

Plant profit maximization improves predictions of European forest responses to drought

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Summary

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- Knowledge of how water stress impacts the carbon and water cycles is a key uncertainty in terrestrial biosphere models.
- We tested a new profit maximization model, where photosynthetic uptake of CO₂ is optimally traded against plant hydraulic function, as an alternative to the empirical functions commonly used in models to regulate gas exchange during periods of water stress. We conducted a multi-site evaluation of this model at the ecosystem scale, before and during major droughts in Europe. Additionally, we asked whether the maximum hydraulic conductance in the soil–plant continuum k_{\max} (a key model parameter which is not commonly measured) could be predicted from long-term site climate.
- Compared with a control model with an empirical soil moisture function, the profit maximization model improved the simulation of evapotranspiration during the growing season, reducing the normalized mean square error by c. 63%, across mesic and xeric sites. We also showed that k_{\max} could be estimated from long-term climate, with improvements in the simulation of evapotranspiration at eight out of the 10 forest sites during drought.
- Although the generalization of this approach is contingent upon determining k_{\max} , it presents a mechanistic trait-based alternative to regulate canopy gas exchange in global models.

Introduction

Water availability is one of the primary controls of vegetation function, largely responsible for the pronounced seasonal and interannual variability in global CO₂ uptake by terrestrial ecosystems (Ahlström *et al.*, 2015; Jung *et al.*, 2017; Humphrey *et al.*, 2018; Green *et al.*, 2019). As a result, contemporary droughts affecting the Amazon, Australia, Europe, and North America have had considerable impact on ecosystems (e.g. affecting water use efficiency; see Peters *et al.*, 2018), human populations, and economic systems (Ciais *et al.*, 2005; Marengo *et al.*, 2013; van Dijk *et al.*, 2013; Boyer *et al.*, 2013). Critically, the impact of drought is often long-lasting (Kannenbergh *et al.*, 2019). For example, the legacy of the 2003 European drought was apparent beyond the conclusion of the drought, as forests experienced diebacks and pest infestations (Bréda *et al.*, 2006; Stahl *et al.*, 2016). Increases in drought intensity and/or duration, as projected in response to climate change, would therefore have major implications for the terrestrial biosphere (Stocker *et al.*, 2014; Ault *et al.*, 2014; Cook *et al.*, 2015; Zhao & Dai, 2017).

In coupled climate models, land surface models (LSMs) simulate the exchange of carbon (C), water, and energy fluxes between

the land surface and the atmosphere (Pitman, 2003). Land schemes typically use empirical relationships, hereafter referred to as β functions, to reduce canopy gas exchange in response to a decline in soil water availability (Best *et al.*, 2011; Egea *et al.*, 2011). These β functions rely on soil-dependent parameters (e.g. soil moisture content at field capacity and the wilting point), instead of reflecting vegetation adaptations to water availability. β has also been defined based on soil water potential thresholds (Oleson *et al.*, 2013), causing abrupt declines in vegetation function due to declining water availability in the top soil layers (De Kauwe *et al.*, 2015b; Medlyn *et al.*, 2016). Overall, β functions lack both empirical support (Verhoef & Egea, 2014; Medlyn *et al.*, 2016) and theoretical foundation, leading to important intermodel disagreement in the shapes of the functional forms used to limit gas exchange (Desborough, 1997; Medlyn *et al.*, 2016; De Kauwe *et al.*, 2017).

Importantly, the use of β functions contradicts widespread evidence that plants differ in their sensitivity to reduced water availability (Brodrribb & Cochard, 2009; Urli *et al.*, 2013; Li *et al.*, 2017). Explicit representations of plant hydraulics (e.g. segmented into root, stem, and leaf hydraulic elements) offer a mechanistic alternative to empirical soil-dependent β functions

Table 1 Summary of the 10 eddy-covariance sites.

Site name	Country	Latitude	Longitude	PFT ¹	Dominant species	Data ²	Reference
Hyytiälä	Finland	61.85°N	24.29°E	ENF	<i>Pinus sylvestris</i>	FN	Rinne (2000)
Sorø	Denmark	55.49°N	11.64°E	DBF	<i>Fagus sylvatica</i>	FN	Pilegaard <i>et al.</i> (2001)
Loobos	Netherlands	52.17°N	5.74°E	ENF	<i>P. sylvestris</i>	FN	Moors (2012)
Hesse Forest-Sarrebourg	France	48.67°N	7.07°E	DBF	<i>F. sylvatica</i>	LT ³	Granier <i>et al.</i> (2008)
Parco Ticino Forest	Italy	45.20°N	9.06°E	DBF	<i>Populus × canadensis</i>	FN ³	Valentini & Miglietta (2015)
Puéchabon	France	43.74°N	3.60°E	EBF	<i>Quercus ilex</i>	FN	Rambal <i>et al.</i> (2004)
Roccarespampani1	Italy	42.41°N	11.93°E	DBF	<i>Quercus cerris</i>	FN	Rey <i>et al.</i> (2002)
Roccarespampani2		42.39°N	11.92°E				
El Saler1	Spain	39.35°N	0.32°W	ENF	<i>Pinus halepensis</i>	LT ³	Kivimäenpää <i>et al.</i> (2010)
Espirra	Portugal	38.64°N	8.60°W	EBF	<i>Eucalyptus globulus</i>	LT ³	Rodrigues <i>et al.</i> (2011)

¹PFT, plant functional type; ENF, evergreen needleleaf forest; EBF, evergreen broadleaf forest; DBF, deciduous broadleaf forest.

²Data sets: FN, FLUXNET2015; LT, LaThuile.

³Data for the years 2002 and 2003 only are used, either due to a lack of availability in the later years (LT data set) or to missing data (at Parco Ticino Forest).

Table 2 Climate information and average growing-season weighted leaf area index (LAI_{GS}) at the 10 eddy-covariance sites.

Site name	Köppen climate class ¹	MAP ² (mm yr ⁻¹)	T _{air,avg} ² (°C)	D _{avg} ² (kPa)	T _{air,xx} ² (°C)	D _{xx} ² (kPa)	LAI _{GS} ³ (m ² m ⁻²)
Hyytiälä	Dfc	570	9.88	0.34	20.20	1.19	1.34
Sorø	Cfb	568	12.82	0.31	19.70	0.77	1.58
Loobos	Cfb	778	13.40	0.34	22.00	1.14	1.34
Hesse Forest-Sarrebourg	Cfb	753	14.29	0.48	23.50	1.36	2.31
Parco Ticino Forest	Cfa	1026	18.14	0.69	28.00	1.95	0.76
Puéchabon	Csa	772	17.56	0.77	28.00	2.39	1.13
Roccarespampani1	Csa	675	19.71	0.79	29.40	2.13	1.83
Roccarespampani2							1.64
El Saler1	Csa	383	21.29	0.90	30.00	2.21	0.67
Espirra	Csa	736	20.02	0.84	29.00	2.34	0.85

¹Dfc, continental without dry season and with cold summer; Cfb, temperate without dry season and with warm summer; Cfa, temperate without dry season and with hot summer; Csa, temperate with dry and hot summer.

²MAP, mean annual precipitation; average (avg) and extreme (xx) temperature and vapour pressure deficit values are calculated using the CRU TS v.4.03 data sets (Harris *et al.*, 2014) over the 1972–2002 period.

³Average weighted sunlit–shaded LAI values are calculated over the growing season (i.e. April–November) following the procedure detailed in the Supporting Information Methods S7 subsection b.

and hydraulic cost (HC) at the optimal leaf water potential $\Psi_{\text{leaf,opt}}$ (MPa) where profit is maximized:

$$\text{Profit}_{\text{max}} = \max(\text{CG}(\Psi_{\text{leaf}}) - \text{HC}(\Psi_{\text{leaf}})) \in [0, 1] \quad \text{Eqn 1}$$

(Ψ_{leaf} (MPa), leaf water potential; CG and HC are unitless and normalized to 1, which makes them comparable).

In our implementation of the model introduced by Eqn 1, water potential in the soil–plant continuum Ψ (MPa) varies along a continuous transpiration stream (i.e. a single hydraulic conductor): from the root-zone soil water potential Ψ_s (MPa) to Ψ_{leaf} . Ψ_{leaf} cannot drop below the critical leaf water potential indicative of maximum xylem hydraulic failure Ψ_{crit} (MPa). Using a continuous transpiration stream reduces parameterization by removing hydraulic segmentation, but likely results in more marked drought stress because it smooths conductance changes between the root zone and the leaves. We set Ψ_{crit} to match a near-complete hydraulic conductivity loss of 95%, accounting for possible high levels of embolism resistance.

Hydraulic cost The normalized hydraulic cost function reflects the increasing potential damage from cavitation as hydraulic conductance is lost:

$$\text{HC}(\Psi) = \frac{k_{i,\text{max}} - k(\Psi)}{k_{i,\text{max}} - k_{\text{crit}}} \in [0, 1] \quad \text{Eqn 2}$$

($k_{i,\text{max}}$ (mmol m⁻² s⁻¹ MPa⁻¹), instantaneous maximum hydraulic conductance in the soil–plant continuum after accounting for water stress – i.e. k_{max} evaluated at Ψ_s ; k_{crit} (mmol m⁻² s⁻¹ MPa⁻¹), critically low hydraulic conductance that provokes xylem failure at Ψ_{crit} ; k (mmol m⁻² s⁻¹ MPa⁻¹), hydraulic conductance for any water potential in the soil–plant continuum – see Eqn 3).

Hydraulic conductance is represented by a cumulative Weibull distribution (Neufeld *et al.*, 1992):

$$k(\Psi) = k_{\text{max}} e^{-(\Psi/b)^c} \quad \text{Eqn 3}$$

(k_{\max} ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$), maximum hydraulic conductance in the soil–plant continuum; b (MPa) and c (unitless) are sensitivity and shape parameters of the plant hydraulic vulnerability curve, respectively, and are reconstructed from two P_x parameters – e.g. P_{50} and P_{88} ; see Eqns S8, S9 in Methods S3).

