

Photosynthetic capacity, canopy size and rooting depth mediate response to heat and water stress of annual and perennial grain crops

G. Vico^{a,*}, F.H.M. Tang^{a,b,c}, N.A. Brunsell^d, T.E. Crews^e, G.G. Katul^{f,g}

^a Department of Crop Production Ecology, Swedish University of Agricultural Sciences (SLU), 750 07 Uppsala, Sweden

^b School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

^c Department of Civil Engineering, Monash University, Clayton, Victoria, Australia

^d Department of Geography and Atmospheric Science, University of Kansas, Lawrence, KS, USA 66045

^e The Land Institute, 2440 East Water Well Rd., Salina, KS, 67401, USA

^f Department of Civil and Environmental Engineering, Duke University, Durham, NC, USA 27708

^g Nicholas School for the Environment, Duke University, Durham, NC, USA 27708

ARTICLE INFO

Keywords:

annual wheat
leaf energy exchange
leaf temperature
intermediate wheatgrass
transpiration
water stress

ABSTRACT

Perennial grain crops are promoted as an alternative to annual staple crops to reduce negative environmental effects of agriculture and support a variety of ecosystem services. While perennial grains have undergone extensive testing, their vulnerability to projected future warmer and drier growing conditions remains unclear. To fill this gap, we compared leaf temperature and gas exchange rates of annual wheat and different perennial wheat ideotypes using a multi-layer process-based eco-hydrological model. The model combines leaf-level gas exchange, optimality principles regulating stomatal conductance, energy balance, radiative and momentum transfer inside the canopy, as well as soil water balance. Wheat ideotypes are parameterized based on an extensive review of field data. When compared with annual wheat, perennial wheat ideotypes with high leaf area index had between 12% and 39% higher canopy transpiration and net CO₂ assimilation, depending on their photosynthetic capacity and water status. Differences in leaf temperature and instantaneous water use efficiency between annual wheat and the perennial ideotypes were moderate (-0.5 to +0.4 °C and -6 to +2%, respectively). Low soil water availability did not alter the ranking of ideotypes in terms of canopy temperature and gas exchanges. During a prolonged dry down, cumulated water use was higher and canopy temperature lower in perennial than annual ideotypes, thanks to the deeper roots, whereas cumulated net CO₂ fixation depended on the specific traits and air temperature. Leaf-specific and whole plant characteristics interacted with hydro-meteorological conditions in defining the perennial's vulnerability envelopes to potential heat and water stress. These findings underline the importance of plant characteristics, and particularly leaf area and rooting depth, in defining the suitability of perennial grain crops under future climates.

1. Introduction

Annual crops, particularly grains, are essential for food security across the globe (e.g., Kreitzman et al., 2020; Meyer et al., 2012). Transitioning to perennial grain crops has been proposed as a way to enhance ecosystem services and sustainability of agriculture (e.g., Batello et al., 2014; Crews et al., 2018; Glover et al., 2010; Wagoner, 1990). Perennial crops ensure continuous soil coverage, can increase soil carbon storage (Ledo et al., 2020), improve soil structure and functioning (Duchene et al., 2020; DuPont et al., 2014; Sprunger et al.,

2019), and facilitate exploiting soil water and nutrients (Culman et al., 2013; Sprunger et al., 2018a). Perennial crops can also reduce nutrient leaching (Culman et al., 2013; Huddell et al., 2023; Jungers et al., 2019) and greenhouse gas emissions (Kim et al., 2021). Yet, it remains unclear whether perennial grain crops could support the adaptation of agriculture to changing climates.

Annual and perennial plants differ in many traits, even when considering congeneric species (Liu et al., 2019; Vico et al., 2016). Perennial grain crops are generally taller and have a larger leaf area than annual ones (Bergquist, 2019; Clark et al., 2019). Perennial plants

* Corresponding author: Giulia Vico, Department of Crop Production Ecology, Swedish University of Agricultural Sciences (SLU), Ulls väg 16, PO Box 4043, 750 05 Uppsala, Sweden

E-mail address: giulia.vico@slu.se (G. Vico).

<https://doi.org/10.1016/j.agrformet.2023.109666>

Received 25 July 2022; Received in revised form 26 July 2023; Accepted 15 August 2023

Available online 28 August 2023

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allocate more resources to below- rather than above-ground (Vico et al., 2016) and have larger, deeper roots than annual species (Sleiderink, 2020; Thorup-Kristensen et al., 2020). Both higher and lower stomatal conductance and photosynthetic capacity have been observed in perennial compared with annual species (Jaikumar et al., 2013; Liu et al., 2019; Lundgren and Des Marais, 2020; Vico et al., 2016). When compounded, these differences can have opposite effects on leaf temperature, transpiration and carbon fixation rates, and water use efficiency. Hence, the vulnerability of annual and perennial crops to limiting factors such as heat and water stress can differ considerably.

Canopy structure as well as leaf size and transpiration drive the leaf energy balance and thus leaf temperature (Michaletz et al., 2016). Eddy-covariance flux measurements showed that intermediate wheatgrass – a candidate perennial wheat – was on average aerodynamically less coupled to atmospheric conditions than annual wheat (Sutherlin et al., 2019). A lower aerodynamic coupling can enhance the leaf-to-air temperature difference, leading to higher canopy temperatures in perennial than annual crops, all else being equal. At the same time, under well-watered conditions, the larger transpiring biomass typical of perennial plants enhances transpiration, particularly if associated with higher stomatal conductance. This higher transpiration decreased leaf and canopy temperature as a result of evaporative cooling (Huang et al., 2015). It is thus uncertain whether perennial grain crops could experience higher heat stress than annual crops, for set hydro-meteorological conditions. We are not aware of canopy temperature observations contrasting perennial and annual crops, making it difficult to evaluate the potential adaptation of perennial crops to warming.

Access to soil water stores and its transpiration-driven depletion are key when assessing the vulnerability of crops to increased atmospheric water demands and altered precipitation patterns. The deeper roots typical of perennial plants (Sleiderink, 2020) allow exploitation of soil water stores that are larger and expected to be less subject to drying in the future (Berg et al., 2017). As such, perennial crops might be less vulnerable than annual crops to soil moisture drying trends projected for many regions (Basche and Edelson, 2017; Glover et al., 2010; van Tassel et al., 2014). The beneficial impacts of perennial crops on soil structure (Basche and DeLonge, 2017) could also facilitate water and nutrient retention, particularly under more extreme precipitation events. At the same time, having larger above-ground biomass, soil water storage is depleted faster (Katul et al., 2007; Siqueira et al., 2008), potentially exposing perennial crops to water stress earlier than annual ones. Whether the advantages provided by deeper roots or the disadvantages caused by faster water use prevail depends on the interactions between hydro-meteorological conditions and the plant characteristics. These interactions have so far been explored only via a minimalist model, relying on a simplified description of plant traits and response to hydro-meteorological conditions (Vico and Brunsell, 2018).

Water stress can exacerbate heat stress by reducing the plant evaporative cooling and increasing leaf temperature, all else being the same (Luan and Vico, 2021; Webber et al., 2016). As a result, the trade-off between access to deeper soil water stores and larger water demand defines the vulnerability of perennial crops not only to water stress but also to heat stress. Indeed, heat and water stress have interactive detrimental effects on crops and their yields (e.g., Luan et al., 2021; Matiu et al., 2017). Yet, these joint effects are seldom considered in models and experiments (Rötter et al., 2018) and remain unquantified for perennial grain crops.

Perennial grain crops are currently the focus of intense breeding programs (Crews and Cattani, 2018). The main goal has been to achieve marketable yields comparable with their annual counterparts, while maintaining the advantages of the perennial life habit (Kantar et al., 2016; Pastor-Pastor et al., 2019) and ensuring that the newly selected genotypes are well-suited to future hydro-meteorological conditions (e.g., Araus et al., 2002; Bell et al., 2010). Process-based models can help to disentangle the interactions between plant traits and hydro-climatic conditions. This can support an effective breeding for climate change

adaptation, by clarifying which plant traits or combinations of traits the perennial grain crops should possess to reduce their vulnerability to abiotic stressors expected to become increasingly frequent. This will ensure an effective water use and optimal canopy temperature for carbon fixation, while limiting their dependence on irrigation.

To evaluate the prospects of perennial crops under climate change beyond the limited flux data (Sutherlin et al., 2019), we developed and parameterized a process-based eco-hydrological model. Our model quantifies the profiles of leaf temperature and gas exchange rates within and above the canopy, and how these profiles are affected by and affect soil water dynamics. We explored the interactions of plant characteristics known to change with life habit and growing conditions in defining water use, carbon fixation and the occurrence of heat and water stress. Specifically, we ask i) how are differences in canopy temperature and transpiration and CO₂ assimilation rates mediated by crop characteristics associated to annual vs perennial life habit? ii) under which hydro-meteorological conditions are leaf temperature and gas exchange rates higher in perennial than annual grain crops? and iii) to what extent can deeper roots compensate for higher water demands? While the model is of general applicability, we focused on annual winter wheat, *Triticum aestivum*, and perennial wheat candidates - perennial wheat (*Triticum aestivum* L. × *Thinopyrum* spp.) and intermediate wheatgrass (*Thinopyrum intermedium*). Our results can guide future field experiments to key questions and breeding programs towards the most relevant traits for climate change-adapted perennial grain crops.

2. Material and methods

To answer the above questions, we developed and parameterized a vertically explicit description of the energy and momentum transfer as well as water and carbon balances in the canopy, coupled with soil water dynamics (Fig. 1; Section 2.1). The model estimates profiles of leaf temperature, transpiration and CO₂ assimilation rates, instantaneously and during a soil moisture dry down, as a function of crop characteristics and externally supplied boundary conditions (air temperature, relative humidity, wind velocity and solar radiation above the canopy, and initial soil or root water potential). Annual wheat was used as term of comparison. From that, several plausible perennial wheat ideotypes were constructed (Fig. 2) by altering the model parameters based on literature data (Section 2.2). We explored a variety of hydro-meteorological conditions in snapshots and during a dry down (Section 2.3).

2.1. Model

The model comprises four interdependent modules, quantifying layer-wise i) the micrometeorological conditions above and inside the canopy (mean wind velocity, air temperature, radiation transmission and absorption; Section 2.1.1); ii) the water flow along the soil-plant-atmosphere system, based on stomatal optimization theory and coupling with leaf carbon exchanges (Section 2.1.2); iii) the leaf energy balance (Section 2.1.3); and iv) the soil water dynamics (Section 2.1.4). We assume that fluxes equilibrate instantaneously with their driving forces and above-ground canopy water storage can be ignored relative to soil water storage. The model equations were solved numerically (Supplementary Information, SI, Section 4

2.1.1. Micrometeorological conditions above and inside the canopy

Mean wind velocity $U(z)$ and air temperature $T_a(z)$ profiles were determined by solving the mean momentum and heat balance equations at height z . The turbulent fluxes were ‘closed’ using a first-order closure scheme (SI, Section 1.1). For simplicity, the relative air humidity and air CO₂ concentration were considered constant with height (i.e., well mixed) within the canopy and approximated by their conditions above the canopy. As a consequence, the vapor pressure deficit profile $D(z)$ followed that of $T_a(z)$.

