Review

Agriculture in silico: Perspectives on radiative transfer optimization using vegetation modeling

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ABSTRACT

Advancing crop yield within limited agricultural land use is crucial to alleviate potential food shortages from the increasing world population. While genetic breeding holds great potential in improving crop yield, real-world practices are often constrained by the limitations of scaling the laboratory findings with respect to coupled environmental feedback and limited tools to project the optimal strategies based on environment and crop traits such as crop density management. Aided by a process- and trait-based vegetation model, we review and theoretically evaluate approaches that aim to improve crop yield through canopy radiative transfer optimization. The evaluated approaches include trait breeding (e.g. leaf color and chlorophyll action spectrum), canopy structure (e.g. canopy density and spacing), and environment manipulation (e.g. supplemental radiation intensity and source). We prototype vegetation modeling applications that can theoretically explore the potentials of a number of approaches at various setups that otherwise require tremendous effort in the real world, and propose to use vegetation modeling to guide more efficient agricultural practices. Future elaborations in vegetation modeling with respect to more physiological representations of vegetation processes, quantification of maintenance costs, and utilization of remote sensing data would further advance the utilization of modeling in agriculture.

1. Introduction

World population is expected to reach 10 billion by the end of the 2050s, according to the 2022 revision of World Population Prospects by the United Nations following the scenario of medium-fertility variant. Compared to the estimate of 7.88 billion in 2021, the 27% population increase may require increasing agricultural land use, thus resulting in extra CO_2 and methane (CH_4) emissions, slowing down global carbon neutralization, and accelerating global warming. Therefore, it is crucial to improve the crop yield per ground area. The commonly used approaches include breeding (Chen and Blankenship, 2011; De Souza et al., 2022; Furbank et al., 2020; Tester and Langridge, 2010; Varshney et al., 2009), crop density optimization (Deng et al., 2012; French et al., 2016; Gimplinger et al., 2008; Tokatlidis, 2017), mulching (Gao et al., 2019; Kader et al., 2017; Sinkevičienė et al., 2009; Sun et al., 2020), optimized irrigation (Fanadzo and Ncube, 2018; Lorite et al., 2004; Sandhu et al., 2019), proper fertilization (Jagadamma et al., 2008; Meena et al., 2014; Zhang et al., 2009), and vertical farming (Asseng et al., 2020; Beacham et al., 2019; Touliatos et al., 2016). These approaches can be categorized into several types, including trait enhancement (breeding), water use (irrigation, fertilization, and mulching), and light use (density control and vertical farming).

However, despite the well-acknowledged benefits of these approaches in theory or proven in the lab and research sites, real-world application may run into endless trials because of the lack of a generalized tool to find the optimal practices under certain environments and crop traits, e.g. finding the optimal crop density and spacing prior to sowing (Hammer et al., 2019). Further, crop breeding may also lack hints on the optimal ranges of the target traits based on the environment other than the optimal laboratory environment, e.g. optimal chlorophyll (chl) content (Li et al., 2022). Among the limitations, improving light use efficiency (LUE) is largely restricted by the inability to quantitatively monitor canopy radiative transfer and hence radiation utilization within the canopy. One solution to the problem is to combine agricultural practices and vegetation models with adequate complexity, e.g. using models with hyperspectral radiative transfer scheme for leaf pigment- and/or light source-related approaches (Chen et al., 2022; Chen and Blankenship, 2011; Zhen and Bugbee, 2020a).

Radiative transfer within the canopy is impacted by both leaf traits, e.g. leaf pigment contents and canopy structure, e.g. leaf area index (LAI)

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and clumping index (CI) (Chen et al., 2012; Féret et al., 2021; Jacquemoud and Baret, 1990; van der Tol et al., 2009). At leaf level, when chl content increases, light absorption ratio increases (canopy absorbs more light), but light transmittance ratio decreases (absorbed light distribution is more uneven) (Evans, 1996; Jacquemoud and Baret, 1990). As photosynthetic rate saturates with higher radiation (Farquhar et al., 1980), it is theoretically expected that higher chl content results in declined crop-integrated productivity when exceeding a threshold, because less light is available in the lower canopy. At canopy level, crop density and spacing impact how light transmits and scatters within the canopy. Higher LAI and CI both result in higher total absorbed radiation but more uneven absorbed radiation (Campbell and Norman, 1998; Chen et al., 2012; Wang et al., 2021). Although lower chl content and CI would result in declined total absorbed radiation, the more favorable radiation environment in the lower canopy might result in a higher overall photosynthetic gain. Thus, optimizing leaf absorption features and canopy structure through accurately quantifying canopy radiative transfer may have substantial potential in improving crop productivity (Li et al., 2021; Nobel and Long, 1985).

In this study, we review researches aiming to optimize crop light harvesting, evaluate the approaches through a theoretical framework based on vegetation modeling, and explore the potential of vegetation modeling in future agricultural practice to improve crop productivity. We use the soil-plant-air continuum module of the next-generation land surface model of CliMA Land (Wang et al., 2023) to prototype the agricultural applications. More details can be found in https://github.com/CliMA/Land and Wang et al. (2021, 2023). We structure the paper to cover three key aspects regarding crop light harvesting (Fig. 1), including chl absorption, canopy structure, and light supplementation, which correspond to the three stages of prior to sowing—traits breeding, during sowing—canopy structure optimization, and post sowing—environment manipulation, respectively.