Here, k_{\max} represents the maximum conductance of a single hydraulic conductor connecting the root zone to the leaves. In segmented representations of plant hydraulics, this parameterization would vary between the rhizosphere, roots, stem, and so on. Our approach combines all the hydraulic elements in the soil–plant continuum, hence encompassing maximum rhizosphere conductance as well as maximum whole plant hydraulic conductance.

k drops with soil water depletion, owing to xylem embolism, and recovers with soil water recharge (i.e. we assume perfect and instantaneously reversible embolism). Hence, the supply of water for transpiration from the root zone depends on plant hydraulic vulnerability and photosynthetic demand (via CG in Eqn 1), for any steady-state pressure drop between Ψ_s and Ψ_{leaf} (Sperry & Love, 2015):

$$E(\Psi_{\text{leaf}}) = \int_{\Psi_s}^{\Psi_{\text{leaf}}} k(\Psi) d\Psi \quad \text{Eqn 4}$$

(E is expressed in $\text{mmol m}^{-2} \text{s}^{-1}$).

Carbon gain The normalized C gain function represents a marginally decreasing C gain as leaf water potential becomes more negative:

$$\text{CG}(\Psi_{\text{leaf}}) = \frac{A(\Psi_{\text{leaf}})}{A_{\max}} \in [0, 1] \quad \text{Eqn 5}$$

(A ($\mu\text{mol m}^{-2} \text{s}^{-1}$), photosynthetic uptake at each corresponding Ψ_{leaf} ; A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$), instantaneous maximum over the range of Ψ_{leaf}).

The diffusive supply of CO_2 uses Fick's first law to represent the CO_2 flux from the ambient air C_a ($\mu\text{mol mol}^{-1}$) into the leaf intercellular air spaces C_i ($\mu\text{mol mol}^{-1}$):

$$A(\Psi_{\text{leaf}}) = g_c(\Psi_{\text{leaf}})(C_a - C_i(\Psi_{\text{leaf}})) \quad \text{Eqn 6}$$

(g_c ($\text{mol m}^{-2} \text{s}^{-1}$), CO_2 diffusive leaf conductance; C_i is obtained at Ψ_{leaf} by solving a system comprising Eqn 6 and a biochemical photosynthesis model (Farquhar *et al.*, 1980) of net photosynthesis A_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$); see Methods S1).

In Eqn 6, g_c varies with Ψ_{leaf} . To solve for g_c , leaf-to-air vapour pressure deficit D_{leaf} (kPa), and leaf temperature T_{leaf} ($^{\circ}\text{C}$) (at a given Ψ_{leaf}), we build a system of three expressions of $E(\Psi_{\text{leaf}})$: (1) E given by the supply function (Eqn 4); (2) E meeting the atmospheric demand for water (i.e. equating $1.57g_cD_{\text{leaf}}$, where 1.57 converts from conductance to CO_2 to total leaf conductance to water vapour); and (3) E given by the Penman–Monteith equation following radiative and thermodynamic constraints imposed on T_{leaf} (see Eqn S7), and thus on D_{leaf} .

Whilst the second equation of this system (atmospheric demand for E) implies a perfect coupling between the leaves and the atmosphere, stomatal feedbacks are theoretically accounted for via the plant hydraulic vulnerability in the supply equation (see Eqn 4).

Calculating the maximum hydraulic conductance k_{\max}

As discussed in the Introduction section, the key model parameter k_{\max} is not readily available. Katul *et al.* (2003) and Sperry *et al.* (2017) suggested a non-instantaneous (but not clearly defined) timescale of optimality, on which hydraulic plant traits would coordinate with photosynthetic traits. This hypothesis would reduce parameterization and be supported by leaf-level (e.g. Brodribb & Feild, 2000) and stand-level (e.g. Lai *et al.*, 2002) experimental evidence.

k_{\max} behavioural plasticity Sperry *et al.* (2017) suggested that, to maintain an optimal $C_i : C_a$ ratio of 0.7, k_{\max} should be coordinated with respect to both Eqn 1 and the maximum carboxylation rate at 25°C ($V_{\text{cmax},25}$) (see Fig. 3b in Sperry *et al.*, 2017). With that assumption, plants always follow the profit maximization approach, even at longer timescales; the possibility of long-term strategies oriented toward greater C accumulation, or greater water conservation, is ignored.

Here, we extend the Sperry *et al.* (2017) coordination hypothesis to add two alternative solutions for k_{\max} , because we have no *a priori* knowledge of how, and whether, hydraulic and photosynthetic trait coordination varies across plant species. We test the idea that a degree of plasticity in k_{\max} would feed back on $\Psi_{\text{leaf, opt}}$, and by extension on the water and C fluxes, so as to allow for behavioural plasticity in k_{\max} at longer timescales.

All our solutions for k_{\max} are calculated assuming well-watered conditions. For the first solution, $k_{\max, \text{opt}}$, we calculate the value of k_{\max} that yields $C_i : C_a = 0.7$ at $\Psi_{\text{leaf, opt}}$, following Eqn 1, as Sperry *et al.* (2017) did. $\Psi_{\text{leaf, opt}}$ corresponds to levels of embolism that vary depending on the vulnerability curve, $V_{\text{cmax},25}$, and soil water potential. For the second solution, $k_{\max, \text{high}}$, we calculate the value of k_{\max} that yields $C_i : C_a = 0.7$ immediately before Ψ_{leaf} equals P_{12} . P_{12} is the water potential at a 12% loss in xylem conductivity, which coincides with the onset of xylem embolism (Choat *et al.*, 2018). $k_{\max, \text{high}}$ is independent of Eqn 1 but makes use of Eqns 3, 4 and 6, and $k_{\max, \text{high}}$ is again coordinated with $V_{\text{cmax},25}$ so as to achieve $C_i : C_a = 0.7$. For the third solution, $k_{\max, \text{low}}$, we calculate the value of k_{\max} that yields $C_i : C_a = 0.7$ immediately before hydraulic cost offsets net profit. Mathematically, hydraulic cost exceeds profit when $\text{CG}(\Psi) = 2\text{HC}(\Psi)$. This third solution is the one for which the percentage loss in conductivity at Ψ_{leaf} ought to be the greatest (except in cases where the parameterized vulnerability curves indicate very negative hydraulic safety margins). Eqns 2–6 are used to determine $k_{\max, \text{low}}$.

$k_{\max, \text{high}}$ and $k_{\max, \text{low}}$ are intended as indicators of possible alternative longer term optimization strategies, since coordination between them and $C_i : C_a = 0.7$ may not always be physiologically meaningful. $C_i : C_a = 0.7$ might never be observed near the onset of xylem embolism for drought-avoiding species, but it

is unclear what a more appropriate value would be. Note, assuming these alternative set points is analogous to assuming different soil water availabilities upon the calculation of $k_{\max,\text{opt}}$.

In all three cases, once k_{\max} has been calculated, it is used as an input parameter for the profit maximization algorithm (see Profit maximization approach subsection), which simulates actual model outputs on an instantaneous basis. Fig. 1 illustrates how using values of $k_{\max,\text{high}}$ and $k_{\max,\text{low}}$ might alter the instantaneous profit maximization compared with $k_{\max,\text{opt}}$. In Fig. 1, $k_{\max,\text{high}}$ maximizes profit at smaller HC and CG compared with the two other solutions, displaying a more conservative water use strategy. On the contrary, $k_{\max,\text{low}}$ achieves maximum profit at higher HC and CG compared with the two other solutions, displaying a more profligate water use.

Fig. 1 demonstrates an example of the relative behaviours of $k_{\max,\text{opt}}$, $k_{\max,\text{high}}$, and $k_{\max,\text{low}}$. These relative behaviours are determined by the plant's vulnerability curve and, as such, vary from species to species.

k_{\max} adjustments to climate Another uncertainty pertains to the coordination of k_{\max} with photosynthetic traits and climate. Fig. 2 displays the theoretical response of $k_{\max,\text{opt}}$ (from our first k_{\max} solution) to changes in atmospheric conditions. Fig. 2a shows the relationship between increasing $V_{\text{cmax},25}$ and increasing $k_{\max,\text{opt}}$. As vapour pressure deficit D increases, $k_{\max,\text{opt}}$ further increases for a given $V_{\text{cmax},25}$, albeit logarithmically. In Fig. 2b,

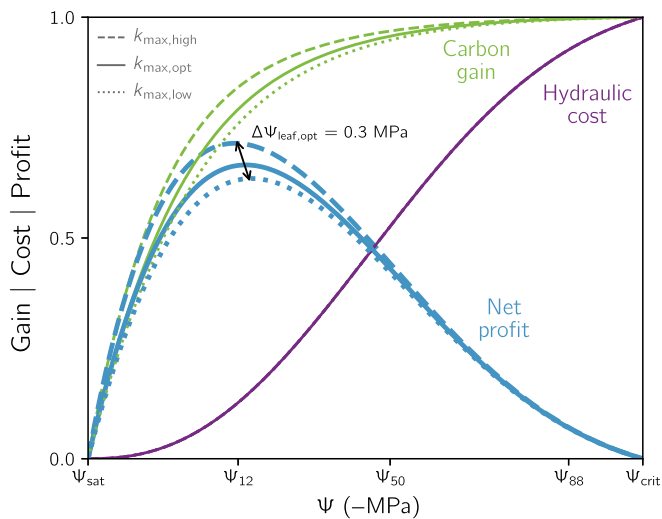


Fig. 1 An example of the instantaneous profit maximization algorithm. The carbon gain (green), hydraulic cost (purple), and net profit (blue) are shown as functions of the transpiration stream, which ranges between the soil water potential at saturation Ψ_{sat} and the critical water potential Ψ_{crit} . Maximum hydraulic conductance k_{\max} was calculated for each of the three behavioural solutions (i.e. $k_{\max,\text{high}}$, $k_{\max,\text{opt}}$, and $k_{\max,\text{low}}$; see the Calculating the maximum hydraulic conductance k_{\max} subsection of the Materials and Methods), before being used as an input the model. The dashed and dotted lines illustrate the impacts of alternative strategies for k_{\max} on the maximum profit; the optimal leaf water potentials at which profit it maximized $\Psi_{\text{leaf,opt}}$ span a range of 0.4 MPa between the instantaneous model run using $k_{\max,\text{high}}$ and the one using $k_{\max,\text{low}}$. The species used in this example is *Juniperus virginiana* ($P_{50} = -6.6$ MPa and $P_{88} = -10.5$ MPa; Choat *et al.*, 2012), with $V_{\text{cmax},25} = 100 \mu\text{mol m}^{-2} \text{s}^{-1}$, $T_{\text{air}} = 25^\circ\text{C}$ and $D = 1$ kPa, $\Psi_s = -0.8$ kPa, and $\text{LAI} = 2 \text{ m}^2 \text{ m}^{-2}$.