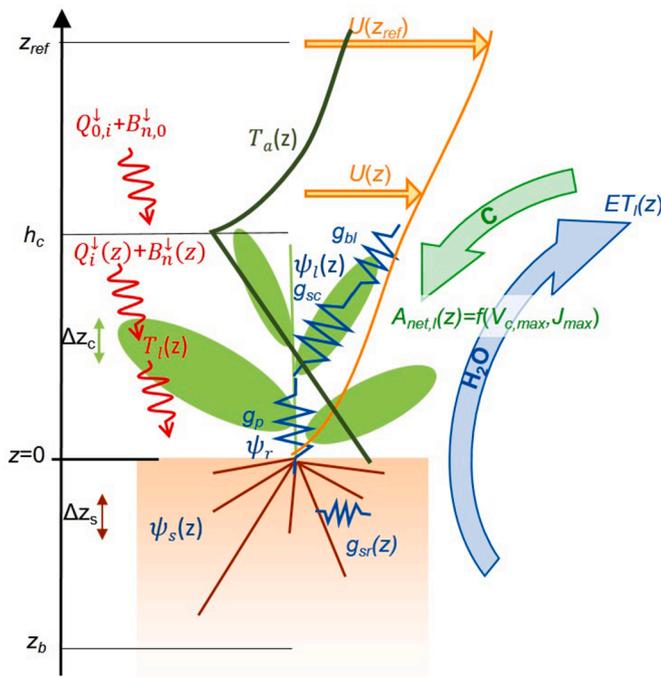


Fig. 1. Scheme of the multi-layer eco-hydrological model. The model describes the energy and mass exchanges within a stand with canopy height h_c , from soil at depth z_b to height z_{ref} above ground, with z being positive upwards. For each layer Δz_c above ground, the radiation and leaf energy balance (accounting for incoming and transmitted short- and long-wave radiation, Q_i^{\downarrow} and B_n^{\downarrow} ; in red) and momentum transfer are formulated. The model determines mean air temperature $T_a(z)$ (dark green) and wind velocity $U(z)$ (orange), as well as the carbon and water balances in the closed canopy, and, from these, leaf-level net CO_2 assimilation and transpiration rates, $A_{net,l}(z)$ and $ET_l(z)$ (light green and blue, respectively), and the leaf temperature, $T_l(z)$. For the snapshot simulations, the root collar potential, ψ_r , is set and only the above-ground part of the model is run. Conversely, when exploring a dry down, the above-ground part is coupled with a multi-layered soil water balance model, providing the soil water potential profile $\psi_s(z)$, calculated over each layer Δz_s by continuity equation. Water moves along a series of conductances (dark blue), from the soil (g_{sr}), through the plant (g_p), leaf (g_{sc}) and boundary layer (g_{bl}) to the atmosphere. The hydro-meteorological conditions at a reference height above the canopy, z_{ref} , are externally supplied and imposed on the crop system (Table 1). Water flows freely at z_b .

The absorbed short-wave radiation $Q^{\downarrow}(z)$ was obtained using a simplified radiation transmission model, whereby the radiation attenuates exponentially with canopy depth, thus depending on leaf area (SI, Section 1.2).

2.1.2. Water flow along the soil-plant-atmosphere system and leaf water and carbon exchanges

Soil water potential and atmospheric water demand drive canopy transpiration, creating a soil-plant-atmosphere system, which couples the leaf water and energy balances. The leaf-level transpiration rate, ET_l , results from the balance of water supplied via root water uptake and transport inside the plant, along a pressure gradient from the soil to the leaves, and water losses through the leaves, regulated by leaf conductance and atmospheric water vapor demand. The coupling of the leaf water exchange to the CO_2 fixation via the stomatal optimization allows estimating the net leaf-level CO_2 assimilation rate, $A_{net,l}$. Integration of ET_l and $A_{net,l}$ over the canopy profile provides the canopy transpiration and net CO_2 assimilation (ET_c and $A_{net,c}$).

Root water uptake and transport inside the plant were modelled via an integrated form of Darcy's law (Manzoni et al., 2013), considering soil-to-root, plant, and leaf conductances (SI, Section 2). The soil-to-root

conductance, $g_{sr}(z)$, depends on root characteristics (root dry weight density profile, $RWD(z)$, average root tissue density, RTD , and root radius, r_r) as well as soil hydraulic conductance in each soil layer (SI, Eq. 16; Lhomme, 1998). The plant conductance reduces non-linearly with increasingly negative canopy-averaged leaf water potential, from an ideotype-specific maximum value, $g_{p,max}$ (SI, Eq. 17; Manzoni et al., 2013). The leaf conductance to water vapor, g_v , is represented as the series of stomatal and leaf boundary layer conductances (SI, Section 2.2). We obtained the leaf-level stomatal conductance based on the optimization principle, assuming the leaf maximizes the net carbon fixation over a given period, under set water availability (Buckley et al., 2017). Both RuBisCO and electron transport rate limitations to gross photosynthesis are considered using a hyperbolic approximation of the original Farquhar model (Farquhar et al., 1980; Vico et al., 2013). This approach allows retaining key physiological parameters, such as maximum carboxylation rate, $V_{c,max}$, and electron transport rate, J_{max} , and their dependences on water availability and leaf temperature (Bernacchi et al., 2001; Medlyn et al., 2002; Vico and Porporato, 2008). Leaf day respiration is set to a fraction of $V_{c,max}$, and hence depends also on water availability and leaf temperature. In parallel to stomatal conductance, we also considered a minimum loss of water that is not directly controlled by the plant, which decreases with declining leaf water potential (cuticular conductance; Duursma et al., 2019; Luan and Vico, 2021). The leaf boundary layer conductance depends on mean wind velocity, $U(z)$, and leaf size, d_l (Campbell and Norman, 1998).

2.1.3. Leaf energy balance and leaf temperature

The leaf temperature at height z inside the canopy, $T_l(z)$, is calculated based on the leaf energy balance. This balance considers the net absorbed short- and long-wave radiation and the sensible and latent heat losses (Campbell and Norman, 1998), along with their dependences on leaf and air temperature and their coupling with the canopy momentum balance, transpiration, and leaf activity (SI, Section 3).

2.1.4. Soil water dynamics

When extending the simulations to a soil moisture dry down, the above modules are coupled with a layer-wise description of the soil water dynamics. The vertical water flux is given by gravity and differences in soil water potential, $\psi_s(z)$. The layer-specific sink term is set equal to a fraction of the canopy transpiration, ET_c (Section 2.1.2) proportional to the local soil-to-root conductance, $g_{sr}(z)$. For simplicity, plant mediated hydraulic distribution is neglected. Agricultural fields are typically flat and with rather homogeneous conditions above- and below-ground, so we did not consider lateral movements of soil water. No flux was considered at the soil surface, in line with the focus on a dry down (i.e., no rainfall or irrigation) and closed canopy (i.e., reduced soil water evaporation).

2.2. Selection of crop parameters for the annual and perennial wheat ideotypes

We parameterized the model for two crops with similar agronomic features but contrasting life habit: annual wheat and a perennial alternative to that. Perennial wheat (*Triticum aestivum* L. \times *Thinopyrum* spp.) and intermediate wheatgrass (*Thinopyrum intermedium*) have been the target of extensive breeding (e.g., Hayes et al., 2018), with testing of varieties from different selection cycles.

The key traits known to change with life habit relate to canopy characteristics, photosynthesis, and root biomass and its distribution (Bergquist et al., 2019; Clark et al., 2019; Duchene et al., 2020; Jaikumar et al., 2013; Sprunger et al., 2018b; Vico et al., 2016). We thus used the parameterization of annual wheat in Luan and Vico (2021; Table S2) also for perennial wheat and changed only the parameters expected to vary with life habit. None of the perennial wheat or wheatgrass hybrids currently available have been fully characterized with reference to

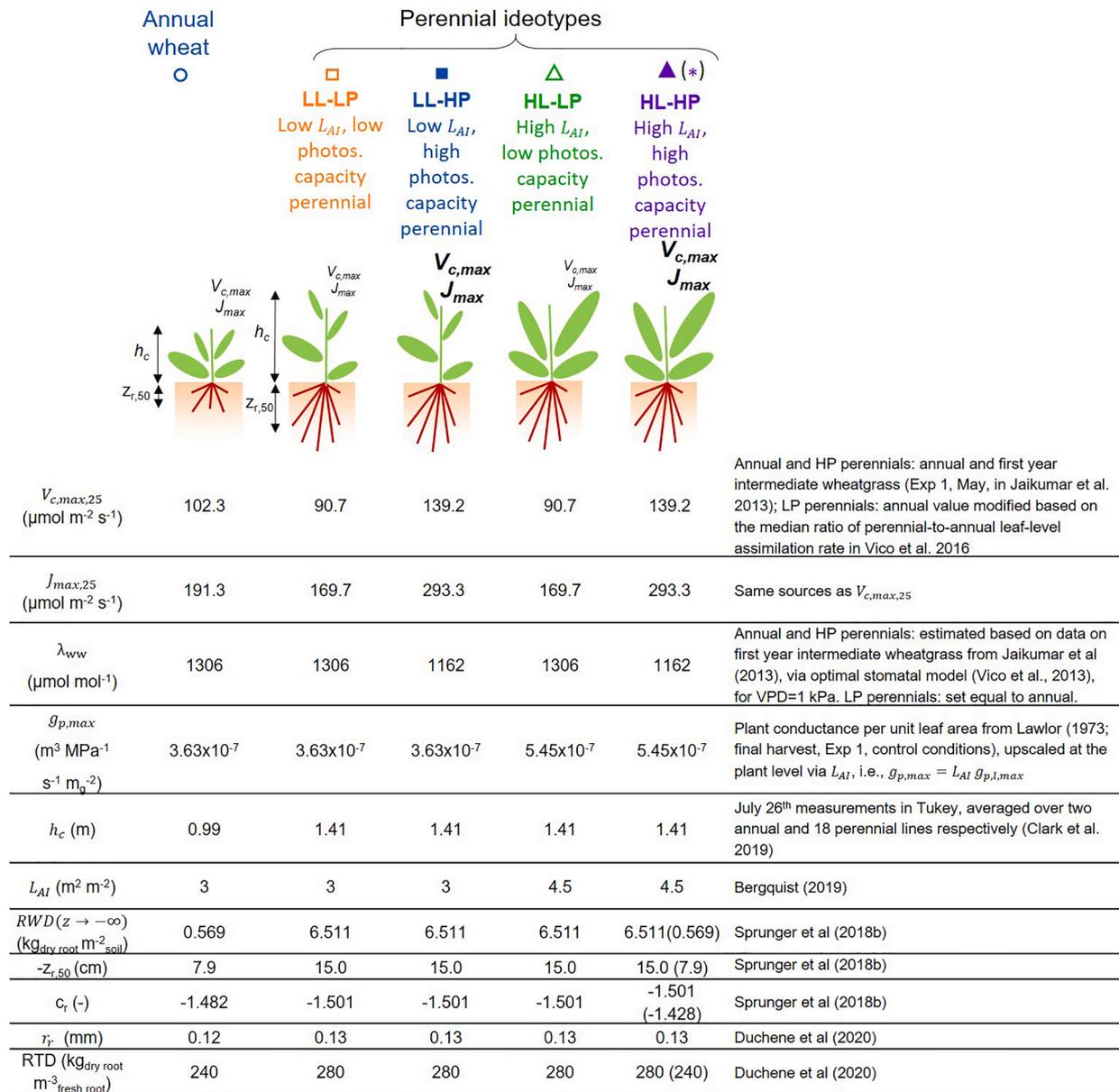


Fig. 2. Summary of annual and perennial ideotypes considered and their characteristics and sources: photosynthetic capacity (maximum carboxylation and electron transport rates at 25°C, $V_{c,max,25}$ and $J_{max,25}$, and marginal water use efficiency under well-watered conditions λ_{ww}), maximum plant conductance $g_{p,max}$, plant structure (canopy height h_c and leaf area index L_{AI}) and root features (soil depth above which 50% of the roots are located $z_{r,50}$, mean root radius r_r , root dry weight density, RWD , root tissue density, RTD , and root profile steepness, c_r). We considered annual wheat (far left; blue open symbol) and four perennial wheat ideotypes (other columns), combining low and high leaf area index (LL and HL respectively), and low and high photosynthetic capacity (LP and HP respectively). In addition, the case of HL-HP with root parameters equal to annual wheat (in brackets) is examined in the dry down simulations.

photosynthetic capacity, plant and root architecture. Furthermore, few experiments contrast these perennial hybrids with annual wheat under the same conditions. Given the uncertainty in perennial wheat characteristics, we explored several perennial ideotypes differing in key traits (Fig. 2), based on literature data mostly relative to perennial wheat and intermediate wheatgrass, but in some cases contrasting congeneric annual and perennial species. We refer to these ideotypes generically as perennial wheat.

