Opinion Paper

A canopy conundrum: can wind-induced movement help to increase crop productivity by relieving photosynthetic limitations?

Running Title: Wind Movement and Productivity

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Highlight

Wind-induced movement is a ubiquitous property of all crops yet has not been accounted for with reference to photosynthesis. We put forward the opinion that we should manipulate crop biomechanical properties specifically to improve wind-induced light patterning which in turn will enhance dynamic photosynthesis.

Abstract

Wind-induced movement is a ubiquitous occurrence for all plants grown in natural or agricultural settings and in the context of high, damaging wind speeds it has been well studied. However, the impact of lower wind speeds (that do not cause any damage) on mode of movement, light transmission and photosynthetic properties has, surprisingly, not been fully explored. This is likely to be influenced by biomechanical properties and architectural features of the plant and canopy. A limited number of eco-physiological studies have indicated that movement in wind has the potential to alter light distribution within canopies, improving canopy productivity by relieving photosynthetic limitations. Given the current interest in canopy photosynthesis is timely to consider such movement in terms of crop yield progress. This opinion article sets out the background to wind-induced crop movement and argues that plant biomechanical properties may have a role in the optimisation of whole canopy photosynthesis via established physiological processes. We discuss how this could be achieved using canopy models.

Key Words

Canopies, Crops, Movement, Photosynthesis, Productivity, Wind, Yield, Dynamic

Introduction: setting out the problem

It is well known that high wind speeds can cause physical damage to crops and result in substantial losses to yield. 'Fatal' events in high winds such as canopy lodging resulting from stem breakage have received attention and as a result there has been much progress in understanding the underlying mechanisms (Kashiwagi *et al.*, 2008*b*; Berry and Spink, 2012; Piñera-Chavez *et al.*, 2016*a*). However physical movement of a plant canopy resulting from much lower wind speeds (for example up to 6 m s^{-1}) that do not threaten damage to the plant is a common feature of field settings, yet its contribution to global crop yield has been overlooked. Evidence from both natural and agricultural systems has suggested that perturbations at such low wind speeds may be small but still have the potential to significantly influence whole canopy photosynthesis by altering the light available to photosynthetic tissue lower in the canopy (Roden and Pearcy, 1993*a*,*b*; Roden, 2003; Burgess *et al.*, 2016). The range of consequences of wind movement for plant function are also far- reaching, including effects to both the biotic and abiotic environment and the microclimate surrounding plants; all of which translate to differences in productivity. However, despite its ubiquitous nature, there are many fundamental questions remaining and wind-induced movement remains an unknown factor in terms of photosynthetic productivity. Recent increased interest in canopy photosynthesis means that it is timely to consider movement in terms of crop yield progress. In this paper we put the problem in context, drawing in part from existing knowledge from eco-physiological studies and focus on light as a substantial factor with consideration of others. We will not consider high speeds that result in reductions in size, lodging and damage although we do make reference to these factors, in terms of how features with their prevalence may influence overall movement (see (Baker *et al.*, 1998; Cleugh *et al.*, 1998; Berry *et al.*, 2003, 2007; de Langre, 2008). We discuss the ways in which mathematical modelling and computer vision can be applied to this problem (Burgess *et al.*, 2016). We largely refer to a canopy as a crop monoculture such as wheat or rice and analyse ways in which plant biomechanical properties could be altered to enhance productivity in these species.

The lack of understanding on the influence of low wind speeds on crops is partly due to the complexity of techniques required for measurement and analysis. Wind-induced movement is a stochastic process, determined by many different factors, making it difficult to quantify and measure, or to link to light patterning and photosynthetic yield. Whilst movement within a canopy may at first appear simple, in reality movement caused by wind is highly complex and difficult to describe mathematically. It involves interactions between multiple types of plant organs, with varying physical properties, and the specific environmental conditions present. For example: leaves can bend or twist around different axes (partly dependent and constrained by growth angle and water status); leaves are displaced at different rates in relation to each other; the biomechanical properties of individual structures will change throughout growth and development; wind speed and direction are very complex and can change rapidly over short time scales, with large variation in eddy size, frequency and distribution; and solar angle changes throughout the day and year meaning that the light patterns will alter even if wind speed and direction remains the same. Wind properties above the canopy can be very different to those within the canopy and hence different leaves will be subject to very different forces. An overview of some of these different factors determining movement during wind is given in Figure 1.

