Crop and Environment 1 (2022) 74–85

Contents lists available at ScienceDirect

Crop and Environment

journal homepage: www.journals.elsevier.com/crop-and-environment

Review

Casting light on the architecture of crop yield

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ARTICLE INFO

Keywords:
Canopy architecture
Canopy function
Crop yield
Light interception
Photosynthesis

ABSTRACT

Crop canopy architecture is a central component of yield. The arrangement of leaves in three-dimensional space defines the efficiency of absorption of radiation and its conversion into dry matter at the canopy level. The description of architecture is normally associated with light since the optimal distribution of light is associated with that of other essential components such as nitrogen and pigments. However, architecture has been influenced by a number of other unrelated processes through breeding and selection that may have acted independently or even against light use efficiency. This review attempts to provide a broad view and interpretation of canopy architectural properties and the factors affecting crop architecture starting with evolution, domestication, climatic conditions and cultivation patterns, predominantly focusing on field grown agricultural crops. Using examples of modelling with a virtual canopy, we will discuss how architectural traits affect light interception and photosynthesis. Finally, we will discuss the future of architectural research: the concept of the ideal plant type (the ideotype) and which features we can expect to see, as well as the social constraints that may govern future crop architecture.

1. Introduction

Architecture, the arrangement of leaf material in three-dimensional (3D) space, is critical in determining plant performance. Structural traits are determined by genetics but will also be shaped by environmental conditions plus human interaction and management resulting in a wide range of possible plant and canopy architectures (Fig. 1). Structural traits are integral to canopy function, determining the interception and use of resources, altering the distribution and movement of water, light and gases and influencing the prevalence of pests, diseases and pollinators. Architecture is particularly important in determining the light environment, and subsequently the photosynthetic productivity of plant canopies. Photosynthesis, in turn, is closely linked to potential yield (Murchie et al., 2009; Zhu et al., 2010). Hence canopy architecture is most frequently discussed and rationalised in the context of light interception and photosynthetic efficiency. This is particularly the case recently with the interest in improvement of photosynthesis for yield potential improvement.

However, whilst the primary goal of many plant breeding programmes is to increase crop yields, this does not always occur with conscious selection of optimised architectural traits meaning that crop canopy structure has diverse influences which do not necessarily coordinate with photosynthetic efficiency. This perspective is not often considered. Within this review, we will provide a new and comprehensive overview of the factors that have shaped crop canopy architecture, with a focus on field-grown agricultural crops such as cereals. First, we discuss the factors affecting crop architecture from evolution including domestication, climatic conditions and cultivation patterns. Using examples of modelling with a virtual canopy, we will discuss how different architectural traits can affect light interception and photosynthesis in crops. Finally, we will discuss the future of architectural research: the concept of the ideal plant type (the ideotype) and which features we can expect to see, as well as the social constraints that may govern future crop architecture. For the sake of clarity, we consider mature canopies but we appreciate the critical importance of progress through distinct developmental stages and its influence on overall yield. We focus on crops such as cereals due to the large areas given to the cultivation and whilst much of the content is applicable to horticultural crops and orchard trees, this is not the primary application of discussed principles and optimal architecture types may differ dependent on environment.

2. The determinants of architecture

2.1. Biogeography, weather and climate

Both climatic conditions and evolutionary pathways are important in determining architectural properties of plants. Vascular plants evolved as

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https://doi.org/10.1016/j.crope.2022.03.009
Received 22 December 2021; Received in revised form 25 February 2022; Accepted 28 February 2022

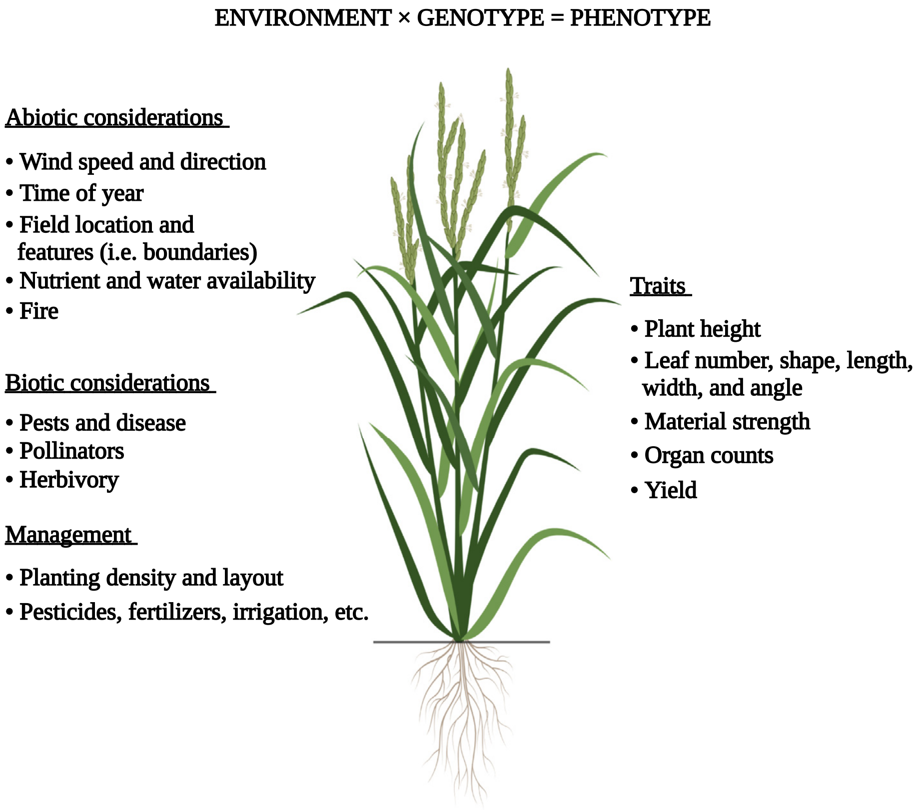

Fig. 1. Overview of features affecting plant architecture. The phenotype is determined by genetics as well as local environmental conditions.

a monophyletic clade which subsequently diversified into the range of architectural types now found in living and fossil species (Sussex and Kerk, 2001). Most developmental strategies arise as a balance between deterministic genetic control combined with plasticity resulting from local climatic conditions (Halle, 1999). In the most basic sense, this allows plants to be grouped into architectural models based on the internal processes that govern plant growth form (Barthélémy et al., 1997; Halle et al., 1978). From such analyses, 23 architectural models were identified, based on features such as the position of branching patterns, growth axis and sexual structures, to which most extant seed plants can be assigned. More recent work has proposed an additional 12 architectural models for dichotomous branching plants, the majority of which are extinct or present in non-vascular or non-seed plants (Chomicki et al., 2017; Gola, 2014; Halle, 2004). These dichotomous structures became less prevalent during the Palaeozoic, coinciding with a reduction in atmospheric CO_2 concentrations and the rise of megaphyll leaves, enabling axillary branching structures to outcompete (Chomicki et al., 2017). To a large extent, all architectural models are determined by the spatial and temporal behaviour of meristems and phytomers–continuous or intermittent activity, vegetative versus reproductive growth, axillary versus terminal branching or, equal versus unequal phytomer growth. Many of these features are associated with hormone regulation and pathways. Understanding of the underlying genetic and physiological components will thus enable a greater understanding of the evolution of architectural types plus enable future expansion of architectural types through manipulation of meristem function (Sussex and Kerk, 2001).