We focused on the period around flowering, assuming a closed canopy. More developed canopies lead to faster soil water uptake, and hence a higher risk of water stress, and a weaker aerodynamic coupling between canopy and atmosphere, and hence more marked differences between leaf and air temperatures. Furthermore, yields of annual wheat are most sensitive to water and heat stress around flowering (Daryanto et al., 2017; Porter and Gawith, 1999). Nevertheless, the model could be

applied to other phenological stages, by altering the canopy features (chiefly leaf area index and canopy height), and consequently the fluid dynamic parameters, and root distribution. Early in the season, with sparser canopies, soil water evaporation from the top soil layer needs to be accounted for.

2.2.1. Photosynthesis and stomatal conductance parameters ($V_{c,max,25}$, $J_{max,25}$, and λ_{ww})

Compared with annual wheat, first-year intermediate wheatgrass had respectively 36% and 53% higher maximum carboxylation rate and electron transport rate, $V_{c,max,25}$ and $J_{max,25}$, but a similar CO_2 compensation point at 25°C, in a field experiment in Michigan (Jaikummar et al., 2013). The same pattern also emerged in perennial wheat and rye and in second-year intermediate wheatgrass. Yet, among congeneric annual and perennial species, the median leaf-level assimilation rate was 11.3%

lower in perennial than annual species (Vico et al., 2016). This lower assimilation rate is in line with the leaf economic spectrum (Wright et al., 2004), whereby longer-living plants exhibit traits typically associated to slower growth, including lower photosynthetic rate. Because of this uncertainty in leaf-level activity, we considered two sets of perennial ideotypes: ‘high’ photosynthetic capacity perennial ideotypes (HP), setting $V_{c,max,25}$ and $J_{max,25}$ respectively 36% and 53% higher than the values for annual wheat (as in Jaikumar et al., 2013); and ‘low’ photosynthetic capacity perennial ideotypes (LP), with $V_{c,max,25}$ and $J_{max,25}$ reduced by 11.3% in the perennial relative to annual wheat, as per the observed median difference in leaf-level assimilation rate between congeneric species (as in Vico et al., 2016). We assumed that optical properties of the leaves did not co-vary with photosynthetic capacity.

No information is currently available on the marginal water use efficiency, λ_{ww} , needed for the leaf-level stomatal conductance calculations. Nevertheless, differences in photosynthetic capacity and stomatal conductances can indicate differences in λ_{ww} . For the high photosynthetic capacity perennial ideotypes, we determined the marginal water use efficiency under well-watered conditions, λ_{ww} based on observations from Jaikumar et al. (2013). Specifically, we selected λ_{ww} so that the observed stomatal conductance is matched by that predicted by the stomatal optimization model (Eq. 5 in Vico et al., 2013), for the observed photosynthetic parameters ($V_{c,max,25}$, $J_{max,25}$, CO_2 compensation point) and ratio of leaf intercellular to ambient CO_2 concentration (Table 2 and 4 in Jaikumar et al., 2013). The calculated λ_{ww} for intermediate wheatgrass was 2% and 26% lower in first- and second-year plants respectively compared with annual wheat. λ_{ww} was lower than that for the annual species also for perennial wheat and rye (SI, Fig. S2). Based on these calculations, we set λ_{ww} to $1306 \mu\text{mol mol}^{-1}$ for annual wheat and to $1162 \mu\text{mol mol}^{-1}$ for HP perennial ideotypes, which correspond to the values at 25°C and 1 kPa of water pressure deficit for first-year wheatgrass. No similar estimate is possible for the LP perennial ideotypes, due to the lack of data on stomatal conductance associated with the chosen photosynthetic capacity. Nevertheless, the LP perennial ideotypes have $V_{c,max}$ and J_{max} just 11% lower than the annual, so we set λ_{ww} to the value of annual wheat. A plausibility argument for this choice is that long-term intercellular-to-ambient CO_2 concentrations are similar for the same vapor pressure deficit (Katul et al., 2010, Eq. 15). Sensitivity analyses showed that the effects of changes in λ_{ww} are small, compared with those of other parameters.

Lacking specific information, we assumed the same effects of temperature on metabolic rates, water availability on soil-to-root and plant conductances, and marginal water use efficiency to water stress for annual and perennial wheat. These were set as in Manzoni et al. (2011b); Manzoni et al. (2013); Medlyn et al. (2002); Vico and Porporato (2008); Zhou et al. (2013).

2.2.2. Canopy characteristics (h_c and L_{AI}) and plant water conductance ($g_{p,l,max}$)

Perennial wheatgrass varieties had similar plant height soon after the beginning of flowering, but were taller than annual wheat varieties later in the growing season (Clark et al., 2019; Zimbric et al., 2021). In line with the focus on the period around flowering, in all perennial ideotypes we set canopy height h_c 43% higher than annual, based on data collected in Washington from Clark et al. (2019). The resulting canopy height for intermediate wheatgrass matches observations in Wisconsin (Zimbric et al., 2021) and Minnesota (Jungers et al., 2018), but is higher than observations for both intermediate wheatgrass and perennial wheat in Michigan (Tinsley, 2012).

Perennial wild and domesticated species also had larger biomass than their congeneric counterparts, already during their first year (Vico et al., 2016), pointing to potentially higher leaf area index, L_{AI} , in perennial species. Yet, L_{AI} and biomass do not necessarily scale in the same way in plants with annual and perennial life habit because perennial plants have lower specific leaf area (Jaikumar et al., 2013;

Vico et al., 2016). Indeed, L_{AI} was the same, or only marginally different in annual wheat and first-year perennial wheat around flowering, and ranging from around $2 \text{ m}^2 \text{ m}^{-2}$ in Washington (Clark et al., 2019) to $3\text{--}4 \text{ m}^2 \text{ m}^{-2}$ in Minnesota (Bergquist, 2019). Nevertheless, L_{AI} increased from $2\text{--}3 \text{ m}^2 \text{ m}^{-2}$ in first-year perennial wheat and intermediate wheatgrass to $4\text{--}6 \text{ m}^2 \text{ m}^{-2}$ in second-year plants in Wisconsin (Tinsley, 2012) and from $3\text{--}4$ to $5\text{--}6 \text{ m}^2 \text{ m}^{-2}$ in Minnesota (Bergquist, 2019). Similarly, second-year intermediate wheatgrass had L_{AI} of $4\text{--}5 \text{ m}^2 \text{ m}^{-2}$ in the summer months in Nebraska (Mitchell et al., 1998). Because L_{AI} is key in defining the aerodynamic coupling between the canopy and the atmosphere and hence leaf temperature, we considered two sets of perennial ideotypes, one with the same L_{AI} as annual wheat ($3 \text{ m}^2 \text{ m}^{-2}$, the ‘LL’ perennial), and the other, the high L_{AI} (HL) perennial, with L_{AI} of $4.5 \text{ m}^2 \text{ m}^{-2}$. The leaf area density is assumed to be uniformly distributed with height above the ground (z), in line with observations in rice, switchgrass and mixed grassland (Katul et al., 2004; Manzoni et al., 2011a).

Finally, lacking specific information, we assumed the same maximum plant hydraulic conductance per unit leaf area, $g_{p,l,max}$, for annual and perennial ideotypes, and set the value relative to well-watered conditions equal to $1.21 \cdot 10^{-4} \text{ kg MPa}^{-1} \text{ s}^{-1} \text{ m}^2$ (Lawlor, 1973). $g_{p,l,max}$ is scaled up to the whole plant by multiplication by L_{AI} . As a result, high L_{AI} perennial ideotypes have higher plant conductance (per unit ground area) under well-watered conditions, $g_{p,max}$, than annual and low L_{AI} perennial ideotypes.

2.2.3. Root biomass and distribution in the soil

Perennial plants tend to invest more resources below ground (Vico et al., 2016), have deeper roots (Cox et al., 2006; DuPont et al., 2014; Monti and Zatta, 2009; Sprunger et al., 2018b), and take up water from deeper layers (Clement et al., 2022; Vilela et al., 2018), compared with their annual counterparts and crops in general.

Observed total root dry weight was 0.569 and $6.511 \text{ kg}_{\text{dry root}} \text{ m}_{\text{soil}}^{-2}$ in annual wheat and intermediate wheatgrass respectively (Sprunger et al., 2018b). We thus set the total root dry weight density, $RWD(z \rightarrow \infty)$, to these values. Observed root dry weight density cumulative profile, $RWD(z)$ (Sprunger et al., 2018b) was well described by the relation proposed by Schenk and Jackson (2002) (SI, Eq. 23), after fitting the two parameters – depth above which 50% of the roots are located, $z_{r,50}$, and steepness of the profile, c_r . This fitting shows that 50% of roots were located in the top 7.9 cm and 15 cm for annual wheat and intermediate wheatgrass respectively (SI, Section 6.1). These root profiles are shallower than those observed under low fertilization (Sprunger et al., 2018b) and, in general, emerging from other point observations. For example, perennial grasslands and annual wheat had 74% and 68% and of their root biomass in the top 0.4 m respectively (DuPont et al., 2014), i.e. 18–13% less root biomass than expected based on Eq. 23 (in SI) fitted to data of Sprunger et al. (2018b). Rhizotrone observations showed root carbon inputs by intermediate wheatgrass till 3.6 m depths, with 45% of inputs in the top 0.25 m (Peixoto et al., 2020): this is 23% lower than predicted by the fitted Eq. 23 (in SI). Similarly, annual wheat had 95% of the roots in the top 1 m, with 50% of them in the top 0.17 m, according to a synthesis of root profiles (Fan et al., 2016), while the fitted $RWD(z)$ profile would set the values at 98% and 75% respectively. Nevertheless, none of these experiments included annual and perennial crops side by side – the only other comparison being a potted experiment showing no difference in rooting depth between annual and perennial wheat seedlings (Ward et al., 2011). Because of the remaining large uncertainty in rooting depth of perennial wheat, particularly after the first year, we also considered the extreme case of a perennial with rooting depth equal to that of the annual in the soil water dynamics analyses (Section 3.2).

Finally, first-year intermediate wheatgrass had 8% higher average root radius, r_r , than annual wheat in a field experiment in France (Duchene et al., 2020). Based on this, we set r_r to 0.12 mm for annual wheat and 0.13 mm for perennial wheat. From the same experiment,

root tissue density, RTD , could be estimated to be 240 and 280 $\text{kg}_{\text{dry root}} \text{m}^{-3}_{\text{fresh root}}$ in annual wheat and intermediate wheatgrass respectively (Duchene et al., 2020).

The larger root biomass and higher root tissue density and radius of deep-rooted perennial ideotypes compared with annual wheat lead to a ten-fold higher soil-root conductance under well-watered conditions, at the depth with highest root biomass for each ideotype.

2.3. Hydro-meteorological conditions

In the first set of analyses (Sections 3.1-3.2; Figs. 3-5), we focused on the canopy-to-atmosphere coupling and effects of water availability. We thus prescribed the root collar water potential, ψ_r , as a boundary condition, looking at a *snapshot*. In the second set of analyses, we considered the temporal co-evolution of soil water content, canopy fluxes and temperature, over an extended period without precipitation, i.e., looking at a *dry down*, thus evaluating how the instantaneous differences in canopy fluxes evolve in time (Section 3.3). In all simulations, a sandy loam soil was assumed.