2. Chlorophyll absorption

Chl a and b and carotenoids are the main pigments to harvest light in higher plants (Gao et al., 2018; Mazor et al., 2015; Wei et al., 2016). Both chl a and b have the highest absorption ratio for blue and red light, and a relatively lower but still high enough absorption ratio for green light (Lichtenthaler, 1987; Lichtenthaler and Buschmann, 2001; Linschitz and Sarkanen, 1958; Peters and Noble, 2014). As most of the visible light that may be used for photosynthesis is absorbed by leaves in the upper canopy, productivity of shaded leaves in the lower canopy is largely limited by light availability. To address the problem, two possible crop breeding

strategies that impact light absorption within the canopy have been explored extensively in recent years, including regulating the chl content (Cardona et al., 2018; Gu et al., 2017; Melis, 2009; Schüler et al., 2020; Slattery et al., 2017; Slattery and Ort, 2021; Wang et al., 2022) and modifying the chl absorption feature (Cardona et al., 2018; Chen and Blankenship, 2011; Elias et al., 2021; Kato et al., 2020; Nürnberg et al., 2018).

2.1. Chlorophyll content optimization

Natural selection forces from competition within and among species have resulted in various strategies of plants to compete for limited light, water, and nutrients (Craine and Dybzinski, 2013; Ewel and Mazzarino, 2008; Gundel et al., 2014). However, the competition would lead to non-optimized light, water, or nutrient utilization (Coomes and Allen, 2007; Hautier et al., 2009; Weiner, 1986). For example, plants are often "forced" to grow taller to compete for light and invest more chloroplasts in the upper canopy to use the excessive light, which otherwise would be "stolen" by the competitors. Thus, it is often found that chl is over-invested in plants (Ainsworth et al., 2012; Slattery et al., 2017; Zhu et al., 2010). Promisingly, lower chl content, in theory, would benefit plants in terms of canopy radiative transfer given that absorbed light could be more evenly distributed within the canopy (Ainsworth et al., 2012; Gu et al., 2017; Ort et al., 2011). In many cases, breeding can be treated as a way to liberate plant traits from the constraints of the natural selection force since competition pressure is minimized in cropland.

An increasing amount of research has been focused on leaf color mutants with lower chl contents to improve crop yield for various crops (Cheng et al., 2022; Li et al., 2016, 2022; Lin et al., 2022; Zhong et al., 2015, 2023). However, it remains unknown how some important metabolic pathways (such as photosynthesis) are involved and regulated in leaf color variations. As a result, most research has reported negative results, which probably resulted from either changes in the metabolic pathways or non-optimized chl contents, e.g. when leaf chl content is too low. Among the positive results, Zhong et al. (2015) found a non-significant difference between two breeds of maize. Gu et al. (2016, 2017) found reduced growth duration and elevated yield for a chl-deficit mutant rice variety because of higher stomatal conductance. Slattery et al. (2017) found similar yields between a mutant and the wild type per unit leaf area, though not over-yielding the wild type.

We note that research focused on leaf-level traits and measurements may not be a good proxy for crop yield as in Zhong et al. (2015) and Slattery et al. (2017). As the less green mutants absorb less light at the same crop canopy density, the optimal crop density ought to be higher for
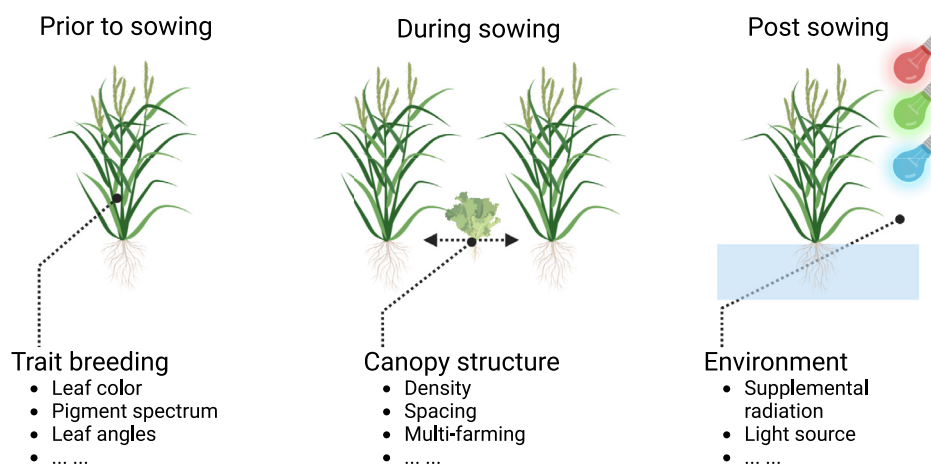
Fig. 1. Strategies that can be used to improve crop yield through canopy radiation optimization, including trait breeding prior to sowing, canopy structure management during sowing, and environment manipulation after sowing.

these less green mutants compared to the wild type. Thus, a fair comparison of yields should be the yields at the optimized canopy structure. Gu et al. (2017) found rice yield was significantly elevated when growing at higher density. However, the optimal crop density reported at one site would not be useful for other sites with contrasting weather scenarios. Therefore, it is crucial to develop a method to theoretically determine the optimal traits and canopy structure based on the local environment such as temperature, radiation, and precipitation.