The global distribution of architectural types is uneven, suggesting that certain architectures are more suitable for given habitats (Brunig, 1976; Moncrieff et al., 2014). Architecture will be affected by both abiotic and biotic features of the environment as well as geological history. For example, habitats closer to the equator experience more similar weather conditions all year round, thus continuous plant growth is largely restricted to tropical regions. In comparison, seasonality, whether that encompasses a period of reduced temperature or rainfall, will impact development. In woody plants, rhythmic growth enables protection of sensitive plant tissues from adverse conditions. An alternative is the evolution of the herbaceous habit; with many temperate herbaceous species evolving from ancestral tropical woody plants (Beaulieu et al., 2013; Chomicki et al., 2017; Zanne et al., 2014). In comparison, Moncrieff et al. (2014) found distinct differences between African and Australian savannah tree taxa. They attributed the differences not to disparities in the environmental conditions in which the trees grew, but rather in the differing evolutionary history of African versus Australian savannas. Traits will also depend upon niche differentiation over time or other features of the environment such as fire risk. For example, forest successional species often differ in their reiteration potential, with early successional species having restricted potential due to reduced growth rates (Chomicki et al., 2017; Millet et al., 1999). Fire tolerance structure often encompass bud protection mechanisms including resprouting or reduced branching (Crisp et al., 2011; Staver et al., 2012).

2.2. Domestication

Plant architecture is economically important as it will determine key traits in crop and ornamental plants plus cultivated forest stands (Teichmann and Muhr, 2015). As such, architecture represents one of the core targets for improvement during domestication and breeding programmes. The resulting structure of modern cultivars is a result of the genetic basis of the progenitors combined with ecological diversification and local cultural pressures. Within crop plants, architectural traits have evolved over thousands of years during the process of domestication. Whilst the genetic changes associated with domestication have mainly been studied for members of the grass family, these only represent a small proportion of the domesticated food crops, with approximately 2,500 species found in over 160 plant families including both monocots and eudicots as well as non-flowering plants (Meyer and Purugganan, 2013). A common set of targeted traits include loss of seed shattering, dormancy, branch angle or pattern and internode elongation; collectively referred to as the “domestication syndrome” and almost all domestication events entail improvements in yield, abiotic and biotic stress resistance plus improvements in nutritional quality (Abbo et al., 2014; Flint-Garcia, 2013; Sakuma et al., 2011; Teichmann and Muhr, 2015; Teo et al., 2014; Zhang and Yuan, 2014; Zohary et al., 2015). Yield increases can either occur through an increase in seed number as seen in rice, or through maintenance of number but an increase in individual fruit size like in tomatoes and aubergine (Si et al., 2016; Zhu et al., 2018).

Cereal crops were domesticated from wild grasses and have undergone continual breeding and selection for thousands of years. Domestication in cereals is largely associated with changes in the pattern and timing of branching which influences both vegetative and inflorescent structures (Doust, 2007). Whilst inflorescent branching determines the number of seeds produced by each reproductive structure, vegetative branching will determine overall biomass and is more susceptible to environmental conditions (Doust, 2007). Vegetative branching in cereals is separated into two main classes: those with multiple basal tillers such as wheat or rice, or those with more prominent axillary branching and fewer, or only one, main stem such as sorghum, maize and millets (Teichmann and Muhr, 2015). Whilst both sets evolved from wild grasses with a similar growth habit, the former may be related to grazing pressures or other ecological factors whereby semi-independence of tillers from the primary shoot provides an advantage. Compared to wild relatives, domesticated cereals have reduced levels of vegetative branching and the genetic regions and environmental variables contributing to this have been identified (Doust and Kellogg, 2006; Duggan et al., 2005; Ishikawa et al., 2005; Li et al., 2003). For maize, the wild relatives (collectively called teosinte) develop multiple axillary branches resulting in multiple female inflorescences. In comparison, the modern cultivars of maize generally contain only a single female inflorescence (ear), through changes in the expression of *TEOSINTE BRANCHED 1* (*TB1*) (Doebley et al., 1997; Meyer and Purugganan, 2013). This is likely to have arisen through selection pressure upon ear architecture, to support a single large ear at the expense of branching (Yang et al., 2019). Whilst each of the cereal species were domesticated independently from each other, the advent of molecular techniques indicates that the domestication of several species may select upon the same genes or gene pathways (Doust, 2007; Meyer and Purugganan, 2013; Paterson et al., 1995). Thus similarly, *TB1* was selected for during the domestication of pearl millet and rice (Remigereau et al., 2011; Lu et al., 2013). In addition to tillering, the angle between the tiller and the culm is important for rice cultivation to enable dense cultivation whilst balancing weed suppression (Haefele et al., 2004; Wang and Li, 2006). Genes have also been identified that are associated with the orientation of branching structure such as the erect growth habit in Asian rice, controlled by the *PROSTATE GROWTH 1* (*PROG1*) gene, as well as *TILLER ANGLE CONTROL 1* (*TAC1*) (Jin et al., 2008; Yu et al., 2007).

Similar to the domestication of wild grasses, the evolution of root and tuber crops commonly coincides with reduced branching (Meyer and Purugganan, 2013). Within carrots, this encompasses minimal lateral root branching and a biennial growth habit to support non-woody root growth (Iorizzo et al., 2013). In contrast, within fruit and timber trees, the degree of branching is economically important due to the contribution of leaves to specific leaf area, and early canopy closure is crucial for weed suppression. Therefore, gene and cultivation techniques are selected that often increase branching rate (Teichmann and Muhr, 2015).

