil temperature), and plant water transport (i.e. root density, leaf area, plant height, quantum efficiency for photosynthesis, and stomata sensitivity). For each model output parameter (i.e. the difference of  $\psi_s$ ,  $\psi_x$ ,  $\psi_l$ , T, A,  $g_s$ , Ci for two consecutive days), a Jacobian matrix **J** was defined as the matrix of the partial derivatives of the relative model output ( $Out_{rel}$ ) with respect to normalized model input parameters ( $par_{norm}$ ). The **J** matrix was calculated as:

$$\mathbf{J} = [j_k]_{1 \leq k \leq m}, \text{ with } j_k = \frac{\delta Out_{rel}}{\delta par_{norm,k}} \quad (1)$$

$m$  indicates the number of parameters and  $\delta Out_{rel}$  are the relative model outputs.  $\delta Out_{rel}$  was calculated as:

$$\delta Out_{rel} = \frac{100 \cdot \delta Out}{Out_{orig}} \quad (2)$$

where  $Out_{orig}$  is the original model output without any parameter change. Parameters were normalized assuming a uniform distribution over their variation range to make differently scaled parameters comparable. Normalized parameters were calculated as:

$$par_{norm} = \frac{par}{par_{max} - par_{min}} \quad (3)$$

For this particular experiment, Jacobians ( $j_k$ ) were calculated for each parameter through perturbing the parameter by 1% of its theoretical variation range (Table C1). Obtained  $j_k$  values describe the influence of parameter  $par_k$  on the model output  $Out_{rel}$ . It must be noted that this linear error analysis does not account for correlations between parameters.

**Table C1**

Parameters and their value ranges assessed in a local sensitivity analysis. For well watered conditions, soil water content was set to  $0.0027 \text{ m}^3 \text{ m}^{-3}$ , for dry conditions to  $0.0011 \text{ m}^3 \text{ m}^{-3}$ . For low light conditions, photosynthetic photon flux density was set to  $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , for high light conditions to  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . For photosynthetic photon flux density, air temperature and vapour pressure deficit, a typical diurnal course was assumed and indicated initial values represent the maximum value of the diurnal. Value ranges were partly obtained from Garcia-Tejera et al. (2017).

Parameter	Min	Max	$\delta par$ (1%)	Initial value
Soil water content [ $\text{m}^3 \text{ m}^{-3}$ ]	0.01	0.3	0.0029	0.0027/ 0.0011
Soil type [–]	sandy loam	loam		loam
Plant height [m]	0.1	10	0.099	1.0
Root length density [m (root) $\text{m}^{-3}$ (soil)]	5.0e003	1.56e005	1.5e003	1.56e005
Leaf Area Index [ $\text{m}^2 \text{ m}^{-2}$ ]	0.1	10	0.099	2.0
Sensitivity of stomata [MPa; MPa]	1.6; –1.6	3.2; –3.2	0.016; –0.016	1.6; –1.6
Quantum efficiency [–]	0.5	1.0	0.005	0.9
Photosynthetic Photon Flux [ $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ]	0	2500	25	max. 500/ 2000
Air temperature [°C]	5	35	0.3	max. 20
Vapour Pressure Deficit [kPa]	0.1	10	0.099	max. 2.5
Air Pressure [kPa]	80	120	1	100

#### Appendix D. Changes in plant – light interaction using SCOPE model

A sensitivity analysis was applied to quantify the impact of vegetation and environmental parameters on observable radiation reflected and emitted from vegetation canopies as well as plant transpiration as most direct indicator of water movement in plants. Two homogeneous vegetation canopies were considered, a healthy canopy under low environmental stress and a stressed canopy under harsh environmental conditions. We simulated top-of-canopy signals assuming accurate atmospheric compensation of remote sensing signals. We particularly varied two biochemical variables (i.e. leaf chlorophyll content (LCH), leaf water content (LWC)), two structural properties (i.e., leaf area index (LAI), leaf inclination distribution function (LIDF)), and the environmental variable air temperature  $T_{air}$ .

We used the SCOPE model as introduced by van der Tol et al. (2009) and changed model parameters as indicated in Table D1 for a vital and a stressed canopy. Resulting relative differences in simulated radiance, fluorescence and transpiration are quantified and presented in Figures 3 and 4. SCOPE allows simulating surface reflectance and the emitted sun-induced chlorophyll fluorescence with a spectral resolution (full width half maximum, FWHM) of 1.0 nm and a spectral sampling interval (SSI) of 1.0 nm. SCOPE is a combined model comprising an energy balance model providing simulations of photosynthesis, chlorophyll fluorescence and skin temperature at leaf level, the leaf and canopy radiative transfer (RT) models PROSPECT (Jacquemoud and Baret, 1990) and SAIL (Verhoef and Bach, 2007) to calculate ToC reflectance and transmittance, a RT model for chlorophyll fluorescence based on the FluorSAIL model (Miller et al., 2005), and a numerical RT model for thermal radiation based on Verhoef and Bach (2007).

**Table D1**

Model parameters for the SCOPE based analysis of plant-light interactions. Parameter ranges were partly obtained from van der Tol et al. (2009).

Parameter	Min	Max	$\delta par$ (1%)	Vital	Stressed
<b>Biochemistry</b>					
Leaf chlorophyll content [ $\mu\text{g cm}^{-2}$ ]	0	80	0.8	60	20
Leaf water content [ $\text{g cm}^{-2}$ ]	0	0.02	0.002	0.015	0.005
<b>Structure</b>					
Leaf inclination angle parameters [ $\text{g cm}^{-2}$ ]	–0.35/ –0.25	0/0	–0.0035/ –0.0025	–0.3535 <sup>a</sup> /–0.2525 <sup>a</sup>	
Leaf Area Index [ $\text{m}^2 \text{ m}^{-2}$ ]	0	10	0.1	5	0.5
<b>Environment</b>					
Leaf temperature [°C]	5	35	0.3	20	30

<sup>a</sup> Corresponds to an average leaf zenith angle of 60°.

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