Here, we prototype an application for chl content optimization based on the soil-plant-air continuum module from the CliMA Land model, which is capable of simulating hyperspectral canopy radiative transfer (Wang et al., 2021, 2023). Lower chl content, in theory, results in lower total absorbed radiation, lower absorbed radiation in the upper canopy, and higher absorbed radiation in the lower canopy (Fig. 2A). The more evenly distributed absorbed radiation might result in elevated canopy-level carbon gain. For example, in our simulation of a crop field with dense canopy (LAI = 4), when we set the total chl content to 60 µg cm^{-2} leaf area, the integrated photosynthetically active radiation absorbed by photosynthetic pigments (ΣAPAR) is 1,206 µmol m^{-2} s^{-1}, whereas the integrated gross photosynthetic rate (ΣA, also known as gross primary productivity) is 28.0 µmol m^{-2} s^{-1} (Fig. 2A). When we reduce chl to 35 µg cm^{-2}, ΣAPAR decreases to 1,151 µmol m^{-2} s^{-1}, whereas ΣA increases to 28.4 µmol m^{-2} s^{-1} (Fig. 2A). When we further decrease chl to 10 µg cm^{-2}, ΣAPAR decreases to 928 µmol m^{-2} s^{-1}, whereas ΣA increases to 28.8 µmol m^{-2} s^{-1} (Fig. 2A).

However, ΣA does not always increase with lower chl content, and the exceptions are when chl content is too low (lower than 10 µg cm^{-2}) to absorb enough radiation to photosynthesize (Fig. 2B) and when LAI is too low (lower than 2.5) for the benefit of a more evenly distributed APAR to show up (Fig. 2B). The improvement in productivity only shows up when canopy density is high (LAI ≥ 3). However, the magnitude of the improvement could be marginal except for extremely dense canopies (LAI ≥ 5). Therefore, whether lower chl content benefits crop yield depends on the local environment and canopy structure, and it is only recommended for crops with dense canopy, which can be achieved by increasing crop density (Gu et al., 2017).

Note that as lower chl content mutants absorb less light, the growth rate at the seedling stage would be slower, because LAI is low at the seedling stage. Thus the overall accumulation of photosynthate might be less than the modeled value. Thus, optimizing chl content at different growing stages also holds great potential to improve crop yield. Moreover, lower chl content mutants would have lower leaf temperature

because of the energy balance, potentially benefiting plants in temperature- and drought-stress environments. A detailed model that accounts for the dynamic weather and growth of crops would better guide the optimization of chl content and crop density, thus alleviating the increasing food demand from limited cropland.
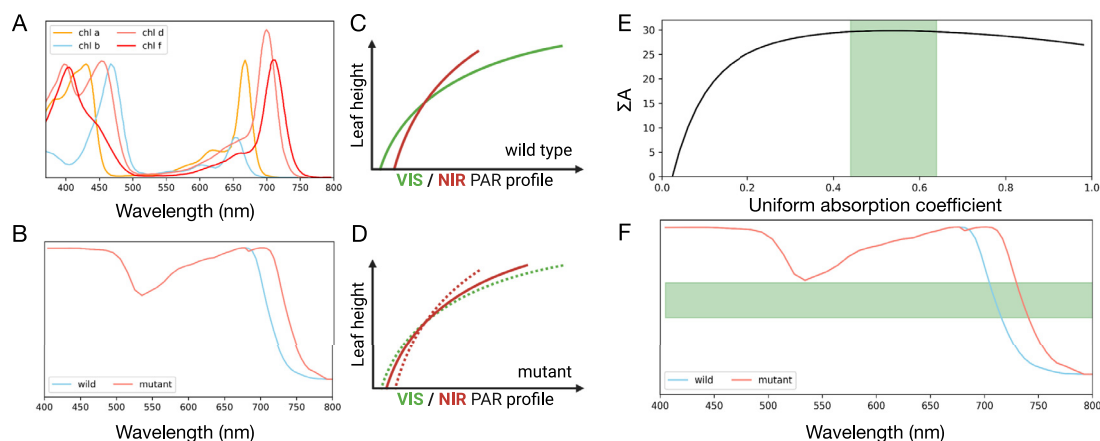
2.2. Chlorophyll absorption coefficient

Providing supplemental light is a common practice to improve the plant growth rate in the greenhouse and growth chamber, though it is costly and less applicable to the field. An energy-free approach is to extend the absorption spectrum window of photosystems and light harvest complexes (Chen and Blankenship, 2011), for example, near infrared (NIR) light with wavelengths ranging from 700 to 750 nm (because ultraviolet light may damage the photosynthesis machinery). According to the American Society for Testing and Materials (ASTM) G-173-03 standard tables, the land surface on average receives approximately 60 W m^{-2} solar energy from far-red NIR ranging from 700 to 750 nm (364 µmol m^{-2} s^{-1} photons), compared to 430 W m^{-2} visible light ranging from 400 to 700 nm (1,980 µmol m^{-2} s^{-1} photons). If plants can absorb far-red NIR for photosynthesis as efficiently as visible light, there could be an up to 18% increase in total absorbed photons (actual increase in productivity will be lower because of the non-linearity between photosynthetic rate and radiation).