More recently in the evolution of modern crop varieties are the significant architectural changes coinciding with the green revolution. Introduction of dwarfing genes led to large reduction in the stature of staple cereals. Within rice, *semidwarf 1 (SD1)* is responsible for a reduction in culm length whereas in wheat, the *Reduced height (Rht)* genes limited yield loss associated with lodging events with simultaneously increasing the proportion of assimilate partitioned to the grain (Hedden, 2003; Pearce et al., 2011). Where and how these genes arose is debatable, with evidence suggesting that *SD1* was originally selected by early Japanese farmers thousands of years prior to the green revolution, however both influence the action and production of gibberellin plant hormones (Asano et al., 2011). As such, dwarfing genes are prevalent among many crop varieties and more recent interest has arisen in translating similar effects into other crop plants such as brassicas (Choudhary and Jambhulkar, 2016).

Diversity is created in populations as domesticated crops evolve and spread from their initial geographical range and adapt to new environmental conditions and cultural preferences. In most instances, the cultural traits will have evolved under conscious selection (Grobman et al., 2012; Knüpffer et al., 2003). This may involve the introduction of traits that reduce the fitness of plants if cultivated under ‘wild’ conditions, but increased fitness under human exploitation. Domestication within the brassicas highlights the wide range of possible forms which can be generated from the same wild progenitor by targeting different organs or genetics (Fernie and Yan, 2019). From the progenitor wild mustard (*Brassica oleracea*) selection of stem traits generated kohlrabi; on flower traits generated broccoli; terminal bud selection led to cabbage; axillary buds led to brussels sprouts; leaves led to kale and collard greens whilst alteration in allopolyploidy led to rutabaga (*Brassica napus*) and Chinese cabbage (*Brassica campestris*) (Fernie and Yan, 2019; Vaughan and Geissler, 2009).

It is possible that domestication events have led to a limited ability to alter architectural traits further. Within many crop species, artificial selection of wild progenitors led to a genome-wide reduction in genetic diversity, as seen in soybean, rice, wheat, maize and barley (Haudry et al., 2007; Hyten et al., 2006; Tanksley and McCouch, 1997). Within maize, a genetic bottleneck led to a substantial loss in genetic variance compared with teosinte; particularly as a result of morphological changes relating altered branching (Yang et al., 2019). These studies indicated that depending on the desired end product, other canopy architectural traits may be constrained. In comparison, einkorn wheat, carrot and chicory have maintained the same amount of genetic diversity as their wild counterparts (Iorizzo et al., 2013; Kilian et al., 2007). The potential for a genetic bottleneck depends upon the length of domestication, mating system and breeding practices. Within carrots, outcrossing has contributed to the maintenance of diversity, with genetic purity requiring geographical segregation of up to 5 km, which is unlikely to have been maintained by early carrot breeders (Glémin et al., 2006; Simon, 2010). In domesticated apples, self-incompatibility, a long lifespan and introgression from wild relatives via open-pollination has maintained genetic diversity despite the use of vegetative propagation by grafting (Cornille et al., 2012). In crops where genetic diversity has been reduced, cultivation in less suitable areas leads to global variation in cultivation efficiency. For example, yields of cassava in sub-Saharan Africa are a third of those in South East Asia, partly attributable to the application of fertilisers in Asia but not Africa (FAO, 2015).

2.3. Cultivation and management

This review is largely concerned with alterations in architecture that are genetic in origin, especially those that derive from domestication and breeding but we recognise the importance of ‘plasticity’ in the plant form. Here we merely provide a brief synopsis of relevant points. Agronomic practices and environment have a role to play, such as resource availability, timing of fertiliser application and planting density. The exogenous application of plant growth regulators (PGRs) with the purpose of altering plant height and achieving uniform growth is common practice and provides a practical example of the importance of architecture to growers. Another common example is that of tillering in cereals. Tillers are shoots that arise from the base of the plant and their emergence is influenced by conditions such as light, nutrition and water. They enable the plant to compensate leaf area and architecture according to planting density and competition from neighbours and to adjust to availability of resources for growth (Evers et al., 2007; Longnecker et al., 1993; Zhong et al., 2002).

Leaf erectness is less effective for weed competition than horizontal leaves and this has implications for planting density. For example, irrigated rice has a short life cycle and less need to compete with weeds. In this case upright leaves and a high tiller density can permit the rapid accumulation of a high leaf area index needed to achieve high canopy photosynthetic rates and maximise yield (Ong and Monteith, 1992).

Cropping systems are diverse and can include multiple species in the same physical location, a practice that can help to enhance and conserve resources (Brooker et al., 2014; Li et al., 2003). Architecture of component crops and of the combined multispecies canopy both contribute to the efficiency of light utilisation for example by placing C4 leaves in the upper layers and broadleaf C3 species in the lower layers (Burgess et al., 2017a,b).

2.4. *Biotic determinants of architecture*

Other features impacting architecture include herbivory, pollination, pests and diseases. Herbivory will induce architectural types that protect the most edible plant material, such as 'cage' architecture and will also affect the spatial arrangement, density and composition of a habitat (Cadenasso and Pickett, 2000; Charles-Dominique et al., 2017). Certain traits are linked to the distribution and density of pollinators, which is in part linked to suitable weather conditions (Prusinkiewicz et al., 2007). Similarly, the incidence of pests and diseases will be determined by a combination of architecture and local environmental conditions and will, in turn, alter structural traits. The severity of disease is dependent on the initial inoculum pressure combined with climatic conditions and canopy architecture (Tivoli et al., 2013). In the case of fungal or bacterial pathogens, increased severity is often associated with traits that favour a more humid microclimate, a reduction in air movement and increased rates of senescence (Chang et al., 2007; Coyne et al., 1974; Richard et al., 2012; Tivoli et al., 2013).

3. The biological importance of architecture

The largest effect that architecture has on plants is changes to the environmental conditions inside plant canopies. Whilst all abiotic factors are influenced by the structural traits, here only light will be considered although the whole microclimate within a crop canopy will be altered. As the key driver of photosynthesis, the light quantity and quality subject on a leaf is critical in determining productivity and biomass accumulation. Light poses a two-fold challenge to the plant–the need to use as many photons as efficiently as possible whilst simultaneously preventing harm caused by excessive radiation. Achieving the optimal balance between these two states is critical for maximising productivity and mitigating damage (Burgess et al., 2015; Demmig-Adams et al., 2012; Retkute et al., 2015; Townsend et al., 2018). Leaf photosynthesis responds non-linearly to light intensity, and intensities can vary from limited to excessive dependent on canopy location. Features such as leaf number, angle, size, shape and composition, structural support features plus the arrangement of this material in 3D space will determine the specific characteristics of light reaching photosynthesising tissue. The effect of leaf angle on light interception and carbon gain can be seen in Fig. 2.