$V_{\text{cmax},25}$ is fixed and $k_{\max,\text{opt}}$ is constrained by T_{air} ; it declines above 25°C .

Fig. 2 shows that assuming $T_{\text{air}} = 25^\circ\text{C}$ and $D = 1$ kPa, as Sperry *et al.* (2017) did, might not be appropriate for the calculation of k_{\max} . As such, we test two scenarios to estimate whether the previously introduced k_{\max} behavioural plasticity displays further adjustment to average climatic conditions or hotter and drier conditions (see the Model spin-up and experiments – k_{\max} adjustments to climate subsection). The first scenario represents the background conditions under which plants grow. The second scenario will help us gauge the degree to which they might make hydraulic adjustments to cope with extreme growing conditions.

Modelling framework

We hereafter refer to the default model, embedding the Medlyn *et al.* (2011) stomatal model, as the ‘Control model’ and to the profit maximization approach as the ‘Profit_{max} model’. Both models were implemented within the same tractable LSM and forced by half-hourly meteorological inputs (i.e. photosynthetically active radiation, air temperature, precipitation, vapour pressure deficit, atmospheric pressure, and wind speed), which makes results directly comparable. Our LSM represents many of the core processes used across LSMs, albeit simplified. Notes S1 and Figs S2–S5 show a broad agreement between the Control model and the CABLE LSM (CABLE-2.0, revision 5320; Kowalczyk *et al.*, 2006; Wang *et al.*, 2011). We now summarise the key features of the tractable LSM, but see Methods S1–S6 for more information.

We used a two-big-leaf approximation (Wang & Leuning, 1998), differentiating the radiation absorbed by sunlit and shaded leaves to simulate canopy fluxes. Soil hydrology was represented using a water balance ‘tipping bucket’ model.

In the Control model, water stress impacts canopy fluxes by down-regulating the slope of the sensitivity of A_n to g_s , depending on the empirical soil-moisture stress factor β :

$$\beta = \frac{\theta - \theta_{\text{wp}}}{\theta_{\text{fc}} - \theta_{\text{wp}}} \quad \text{Eqn 7}$$

(θ ($\text{m}^3 \text{ m}^{-3}$), volumetric soil moisture; θ_{wp} ($\text{m}^3 \text{ m}^{-3}$) and θ_{fc} ($\text{m}^3 \text{ m}^{-3}$), volumetric soil moisture contents at wilting point and field capacity, respectively).

The Profit_{max} model transforms θ to Ψ_s via the Clapp and Hornberger water retention equation (Clapp & Hornberger, 1978; see Eqn S11), for use in the calculations related to the transpiration stream.

Forcing and site data

We tested the modelling framework at 10 European eddy-covariance sites on a latitudinal gradient (Table 1) over the years preceding and during two severe droughts: the 2003 continental and 2006 regional heat wave and drought events in Europe. Attention was given to diversity in climate (Table 2) and forest type (Table 1), to encompass a broad range of tree functional traits

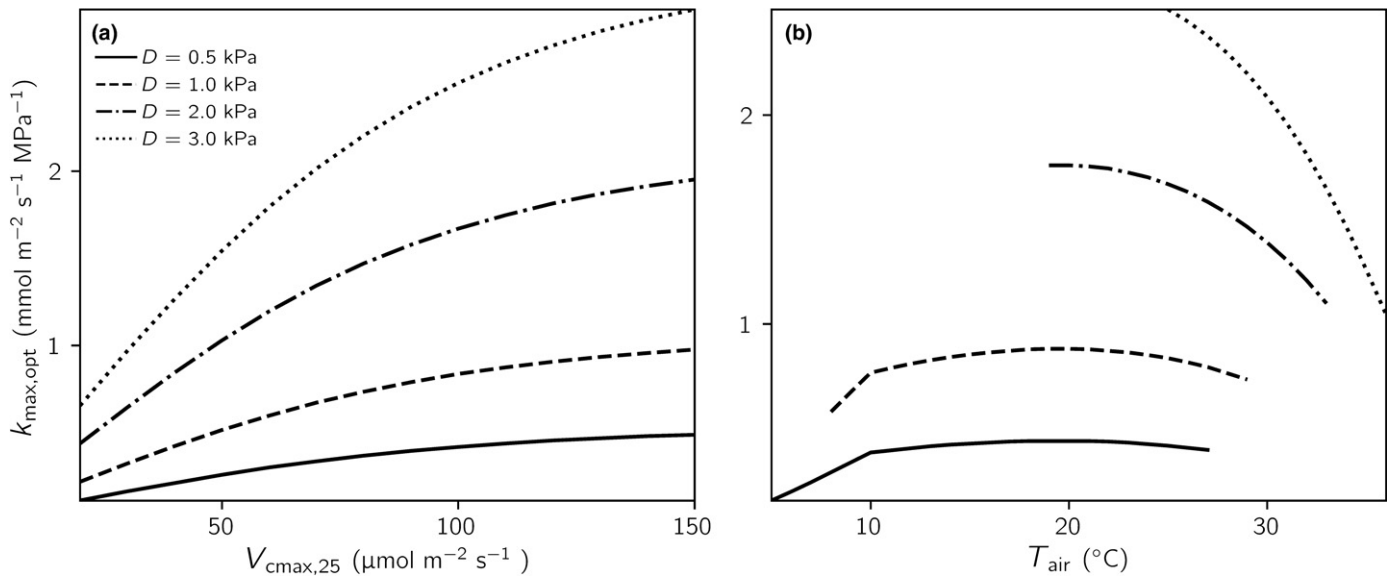


Fig. 2 The sensitivity of the modelled optimal coordination between the maximum hydraulic conductance $k_{\max, \text{opt}}$ and (a) the maximum carboxylation rate at 25°C $V_{c\max, 25}$ and (b) air temperature T_{air} , both depending on vapour pressure deficit D . (a) $k_{\max, \text{opt}}$ increases near proportionally with $V_{c\max, 25}$ and in a logarithmic fashion with D ; T_{air} is fixed to 25°C. (b) $k_{\max, \text{opt}}$ increases with T_{air} , before decreasing (sharply at the two highest D) starting between 20 and 25 °C; $V_{c\max, 25}$ is set to 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The valid range for $k_{\max, \text{opt}}$ is constrained by physically plausible co-occurring values of T_{air} and D under a relative humidity spanning 5–95%. The species used in this example is *Juniperus virginiana* ($P_{50} = -6.6$ MPa and $P_{88} = -10.5$ MPa; Choat *et al.*, 2012), with $\Psi_s = -0.8$ kPa and LAI = 2 $\text{m}^2 \text{m}^{-2}$.

(Table S2). Half-hourly meteorological forcing data, as well as latent heat – converted to evapotranspiration (ET) – and gross primary productivity (GPP) data used to evaluate the framework, originate from the marginal distribution sampling gap-filled FLUXNET2015 and LaThuile data sets (<http://fluxnet.fluxdata.org>) and were preprocessed using the FLUXNETLSM v.1.0 R package (Ukkola *et al.*, 2017). The GPP data in the FLUXNET2015 and LaThuile data sets are not actually measured, but rather estimated from measured net ecosystem exchange data using a nighttime partitioning approach (Reichstein *et al.*, 2005).

The model was run using site-specific prescribed phenologies (see Methods S7 subsection a) derived from the 8-d MODIS MOD15A2H v.6 leaf area index (LAI) product (Myneni *et al.*, 2015). The total effective root-zone depth of the ‘tipping bucket’ model was set between 0.3 and 1.20 m across sites (see Table S1 for the site-specific values and Methods S8 subsection a for how they were obtained). Species-specific trait data, as well as broader plant functional type (PFT) parameters used to run the LSM are provided in Tables S2–S5.

Model spin-up and experiments

Drought events were modelled by running the Control and Profit_{max} models for the calendar years of drought occurrence (2003 and 2006). The years before drought (2002 and 2005) were also modelled to act as reference conditions. The Control model was spun up to initialise the root-zone soil moisture state available to both the Control and the Profit_{max} at the beginning of each year. This spin-up was either forced with the flux tower’s meteorological record for the previous year, when available, or with the average site climatology.

k_{\max} calibration Objective (1) (see Introduction section) was addressed by calibrating k_{\max} to assess whether the Profit_{max} model can better explain the observed ET and GPP than the Control model (see Notes S2 and Fig. S6 for a calibration of the Control). To calibrate k_{\max} , we first calculated $k_{\max, \text{opt}}$ at $T_{\text{air}} = 25^{\circ}\text{C}$ and $D = 1$ kPa. This reference $k_{\max, \text{opt}}$ was then used to generate a sequence of possible values for k_{\max} . Twelve values were evenly selected between 25% and 95% of $k_{\max, \text{opt}}$ and a further 12 values were evenly distributed between 105 and 250% of $k_{\max, \text{opt}}$. The reference $k_{\max, \text{opt}}$ itself was added to the sequence, which led to a total of 25 values being used as parameter inputs to run each of the drought and nondrought years. The best calibrated k_{\max} value was selected following the procedure detailed in the Model performance assessment – Selection of best-performing configurations within each of the experiments subsection.

k_{\max} adjustments to climate Objective (2) (see Introduction section) was addressed by calculating the site-level k_{\max} following the strategies in Table 3: the $k_{\max, \text{opt}}$, $k_{\max, \text{high}}$, and $k_{\max, \text{low}}$ (introduced in the Calculating the maximum hydraulic conductance $k_{\max} - k_{\max}$ behavioural plasticity subsection) were each adjusted depending on long-term climate. We used coarser resolution meteorological data, from the 4.03 release of the Climate Research Unit TS data set (CRU TS v.4.03; Harris *et al.*, 2014) for the 1972–2002 period, to define two contrasting climate scenarios based on T_{air} and D :

(1) An ‘Average’ scenario, where CRU monthly daily mean air temperature was averaged over the growing season ($T_{\text{air, avg}}$, $^{\circ}\text{C}$); that is, April–November between 1972 and 2002. Average monthly vapour pressure deficit D_{avg} (kPa) was calculated via Tetens’s equation for saturation vapor pressure (Monteith &

Unsworth, 1990), using air temperature and monthly average actual vapour pressure over the growing season.