However, chl a and b in the photosystems and light harvest complexes of higher plants can only utilize a very limited fraction of far-red NIR because of the very low absorption ratio (Fig. 3A) (Hogewoning et al., 2012; Jacquemoud and Baret, 1990; Wientjes and Croce, 2011). Comparatively, chl d and f in some organisms like algae and cyanobacteria are more red-shifted with NIR action spectrum peaks around 710 nm (chl d) and 745 nm (chl f) (Fig. 3A) (Chen and Blankenship, 2011; Elias et al., 2021; Nürnberg et al., 2018). Further, the similarities among chl a, d, and f make it possible to replace chl a with d and/or f in higher plants.

While this approach sounds very promising for shaded plants that live in the lower canopy where far-red light is abundant, its potential in main crops could be limited if not be properly implemented. The reason is that if a plant can absorb far-red light as effectively as red light (Fig. 3B), the APAR from far-red light will be more in the upper canopy but less in the lower canopy, while the APAR from visible light will be unchanged (Fig. 3C, D). This would result in a more uneven APAR distribution and neutralize the boost in photosynthesis from higher ΣAPAR. When we run the CliMA Land model with two settings (one default setting with low far-
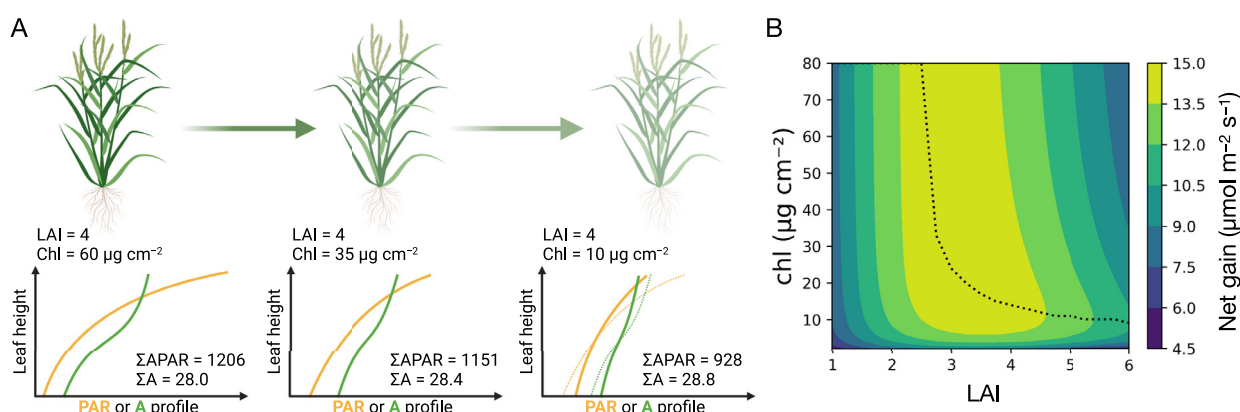
Fig. 2. Example of chlorophyll (chl) content optimization. A, example of canopy radiation and photosynthesis profiles at three different canopy settings. ΣAPAR is the integrated photosynthetically active radiation absorbed by photosynthetic pigments in µmol photons m^{-2} s^{-1}, and ΣA is the integrated gross photosynthetic rate in µmol CO$_2$ m^{-2} s^{-1}; B, instantaneous net carbon gain as a proxy of crop yield at various settings of leaf area index (LAI) and chl. Carbon gain is computed as net primary productivity (NPP) minus biomass investment in leaf area (C$_{biomass}$) normalized based on leaf life span (LS): NPP − C$_{biomass}$/LS. The dashed curve plots the optimal chl at each LAI that has the highest yield. The simulations were performed for a time instant using soil-plant-air continuum module from the CliMA Land model (Wang et al., 2021, 2023).

Fig. 3. Example of chlorophyll (chl) absorption coefficient optimization. A, absorption spectra of chl a, b, d, and f; B, leaf absorption spectrum for "wild type" and "mutant", of which far-red absorption increases; C, wild type photosynthetically active radiation (PAR) profiles of visible (VIS) and near infrared radiation (NIR); D, mutant PAR profiles of VIS and NIR; E, canopy integrated gross photosynthetic rate (ΣA) at various uniform absorption coefficients, shaded green marks the optimal range of a uniform absorption coefficient; F, comparison of hyperspectral absorption coefficient and optimal uniform absorption coefficient.

red absorption and one setting with high far-red absorption), we find that although ΣAPAR increases from 1,166 to 1,230 μmol m^{-2} s^{-1}, ΣA only increases marginally from 28.3 to 28.4 μmol m^{-2} s^{-1}.