The spatial arrangement of plant material creates a complex pattern of light, typically resulting in progressively lowered light levels superimposed with high light patches or "light flecks" (Durand et al., 2021; Townsend et al., 2018). The cellular and molecular features of photosynthesising tissue can acclimate to these light levels, either during development (i.e. developmental acclimation) or changes in mature tissue over a period of days (i.e. dynamic acclimation) (Retkute et al., 2015; Townsend et al., 2018; Walters, 2005). This enables foliage photosynthetic potential to increase with increasing light availability and enable exploitation of high light events. There is substantial variation between species in their ability to acclimate, with plants from semi-shaded environments exhibiting the greatest plasticity in acclimation capacity (Murchie and Horton, 1997). The ability for individual plant leaves to acclimate is also dependent upon leaf age and availability of nutrients, species-specific differences in cellular division and expansion, chlorophyll content and ratios, and changes in the composition and activity of photosynthetic enzymes (Carmo-Silva and Salvucci, 2013; Field, 1981; Hikosaka, 2005; Murchie et al., 2002; Niedermaier et al., 2020; Orr et al.,

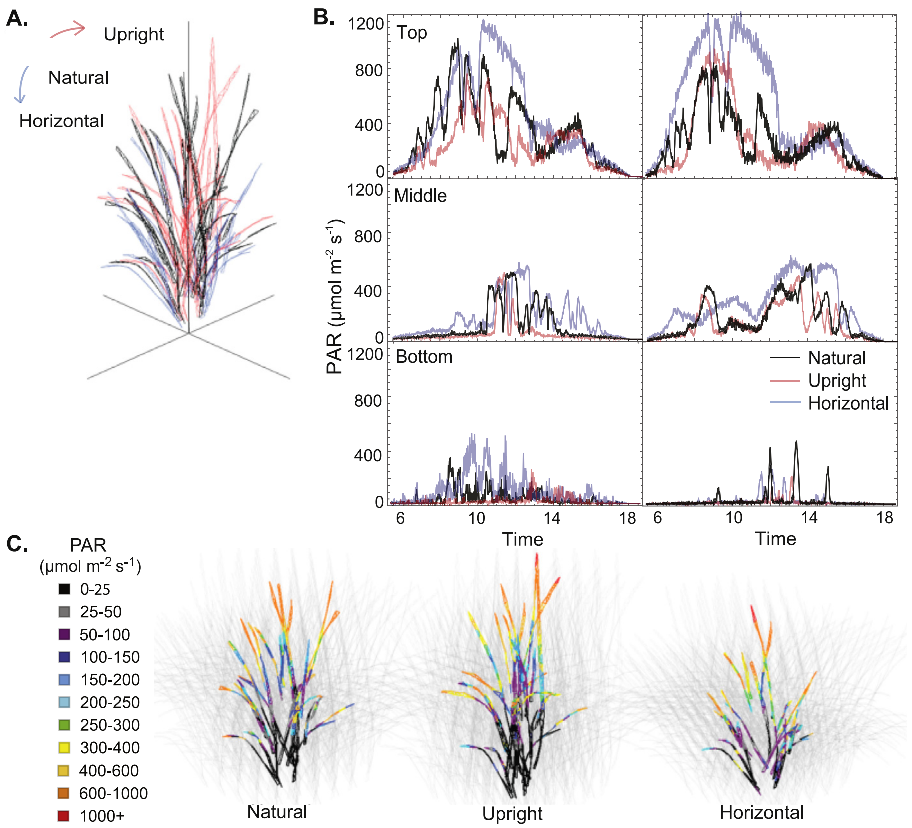

Fig. 2. Changes in light interception in a simulated rice canopy subject to altered leaf angle. (**A**) Schematic of plant distortion indicating the leaf position in each plant where leaves were manually separated and rotated 10° towards or away from the central axis, (**B**) Selected light patterns over the whole day for fixed leaf positions for the three different orientations and (**C**) Each reconstructed rice canopy (5 x 5 plants) with the central plant in bold where maximum PAR ranges are colour coded for 1200 h.

2016; Pons et al., 2001; 2005; Stiles and Van Volkenburgh, 2002). Anatomical and molecular differences in leaves resulting from acclimation enables higher efficiency under local light conditions but will also influence the attenuation of different wavelengths to lower canopy layers. Depending upon the species, photosynthetic capacity can vary between two and 20 folds from the canopy top to bottom.

In all higher plants, the photosynthetic photoreceptors chlorophyll *a* and *b* along with accessory pigments such as the carotenoids absorb wavelengths between 400 and 740 nm for use in photosynthesis (Croce et al., 2003; Demmig-adams et al., 2014; Zhu et al., 2008). Photons of wavelengths between 400 and 700 nm are therefore referred to as photosynthetically active radiation (PAR) (Hogewoning et al., 2012). Some work utilises 400–740 nm, which may be acceptable as within the PAR range because far-red (FR) light can be intercepted by photosystems and drive photosynthesis (Smith et al., 2017; Zhen and Bugbee, 2020). However different wavelengths of PAR are absorbed with varying efficiency, with peaks in the blue (B, 400–500 nm) and red (R, 600–700 nm) and, depending on species, complete reflection of up to 50% of the green (G, 500–600 nm) (Hogewoning et al., 2012; Smith et al., 2017; Terashima et al., 2009; Zhu et al., 2008;). The sunlight spectrum contains R, G and B photons, all of which are capable of driving photosynthesis with high quantum efficiency once absorbed by leaves. However, properties of the leaf and canopy determine the attenuation of different wavelengths to lower canopy layers, and thus the proportion of each wavelength reaching specific chloroplasts (Franklin, 2008; Terashima et al., 2009). As sunlight passes through a plant canopy, chloroplasts preferentially remove R and B wavelengths, with up to 80% of G wavelengths being transmitted through the chloroplast (Evans and Anderson, 1987; Smith et al., 2017; Terashima et al., 2009). Coupled with the highly refractive properties of leaves, this results in a greater proportion of G photons reaching deeper into leaf tissue and lower canopy layers (Smith et al., 2017; Sun et al., 1998). Similarly, plant canopies show a large gradient in R to FR photons, with an enrichment of FR photons in lower layers. This is associated with the shade response, and often leads to elongation and altered partitioning of resources. Whilst not conventionally viewed as efficient wavelengths, recent evidence suggests a role for FR and G photons in driving and maintaining photosynthesis, particularly in lower canopy layers (Smith et al., 2017; Zhen and Bugbee, 2020).