In the snapshot analyses, plant water status was set a priori via the root collar water potential, ψ_r . As the baseline, we considered a well-watered condition ($\psi_r = -0.1$ MPa), but explored also moderate water stress ($\psi_r = -1$ MPa; Table 1). Above the canopy, we considered a baseline air temperature ($T_a(z = 2 \text{ m})$), relative humidity (RH) and wind velocity above the canopy ($U(z = 2 \text{ m})$) and then individually modified some of these conditions as expected under future climates (higher temperatures, lower wind velocity and soil water content; Berg et al., 2017; IPCC, 2021; McVicar et al., 2012; Table 1). In line with model predictions (Ficklin and Novick, 2017), RH was not changed with air temperature, so that vapor pressure deficit (D) increases exponentially with warming. Incoming radiation at the top of the canopy ($Q^{\downarrow}(h_c)$) was set to 800 W m^{-2} , irrespective of ideotype.

The dry down simulation extended over a 15-day period without precipitation, during which soil water potential was allowed to vary dynamically, starting from a uniform profile set at -0.1 MPa, independent of ideotype. Differently from the snapshot analyses, root collar water potential was calculated at each time step of the dry down, based on the continuity equation (SI, Section 2.1). During the dry down, solar radiation followed the local daily cycle of direct and diffuse radiation on a horizontal surface, assuming clear skies (Dingman, 1994), with day length corresponding to July 15th and subsequent days at 40° latitude N, despite the higher requirement of growing degree days in perennial than annual wheat (Jungers, 2018; USDA, 2022). Also $T_a(z = 2 \text{ m})$ and RH varied during the day, with daily averages equal to the snapshot conditions, but following a sinusoidal diurnal pattern, with an amplitude of 10°C for $T_a(z = 2 \text{ m})$ and 40% for relative humidity. $T_a(z = 2 \text{ m})$ and RH were in counter-phase, with the maximum of $T_a(z = 2 \text{ m})$ and minimum of RH at 2 pm solar time (Table 1).

3. Results

3.1. Role of plant characteristics in defining profiles of key variables under set hydro-meteorological conditions (snapshot analyses)

For set hydro-meteorological conditions, mean wind velocity and shortwave radiation declined from top to bottom in the canopy, as expected from attenuation theories (Fig. 3A,C). The modeled profile of mean air temperature T_a was rather flat, with $\sim 1^\circ \text{C}$ warming from top to bottom of the canopy (Fig. 3B) – the result of the balancing between reduced wind velocity U (and hence leaf boundary layer conductance to heat) and increased leaf-to-air temperature difference. Leaf temperature, T_l , was reduced deeper in the canopy (Fig. 3K), along with shortwave radiation Q_{short} (Fig. 3C), despite the lowering U and hence leaf-air coupling. Both stomatal and cuticular conductance g_{sc} and net CO_2 assimilation rate per unit leaf area, $A_{\text{net},l}$, generally declined with canopy

depth (i.e., with decreasing z ; Fig. 3E,G), as the result of reduced light availability (Fig. 3C) and lower T_l (Fig. 3K), and in spite of the less negative leaf water potential ψ_l deeper in the canopy (Fig. 3H). Conversely, maximum carboxylation, $V_{c,\text{max}}$, was slightly reduced only deep in the canopy (Fig. 3F) following leaf temperature (Fig. 3K), but increased in the top of the canopy in high photosynthetic capacity (solid lines) following the sharp increase in ψ_l in those ideotypes (Fig. 3H). Transpiration rate decreased from top to bottom in the canopy (Fig. 3I), following g_{sc} and wind velocity and hence leaf boundary layer conductance (not shown).

While these general patterns are mostly independent of plant characteristics, there were some differences in the profiles among ideotypes (line types in Fig. 3). L_{AI} was most relevant in defining conditions and functioning at the bottom of the canopy, while photosynthetic capacity was more important at the top. Annual wheat (dotted blue line) had intermediate profiles among the perennial ideotypes, but most similar to LL-LP (orange line), despite the differences in canopy height and photosynthetic capacity and consequently wind velocity. More in detail, for a fixed z/h_c , wind velocity U was lower in annual wheat than in the perennial ideotypes (Fig. 3A; dotted vs dashed and solid lines), which were taller. The difference was largest at the top of the canopy, reaching 0.5 m s^{-1} . This was the case also for the high L_{AI} perennial ideotypes (green and violet lines), which have a leaf area density comparable with that of annual wheat – the result of higher h_c and L_{AI} . For set incoming radiation at the top of the canopy, absorbed shortwave radiation Q_{short} depended only on the ideotype L_{AI} (SI, Eq. 9-11) and was lower in the high L_{AI} perennials (violet and green lines) than in the other perennial ideotypes and annual wheat (Fig. 3C). Compared with the other ideotypes with the same L_{AI} , higher photosynthetic capacity resulted in higher g_{sc} , $A_{\text{net},l}$ and ET_l , as well as more negative ψ_l at all heights, particularly high in the canopy (Fig. 3E,G-I). Profiles of T_l were also steeper for high photosynthetic capacity ideotypes (Fig. 3K). Differences in photosynthetic capacity and L_{AI} partially balanced out so that the high L_{AI} -high photosynthetic capacity (HL-HP, violet lines) and low L_{AI} -low photosynthetic capacity (LL-LP, orange lines) ideotypes had intermediate g_{sc} , $A_{\text{net},l}$, ET_l , and ψ_l . The high L_{AI} -low photosynthetic capacity perennial (HL-LP, green lines) had the lowest gas exchange rates, least negative leaf water potential, whereas the low L_{AI} -high photosynthetic capacity (LL-HP, blue lines) had the highest gas exchange, most negative leaf water potential. Nevertheless, HL-HP and LL-LP ideotypes (violet and orange lines) exhibited the largest difference in T_l among all ideotypes. The HL-HP ideotype was the coolest, because its high L_{AI} reduced radiation transmission inside the canopy.

Compared with annual wheat, perennial ideotypes were between 0.5°C cooler and 0.4°C warmer, depending on canopy position, hydro-meteorological conditions and ideotype (Fig. 4). The highest positive differences occurred at the top of the canopy, where the heating load is highest, whereas the most negative difference occurred deep in the canopy (Fig. 4, top vs bottom row). The entire canopy of the LL-LP ideotype (orange open squares) was warmer than that of annual wheat under all conditions, and warmer than that of the other perennial ideotypes except at the top of the canopy under moderate water stress and higher air temperature.

Compared with annual wheat, all perennial ideotypes except LL-LP (orange open squares) had higher canopy-cumulated net CO_2 assimilation rate, $A_{\text{net},c}$, and canopy transpiration, ET_c , irrespective of hydro-meteorological conditions (Fig. 5A-D). The HL-HP ideotype had the highest difference in $A_{\text{net},c}$ and ET_c compared with annual wheat (up +39 and +37% respectively; Fig. 5A-D; violet closed triangles). Annual-to-perennial differences for LL-HP and HL-LP ideotypes were lower and largely comparable (blue and green symbols respectively) except under warm temperatures and moderate water stress. This small LL-HP to HL-LP difference suggests that L_{AI} and photosynthetic capacity have opposite balancing effects on transpiration, and even more so on net CO_2 fixation. The LL-LP ideotype (orange open squares) fixed 4-6% less CO_2

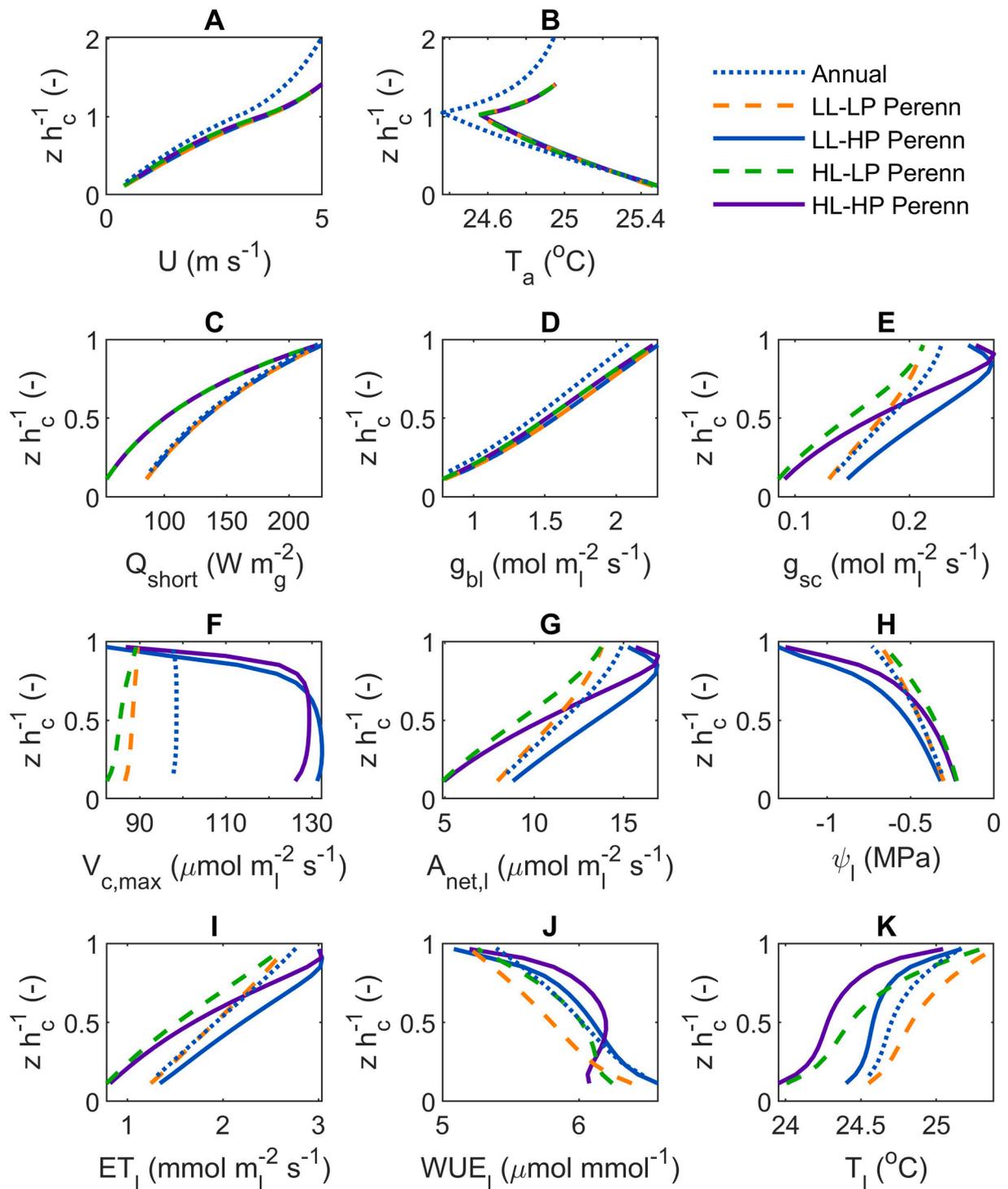


Fig. 3. Profiles of key model variables (panels) for annual and perennial wheat ideotypes (lines), for hydro-meteorological conditions set at the baseline snapshot conditions (Table 1). A) wind velocity $U(z)$, B) air temperature $T_a(z)$, C) absorbed shortwave radiation $Q_{short}(z)$ (per unit ground area), including near-infrared (NIR) and photosynthetically active radiation (PAR) wavelengths, D) leaf boundary layer conductance $g_{bl}(z)$ (per unit leaf area), E) parallel of stomatal and cuticular conductances $g_{sc}(z)$ (per unit leaf area), F) maximum carboxylation rate $V_{c,max}(z)$ (per unit leaf area), G) net CO_2 assimilation rate $A_{net,l}(z)$ (per unit leaf area), H) leaf water potential $\psi_l(z)$, I) transpiration rate $ET_l(z)$ (per unit leaf area), J) leaf-level instantaneous water use efficiency, $WUE_l(z) = A_{net,l}(z)/ET_l(z)$, and K) leaf temperature, $T_l(z)$. Lines refer to the ideotypes: annual wheat (dotted lines) and perennial wheat (dashed and solid lines). The four perennial ideotypes differ in their L_{AI} and photosynthetic capacity (Fig. 2): low L_{AI} -low photosynthetic capacity (LL-LP; orange), low L_{AI} -high photosynthetic capacity (LL-HP; blue), high L_{AI} -low photosynthetic capacity (HL-LP; green) and high L_{AI} -high photosynthetic capacity (HL-HP; violet). All heights are normalized by canopy height, h_c , i.e., $z/h_c=1$ is the top of the canopy, which is higher in perennial ideotypes than annual wheat (Fig. 2). $U(z)$ and $T_a(z)$ of the perennial ideotypes largely overlap (Fig. 3A,B). $Q_{short}(z)$ profiles of ideotypes with the same L_{AI} coincide (Fig. 3C), with the curve to the left corresponding to high L_{AI} perennial ideotypes and that on the right to low L_{AI} perennial ideotypes and annual wheat.