If we imagine the absorption coefficient as a "trait" that can be modulated by plants, there is a trade-off that plants need to deal with. If the coefficient is too high, absorbed light will be too unevenly distributed, and the overall carbon gain might decrease with a higher absorption coefficient beyond the threshold (Fig. 3E). If the coefficient is too low, plants will not be able to absorb enough radiation even in the upper canopy. Optimally, keeping the absorption coefficient within an intermediate range would benefit plants most (as marked in green in Fig. 3E). Because of this tradeoff, supplementing NIR in addition to regular visible light benefits plants more through the higher transmittance resulting from a lower absorption coefficient of NIR. Thus, in theory, extending the action spectrum of photosystems to NIR may not help improve crop yield significantly in many scenarios (target coefficient is higher than the optimum) (Fig. 3F), because more NIR would be absorbed by the upper canopy where the photosynthetic rate already saturates with absorbed radiation (there is only less than 0.3% increase of ΣA in our simulation). Moreover, plants might suffer from heat stress because the upper canopy absorbs extra energy from NIR.

Therefore, it is expected that the approach to extend crops' action spectrum benefits more shaded plants that are exposed to a higher fraction of NIR. Once chl d and f are successfully implemented in crops, mixed cropping would benefit more as solar radiation can be more efficiently utilized, e.g. regular plants in the upper canopy and gene-mutated plants in the lower canopy. Vertical farming would also benefit from this technical advance because of the lower energy cost for generating the same amount of NIR photons.

3. Canopy structure

Optimizing canopy structure is a breeding-free approach to improve crop yield, and has shown great potential in real-world practices such as crop density control (Baloch et al., 2002; Chaperpa et al., 2020; Kisić et al., 2010; Thornley, 1983) and mixed cropping (Agegnehu et al., 2006; Lizarazo et al., 2020). However, there is no static strategy for any crop, given their differences in traits and variations in different local environments. Thus, optimizing canopy structure based on crop traits and the environment is highly demanded to maximally advance crop yield. Here we prototype another application using our vegetation model to project the optimal canopy structure regarding crop density and spacing for a single crop system and a combination of two crops within a vertical canopy. We note that improved crop yield by optimizing canopy

structure is actually realized by optimizing the radiative transfer within the canopy, which is extremely difficult to do in the real world because of the difficulty in monitoring the whole canopy radiation profile. Comparatively, theoretical analysis empowered by vegetation modeling will help provide quantitative guidance over this optimization.

3.1. Crop density and spacing

A common practice to improve crop yield is to adjust the crop density (Bleasdale and Nelder, 1960; Willey and Heath, 1969), e.g. increasing the density when water and light resources are abundant. For example, when we adjust the LAI from 3 to 4 in our model, ΣAPAR increases from 1,111 to 1,166 μmol m^{-2} s^{-1}, PAR profile becomes more uneven, and ΣA increases from 25.7 to 28.3 μmol m^{-2} s^{-1} (Fig. 4A). However, the increase in ΣA from higher LAI is at the cost of increasing leaves, and thus the net yield cannot increase indefinitely with higher LAI (Fig. 4B).

When crop density is fixed, one could also improve the canopy radiative transfer by altering the spacing among individuals. This change in canopy structure can be represented in vegetation models using a bulk property of the canopy called CI (Braghiere et al., 2021; Chen et al., 2012; Pinty et al., 2006). For example, increasing the space (corresponding to canopy with lower CI) will increase the probability of leaves exposed to direct radiation in the lower canopy, but decrease the light absorption in the upper canopy (Fig. 4A). When we adjust the CI from 1.0 to 0.7 (LAI = 3), we find that ΣA increases from 25.7 to 26.5 μmol m^{-2} s^{-1} even though ΣAPAR decreases from 1,111 to 1,009 μmol m^{-2} s^{-1} (Fig. 4A).

In theory, when crop density is low, plants are less constrained by light availability, and changing spacing would make a marginal difference (Fig. 4B). However, when the crop density is high, a high LAI would result in a more uneven absorbed radiation distribution, and adding space would help make the vertical APAR distribution less uneven. Thus, it is expected that adding proper spacing will benefit to the yield, and the optimal spacing would be higher for denser canopy (Fig. 4B). When crop traits change, for instance, with the decreases of chl content, the optimal canopy structure would change accordingly, and adjusting the crop density and spacing based on crop traits has great potential to advance crop yield (Fig. 4B).