In full sunlight, there is a predictable temporal effect for light reaching the top of the canopy caused by solar movement, which results in a spatial shifting of light patterns according to time of day, as well as corresponding changes in the spectral composition. Light used to drive photosynthesis can be split into three components dependent on the directionality of light: 1) direct light, which comes directly from a source (the sun); 2) diffused light, which comes from all directions and 3) scattered or transmitted light, which has passed through or been re-emitted by an object (Durand et al., 2021). Under full sun conditions, direct light accounts for up to 85% of total radiation, with the proportion of diffuse radiation increasing as the sun approaches the horizon. The position of the sun in relation to canopy structure, combined with the length of the day is therefore integral in determining overall light interception. Therefore, geographical location or latitude will have contrasting effects on plant performance. Traits such as leaf inclination angle and leaf area are critical in determining the flux of solar radiation (Ezcurra et al., 1991; Falster and Westoby, 2003). Plants containing erect leaf stature tend to have a decreased light interception when the sun is directly overhead (i.e. during midday hours or low latitudes) but increases light capture at lower solar angles (i.e. start/end of the day or during seasonal changes in the higher latitude regions).

However, the true pattern of light within a canopy will depend upon these factors in combination with other weather patterns, including cloud cover and the displacement of leaf material brought about by wind. Early work predicted that alterations in leaf angle caused by wind can influence canopy photosynthesis (Caldwell, 1970). However, the effects of wind are likely to be very different for different canopy types. A planophile canopy, containing horizontal leaves, should offer less opportunity for light penetration since distortion is unlikely to alter leaf angle substantially. In comparison, an erectophile canopy, such as rice or wheat, will absorb more or less light depending on the angle of foliage, and hence their position relative to the sun. Thus wind may distort the canopy such that there is an increased chance of light penetration to lower layers (Burgess et al., 2016, 2018). This has previously been shown in tree canopies where fluttering leaves at the top of an Aspen canopy altered the spatial distribution of light and enhanced photosynthesis in lower leaf layers (Roden and Pearcy, 1993a,b). The effect of this distortion will be dependent on geographical location, wind speed and direction plus architectural traits. This can be seen in Fig. 3, whereby wind-induced distortion can be simulated through full body distortion of rice (e.g. tipping the whole plant over).

The true effect of wind-induced movement will depend upon the features of individual organs, whole plant structure and the presence and structure of neighbouring plants (Burgess et al., 2018; Doaré et al., 2004; 2021; Durand et al., 2021). Traits such as plant height, material strength, organ dimensions and projected area across the plane of movement are important factors in determining the mechanical response of plants when subject to wind. Dependent on architectural features, light intensity can

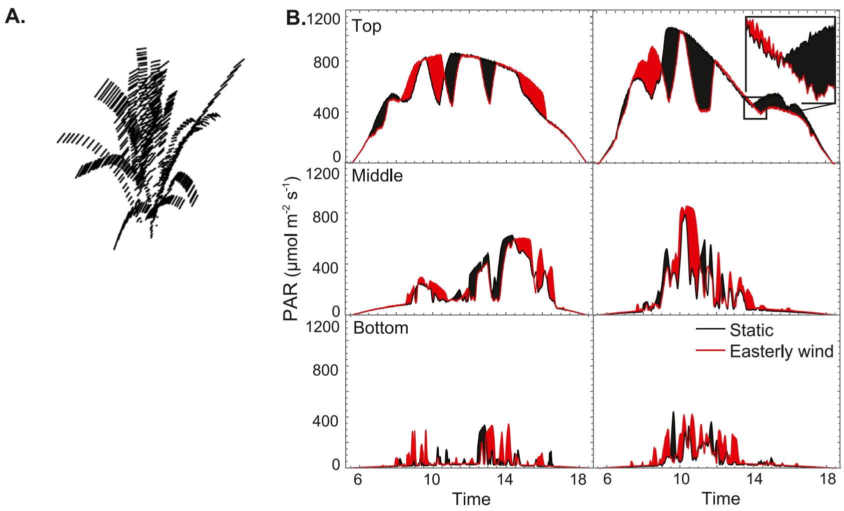

Fig. 3. Changes in light interception in a simulated rice canopy subject to wind, adapted from Burgess et al. (2016). (**A**) Schematic of plant distortion indicating centre of each triangle before and after simulated mechanical canopy excitation and (**B**) Example light patterns received at three different canopy positions where red shading indicates a higher light intensity in the simulation subject to an Easterly wind distortion and black shading indicates a higher light intensity in the natural, non-distorted position. The inset presents a zoomed in section of light pattern indicating higher frequency dynamic changes in light intensity.

differ over the scale of sub-seconds (Burgess et al., 2021; Durand et al., 2021). The full effects of wind-induced movement and canopy architecture can be seen within a recent study that compares measured light dynamics within a field-grown wheat canopy versus a modelled simulation in which the canopy is static (Burgess et al., 2021). Change in PAR, the duration of light flecks and time between light flecks are a result of movement combined with features such as plant height and canopy openness, with up to a ten-fold difference in the length of flecks with and without wind presence (Fig. 4). This highlights the dynamic light environment to which plants are exposed and the importance of assessment of photosynthetic response over varying time scales (Demmig-Adams et al., 2012; Murchie et al., 2018).

Cloud cover increases the proportion of diffused light, with up to 100% of radiation being classed as diffuse. Although the amount of diffuse radiation in the atmosphere has not changed, recent decades have seen large fluctuations (Warren et al., 2007). One of the remarkable effects of diffuse radiation is that it increases the canopy radiation use efficiency, presumably due to the lack of light-saturated photosynthetic leaf area in the canopy (Sinclair and Muchow 1999). It also appears to penetrate canopies and leaves more effectively than direct radiation (Broderson and Vogelmann 2010). However, there is a lack of research into the relative effectiveness of canopy architecture to utilise diffuse or direct radiation more effectively. It seems likely that upright canopies are able to utilise direct radiation more effectively to drive higher canopy photosynthetic rates (Richards et al., 2019).

4. Measurement of canopy structure

Understanding the links between genotype, phenotype and the environment will be critical in improving the productivity of our agricultural systems. However, this is, in part, limited by the ability to quantitively describe the capture and use of resources by the system. This must be considered for each location, with potential benefits occurring over a spatial scale (i.e. maximising instantaneous resource capture) or a temporal scale (i.e. extending the growing season or improving overall resource capture). Manual measurements can be made using readily available equipment such as leaf area meters (destructive) for leaf area index (LAI: leaf area per unit ground area), and leaf angle (mobile phones with accelerometers). There is a plethora of manual equipment available for field sensing of standard canopy traits such as LAI, extinction coefficient and fractional interception including light sensors, light bars and ceptometers (Murchie et al., 2018). Remote sensing using Normalised Difference Vegetation Index (NDVI) and other hyperspectral approaches can also be used in high throughput ways. Remote sensing using hyperspectral reflectance combines with statistical regression has also been used to predict 'high level' traits such as canopy radiation use efficiency (Robles-Zazueta et al., 2021).