(2) An 'Extreme' scenario, where the 90th percentile of CRU monthly average daily maximum temperature was used to calculate $T_{\text{air,xx}}$ (°C). The associated vapour pressure deficit D_{xx} (kPa) was calculated as just noted.

All the $k_{\text{max,opt}}$, $k_{\text{max,high}}$ and $k_{\text{max,low}}$ were calculated for the soil water potential at saturation, given that the plants' vulnerability curves already account for sensitivity to water stress. The site average growing-season weighted sunlit–shaded LAI (see Table 2), but not the rooting depth, was used to scale the estimates from the leaf up to the ecosystem, assuming that a composite shaded–sunlit leaf proxy is representative of the stand's most productive state (see Methods S7 subsection b).

Table 2 summarises the sites' climate scenario information and the composite LAIs, whereas Table 3 provides an overview of the model experiments and configurations.

Model performance assessment

We applied the benchmarking methodology from the Protocol for the Analysis of Land Surface Models (PALS) Land Surface Model Benchmarking Evaluation Project (PLUMBER; Best *et al.*, 2015) to assess model performance. This methodology combines several statistical metrics to produce a comprehensive assessment of model skill, overcoming the shortcomings of individual metrics.

Five common statistical measures were used: normalized mean square error (NMSE), mean absolute error (MAE), standard deviation (SD), and the 5th and 95th percentile values (p_5 and p_{95}) indicative of agreement between the simulated and observed distributions. Following PLUMBER (Best *et al.*, 2015), we calculated the absolute difference between 1 and the ratio of modelled to observed SD, and the absolute distances between the modelled and observed p_5 and p_{95} .

For each statistical metric, we assigned quantile ranks between 0 (best performance) and 1 (worst performance) to the model configurations within an experiment (see the Model spin-up and experiments – k_{max} calibration and k_{max} adjustments to climate subsections); that is, we ranked the configurations relative to what the best performance could be following a quantile distribution. We then averaged each configuration's quantile ranks across the metrics. We therefore obtained an average quantile rank for each configuration, within each experiment. Notably, unlike averaging absolute ranks, averaging quantile ranks considers the configurations' relative performance across the statistical metrics.

Table 3 Summary of the two experiments conducted to estimate the maximum hydraulic conductance k_{max} and of the model configurations evaluated within each experiment.

	Experiments		
	Calibration	Adjustments to climate	
Profit _{max} configurations	25 values around the $k_{\text{max,opt}}$ at $T_{\text{air}} = 25^\circ\text{C}$ and $D = 1$ kPa	6 k_{max} values: 3 solutions × 2 climate scenarios $k_{\text{max,high}}$ $k_{\text{max,opt}}$ $k_{\text{max,low}}$	Average scenario Extreme scenario

Selection of best-performing configurations within each of the experiments To select the best calibrated configuration (objective (1)) and the best climate configuration (Average or Extreme scenario used to derive k_{max} ; objective (2)), we constrained the half-hourly data between April and July in 2002 and 2003. In doing so, we limited the effects of the dry-downs in selecting the configurations; that is, we did not calibrate k_{max} on the drought months in 2003 (July–October). We opted to select the best-performing configurations against the observed ET only, given that GPP is not directly observed but, rather, estimated at eddy-covariance sites.

Although we did not train the Profit_{max} model's algorithm to match the observed data, selecting the best-performing configurations based on a subset of data (ET restricted between April and July in 2002 and 2003) has consequences. We expect the ET predictions to be reasonably close to the observations between April and July in 2002 and 2003, because they will be made in sample. At any other time (i.e. between July and November in 2002 and 2003, and 2005 and 2006), the Profit_{max} model's ET predictions will be out-of-sample. The model's ability to match the observations will then depend, first, on its skill (e.g. in terms of partitioning ET into transpiration and soil evaporation) and, second, on changes in the vegetation properties, including potential legacy effects (in 2005 and 2006) of the 2003 drought on k_{max} . In contrast to the ET predictions, the GPP predictions are always made out of sample.

Evaluating the experiments' best-performing configurations and the Control model In the Model evaluation section, we gauge the effects of selecting each experiment's best-performing configuration (i.e. best calibration and best climate configuration) against ET only. To conduct this analysis, we first evaluated the Profit_{max} model's ability to simulate both (partially out-of-sample) ET and (effectively out-of-sample) GPP over the full April–November periods. Then, again, we combined the statistical metrics into quantile ranks for each of the best configurations and the Control model, relative to the observations.

Code

All model and analysis code are freely available from https://github.com/ManonSabot/Profit_Maximisation_European_Forests (Sabot, 2019).

Results

Model evaluation

Fig. 3 shows each site's average quantile ranks attained by the best model configurations and by the Control model, for GPP (Fig. 3a,c) and ET (Fig. 3b,d). Fig. 3(a,b) shows drought years and Fig. 3(c,d) shows nondrought years. Lower ranks equate to better overall performance, and box plots on the left of the figure summarise results across the entire period. Overall for ET, the calibration (light green, average quantile rank $\mu = 0.44$) and the best $k_{\text{max,opt}}$ among the Average and Extreme scenarios (best

climate configuration summarized in dark green, $\mu = 0.55$) outperformed the Control model (purple, $\mu = 0.74$). For GPP, the performances of the best calibration ($\mu = 0.56$), of the best climate configuration ($\mu = 0.59$), and of the Control model ($\mu = 0.61$) were similar. Selecting for one model output – as we did by selecting the best configurations by evaluating their skill in reproducing ET observations alone – is likely to degrade performance of other outputs (Abramowitz *et al.*, 2019; Herger *et al.*, 2019), but in the case of the Profit_{max} model it did not lead to significant losses in overall GPP performance.

The best Profit_{max} configurations from the two experiments improved on the simulated ET for each individual statistical metric of performance across all sites and years, relative to the Control model (not shown in Fig. 3). ET deviations (i.e. NMSE) were reduced by *c.* 63% in the best calibration and by *c.* 54% in the best climate configuration, which reflects an increase in temporal coincidence with the observations. Accuracy increased (i.e. the MAE decreased) by *c.* 29% for the best calibration and by *c.* 23% for the best climate configuration. The error in variability (i.e. SD metric) decreased by *c.* 41% for the best calibration and by *c.* 24% for the best climate configuration. Finally, the Profit_{max} displayed increased ability in better capturing the tails of the distribution, by 14% and 13% for the p_5 metric for the best calibration and the best climate configuration, respectively (see the Model performance assessment – Evaluating the experiments’ best-performing configurations and the Control model subsection of the Materials and Methods), and by 54% and 26% for the p_{95} metric for the best calibration and the best climate configuration, respectively.

We expected a closer fit between the observed and calibrated Profit_{max} model’s ET flux in the nondrought years (2002 and 2005), because k_{max} was not calibrated on the drought periods. Yet, at three sites (Parco Ticino, Puéchabon, and Roccarespampani1) the calibrated Profit_{max} model better simulated ET in the drought years than in 2002 and 2005. Relative to the Control model, improvements in the simulation of ET were larger in the drought years than in 2002 and 2005, for both the Profit_{max} model’s best calibration and its best climate configuration. In the drought years, the Profit_{max} model outperformed the Control model for ET at eight out of 10 sites. In the nondrought years, it did so at seven sites for the best calibration and at six sites for the best climate configuration (see Fig. 3). Figs 4 and 5 show time series comparisons of the Control model with the Profit_{max} model’s best calibration between April and November during the drought years (the best climate configurations are shown in Figs 6 and 7). Large improvements in the simulated ET are evident at Hyytialä, Parco Ticino, Roccarespampani1, and El Saler. At Hesse, the Profit_{max} significantly reduced ET biases (Figs 4n, 6n, S7n before June), but was still outranked by the Control (see Fig. 3).

Model behaviour

In the Control model, under well-watered conditions, photosynthetic water use efficiency (WUE) is set based on the empirical g_1 parameter and stomatal sensitivity to D (see Methods S4). In the Profit_{max} model, the instantaneous WUE varies optimally

depending on the potential to increase C gain versus the incurred risk of hydraulic function loss, even under well-watered conditions. Fig. 8a shows the effective g_1 parameter implied by the behaviour of the Profit_{max} model across the 10 sites. At Roccarespampani 1 and 2, the Profit_{max} model suggests a more conservative water use strategy than the Control model (lower g_1) to better match the observations. Conversely, the Profit_{max} model implies a more profligate water use strategy (higher g_1) at Hyytialä. In either case, the resulting changes in E do not linearly translate to marked changes in GPP because of the nonlinear relationship between g_s and A_n (e.g. Figs 4a,b, 5e,f). Indeed, when stomata are fully open, A_n is primarily limited by the rate of ribulose-1,5-bisphosphate regeneration (see Methods S1) and thus relatively insensitive to variations in stomatal conductance.

Behavioural differences between the models are also explained by their contrasting sensitivities to D . The Profit_{max} approach does not *a priori* set the sensitivity to D , whereas the Control model assumes g_s to be proportional to $1/D^{0.5}$ in the absence of water stress (Medlyn *et al.*, 2011). Both panels of Fig. 8 show a wide variation in the sensitivity of g_s to D across the 10 sites, varying between 0.48 and 0.84, and averaging 0.62 (cf. findings of Oren *et al.* (1999)).