3.2. Mixed cropping

Competition for light, nutrients, and water typically results in overinvested chl content in the upper canopy and unnecessary root investment (Ainsworth et al., 2012; Casper and Jackson, 1997; Schenk, 2006; Slattery et al., 2017; Zhu et al., 2010), making it impractical to
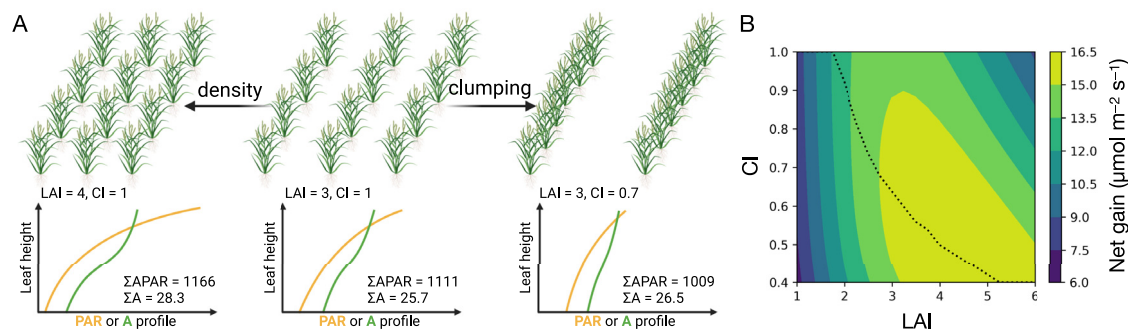
Fig. 4. Example of canopy structure optimization. A, canopy structure can be adjusted through crop density or spacing (clumping); B, carbon gain at various combinations of leaf area index (LAI) and clumping index (CI). The dotted line plots the optimal CI at different LAI settings.

grow under-story crops because of the limited light resources. Although plants do show vertical heterogeneity of chl content (Mänd et al., 2013; Moulin et al., 2003), the profile is likely not optimized for productivity. However, this optimality could be achieved by mixing crops in the field to create an artificially optimized vertical profile. However, we note that if the crops have similar chl contents or compositions, mixed cropping would not benefit the overall yield in terms of radiation.

Promisingly, the success of leaf color mutants and the potential inclusion of chl d and f make this artificial optimization possible through modulating the light absorption among crops with different heights. Thus, we theorize two scenarios here, a regular lower canopy crop mixed with a less green mutant in the upper canopy and a regular upper canopy crop mixed with a chl d + f breed in the lower canopy (Fig. 5). For the first scenario, the canopy radiation profile would be more evenly distributed even though total radiation decreases. Our simulation supports the hypothesis as ΣAPAR decreases from 1,111 to 989 μmol m^{-2} s^{-1} and ΣA increases from 25.7 to 26.3 μmol m^{-2} s^{-1}. For the second scenario, the upper canopy APAR profile would be unchanged, but the lower APAR profile will be higher because of the extra NIR absorption. Our simulation also supports this hypothesis as ΣAPAR increases to 1,138 μmol m^{-2} s^{-1} and ΣA increases to 26.1 μmol m^{-2} s^{-1}. Based on the simulations, it is expected that the combination of low chl mutant in the upper canopy and chl d + f breed in the lower canopy may result in even higher productivity.

Optimization over the mixed cropping systems would help further advance the crop yield, and the possible ways include the optimization of

(1) chl contents and compositions for upper and lower canopy crops, (2) faction of upper and lower canopy crops, (3) crop density, and (4) crop spacing. A well-calibrated vegetation model would help find the optimal combination of crops based on crop traits and local environment, thus allowing for more effective radiation utilization in mixed cropping systems.
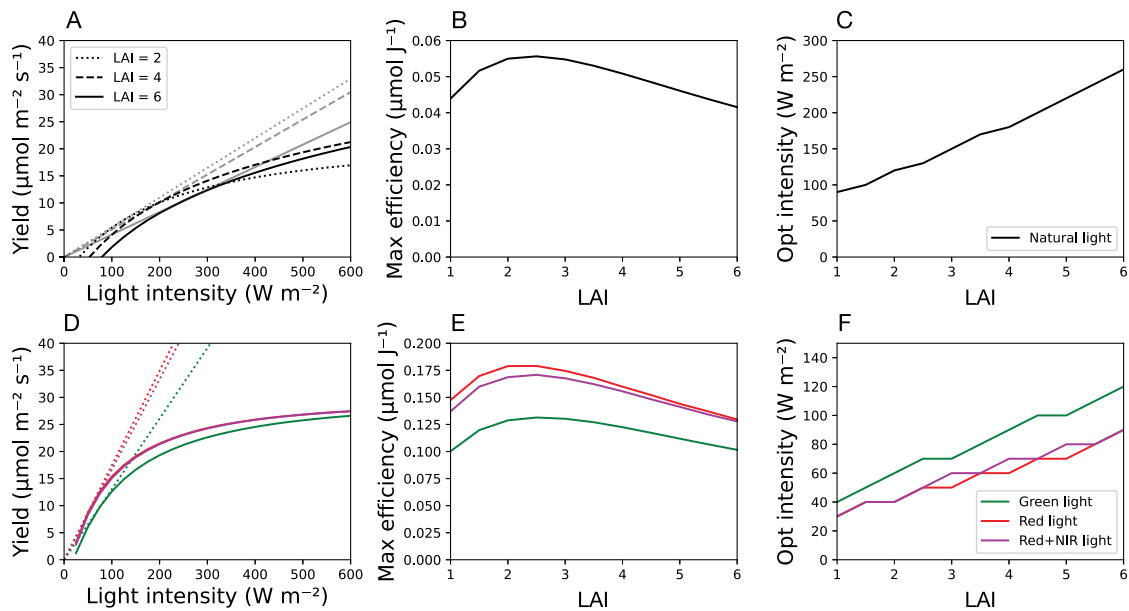
4. Light source