For overall assessment of plant productivity and yield, detailed quantification of structures is necessary. The desire to create geometrically accurate 3D models of plants has led to the development of a number of different techniques to capture plant architecture (e.g. (Gibbs et al., 2019a,b; Godin and Sinoquet, 2005; Hui et al., 2018;; Pound et al., 2014; Song et al., 2013; Watanabe et al., 2005; Quan et al., 2006). Such approaches could provide an initial screening for assessing crop performance before more time-, labour- and space-incentives methods are used (Burgess et al., 2015a,b; Burgess et al., 2017a,b; Evers et al., 2019; Godin and Sinoquet, 2005).

Canopy architecture can be quantified and represented using both destructive and non-destructive approaches (Anderson, 1971; Bréda, 2003; Campbell and Norman, 1989; Chen et al., 1997; Jonckheere et al., 2004; Ross, 1981; Weiss et al., 2004; Wilson, 1963). Destructive methods require identification of key architectural features, defined by a number of different parameters such as counts, dimensions and angles, taking averages across a number of plants, then reconstructing a representative canopy (Alarcon and Sassenrath, 2011; Song et al., 2013; Watanabe et al., 2005). However, reconstructing the plant structure from data, *in silico*, is often time-consuming and tedious due to the rigorous measurements required (Fourcaud et al., 2008; Vos et al., 2009). Non-destructive methods can be broadly split into two categories with differing levels

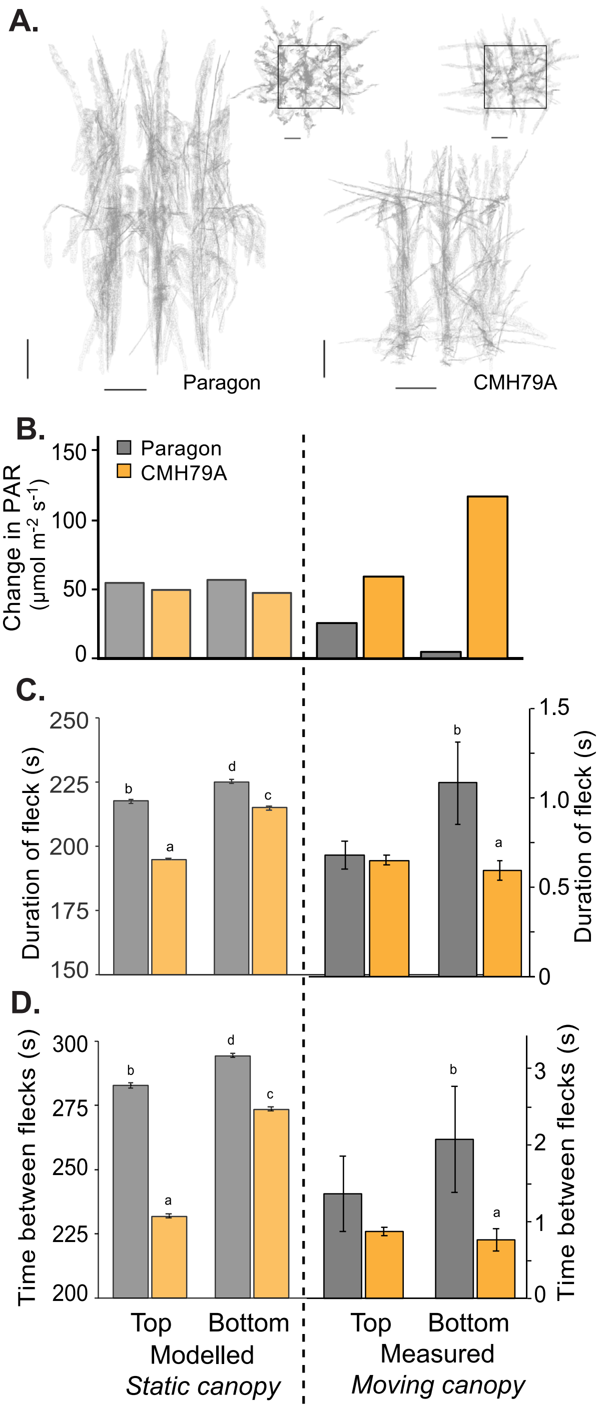

Fig. 4. Changes in the magnitude and duration of sunflecks in two architecturally contrasting wheat canopies, with and without wind-induced movement adapted from Burgess et al. (2021). Values given for the top and bottom half of each canopy, respectively. (**A**) Overview of structural differences between the two contrasting wheat lines, Paragon and CMH79. The scale bar indicates 10 cm whilst the top right insert shows the top-down view of each canopy with the ray tracing boundaries depicted by the outline. (**B**) Absolute change in PAR during a sunfleck relative to the background irradiance. (**C**) Duration of sunfleck and (**D**) Time between each sunfleck where bars indicate the mean ± SE and different letters indicate significant differences following ANOVA and post hoc Tukey's test at the P < 0.05 level.

of accuracy. Low accuracy methods use approximations of plant 3D structure in which leaf angle can be assumed to be constant (e.g. Pagès et al., 2009) or follow an ellipsoidal or spherical distribution (Farque et al., 2001; Rakocevic et al., 2000). This is particularly relevant to crops that exhibit regular and coordinated development, such as rice and wheat (Evers et al., 2005; Pagès and Drouet, 2007; Zheng et al., 2008). However, for plants which exhibit highly heterogeneous canopies, the use of standard leaf angle distributions can lead to a 4–15% difference in calculated photosynthesis values compared to 3D models with explicitly described leaf angles (Sarlikioti et al., 2011).

Alternatively, highly accurate methods rely of digitising a pre-existing structure, but using a set of images as a basis. The image-based models are highly desirable as a method of plant phenotyping, with the information needed to calculate a number of plant traits including leaf areas and angles, plant height, etc. (Burgess et al., 2015; Burgess et al., 2017a, b; Deery et al., 2014; Foo et al., 2020; Houle et al., 2010; Santos and Oliviera, 2012; White et al., 2012). However, the complexity of plant architecture means that image-based approaches are often challenging. In particular, similarities between multiple small leaf segments, lack of texture for feature matching and the high amount of self-occlusion lead to difficulties during reconstruction (Pound et al., 2014; Gibbs et al., 2019a, b). The models produced may also be of limited application. For example, the silhouette-based method produces a static model which cannot be used for modelling aspects such as plant or leaf movement and the point cloud data cannot be used for modelling photosynthesis; for this surface detail is required (see Burgess et al., 2017b; Pound et al., 2014).