To understand how the Profit_{max}’s instantaneous regulation of WUE affects plant water use during the growing season, we analysed the best calibration’s partitioning of ET into transpiration and soil evaporation, compared with that of the Control model. At all sites besides Roccarespampani 1 and 2, the ratio of transpiration to ET was increased and the ratio of soil evaporation to ET was decreased. These changes in partitioning led to delays in

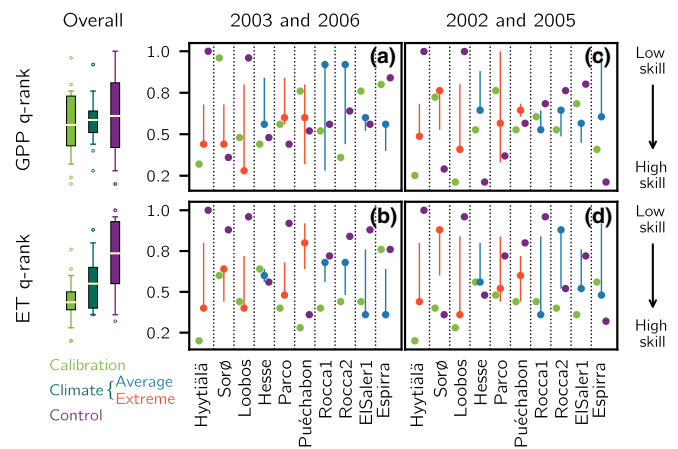


Fig. 3 Quantile ranks (q-rank) of the best configurations of the Profit_{max} model compared with the Control model: (a, b) across drought and (c, d) nondrought years; (a, c) for gross primary productivity (GPP); (b, d) evapotranspiration (ET). The vertical lines – blue (Average scenario) or red (Extreme scenario) – correspond to the best climate configuration’s range of ranks across the three behavioural solutions for the maximum hydraulic conductance. The box-and-whisker plots to the left of the figure summarise the ranks across sites but do not account for the behavioural range shown by the vertical lines. In the box-and-whisker plots, the horizontal yellow line shows the average overall quantile rank and the box shows the interquartile range; the whiskers extend to the 10th and 90th percentile values of the ranks, with dots outside of the whiskers showing outliers.

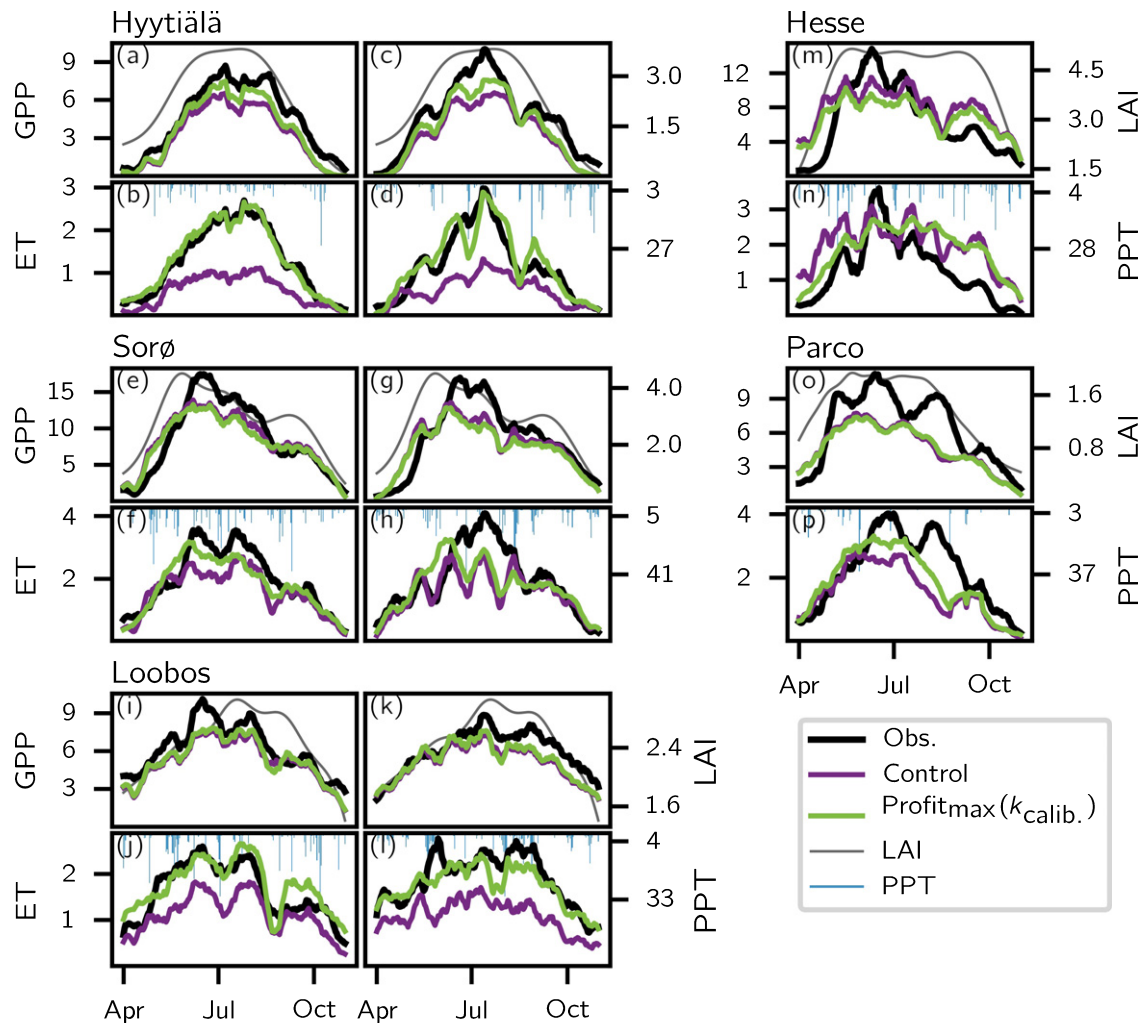


Fig. 4 A 14-d running average of the carbon (C) and water fluxes predicted by the best selected calibration configuration from the Profit_{max} model (green line) at the five northernmost eddy-covariance sites during (a, b, e, f, i, j, m, n, o, p) the 2003 and (c, d, g, h, k, l) the 2006 European drought events, compared with the Control model (purple line) and with the observations (black line). Grey lines show the prescribed phenologies (leaf area index (LAI), $\text{m}^2 \text{m}^{-2}$) and blue bars the precipitation (PPT, mm d^{-1}). The gross primary productivity (GPP) units are $\text{g C m}^{-2} \text{d}^{-1}$ and the evapotranspiration (ET) units are mm d^{-1} .

the overestimations of the rate and magnitude of dry-down simulated by the Control model (seen in many LSMs; Ukkola *et al.*, 2016) by up to 2 months (e.g. Fig. 5f,p in the Profit_{max}), on par with the observations. Fig. 9 illustrates how the Profit_{max} mechanically shifted the plants' ability to transpire as a function of soil water availability, from where canopy gas exchanges are maximized to where plants begin to wilt. This led to greater transpiration under drier conditions (e.g. Fig. 5j) whereby, at seven out of the 10 sites (not shown), the stomata were still not fully closed past the threshold for the wilting point of -1.5 MPa commonly used in LSMs (see Fig. 9 for an example at two sites). By contrast, the soil water potential never dropped below -0.9 MPa in the Control model.

Crucially, the Profit_{max} model's ability to simulate more realistic WUEs (e.g. Figs 4b,p, 5b,p) and to transpire for longer could lead to more realistic annual ET and GPP modelled fluxes. Puéchabon excepted, the best calibration's total ET estimates between April and November were always closer ($> 75\%$ closer at

five out of 10 sites) to the observations than the Control model's. For example, at Hyttiälä, the calibrated Profit_{max} model simulated a total ET of 562 mm between April and November, compared with 537 mm and 253 mm in the observed data and Control model, respectively; over that period, its total simulated GPP was 1620 g C, compared with 2055 g C and 1423 g C in the observed data and Control model, respectively.

Predicted stand k_{max}

In this study, we explored whether each site's stand k_{max} could be derived from the multi-decadal (30 yr) climate, assuming hydraulic adjustments on that timescale. Fig. 10 shows the wide range of k_{max} values ($0.08\text{--}2.53 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$) obtained from the two climate scenarios (Average and Extreme). We found those values to be in good agreement with the literature (cf. Notes S3 and Table S6 for a qualitative comparison). Even though the calculations of k_{max} were performed without knowledge of site

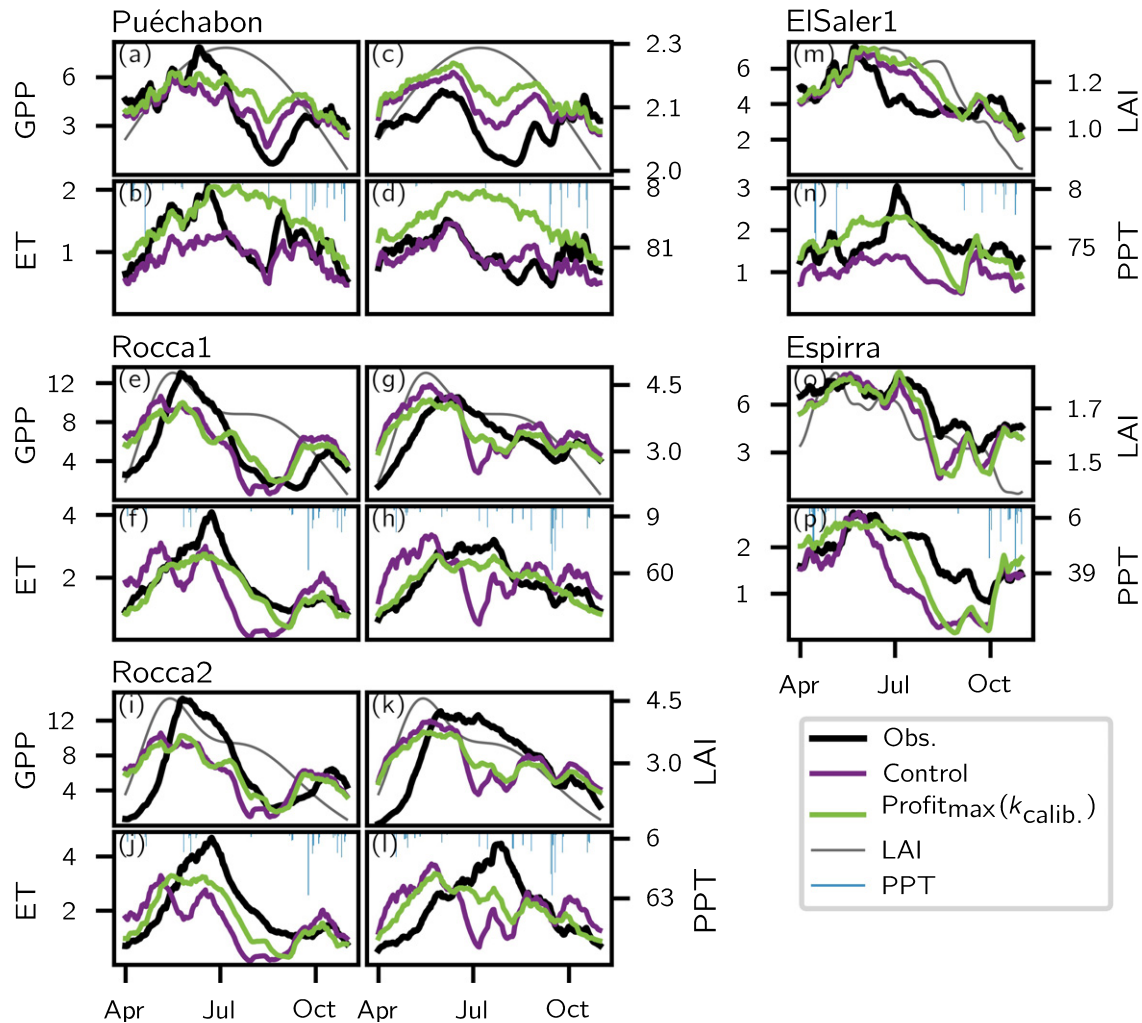


Fig. 5 A 14-d running average of the carbon (C) and water fluxes predicted by the best selected calibration configuration from the Profit_{max} model (green line) at the five southernmost eddy-covariance sites during (a, b, e, f, i, j, m, n, o, p) the 2003 and (c, d, g, h, k, l) the 2006 European drought events, compared with the Control model (purple line) and with the observations (black line). Grey lines show the prescribed phenologies (leaf area index (LAI), m² m⁻²) and blue bars the precipitation (PPT, mm d⁻¹). The gross primary productivity (GPP) units are g C m⁻² d⁻¹ and the evapotranspiration (ET) units are mm d⁻¹.