Vertical farming is an important step toward sustainability in urban areas for either productivity or personal interest (Asseng et al., 2020; Beacham et al., 2019; Touliatos et al., 2016). Due to the limitation of natural radiation, people often require an external radiation supply. Thus, maximally reducing the energy invested in the radiation supply while maintaining equivalent production is highly recommended (Van Delden et al., 2021; Zhen and Bugbee, 2020a, 2020b). Here, we focus on maximizing energy use efficiency to maximize the net carbon gain per unit energy investment. In this case, there are at least two important decisions to make: (1) how much energy to use per module in a vertical setup and (2) what is the best light source to use in terms of its spectrum.

In our model simulation using the natural light spectrum (with direct and diffuse radiation ranging from 400 to 2,500 nm), the relationship between light intensity and crop yield changes with LAI. The higher LAI requires higher minimum light intensity to compensate for leaf respiration (Fig. 6A). The yield-to-energy ratio increases and then decreases with higher light intensity (Fig. 6A). In other words, for any given canopy structure and light source, there is an optimal light intensity that gives
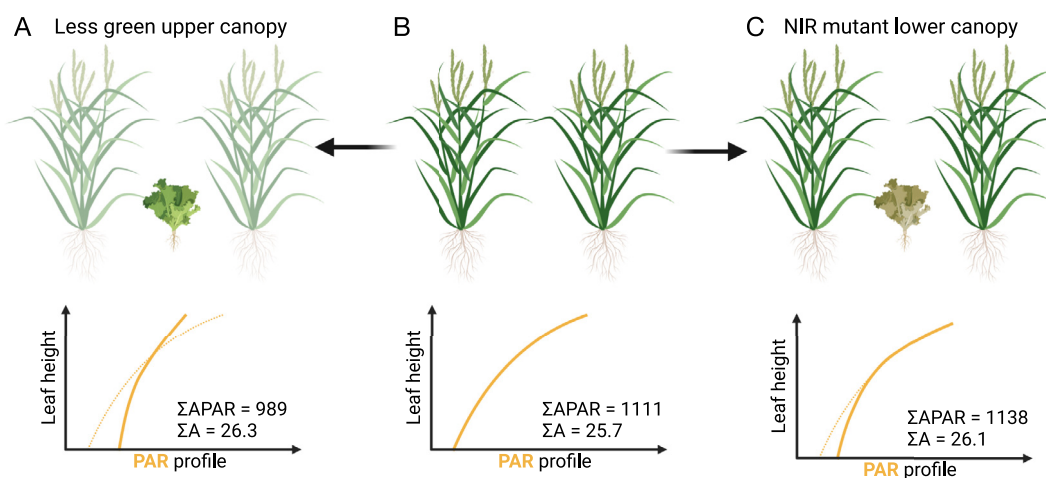
Fig. 5. Example of mixed cropping. A, mixed crop system (leaf area index, LAI = 3) with a less green mutant upper canopy and a normal lower canopy crop; B, single crop system with a LAI of 3; C, mixed crop system (LAI = 3) with a normal upper canopy crop and a chl d + f breed in the lower canopy.

Fig. 6. Example of light source optimization. A, relationship between crop yield and natural light intensity at three leaf area index (LAI) settings. Gray lines label the cases when the yield-to-energy ratio is maximum. The yield is normalized per second by subtracting construction and respiration costs; B, relationship between LAI and maximum (Max) efficiency derived from panel A for natural light; C, optimal (Opt) light intensity that gives maximum efficiency at different LAI; D, relationship between crop yield and supplemental light intensity using three light sources: green only, red only, and red + NIR. Dotted lines label the case when the yield-to-energy ratio is maximum; E, relationship between LAI and maximum efficiency for the three light sources; F, optimal light intensity that gives maximum efficiency at different LAI.

maximized LUE. The maximum LUE increases and then decreases with higher LAI, suggesting an optimal canopy structure for maximum energy use efficiency (Fig. 6B). Moreover, the optimal light intensity increases with higher LAI (Fig. 6C). This suggests that optimal light intensity needs to be adjusted dynamically during crop growth to optimize energy use.

When switch from the natural light spectrum to an artificial light spectrum (diffuse light only), we find similar relationships between crop yield and light intensity, and the maximum occurs earlier compared to natural light as the natural light contains a substantial amount longer wavelength NIR that is not feasible for photosynthesis (Fig. 6D). Similar to natural light, the relationship between maximum LUE also increases and then decreases with higher LAI, but the magnitude of maximum LUE is much higher compared to natural light (Fig. 6E). Optimal light intensity also increases with higher LAI, and is highest for green light because of the higher energy per unit photon (Fig. 6F).