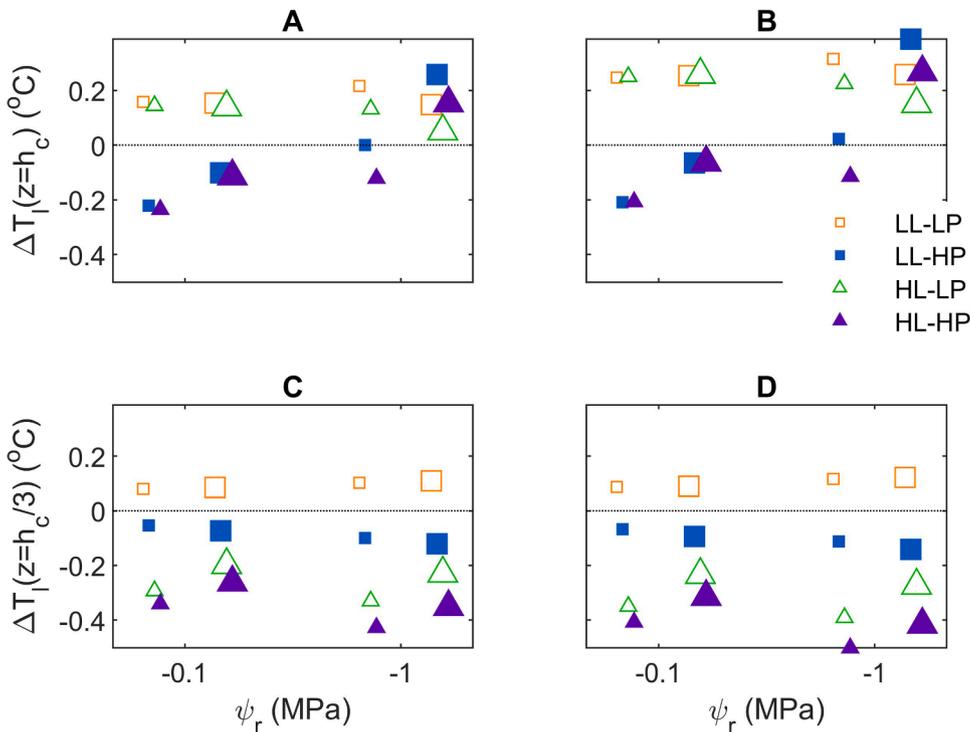


Fig. 4. Annual-to-perennial leaf temperature differences under externally set hydro-meteorological conditions (snapshot; Table 1). Differences in leaf temperature T_l (A, B) at the top of the canopy ($z = h_c$; A, B) and deep into the canopy ($z = h_c/3$; C, D) between perennial ideotypes and annual wheat, with the latter used as term of comparison. Several hydro-meteorological conditions are considered (Table 1). Root collar water potential is set to either at well-watered conditions (set of symbols on the left in each plot) or moderate water stress (sets of symbols on the right in each plot). Air temperature at reference height $T_a(z = 2 \text{ m})$ is set at either $25 \text{ }^\circ\text{C}$ (small symbols) or $30 \text{ }^\circ\text{C}$ (large symbols). Wind velocity at reference height, $U(z = 2 \text{ m})$, is 5 m s^{-1} in the left column and 3 m s^{-1} in the right column. Symbols and colors refer to the different perennial ideotypes (legend): low L_{AI} -low photosynthetic capacity (LL-LP; orange open squares), low L_{AI} -high photosynthetic capacity (LL-HP; blue closed squares), high L_{AI} -low photosynthetic capacity (HL-LP; green open triangles) and high L_{AI} -high photosynthetic capacity (HL-HP; violet closed triangles; Fig. 2). The thin horizontal lines correspond to no difference between the perennial and annual ideotypes; above that, T_l of the perennial ideotype exceeds that of annual wheat.

than annual wheat, but also transpired 3-4% less water. The difference among ideotypes stems from the combination of differences in stomatal conductance (Fig. 3E) and L_{AI} , including their role on the leaf energy balance. Moreover, even small annual-to-perennial differences in leaf-level fluxes can become large when integrated over the canopy, because of the 42% taller canopies and, for the high L_{AI} perennial ideotypes, also 50% higher L_{AI} , compared with annual wheat.

The instantaneous canopy water use efficiency, WUE_c , defined as the ratio of $A_{net,c}$ to ET_c , changed comparably less than $A_{net,c}$ and ET_c across ideotypes and conditions (-6% and +2%; Fig. 5E,F), because of the synergistic changes of $A_{net,c}$ and ET_c . Compared with annual wheat, WUE_c was lower in the perennial ideotypes, except for HL-HP under moderate water stress and cooler conditions (violet triangles) and LL-HP under all conditions (blue squares).

3.2. Role of hydro-meteorological conditions in defining leaf temperature profile and gas exchange rates

More negative root collar water potential increased T_l , particularly in perennial ideotypes compared with annual wheat (left to right pairs of symbols in Fig. 4), to values above $T_a(z = 2 \text{ m})$ (SI, Fig. S3), and more so under reduced wind speed (compare left and right panels in Fig. 4 and SI Fig. S3). Moderate water stress also reduced the difference among perennial ideotypes and caused all perennial ideotypes to be warmer than annual wheat at the top of the canopy, except HL-HP under cooler temperatures (Fig. 4A,B). Deep in the canopy, differences among perennial ideotypes, and from annual wheat, were largely unaffected by plant water status. Air warming above the canopy (i.e., higher $T_a(z = 2 \text{ m})$) increased T_l in all ideotypes (SI, Fig. S3), and slightly reduced the differences among the ideotypes, but did not influence their ranking under well-watered conditions (Fig. 4, small and large symbols). Nevertheless, water stress and warming interactively enhanced leaf temperature at the top of the canopy, and particularly so in high photosynthetic capacity perennial ideotypes (blue square and violet triangle), shifting them from being the coolest to being the warmest ideotypes. Reduced wind velocity above the canopy had a negligible effect.

Water stress enhanced the differences among perennial ideotypes, and between perennial and annual wheat in canopy exchange rates, $A_{net,c}$ and ET_c ; Fig. 5A-D and SI Fig. S4A-D), but did not affect their ranking. Under moderate water stress (left pairs of symbols), $A_{net,c}$ and ET_c were reduced (SI, Fig. S4) but remained higher than annual wheat in all perennial ideotypes except the LL-LP perennial (orange open squares in Fig. 5A-D). Air temperature and wind velocity above the canopy had a secondary role on $A_{net,c}$, and ET_c (compare left and right columns and symbol sizes in Fig. 5), suggesting that energy aspects are more important than aerodynamic ones. Warming and more so water stress altered the ranking of ideotypes with respect to WUE_c , reducing WUE_c in particular for HL-HP perennial ideotypes (Fig. 5E,F; violet closed triangles).

3.3. Co-evolution of canopy temperature, gas exchange and soil water potential during a dry down across ideotypes

During a 15-day dry down, as soil water potential in the rooting zone, ψ_s , progressively declined, leaf temperature at the top of the canopy T_l increased, while canopy net CO_2 assimilation $A_{net,c}$ and transpiration ET_c decreased, as expected (Fig. 6; T_l deeper in the canopy follows similar patterns). Starting from well-watered conditions, shallow roots and, to a lesser extent, high L_{AI} contributed to a faster decline in soil water potential averaged over the root zone (Fig. 6C). Depleted soil water availability reduced water uptake in annual wheat earlier than in the perennial ideotypes, so that, later in the dry down, the average soil water potential was intermediate among the deep-rooted perennial ideotypes. Conversely, the shallow-rooted perennial (dash-dotted lines) had the lowest average soil water potential during the entire dry down, due to its high L_{AI} . When compared layer-wise, the deep-rooted HL-HP ideotype had higher soil volumetric water content than its shallow-rooted counterpart in the top layers of the soil, with the crossing point becoming increasingly shallow as the dry down progressed (SI, Fig. S7; solid vs. dot-dashed violet lines). In the top layers, annual wheat (dotted line in Fig. S7) had soil water potential similar to the deep-rooted HL-HP perennial early in the dry down, and intermediate among the deep-rooted perennial ideotypes as the dry down progressed.