precipitation, the linear regressions (dotted lines) show increases in k_{max} with increasing mean annual precipitation (MAP; see Table 2), suggesting predictable variation in the hydraulic traits across sites. The regression slope was the steepest for the Extreme scenario, with k_{max} values ranging *c.* 2.8 times those of the Average scenario. Note that the relationship between k_{max} and MAP can partially be explained by the relationship between P_{50} and MAP (Li *et al.*, 2018), but that latter relationship alone only explains *c.* one-third of the degree of predictability in k_{max} for a given MAP because species-level values of P_{50} weaken any direct link between P_{50} data and site MAP. The expected relationship between LAI and MAP (Yang *et al.*, 2018) is not a good candidate to explain more of the predictability, as the relationship between k_{max} and MAP holds irrespective of changes in LAI.

Where the best climate predicted k_{max} broadly agreed with the calibrated k_{max} , the Profit_{max} model's climate configuration also had the ability to outperform the Control model (see Fig. 3).

The calibrated k_{max} exceeded that of the Extreme scenario at Hyttiälä and Loobos, but otherwise lay between the values of the Average and Extreme scenarios. The $k_{max,high}$ and $k_{max,low}$ were often smaller than the $k_{max,opt}$ (e.g. Hesse in Fig. 10), as we would expect from species trying to avoid the onset of xylem embolism (Köcher *et al.*, 2012), but this was not always the case (e.g. Puéchabon, where the $k_{max,opt}$ was enveloped by the $k_{max,high}$ and $k_{max,low}$, indicating higher drought tolerance). Overall, no unique climate-driven (i.e. Average or Extreme) or behaviour-driven (i.e. $k_{max,high}$, $k_{max,opt}$ or $k_{max,low}$) pattern explained the improved model performance.

Discussion

Climate models are particularly challenged when it comes to projecting how drought will change in the future (Orlowsky & Seneviratne, 2013). A number of offline LSMs have been

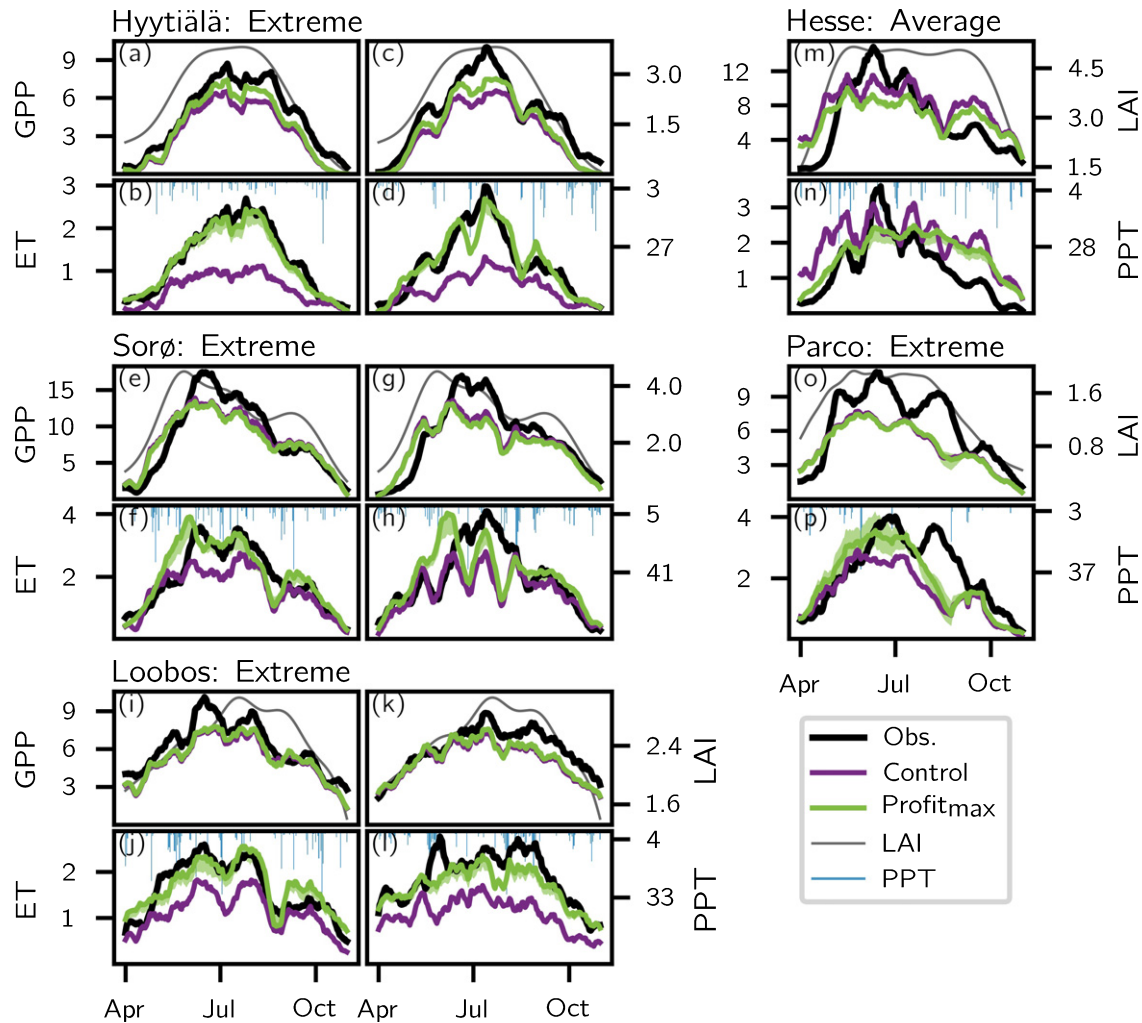


Fig. 6 A 14-d running average of the carbon (C) and water fluxes predicted by the best selected climate configuration from the Profit_{max} model (green) at the five northernmost eddy-covariance sites during (a, b, e, f, i, j, m, n, o, p) the 2003 and (c, d, g, h, k, l) the 2006 European drought events, compared with the Control model (purple line) and with the observations (black line). The green line is the $k_{\max, \text{opt}}$ strategy, and the green shadings encompass the instantaneous range of fluxes predicted by the three behavioural solutions for k_{\max} . Grey lines show the prescribed phenologies (leaf area index (LAI), $\text{m}^2 \text{m}^{-2}$) and blue bars the precipitation (PPT, mm d^{-1}). The gross primary productivity (GPP) units are $\text{g C m}^{-2} \text{d}^{-1}$ and the evapotranspiration (ET) units are mm d^{-1} .

shown to dry out too quickly (Ukkola *et al.*, 2016; Martínez-de la Torre *et al.*, 2019), and coupled-climate models markedly diverge from observations (Ukkola *et al.*, 2018) due to differences in their representation of soil hydraulic processes and vegetation water stress during drought. As root-zone soil moisture availability decreases, the partitioning of net radiation at the vegetated land surface increases sensible heat relative to latent heat. Therefore, if climate models incorrectly represent vegetation responses to drought, it is likely that they also erroneously represent feedbacks to the boundary layer (Donat *et al.*, 2018). This hinders the capacity to capture any land surface amplification of climate extremes (Yunusa *et al.*, 2015; Miralles *et al.*, 2018).

As an alternative to approaches widely used in LSMs, we investigated an optimization approach that considers an evolving trade-off between hydraulic cost and C gain to limit vegetation function during periods of water stress. When

calibrated (via k_{\max}), the Profit_{max} model was able to outperform our Control model, largely improving the simulated ET at eight out of 10 sites (see Fig. 3). Importantly, the Profit_{max} model, with its parameterized behaviour emerging from measured hydraulic traits, showed enhanced skill both outside and during drought. During drought, the k_{\max} model parameter estimated from long-term site climate also led to improvements in simulated ET at eight out of 10 sites. The positive nature of this evaluation at the ecosystem scale opens the door to the incorporation of hydraulic optimization approaches in models.

Can k_{\max} be derived from the climate?