We note that the analysis above is based on our default traits used in the simulations and thus can only serve as a qualitative demonstration of the potential of using vegetation modeling in vertical farming. Notably, our model simulations suggest that vertical farming could substantially benefit from a dynamically modulated light intensity based on plant traits and canopy structure. Moreover, when the canopy becomes extremely dense (LAI > 6), using a mixture of red and NIR light would help give the better transmittance of NIR light (Fig. 6F). We believe that a more mature model with more accurate representations, dynamic trait monitoring, and environmental condition control will help advance vertical farming. For instance, we do not consider electricity-to-light conversion efficiency or any maintenance costs in our prototype application, and accounting for those would make vertical farming more sustainable.

5. Future directions

Vegetation modeling provides a feasible way to more efficiently explore the best approaches to maximize crop yield, and will not be constrained by canopy radiative transfer that we discussed in this review. For example, De Souza et al. (2022) found that accelerating the photoprotection recovery process could substantially improve soybean yield in

a fluctuating light environment. Quantitatively understanding the cost related to the photoprotection recovery would help identify an optimized recovery rate to engineer based on the local climate. Here, we use the trait- and process-based CliMA Land model as an example to outlook the

Table 1
An outlook of how vegetation modeling may help agricultural practice. The listed parameters are supported by CliMA Land model, and can be optimized to improve crop yield.

Parameter	Note
CAR	Leaf carotenoid content (CAR) impacts PAR absorption used for photosynthesis and sustained non-photochemical quenching (Magney et al., 2019; Raczka et al., 2019)
Chl	Leaf chlorophyll content (CHL) impacts PAR absorption used for photosynthesis
HS	Hydraulic system (HS) impacts the water supply to leaves, and hence stomatal behavior
LHA	Leaf hyperspectral absorption (LHA) curves of the pigments impact canopy radiative transfer and light utilization
LMA	Leaf mass per area (LMA) impacts light absorption, particularly shorter wavelength visible light
LWC	Leaf water content (LWC) impacts leaf light absorption feature
PIGMENTS	Other leaf pigments such as anthocyanin and brown pigments would impact the partitioning of PAR into photosynthesis systems
Root	Root distribution within the soil impacts soil water budget and plant hydraulic status
Stomata	Stomatal responses to physiological and environmental cues impact carbon budget of the plant
TD	Temperature dependencies (TDs) of leaf photosynthesis and respiration machinery would impact net assimilation rates of leaves
CI	Clumping index (CI) impacts canopy radiative transfer
LAI	Leaf area index (LAI) impacts canopy radiative transfer
LIDF	Leaf inclination angle distribution function (LIDF) impacts light extinction and scattering coefficient of the canopy
Air	Air temperature, humidity, and CO_2 impact leaf energy, carbon, and water fluxes
Radiation	Supplemental radiation intensity and spectrum impact canopy light profiles
Soil	Soil type impacts plant hydraulic status, and soil albedo impacts canopy light scattering and soil energy balance

potential of utilizing vegetation modeling in agriculture (see Table 1 for more details).

Moreover, an increasing number of research has shown the power of utilizing remote sensing to proxy crop yield (He et al., 2020), retrieve leaf pigment contents (Hernández-Clemente et al., 2012; Zhang et al., 2008), and estimate canopy water content (Humphrey and Frankenberg, 2023; Konings et al., 2021). Using vegetation models along with the remotely sensed data would allow for better monitoring of crop health status. Applications based on this would be of great importance on crop management.

It should be noted that the reliability of the model predictions depends on not only the eco-physiology representations within the model but also the input traits and environmental conditions. In the case of photoprotection recovery dynamics, it would require vegetation models to prognostically model non-photochemical quenching along with photosynthesis (Wang et al., 2020). Moreover, the models need to be well configured and tested with field experiments before using the models for production purposes. We believe that the combination of vegetation modeling and real-world agricultural practices would help boost crop yield more effectively.

6. Conclusions

In the present study, we review the research that aims to improve crop LUE by optimizing the canopy radiation environment and prototyping model applications based on our vegetation model framework. We theoretically evaluate the potential of the agricultural practices, including genetic breeding, canopy structure management, and supplemental light. Given the difficulty in quantitatively monitoring the radiation profile within crop canopy, using modeling tools to simulate crop productivity holds great potential in advancing crop yield. Future efforts in more accurately representing vegetation physiological processes, dynamic plant growth, competition, and maintenance costs related to crop management would help better guide real-world agricultural practices. Further, the vegetation models would also benefit crop breeding and management in other aspects such as plant water relations and remote sensing. We note that changes in large-scale agricultural practices would have substantial impacts on global carbon, water, and energy budgets, and thus help mitigate or intensify global climate change. For example, less green mutants of crops and trees have higher reflectance in the PAR range and would impact the landscape level energy balance. A detailed model that addresses the climate feedback from agricultural practices would help better envision the optimal agricultural strategies with minimal or positive impacts on global warming.

Abbreviations

Not applicable.

Availability of data and materials

The CliMA Land model used for the present study is freely and publicly available at https://github.com/CliMA/Land. Prototype models used to perform the simulations can be found at https://github.com/Yujie-WANG/Published-Codes-Yujie-WANG.

Authors' contributions

All authors contributed equally.

Declaration of competing interest

The authors declare no competing interest.

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