Once detailed structure is known, resource interception and use can be assessed. For example, it is possible to simulate the light environment experienced by individual leaf elements by modelling the radiative exchanges between plant organs (Chelle and Andrieu, 2007). Such approaches account for the fate of a light ray incident upon a leaf surface; whether it is reflected, absorbed or transmitted, and integrate these local processes over the whole structure. The complexity of the integration will depend upon the accuracy of the structural description of the canopy. The 3D plant model obtained in processes described above can be used so that light interception can be calculated using spatial representation of vegetation components (Borel et al., 1991; Chelle et al., 1998; Goel et al., 1991; ; Zhu et al., 2015). Advantages of this approach include fluxes for individual geometric elements and consideration of their size, position and orientation (Burgess et al., 2015; Burgess et al., 2017a,b; Chelle and Andrieu, 2007; Foo et al., 2020).

Alternatively, coupling physical modelling with dynamic growth models could provide a means to link causative genomics with yield models. In functional structural plant models (FSPMs), complementary and competitive interactions between individuals are assessed to determine overall crop performance and, as such, can be used to simulate interactions in complex canopies or multi-species mixtures (Evers et al., 2019; Godin and Sinoquet, 2005;). Crop growth models have been widely used to evaluate the development, growth and yield of crops by combining future climate conditions with the simulation increased temperature or CO_2 physiological effects, such as using Free Air Concentration Enrichment experiments (FACE) (Ainsworth and Long, 2005). This is of particular importance where simulating all environmental changes simultaneously within field experiments is not feasible due to geographical or diurnal variation and where single-factor responses do not account for interactions between variables (Calfapietra et al., 2010).

5. The future of architecture

5.1. The crop "ideotype"

Altering canopy architecture has become one of the primary breeding strategies for improving yield potential for a number of key crops (Khush, 2005; Khan et al., 2015; Reynolds et al., 2000; Rötter et al., 2015). This has led to the concept of an “idealised plant type” or “ideotype”. Erect leaf morphology is a characteristic that repeatedly arises within the concept of an ideotype, particularly for cereals. This feature is key to improvements of Chinese hybrid rice, whereby high leaf angle through to maturity supported an increase in yield potential (Peng et al., 2008). Similarly, erect leaves in wheat have been associated with yield and biomass in key environments (Richards et al., 2019). Erect leaf stature leads to an increased light penetration to deeper canopy layers; unifying light intensities throughout the canopy by avoiding light saturation in uppermost layers and avoid light limitation at lower layers. Furthermore, erect statures permit an increase in overall leaf area, considered here as LAI. As a result, this will maximise net photosynthesis (Clendon and Millen, 1979; Hodanova, 1979; Normile, 1999; Setter et al., 1995; Turitzin and Drake, 1981). Alternatively, varying leaf angle to have upright leaves at the top of the canopy and more horizontal leaves at the bottom ensures maximal interception of light. This can be envisaged with the see the ‘smart’ canopy concept in sorghum in which the genetic control of leaf angle across layers may now be available (Mantilla-Perez and Salas Fernandez, 2017; Mantilla-Perez et al., 2020).

Within dense canopies, steeper leaf angles can potentially lead to an improvement in whole day carbon gain by enhancing light absorption at low solar angles and through a reduction in the susceptibility to photoinhibition and risk of overheating at high solar angles plus a minimised water use relative to carbon gain (Burgess et al., 2015; Cowan et al., 1982; Murchie et al., 1999; Falster and Westoby, 2003; King, 1997; Werner et al., 2001). As such, the erect ideotype is predicted to be most effective in low latitudes (Peng et al., 2008). Such characteristics are in line with previous work to predict the optimal leaf angle according to latitude and work in *Arabidopsis thaliana* (Burgess et al., 2017a,b; Herbert, 2003; Hopkins et al., 2008). Correlations between architectural traits and latitude have also been seen within tree species, with a linear decrease in petiole length with an increase in latitude and change in leaf arrangement (King and Maindonald, 1999). However, despite this, there is still variation amongst varieties and erect leaf stature is not a widespread trait.

As well as leaf stature, LAI is one of the most important canopy architectural traits determining overall productivity. LAI is highly dynamic during the growing season and determines the competitive interactions between individuals and weeds as well as overall resource capture. The persistence of LAI with time is called the leaf area duration (LAD). As LAI increases, and thus the canopy become denser, more solar radiation will be absorbed or reflected and less will be transmitted to lower canopy layers (Bonan, 2002). Different architectures can have the same LAI due to the arrangement or stacking of the foliage yet intercept light very differently. This is particularly relevant in situations whereby LAI is not distributed equally along the vertical axis. If LAI and LAD are maximised, in theory interception will be optimised (Beadle and Long, 1985). Higher LAI during canopy development benefits light interception whilst reducing competition from weeds (Haefele et al., 2004; Hubbart et al., 2012). However, at maturity, fractional interception (the amount of light intercepted by the canopy) should be as close to 1 as possible, indicating full absorption of light by the canopy, but should be balanced against respiration cost. It is therefore advantageous to achieve maximal fractional interception with as low an LAI as possible, as it will conserve resources. However, depending upon the architectural features, there will be an optimal LAI for each given crop, the value of which will be larger for an erect canopy than for a flatter canopy (Goel and Qin, 1994; Hikosaka, 2003). Similarly to other architectural traits, LAI is affected by genetics, local environmental conditions as well as management, including planting density and inputs (Estrada-Campuzano et al., 2012).

An alternative method to unify light intensities is through alteration in the biochemical composition of leaf material to “match” local light conditions and alignment of pigment concentration distribution. This is the concept of canopy ‘optimisation’ and is established in terms of leaf nitrogen (N) gradients where required photosynthetic capacity and hence leaf N content declines in parallel (Hikosaka, 2005). It has been suggested that maintenance of a high leaf N lower in the canopy could benefit in terms of exploitation of brief light bursts (sunflecks) but this depends on the duration and frequency of sunflecks and the cost of maintenance of a high leaf N (Burgess et al. 2018; Sassenrath-Cole and Pearcy 1994). Indeed, the ability of a leaf to rapidly respond to sunflecks and then remove photoprotective processes rapidly has been suggested as a way to increase crop photosynthesis (Kromdijk et al., 2016; Wang et al., 2020). Furthermore, the rate at which photosynthesis can shift from a low to a high state of activation may be critical (Taylor and Long, 2017). The benefits of sunflecks therefore depends on their properties in space and time. This depends on canopy architecture but research into which architectural properties confers optimal sequences of sunflecks is scarce. Some work suggests that a reduced plant height and combined with more upright leaf stature will increase the frequency and reduce the duration of sunflecks (Burgess et al., 2021).