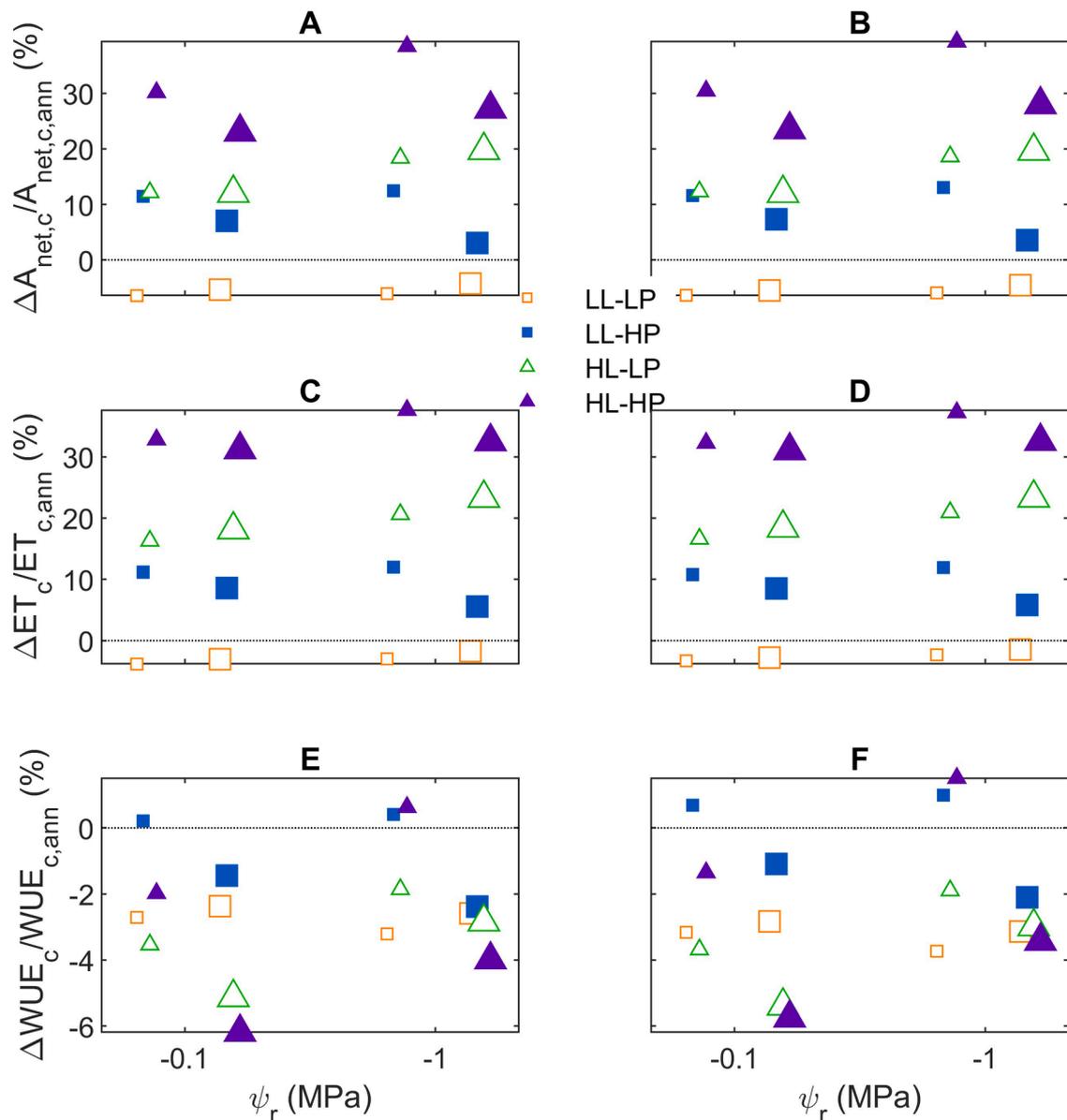


Fig. 5. Annual-to-perennial relative differences in net canopy gas exchange rates per unit ground area for set hydro-meteorological conditions (snapshot; Table 1). Relative differences in (A,B) canopy net CO₂ assimilation rate $A_{net,c}$, (C,D) canopy transpiration rate ET_c , and (E,F) canopy water use efficiency $WUE_c = A_{net,c} / ET_c$. Differences between each perennial ideotype (symbols) and the annual wheat are reported as percentages, using as term of comparison annual wheat grown under the same conditions (subscript ‘ann’). The thin horizontal lines correspond to equal values for perennial and annual ideotypes; symbols above that correspond values larger in the perennial than annual. Root collar water potential, air temperature above the canopy and wind velocity change as in Fig. 4.

The ET_c in the shallow-rooted perennial (dash-dotted violet line) started as high as that of the deep-rooted perennial with the same L_{AI} and photosynthetic capacity (solid violet line), but was reduced to values even below those of annual wheat (dotted blue line) by day 10 of the dry down (Fig. 6G-I). At the end of the 15-day dry down, the shallow-rooted perennial ideotype had the lowest instantaneous ET_c (Fig. 6H), due to the severe water shortage (Fig. 6C), while the annual wheat had the lowest cumulated ET_c (Fig. 6I), due to the combination of low L_{AI} and early reduction in ET_c caused by deteriorating soil water availability.

Among the deep-rooted perennial ideotypes, the higher transpiration rate of the HL-HP perennial early in the dry down, i.e., under well-watered conditions, caused the fastest depletion of ψ_s , whereas the LL-LP perennial had the slowest (violet and orange lines respectively). As the dry down progressed, the more negative ψ_s of HL-HP caused a more pronounced reduction in leaf water potential (not shown) and hence transpiration rate. As a result, ET_c of HL-HP became marginally lower

and leaf temperature higher than those of other deep-rooted perennial ideotypes do. The difference in canopy transpiration rates thus decreased as the dry down progressed, but remained substantial (Fig. 6H). In spite of this, cumulated water requirements remained slightly higher in high L_{AI} ideotypes. The LL-LP perennial had the lowest cumulated water use, but the highest ET_c at the end of the 15-day dry down (Fig. 6I,L; orange lines).

Similar patterns emerged for $A_{net,c}$ rates (Fig. 6D-F), although differences between shallow- and deep-rooted ideotypes were more marked, and those among perennial ideotypes smaller, particularly later in the dry down and when cumulated over the entire dry down (Fig. 6E, F). The shallow-rooted HL-HP perennial ideotype had the lowest cumulated $A_{net,c}$ (Fig. 6F, dot-dashed violet line), because its fast water use under well-watered conditions led to low soil water availability, causing low $A_{net,c}$ despite its higher photosynthetic capacity. Compared to the shallow-rooted HL-HP perennial, $A_{net,c}$ for annual wheat was

Table 1
Summary of hydro-meteorological conditions explored in the snapshot and dry down analyses.

	Snapshot (Fig. 3-5)		15-day dry down (Fig. 6, 7)	
	Baseline value (Fig. 3-5)	Additional level explored (Fig. 4,5)	Baseline value (Fig. 6,7)	Additional levels explored (Fig. 7)
Snapshot only: Root collar water potential ψ_r (MPa)	-0.1 (well-watered)	-1 (moderate water stress)	Calculated by continuity equation	-
Dry down only: Initial soil water potential $\psi_s(z)$ (MPa)	-	-	-0.1 (uniform over the soil profile)	-
Air temperature above the canopy $T_a(z = 2 \text{ m})$ ($^{\circ}\text{C}$)	25	30	Daily average of 25°C and varying sinusoidally, with amplitude of 10°C and maximum at 2 pm	Daily average of 30°C and varying sinusoidally, with amplitude of 10°C and maximum at 2 pm
Air relative humidity RH (%)	60	-	Daily average of 60% and varying sinusoidally, with amplitude of 40% and minimum at 2 pm	-
Incoming radiation at the top of the canopy $Q^{\downarrow}(h_c)$ (W m^{-2})	800	-	Diurnal cycle of clear sky solar radiation on July 15 th and subsequent days at 40N	-
Average wind velocity above the canopy $U(z = 2 \text{ m})$ (m s^{-1})	5	3	5 (and constant)	-

marginally higher, because its low L_{AI} allowed a higher ψ_s throughout the dry down. The high L_{AI} deep-rooted perennial ideotypes had the highest $A_{net,c}$ late in the dry down and when cumulated over its duration.

Canopy-level water use efficiency, WUE_c , deteriorated the most during the dry down in HL-HP perennials, irrespective of the rooting depth (Fig. 6K,L). Low L_{AI} perennial ideotypes and, to a lesser extent annual wheat, maintained the highest and most stable WUE_c .

Warming slightly enhanced the differences among ideotypes in averaged ψ_s , T_i , and $A_{net,c,cum}$, compared with annual wheat, late in the dry down (Fig. 7A-C), but slightly reduced differences for $ET_{c,cum}$ (Fig. 7D). Warming deteriorated $A_{net,c,cum}$ more in perennial than annual ideotypes, so that perennial characteristics became less beneficial or even a disadvantage in terms of total net CO_2 fixation (Fig. 7C). Air temperature did not substantially alter the ranking of ideotypes, except for $A_{net,c,cum}$. Higher air temperature caused a marked reduction in $A_{net,c,cum}$, compared with annual wheat, already early in the dry down (Fig. 7C left) in high photosynthetic capacity perennial ideotypes (blue squares, violet triangle and star). These changes in ranking point to the increasing importance of plant characteristics for CO_2 assimilation under conditions expected to become more frequent in the future. The HL-LP perennial ideotype emerges as the one consistently performing best or among the best across all explored growing conditions, limiting water and heat stress (averaged ψ_s and T_i comparable to annual wheat; Fig. 7A,B) and maintaining high $A_{net,c,cum}$ (Fig. 7C), at the cost of a relatively high water use (Fig. 7D).

4. Discussion

4.1. Methodological considerations

We developed and parameterized a vertically explicit canopy and soil model, describing canopy water, energy and momentum transfers, coupled with soil water dynamics. The model captures the key biophysical processes inside the canopy, including profiles of leaf temperature and water potential, and their non-linear effects on canopy-integrated carbon and water fluxes (Bonan et al., 2022), combining previously tested approaches (e.g., Bassiouni and Vico, 2021; Juang et al., 2008; Launiainen et al., 2015; Manzoni et al., 2011a; Siqueira et al., 2006). The key limitations of the model and their implications are discussed in SI, Section 5. Here we focus on the most consequential methodological aspect: the parameterization.

The model is parameterized primarily based on experimental comparisons of annual wheat with perennial wheat and intermediate wheatgrass lines (Bergquist, 2019; Duchene et al., 2020; Jaikumar et al., 2013; Sprunger et al., 2018b; Ward et al., 2011). Lacking specific information on some traits, we considered also comparisons of wild and domesticated congeneric annual and perennial species (Vico et al., 2016) and annual and perennial grasses in general (Liu et al., 2019). These experimental comparisons provide plausible ranges of plant characteristics known to change with life habit, forming the basis of our ideotypes. Nevertheless, most field experiments focus on specific aspects of plant ecophysiology and hence few traits. The interactive effects of plant characteristics on model outputs underline the importance of simultaneously measuring all the key plant traits when aiming to model a specific variety, and doing so in paired annual and perennial cropping systems when contrasting them.

Despite our extensive literature review (Section 2.2), there remain uncertainties, especially regarding perennial wheat. Of particular relevance for climate change adaptation are plant hydraulics and responses to abiotic stress, which are largely uncharacterized (only cold tolerance has been quantified; Jaikumar et al., 2016). We could not include a life habit-specific response to either temperature for photosynthetic parameters or plant water status for photosynthetic parameters, marginal water use efficiency, and plant conductance. We note that specific leaf area was higher and leaf water potential at loss of turgor less negative in annual compared with perennial species (Liu et al., 2019; Vico et al., 2016). These characteristics are often associated with species occurring in mesic climates (Bartlett et al., 2012), pointing to a reduced sensitivity to water stress in perennial plants. Furthermore, empirical observations show highly variable plant hydraulic conductances and their responses to water availability in annual wheat (Corso et al., 2020; Lawlor, 1973) and among herbaceous species (Locke and Ort, 2015; Mencuccini, 2003), but no information is available on perennial wheat. A sensitivity analysis showed that reducing plant water conductance under well-watered conditions reduces the effects of the plant characteristics known to change with life habit (L_{AI} , photosynthetic capacity, canopy height h_c , marginal water use efficiency under well-watered conditions λ_{ww}).

Another likely important trait above-ground is single leaf size. Smaller leaves enhance leaf boundary layer conductance, all else being the same, causing more marked heating and cooling (Konrad et al., 2021). We are not aware of comparisons of leaf sizes of annual and perennial grain crops. Nevertheless, given potentially large changes in leaf-atmosphere coupling due to leaf size (here accounted for by boundary layer conductance), reduced leaf size in perennial crops could fully counter-balance the potential heating due to taller and larger canopies, suggesting a further avenue for breeding for climate change-adapted perennial grain crops.