The Profit_{max} model relies on key hydraulic traits: values of water potential relating to a specific percentage loss of conductivity (e.g. P_{50}) and k_{\max} . P_x traits are widely measured; it is less clear how one

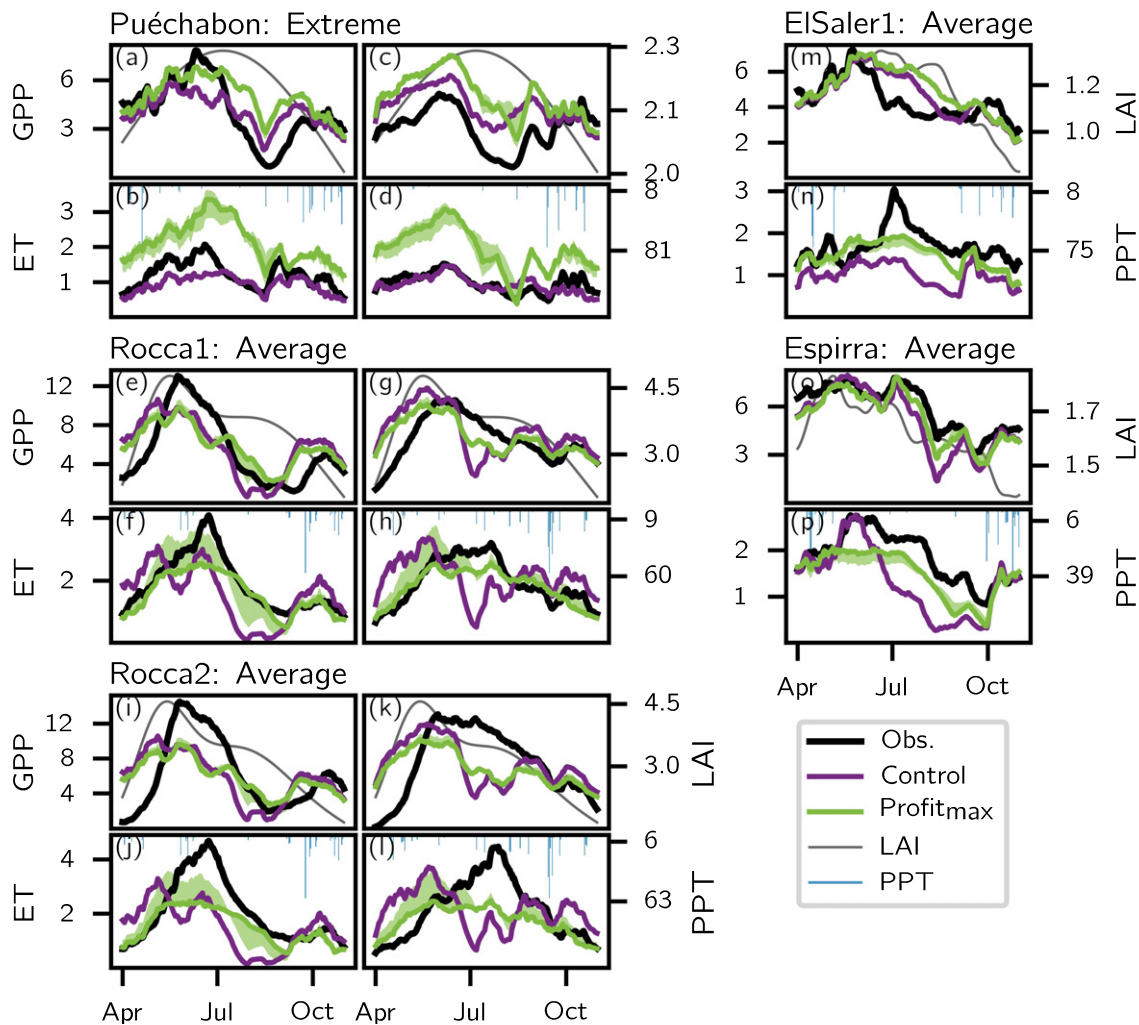


Fig. 7 A 14-d running average of the carbon (C) and water fluxes predicted by the best selected climate configuration from the Profit_{max} model (green) at the five southernmost eddy-covariance sites during (a, b, e, f, i, j, m, n, o, p) the 2003 and (c, d, g, h, k, l) the 2006 European drought events, compared with the Control model (purple line) and with the observations (black line). The green line is the $k_{\max, \text{opt}}$ strategy, and the green shadings encompass the instantaneous range of fluxes predicted by the three behavioural solutions for k_{\max} . Grey lines show the prescribed phenologies (leaf area index (LAI), $\text{m}^2 \text{m}^{-2}$) and blue bars the precipitation (PPT, mm d^{-1}). The gross primary productivity (GPP) units are $\text{g C m}^{-2} \text{d}^{-1}$ and the evapotranspiration (ET) units are mm d^{-1} .

might reliably estimate k_{\max} at the ecosystem scale. k_{\max} is a conceptual representation of the maximum conductance that plants could achieve given their ability to access water under the most favourable conditions, but it has not been commonly reported/derived in existing plant hydraulic literature. Here, we sought to explore whether k_{\max} varied predictively with a measure of climate, first because there is evidence of plant trait adjustments with climate (Atkin & Tjoelker, 2003; Mencuccini, 2003; Carins Murphy *et al.* 2012; Marchin *et al.*, 2016), and second because it led to a more parsimonious model with fewer parameters.

Although MAP is a broad measure of water availability that ignores groundwater effects, we found that k_{\max} increased with increasing MAP (see Fig. 10). This finding makes physical sense, because a stand of plants with low water availability would be limited in its ability to draw water from the soil and to conduct it through to the canopy, compared with a similar stand at a location with higher water availability. We also expected k_{\max} to

increase with vapour pressure deficit (see Fig. 2a) yet be inhibited at high temperatures (see Fig. 2b). Across our 10 sites, we found that the Extreme climate scenario consistently predicted the highest values of k_{\max} , meaning that D was the primary predictor of k_{\max} in the model.

Assuming covariation between k_{\max} and $V_{c_{\max, 25}}$, we estimated k_{\max} for a single value of $V_{c_{\max, 25}}$. In reality, it is likely that k_{\max} varies with $V_{c_{\max, 25}}$ across seasons for instance (Wilson *et al.*, 2000), depending on factors such as climate and soil properties (which likely influence rhizosphere conductance). k_{\max} is also likely to be coupled to plant allocation in individual trees (e.g. root area : leaf area ratio) and to LAI and/or tree density changes at the community scale. Further difficulty arises from the range of hydraulic behaviours observed across phenotypes and within species (Aranda *et al.*, 2005), with plants adjusting their function to different climatic thresholds and/or at different timescales. At intermediate levels of precipitation (between 700 and

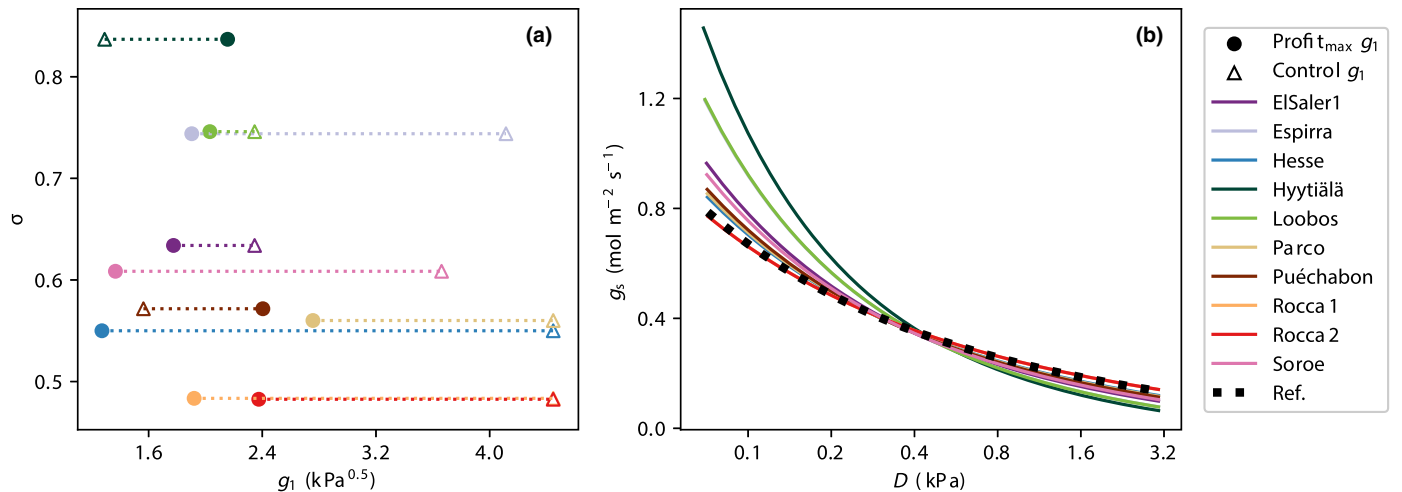


Fig. 8 A comparison of the sensitivity of the Control and calibrated Profit_{max} models' stomatal conductance g_s to vapour pressure deficit D across the 10 eddy-covariance sites. (a) The relationship between the implied water use efficiency g_1 ($\text{kPa}^{0.5}$) of the calibrated Profit_{max} model and its sensitivity to D (σ , unitless). The values of g_1 obtained for the Profit_{max} model were converted from unit kPa^σ to unit $\text{kPa}^{0.5}$ for comparison with the values of g_1 used in the Control model. g_1 and σ were obtained by least-square fitting of the g_s simulated by the calibrated Profit_{max} model to the Medlyn *et al.* (2011) stomatal conductance model. The estimates were produced using the site hydraulic and photosynthetic parameters, for temperatures ranging 10–40°C and D ranging 0.05–3 kPa. The values of g_1 used in the Control model are plotted against the respective sites' σ for visual comparison with those of the Profit_{max} model only, as they correspond to $\sigma = 0.5$. (b) The effect of the various σ on the g_s given by the Control model at 25°C. The input parameter g_1 was set to $2 \text{ kPa}^{0.5}$ for all the curves, but was converted to kPa^σ upon running the Control model with the site-specific values of σ shown in (a). The reference g_s of the Control model ($\sigma = 0.5$) is plotted for comparison. For both (a) and (b), the models were run assuming well-watered conditions.