Recent canopy optimisation studies have suggested leaf chlorophyll concentration should be reduced at the top to aid light penetration whilst efficient light harvesting should be maintained at the bottom (Ort et al., 2015; Walker et al., 2018). This will not affect photosynthetic capacity because at high light levels pigment content per unit leaf area is not limiting. Alternatively, biomechanical properties of plant material can be altered, such that the physical displacement of leaf and stem material will facilitate light penetration to previously shaded leaves. This is consistent with previous work in tree species, whereby leaf fluttering combined with increased photosynthetic induction rates leads to an improved canopy light environment and the corresponding biochemical ability to utilise it (Roden and Pearcy, 1993a,b; Roden, 2003). Modelling approaches have suggested that similar results are also possible within crop species (Burgess et al., 2016, 2018; Gibbs et al., 2019a,b). Changes could be targeted at traits such as sheath or petiole flexibility, stem strength plus altered leaf blade length, and width. It is anticipated that stiffer stems and leaves would lead to lower frequencies and amplitudes of movement in light winds (Burgess et al., 2016, 2018). Changes in canopy biomechanical properties have usually been considered in terms of prevention of lodging damage (Berry et al., 2007), however, its application to improving light dynamics requires further consideration (Burgess et al., 2016, 2021).

Ideotypes have been proposed for a number of crop species. For example, the International Rice Research Institute (IRRI) proposed that upright leaves, low tiller number, a strong culm and large panicles would represent the ideal structure for rice (Dingkuhn et al., 1991; Jiao et al., 2010; Lu et al., 2013; Virk et al., 2004). Within wheat, ideotypes have been suggested with architectural traits reduce the risk of lodging, including a restriction on maximum plant height (Berry et al., 2007; Piñera-Chavez et al., 2016). Ideotypes have also been proposed for other canopy functions. For example, an unfavourable microclimate for disease development can be induced through careful selection of architectural traits. Within bean, stiff upright determinate structures or short indeterminate plant structures consisting of a few main stems and short side branches can limit white mold development through improved air circulation, more rapid leaf drying and improved light interception (Coyne et al., 1974). Within peas, low LAI combined with high internode distance aids to reduce the wetness period and thus limit the effect of Ascochyta blight (Le May et al., 2009).

Modelling approaches have been extensively used in the concept of ideotype design (Gouache et al., 2017; Martre et al., 2015; Rötter et al., 2015; Tao et al., 2017; Van Oijen and Höglind, 2016). Whilst model-assisted ideotype design was traditionally used for low-stress environments, advances in growth modelling and coupling environmental variables enables target traits to be assessed under different scenarios. The ideotype is defined as a set of parameters that define growth and development of a crop and environmental variable can be altered to simulate specific locations or forecasts (Semenov et al., 2014). They can therefore be readily applied to simulation studies to support crop ideotype breeding under altered climatic variables (Rötter et al., 2015). The understanding of canopy optimisation and modelling for light distribution was critical in the development of upright cereal canopies (Mantilla-Perez et al., 2020; Mantilla-Perez and Salas Fernandez, 2017; Peng et al., 2008; Richards et al., 2019). However, the accuracy of process simulations as well as uncertainties over the influence of model parameters may limit the accuracy and applicability of modelling for ideotype design and, in some instance, induces bias when drawing conclusions from a single crop model (Asseng et al., 2013; Rötter et al., 2015; Tao et al., 2017). This is in part limited by the availability of high-quality, long-term empirical datasets for model calibration as well as experimental quantification of model outputs.

5.2. *Where science clashes with preference*

Crop architecture is determined by a combination of genetic, environmental and social factors. Many decisions, including the proposed crop 'ideotype' will shape selection and preference of both commercial breeders and farmers. In some instances, social preference and scientific evidence will conflict, leading to crop choices that are not necessarily considered optimal. In some cases, there may be negative linkages with a given trait (Rasmussen et al., 2015). Alternatively, the proposed 'ideotype' may not perform as well as expected as a result of location, environmental factors, inputs and agronomy (Breseghello and Coelho, 2013; Hammer et al., 2009).

In some instances, obtaining the optimally performing structure requires additional inputs that may not be desirable. For example, erect leaf stature means that a higher LAI and hence higher canopy photosynthesis can be supported, but for maximum efficiency, particularly on a ground area basis, this requires a high input of fertiliser (especially N), which raises cost and reduces sustainability (Burgess et al., 2021). Erect canopies also risk greater weed competition. A combination of canopy architecture types which combines horizontal lower leaves and erect upper leaves has been suggested (Mantilla-Perez et al., 2020). Similarly, a reduction in chlorophyll content especially in the upper regions of the canopy has been shown to increase overall productivity by permitting optimal distribution of light (Walker et al., 2018). This is a particularly interesting suggestion because plant breeders have in the past assumed that deep green leaves equate to higher photosynthesis, something that may have been true until leaf N content reached optimum levels after the introduction of artificial fertilisers. It is possible that continued selection for darker green leaves may have reduced canopy photosynthetic capacity.

6. Conclusion

The architectural forms in which a plant can take are diverse relating to differential coordination between genetics, environmental conditions and management interventions during cultivation and growth. Together the combination of structural traits impact canopy function, determining the spatial and temporal interception of resources, pest and disease dynamics and productivity. Crop architecture is of particular importance in its influence on yield formation which is in turn critical in achieving food security. Historically, architecture has been shaped by many forces and processes, yet still presents a key target for future improvements as we have outlined in this wide-ranging review. This must account for any future changes in climate as well as combatting social preferences that may clash with scientific evidence for productivity. Modelling approaches are likely to be essential in meeting this goal yet we currently lack the detailed datasets, full understanding of the genetic regulation of canopy wide 3D architectural traits and understanding of the growth processes that limit applicability to new ideotype studies.

Declaration of competing interest

The author declares that he/she has no competing interests. Author Erik H. Murchie (Editorial Board member) was not involved in the journal's review or decisions related to this manuscript.

Acknowledgment

This work was supported by the Biotechnology and Biological Sciences Research Council [grant number BB/R004633/1]. AJB is supported by the Leverhulme Trust.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crope.2022.03.009.

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