Root biomass and distribution are rather variable (Cox et al., 2006; DuPont et al., 2014; Monti and Zatta, 2009; Sprunger et al., 2018b; Ward et al., 2011) and crop-specific (Clement et al., 2022), and thus uncertain. Our comparison of shallow- and deep-rooted perennial

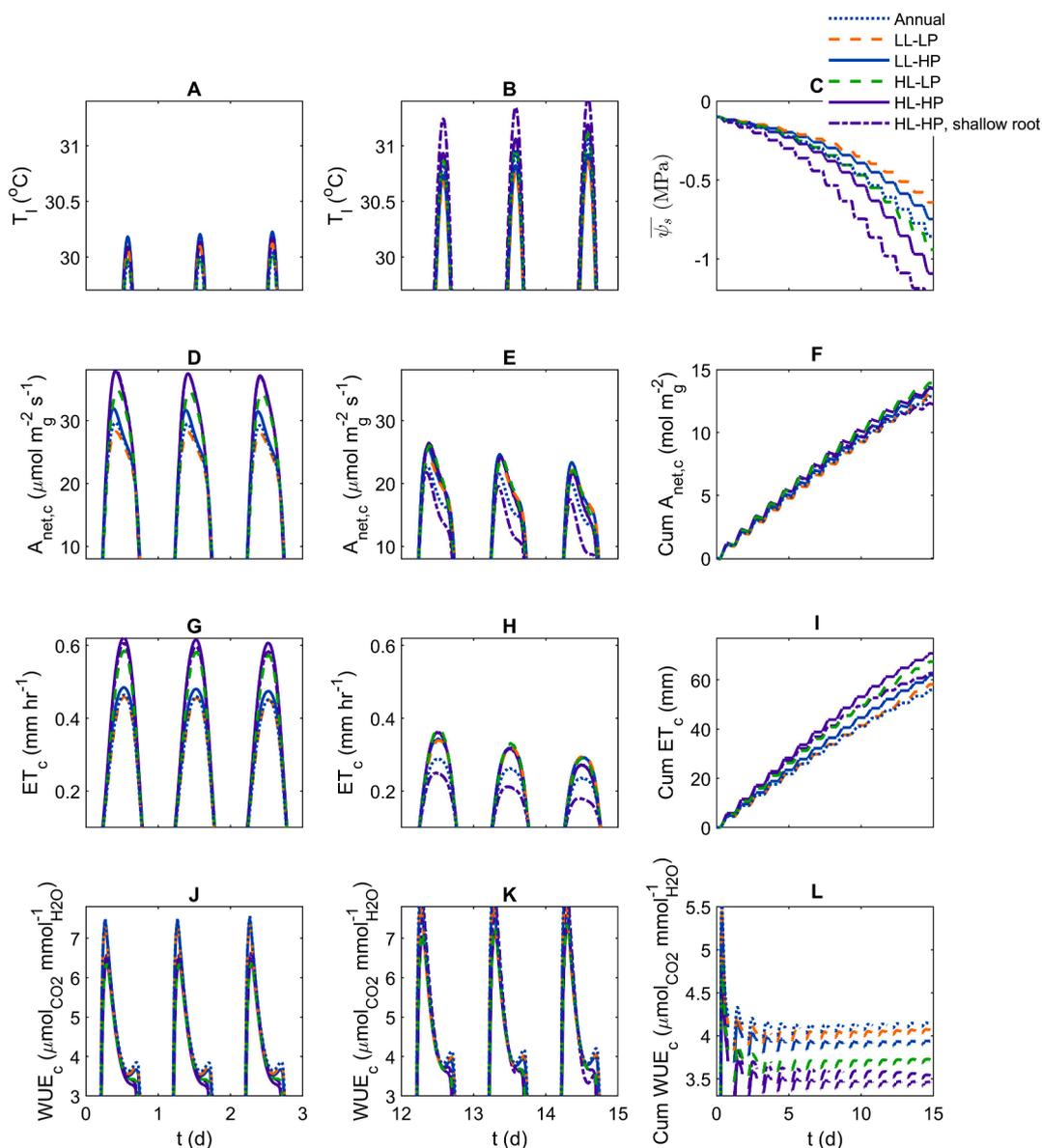


Fig. 6. Leaf temperature and gas exchange during a 15-day dry down. Temporal evolution of (A-B) leaf temperature at the top of the canopy, $T_l(z = h_c)$, (C) soil water potential ψ_s , averaged over the soil profile based on the root distribution of each ideotype, (D,E) instantaneous and (F) cumulated canopy net CO₂ assimilation $A_{net,c}$, (G,H) instantaneous and (I) cumulated canopy transpiration ET_c , (J,K) instantaneous and (L) cumulated canopy water use efficiency, WUE_c . The dry down starts at soil water potential of -0.1 MPa uniform over the whole soil profile. Other hydro-meteorological conditions correspond to baseline values (Table 1). Lines refer to annual wheat (dotted blue line), the deep-rooted perennial ideotypes (solid and dashed lines), and the shallow-rooted HL-HP perennial (dot-dashed violet lines). For graphical clarity, we do not report the dynamics of T_l , $A_{net,c}$, ET_c , and WUE_c over the entire dry down, but only the first and last three days (left and central column). Conversely, the evolution of average ψ_s and the gas exchange cumulated during the dry down are reported in full (right column). To facilitate reading the differences among ideotypes, in the left and central columns, we report only the values relative to the middle of the day (i.e., $T_l(z = h_c) > 29.7$ °C in (A,B), $A_{net,c} > 8$ $\mu\text{mol m}^{-2} \text{s}^{-1}$ (D,E), $ET_c > 0.1$ mm hr^{-1} in (G,H), and $WUE_c > 3$ $\mu\text{mol mol}^{-1}$ in (J,K)). Differences among ideotypes are smaller below these thresholds.

ideotypes shows that root-related plant characteristics are very influential for the occurrence and severity of water (and hence heat) stress during the dry down. Perennial wheat with roots deeper than those reported by Sprunger et al. (2018b) used here (Section 2.2.3; SI, Section 6.1) would have higher net CO₂ assimilation but also higher water transpiration cumulated over the dry down than those depicted in Figs. 6 and 7. Characterizing root-related traits in candidate perennial crops is thus key to assess their vulnerability to heat and water stress.

A further difficulty to compare annual and perennial grain crops is the change in perennial plant characteristics as they age. Most of the available data pertain first-year perennial plants; later year perennial plants often have larger above-ground biomass (Bergquist, 2019; Vico et al., 2016 and references therein). Furthermore, photosynthetic

capacity was reduced in perennial wheat but enhanced in perennial rye from first to second year, based on leaf gas exchange measurements (Jaikumar et al., 2013). Finally, overwintered leaves of perennial wheat had higher photosynthetic capacity than expected assuming an Arrhenius-type dependence on temperature (Jaikumar et al., 2016), similar to the one employed here. Based on our model results, if L_{AI} further increases in later-year perennial plants, we expect higher leaf temperature at the top of the canopy and enhanced canopy transpiration and net CO₂ assimilation, but reduced leaf temperature at the bottom of the canopy, particularly if plant age does not reduce the photosynthetic capacity. The inferred reduction in marginal water use efficiency under well-watered conditions (SI, Fig. S2) would play a secondary role (not shown). Later-year perennial plants also grow deeper roots, as

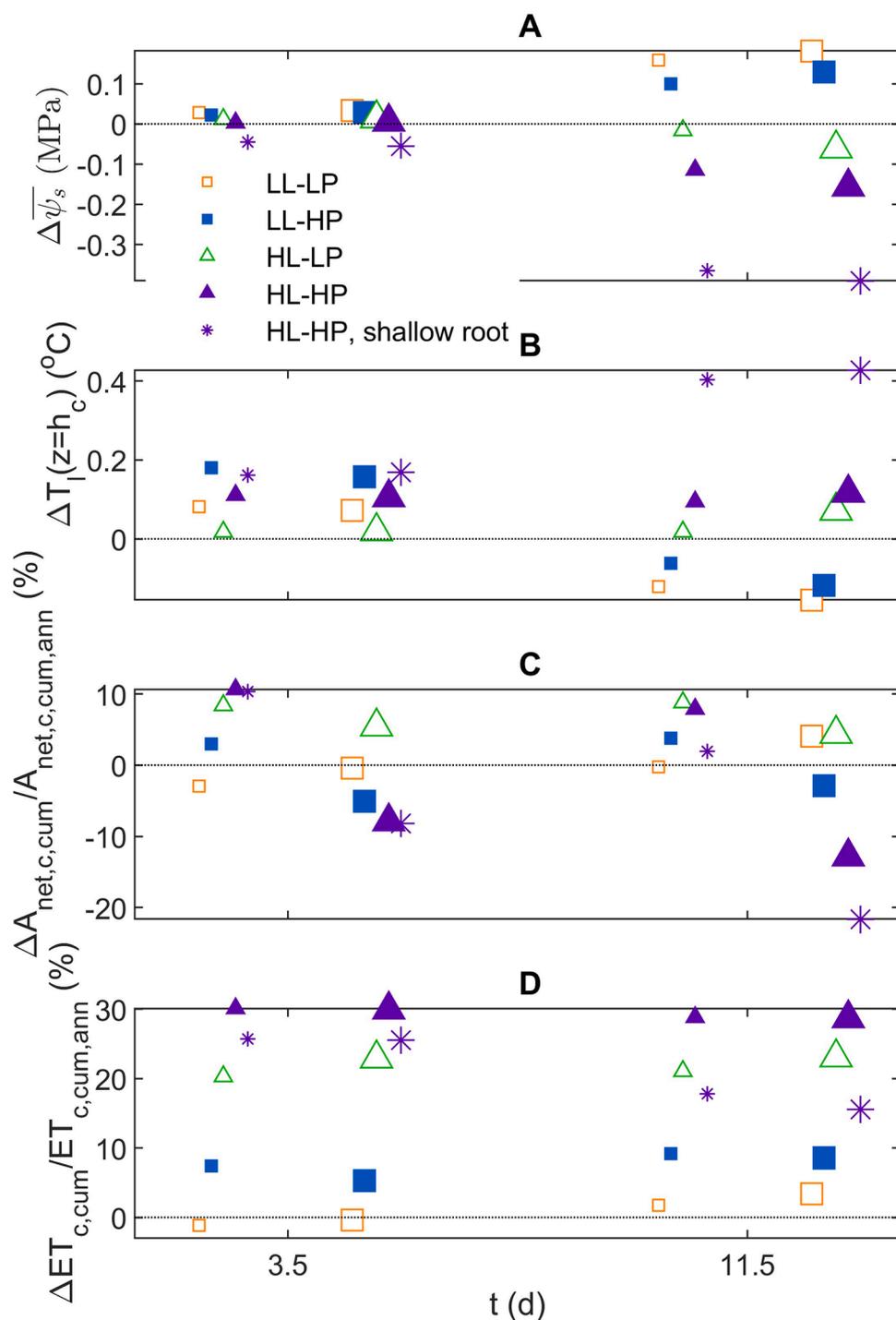


Fig. 7. Comparison of perennial ideotypes to annual wheat after 3.5 and 11.5 days of dry down for average air temperature at reference height $T_a(z = 2 \text{ m})$ of 25 and 30 °C (small and large symbols, respectively). Annual-to-perennial differences in (A) soil water potential ψ_s , averaged by root fraction over the soil profile, (B) leaf temperature at the top of the canopy, $T_l(z = h_c)$, (C) cumulated canopy net CO_2 assimilation $A_{\text{net,c,cum}}$, and (D) cumulated canopy transpiration $ET_{\text{c,cum}}$. We represent the absolute differences of the perennial ideotype with respect to annual wheat for averaged ψ_s and $T_l(z = h_c)$, and percentages for assimilation and transpiration, using the annual wheat under the same conditions as term of comparison (subscript ‘ann’). The dry down began at a soil water potential of -0.1 MPa; wind velocity at reference height, $U(z = 2 \text{ m})$, was set to 5 m s^{-1} (Table 1). Symbols refer to the perennial ideotypes, as specified in the legend and detailed in Fig. 4, with the addition of the shallow-rooted HL-HP perennial ideotype, with root properties equal to those of annual wheat (violet star). The thin horizontal lines correspond to equal values for perennial and annual ideotypes.

evidenced by wheatgrass reducing soil moisture deeper in the soil in the second year (Culman et al., 2013). Deeper roots reduce the effects of prolonged dry downs on canopy temperature and cumulated net CO_2 assimilation, despite higher instantaneous and cumulated transpiration rates.