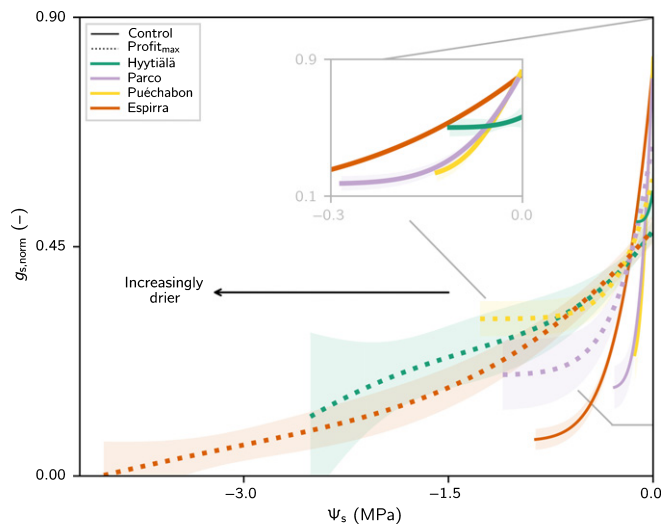


Fig. 9 A comparison of the decline in stomatal conductance g_s with predawn soil water potential Ψ_s , for the Control (plain lines) and the calibrated Profit_{max} (dotted lines) models at a sub-selection of sites. The functional forms emerge from the soil parameters and the β functions in the Control, and from the plant hydraulic traits and the profit maximization algorithm in the best selected calibration. The inset zooms on the functional forms of the g_s - Ψ_s curves from the Control model for $\Psi_s > -0.3$ MPa. The functional forms are made comparable by normalizing g_s by its maximum at a given site. Note that seemingly slow decreases in g_s with Ψ_s can be attributed to the nonlinear relationship between Ψ_s and volumetric soil moisture, whereby small variations in the latter can lead to large variations in the former. To avoid rainfall effects, the data up to 48 h after rain were excluded. To avoid low solar radiation and low temperature effects, the g_s data were restricted between 09:00 h and 15:00 h from April to November across all years. The curves were fitted with a linear generalized additive model, and the shadings show the 95% confidence interval of the fit.

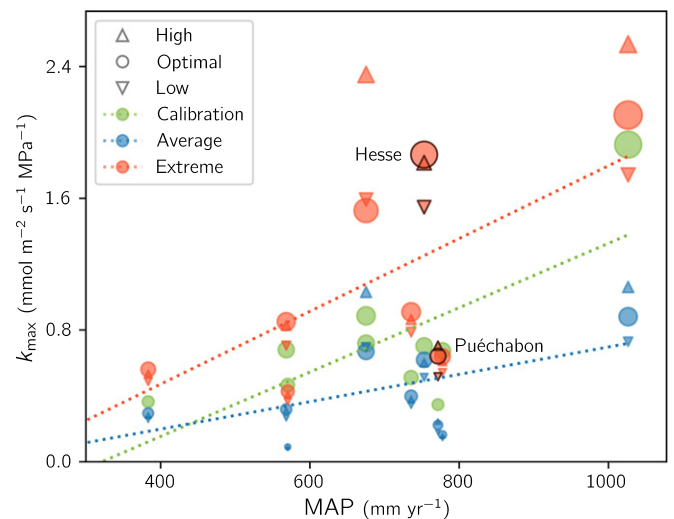


Fig. 10 The estimated site maximum hydraulic conductance k_{max} , for each climate configuration of the Profit_{max} model and for the best selected calibration, shown as a function of mean annual precipitation (MAP; as listed in Table 2). Note, the MAP was not used in the estimation of k_{max} ; however, k_{max} was multiplied by each site's weighted composite LAI, which normalises it to ground area and makes it comparable across sites. Linear regressions are used to show the positive relationship between k_{max} and MAP, with an r^2 of 0.53 and a P -value of 0.02 for the best selected calibration, an r^2 of 0.21 and a P -value of 0.01 for the Average scenario, and an r^2 of 0.30 and a P -value of 0.002 for the Extreme scenario.

800 mm yr^{-1}), diverse hydraulic strategies existed for similar MAPs (see Fig. 10).

Our attempt to estimate k_{max} based on climate is a promising proof of concept. We could further explore alternative climate descriptors, or scenarios, and alternative definitions of

the stand composite LAI (which we assumed to be a fixed value), to derive k_{\max} . Future work may otherwise include exploring the relation between k_{\max} , the (optimal ecosystem) climate and vegetation height, not unlike Liu *et al.* (2019), who showed some coordination between hydraulic traits and maximum plant height across biomes. Approaches relying on measurements of the mean diameter of xylem, which correlates with hydraulic conductivity (e.g. Hagen–Poiseuille law; Limousin *et al.*, 2010), could also be explored as they have previously been tested with some success (Cruiziat *et al.*, 2002). Finally, the use of data-driven approaches, like Bayesian model emulation (Fer *et al.*, 2018), might be an avenue for the calibration of hydraulic traits, allowing optimization schemes to be more widely used in global LSMs.

Improving the simulation of gross primary productivity

Marked improvements in simulated ET, using the Profit_{max} model, were not consistently followed by marked improvements to the simulation of GPP. Selecting the best configurations (see Table 3 for a reminder on what a configuration consists of) based on ET alone was likely to impair the GPP simulations because changes in ET do not linearly translate into changes in GPP. Here, remarkably, the GPP simulations were not degraded. Nevertheless, the recovery of the vegetation following an episode of drought was largely instantaneous (e.g. Fig. 5n). Indeed, the Profit_{max} model only considers instantaneous fluxes and does not directly incorporate mechanistic links between loss of hydraulic function and key turnover of plant tissues (e.g. leaves; see Wolfe *et al.* (2016) and Xu *et al.* (2016)). Since we prescribed LAI based on multi-year climatologies, the model could not capture large observed drops in GPP for a given year. For example, at Puéchabon, where previous years' water stress and drought legacy effects have been shown to affect leaf production in the subsequent years (Rambal *et al.*, 2014), the model failed to capture the GPP drops observed after 2003 (see the Control and Profit_{max} models in Figs 5c, S8c) because it overestimated LAI in scaling from the fluxes from the leaf-level up.

Implementation into state-of-the-art land surface models

Given the good performance of the Profit_{max} model, implementing it into state-of-the-art LSMs to improve the representation of drought–vegetation feedbacks is an attractive option. However, it should be noted that our implementation of the profit maximization approach assumes that the cavitation can be fully recovered upon soil water recharge (as in other hydraulic schemes; e.g. Xu *et al.*, 2016). This assumption is consistent with LSMs that do broadly not account for legacy effects, albeit consistent with the plant hydraulic literature showing that hydraulic repair is not routine in trees (Cochard & Delzon, 2013; Delzon & Cochard, 2014). Incorporating legacy effects is a research gap for the LSM community.

Optimization models can be perceived as computationally expensive for a climate model. Recently, Eller *et al.* (2018) proposed a simpler implementation of the Sperry *et al.* (2017) model with the stomatal optimization model based on xylem hydraulics

(SOX), by removing the continuous transpiration stream. SOX changed the fundamental optimization question asked by Profit_{max} from ‘What is the cavitation risk plants are willing to take to maximise C intake?’ to ‘What is the maximum C intake plants can achieve given a set hydraulic cost?’ We do not know how the practical simplification made by SOX might affect model behaviour across ecosystems, so it is important for future work to compare both assumptions and explore their relative merits. Until such a comparison is made, we argue in favour of maintaining a full optimization on the transpiration stream. Besides, Venturas *et al.* (2018) showed how the Profit_{max} could be used to infer plant mortality, with the advantage of moving past prescribing mortality thresholds (Mencuccini *et al.*, 2019).

In our implementation, we used computationally optimized matrices to solve the optimization (see code), keeping the computation expense small. We also provide a framework to vary (i) the frequency of instantaneous profit maximization (i.e. Eqn 1 every 30 min or longer), (ii) the solving window on the transpiration stream (i.e. instead of Ψ_s to Ψ_{crit} , Ψ_s to $\Psi_{\text{leaf,opt}}(t-1) \pm x\%$ with $t-1$ being the previous time step and the assumption that $\Psi_{\text{leaf,opt}}(t)$ would not depart by more than $x\%$ from the previous one), and (iii) the resolution of the transpiration stream itself (i.e. the increment between two adjacent Ψ values). Preliminary testing (not shown) did not indicate any significant benefit from increasing the resolution of the transpiration stream (i.e. (iii)). Issues arose when the solving window on the transpiration stream was too narrow (i.e. (ii)). Lastly, whilst optimizing up to every third hour did not significantly impact the simulations (i.e. (i)), daily optimizations flattened the model's response to environmental conditions, because they underestimated variations in leaf water potential throughout the day.

Finally, we could apply the Profit_{max} across sites globally, to generate functions to reduce stomatal conductance with decreasing soil water (e.g. Fig. S9). These functions could then be embedded in LSMs in place of the β functions. Although such an approach would be empirical, it would maintain a traceable link to measurable hydraulic traits at no added computation cost to LSMs. This approach will be the subject of future work, because globally connecting hydraulic traits and water limitations on ET in LSMs used in climate models would reduce existing weaknesses during periods of water stress.

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Author contributions

MEBS, MGDK and AJP designed the experiments. AMU pre-processed the eddy covariance data. MEBS developed the theory, implemented the model, and performed the analysis. MEBS, MGDK, AJP, BEM, AV, AMU and GA all contributed to the final manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 A schematic showing the modelling experiments.

Fig. S2 A 14-d running average of the carbon and water fluxes predicted by the Control model at the five northernmost eddy-covariance sites during the 2003 and 2006 European drought events, compared with the CABLE LSM and with the observations.

Fig. S3 A 14-d running average of the carbon and water fluxes predicted by the Control model at the five southernmost eddy-covariance sites during the 2003 and 2006 European drought events, compared with the CABLE LSM and with the observations.

Fig. S4 The predawn volumetric soil water available to the vegetation, as simulated by the Control model and by CABLE, at the five northernmost eddy-covariance sites during the 2003 European drought event.

Fig. S5 The predawn volumetric soil water available to the vegetation, as simulated by the Control model and by CABLE, at the five southernmost eddy-covariance sites during the 2003 European drought event.

Fig. S6 A 14-d running average of the carbon and water fluxes predicted by two different calibrations of the Control model at a sub-selection of sites in 2002, 2003, 2005 and 2006, compared with the calibrated Profit_{max} model, with the reference Control model, and with the observations.

Fig. S7 A 14-d running average of the carbon and water fluxes predicted by the best selected Calibration at the five northernmost eddy-covariance sites in 2002 and 2005, compared with the Control model and with the observations.

Fig. S8 A 14-d running average of the carbon and water fluxes predicted by the best selected Calibration at the five southernmost eddy-covariance sites in 2002 and 2005, compared with the Control model and with the observations.

Fig. S9 The stomatal conductance as a function of the predawn total volumetric soil water available to the vegetation.

Methods S1 Biochemical photosynthesis model.

Methods S2 Energy balance model.

Methods S3 Shape of the vulnerability curves.

Methods S4 Coupling carbon and water.

Methods S5 Scaling from leaf to canopy.

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