It is difficult to know how generalizable our results are among perennial grain crops, because differences in plant characteristics in perennial vs. annual life habit vary. For example, the difference in canopy height between annual wheat and intermediate wheatgrass (Clark et al., 2019) used here is smaller than that observed across a variety of grasses (Liu et al., 2019). Also the difference in leaf-level photosynthetic capacity and assimilation rates varied widely. Higher

values in perennial than annual plants were observed in wheat and rye (Jaikumara et al., 2013) and other perennial species (see references in Lundgren 2020), but the opposite was true when comparing congeneric perennial species (Vico et al., 2016) and no effect of life habit emerged among tropical grasses (Liu et al., 2019). Nevertheless, using the proposed model, we can speculate on how different perennial crops or lines would differ in their vulnerability to abiotic stress based on their characteristics, comparing different ideotypes or varieties for which plant characteristics are known.

4.2. Growing conditions and plant traits interact in defining leaf temperature and gas exchanges

Plant characteristics interacted with hydro-meteorological conditions in defining the differences between perennial and annual ideotypes in leaf temperature and gas exchanges. Process-based models that explicitly account for plant traits and how they affect key biophysical processes in soil and canopy, as the one developed here, allow disentangle the effects of plant characteristics and hydro-meteorological conditions. These aspects are difficult to quantifying separately in field experiments, which are necessarily limited in duration and crop varieties. Yet, understanding the relative role of plant traits and hydro-meteorological conditions is necessary to determine whether perennial grain crops are less vulnerable than their annual equivalent to increasingly frequent abiotic stressors. Furthermore, current perennial crop species are ‘work in progress’, subject to selection (Chapman et al., 2022). Evaluating the role of specific plant characteristics can support breeding for climate change-adapted perennial grain crops, by pointing to the traits needed.

Depending on their characteristics, perennial ideotypes could have canopies up to 0.4 °C warmer or 0.5 °C cooler than annual wheat, with the largest differences under water stress. High photosynthetic capacity enhanced the leaf temperature difference under well-watered conditions and at the top of the canopy, but L_{AI} was the most important factor elsewhere in the canopy and under moderate water stress. We are not aware of comparisons of leaf temperatures between annual and perennial grain crops. Nevertheless, aerodynamic coupling was lower in perennial wheat and grasslands than in annual wheat in the US Mid-West (Sutherlin et al., 2019), suggesting on average warmer-than-air leaf surface temperatures in perennial compared with annual wheat. This was consistently the case in our model results only for the low L_{AI} -low photosynthetic capacity (LP-LL) perennial, whereas differences depended on the interplay between traits and conditions in other ideotypes.

Stomatal and cuticular conductance, g_{sc} , and leaf-level transpiration, ET_l , were higher than annual wheat in high photosynthetic capacity perennial ideotypes, and independent of L_{AI} at the top of the canopy and under well-watered conditions (SI, Fig. S5). Under other conditions, low L_{AI} -high photosynthetic capacity (HP-LL) perennial had the highest g_{sc} , but differences from the annual wheat were small. Leaf-level water use efficiency, WUE_l , was higher than that of annual wheat at the top of the canopy in high L_{AI} perennial ideotypes under well-watered conditions, but lower otherwise (SI, Fig. S6). This dependence on the specific characteristics of the perennial ideotype, position in the canopy, and water availability could explain previous contrasting results relative to stomatal conductance and WUE_l . First-year perennial wheat lines had stomatal conductance per unit leaf area 1.16-1.47 times higher than that of annual wheat (Jaikumar et al., 2013), which is comparable with those we obtain for the high photosynthetic capacity perennial ideotypes, parameterized based on the same photosynthetic data but with additional characteristics taken from other experiments (Fig. 2). Leaf-level water use efficiency was higher in perennial than annual wheat (Jaikumar et al., 2013) and in perennial tropical grasses relative to non-congeneric annual grasses (Liu et al., 2019). Conversely, when comparing congeneric species, no effect of perennial vs. annual life habit on leaf-level transpiration rate and water use efficiency emerged (Vico et al., 2016). Seasonal water use efficiency was also similar between annual and first-year perennial ryegrass, but lower in second-year perennial plants (Neal et al., 2011).

Canopy transpiration and assimilation in perennial ideotypes was up to 39% higher than annual wheat under well-watered conditions (Fig. 5). Irrespective of conditions, high L_{AI} perennial ideotypes had the highest canopy transpiration and assimilation rate, in line with the observed increase in monthly evapotranspiration with L_{AI} in intermediate wheatgrass in Kansas, although L_{AI} covaried with seasonal conditions there (de Oliveira et al., 2018).

Soil water content, gas exchange and leaf temperature evolved during the dry down, depending primarily on rooting depth and L_{AI} (Fig. 6,7). Perennial ideotypes had higher water use than annual wheat, as observed in forage (Neal et al., 2011) and perennial grasses (Basche and Edelson, 2017). Soil moisture of annual wheat was intermediate between high and low L_{AI} deep-rooted perennial ideotypes near the soil surface (SI, Fig. S7). Indeed, in an experiment in Michigan, soil moisture of annual wheat was higher than or comparable with that of intermediate wheatgrass, depending on time of measurement and depth (Culman et al., 2013). Similar patterns also emerged when comparing maize with intermediate wheatgrass and switchgrass in Minnesota (Jungers et al., 2019).

4.3. Suitability of annual and perennial grain crops under changing climates

Growing seasons are becoming warmer and drier in many regions (Cook et al., 2020; IPCC, 2021), and near-surface wind velocity might decline (McVicar et al., 2012). Crops are facing more frequent and intense heat and water stress, and their combinations (Alizadeh et al., 2020). Warming and drying left unaltered the ranking of ideotypes in terms of transpiration or assimilation rate, and water use efficiency, except for cumulated CO_2 assimilation under warming during a dry down. Nevertheless, leaf temperature and instantaneous and cumulated gas exchanges depended on the interplay among metabolic rates (i.e., photosynthetic capacity, defining also day respiration rate), amount of photosynthesizing and transpiring biomass (and hence L_{AI}), access to soil water (and hence root characteristics), and rate of water uptake (and hence soil and plant water status and leaf temperature). Interestingly, changes in L_{AI} and photosynthetic capacity partially balanced out.

Among the hydro-meteorological conditions expected to change in the near future, water availability was the main driver of the differences between annual and perennial ideotypes, in interaction with air temperature. Wind velocity had small effects. Reduced plant water availability reduced snapshot differences in canopy transpiration and assimilation between annual and perennial ideotypes and depleted WUE_c more in perennial than annual wheat (Fig. 5). Differences in transpiration among ideotypes accumulated during a dry down, so that the higher transpiration rates of perennial ideotypes, particularly with high L_{AI} , led to faster soil water depletion (Figs. 6 and 7) and hence higher risk of water stress. This poses the question of whether perennial grain crops are a viable alternative to annual grain crops in precipitation-scarce regions lacking sustainable irrigation sources.

All else being the same, deeper and larger roots were key to maintain high plant water availability and net CO_2 assimilation, and could cancel the negative effects of the larger transpiring biomass during the dry down. This is because the resource allocation patterns typical of each life habit (Vico et al., 2016) are such that the perennial-to-annual difference in root biomass far exceeds that in L_{AI} (Fig. 2). Resistance to dry periods is thus an additional benefit conferred by the typically deeper roots of perennial plants, allowing to tap into deeper water stores, exploiting larger precipitation events and buffering against extended dry periods (Culman et al., 2013; Kirkegaard et al., 2007; Sleiderink, 2020). However, during a dry down, the reduced access to water stores of the shallower roots of annual wheat was mostly compensated by the lower water uptake rate, so that the annual ideotype had only marginally lower cumulated CO_2 assimilation and higher water use efficiency compared with deep-rooted perennial ideotypes. This was not the case for the shallow-rooted perennial (Fig. 6).

Leaf temperature was similar in annual and perennial ideotypes for set conditions, but the faster water use of perennial ideotypes enhanced the risk of heat stress, particularly if the perennial wheat did not have deep roots (Fig. 6B; e.g., Luan and Vico, 2021; Mon et al., 2016; Webber et al., 2016). By causing stomatal closure, elevated air CO_2 concentration could also impair evaporative cooling, warming up the leaves, but would simultaneously reduce transpiration and the risk of water stress.

We did not explicitly consider these effects. Nevertheless, a previous model analysis showed that CO₂ concentration had a minor effect on leaf temperature when compared with single leaf size and wind velocity (Konrad et al., 2021), suggesting our estimated differences in leaf temperatures among ideotypes would hold also under enhanced air CO₂ concentration.

Based on our model analyses, we can conclude that perennial grain crops might be more susceptible to water and indirectly heat stress under future conditions, unless they have access to large and reliably replenished water stores. Deep-rooted perennial ideotypes could consistently provide higher net CO₂ assimilation than annual wheat, when they have high L_{AI} and low photosynthetic capacity, but this came at the cost of higher transpiration.

For an overall assessment of the viability of perennial grain crops under changing climates, we would need to consider also other aspects typical of perennial cropping systems, such as reduced soil disturbance and higher allocation of resources belowground. These contribute to improved soil hydraulic properties (Basche and DeLonge, 2017), infiltration capacity (Basche and DeLonge, 2019), and overall accumulated soil carbon (Crews and Rumsey, 2017; Means et al., 2022). Over time, these changes could confer a further advantage to perennial crops beyond deeper roots in the face of more intermittent precipitation, counterbalancing the risks associated to higher water use of some perennial crops. These long-term feedbacks could be included in the model in a simplified way, by modifying the soil hydraulic parameters, should data be available. Furthermore, reduced soil water content could reduce nutrient leaching (Culman et al., 2013; Jungers et al., 2019), limiting the risk of nutrient limitations for perennial grain crop. Deeper roots can also facilitate nutrient acquisition and in general support sustainable intensification of agriculture (Thorup-Kristensen et al., 2020).

5. Conclusions

Transitioning to perennial grain crops has far-reaching and potentially positive consequences on ecosystem functioning (Crews et al., 2018; Rasche et al., 2017). For perennial grain crops to be an asset for a more sustainable agriculture in the future, they need to provide a variety of ecosystem services, including yields, but also to withstand climate change. Hence, considering the prospects of perennial grain crops as part of future agriculture requires assessing their vulnerability to future climatic conditions (Basche and Edelson, 2017; Glover et al., 2010; van Tassel et al., 2014). To this aim, we developed a process-based model of canopy energy, mass and momentum balance, coupled with soil water dynamics. We parameterized the model based on published data relative to annual wheat and perennial wheat candidates.

There was no consistent difference in leaf temperature, canopy transpiration, CO₂ fixation, and water use efficiency based on annual vs. perennial life habit. Rather, plant characteristics, in interaction with growing conditions, defined the differences in leaf temperature and gas exchange between annual and perennial ideotypes. Perennial ideotypes with deep roots, high leaf area index and, to a lesser extent, high photosynthetic capacity transpired more water and fixed more carbon, and were slightly cooler, than annual wheat, in particular under well-watered conditions. The higher transpiration rate of the perennial ideotypes cumulated during a dry down to higher water needs and more likely water stress, but did not translate in a reduced CO₂ fixation for deep-rooted perennial ideotypes. Altered hydro-meteorological conditions, and in particular low soil water availability, left mostly unchanged which ideotypes had the highest leaf temperature and canopy gas exchange rates.

This key role of the specific plant characteristics and their combinations underlines the importance of considering not only life habit, but also the varieties' specific traits, when assessing the expected changes in vulnerability to climate change, nutrient leaching and demand for irrigation of a shift from annual to perennial grain crops. Moreover, this

exploration provides foresight into considering rooting depth and leaf area as part of the ongoing breeding efforts towards developing climate change-adapted perennial grain crops.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was funded by the Swedish Research Council for Sustainable Development FORMAS grant 2018-00646 to GV, TEC and NAB. We thank Maoya Bassiouni for providing constructive comments on an earlier version of the manuscript, and Simone Faticchi and Stefano Manzoni for discussions on the implementation of the soil water dynamics.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109666.

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