The diverse effects of wind on plant biology

Wind speeds of a sufficient magnitude can affect plant development, structure and function, resulting in reductions in plant size (dwarfing), changes in stem thickness, leaf size and shape and damage to plant surfaces (Grace, 1977, 1988; Ennos, 1997; Smith and Ennos, 2003; de Langre, 2008; Onoda and Anten, 2011). High winds can also cause stem breakage and lodging (for a more comprehensive review see (Berry *et al.*, 2003, 2007). As well as altering the abiotic interactions of the canopy, wind can also alter biotic interactions including insect activity and population growth plus the development and dispersal of pests and diseases within cropping systems (Aylor, 1990; Moser *et al.*, 2009; Shaw, 2012). The wind profile depends upon the structure of the vegetation or other objects within the air flow; which in turn determines the structure and size of eddies (de Langre, 2008). There are additional effects of wind caused by heat and mass transfer, disturbance of CO_2, O_2 and water vapour gradients (de Langre, 2008), the full effect of which will be dependent upon local environmental conditions (Grace, 1988; Burgess *et al.*, 2016). Wind speeds can alter heat and mass transfer which impact upon transpiration and leaf temperature, in turn affecting photosynthesis via stomatal conductance. This process should not be underestimated but in general there is thought to be minimal impact on leaf and canopy photosynthesis by the low to moderate wind speeds observed under optimal growing conditions via this mechanism (Grace, 1988). The effect of wind speeds on boundary layer conductance can be complex but generally a reduction in the mean thickness of the boundary layer occurs with an increase in air flow (Downs and Krizek, 1997). Consequently, the reduction in the vapour pressure gradient between leaf material and the air can lead to a reduced stomatal conductance, transpiration rate and thus higher water use efficiency. Higher temperatures may exacerbate this effect. We also recognise that canopy microclimate is affected by wind movement, for example intra-canopy humidity levels and CO_2 gradients caused by photosynthetic draw-down can be affected by wind and air movement (Buchmann and Ehleringer, 1998). Previous studies have shown the beneficial impact of wind-induced movement in agroforestry systems, whereby reduced wind movement brought about by tree presence can lead to an increased humidity within the crop canopy as less water vapour is removed (Wu and Dalmacio, 1991; Nuberg and Bennell, 2009).

Diversity within plant canopy movement

In reality, it is convenient to divide plant movement into two types: first, that predominantly affecting the structural support (i.e. stem, branch, root system); and second, that affecting the leaves. This is due to the different properties, position and connectivity of each. The contribution of each to overall movement will depend on the local conditions. At low wind speeds, leaf movement is expected to dominate due to their low mass and high surface area whereas at higher wind speeds, stem or branch movement will become more dominant and leaf movement may decrease, with leaves becoming more ‘streamlined’ (e.g. (Speck, 2003). The biomechanical properties of the structures will also determine movement. The response of a branch or an isolated leaf to wind depends upon its length, surface area, tensile strength and mass. For stem structures, low strength and a large mass can lead to breakage, whereas for leaves, mass and surface area will influence movement, particularly fluttering (or equivalent)-type movement. In tree species, the tensile strength of the petiole will determine how far a leaf may bend or whether the leaf may break off at the junction between the petiole and the branch (Derzaph and Hamilton, 2013). The range of motion or risk of breakage will also depend upon the strength of the leaf blade; which is in turn related to the strength of the vein and thus the water status of the leaf (Derzaph and Hamilton, 2013; Gonzalez-Rodrigues *et al.*, 2016).

Whilst analysis of movement in trees has been undertaken (e.g. (Roden and Pearcy, 1993*a*,*b*; Rudnicki *et al.*, 2001; Roden, 2003; Sellier *et al.*, 2006; Moore and Maguire, 2008; Rodriguez *et al.*, 2008; Der Loughian *et al.*, 2014; Tadrist *et al.*, 2014; Gonzalez-Rodrigues *et al.*, 2016), crop canopies arguably present an equally, or even more challenging scenario due to the position of individual plants within a dense community, and thus the interaction of plants with their neighbours (Doaré *et al.*, 2004). For example, individual plants in dense stands demonstrate some mutual support by physical contact, restricting individual stem movement. Furthermore, plant motion and the associated light environment is dependent upon canopy architectural features which are difficult to accurately represent and model in 3-dimensions (3D), especially when confounded by other environmental variables. Difficulties in computer vision with respect to 3D modelling via computer vision arise from challenges posed by occlusion, parallax (the differing appearance of an object from two distinct views), calibration and the processing of large datasets. It is tempting to consider active approaches, in which light is projected from a laser into the scene (Gibbs *et al.*, 2017). The often highly reflective surfaces of leaves, however, make this problematic, as projected light is often reflected away from the imaging device. Biologically relevant data relating realistic canopy architecture, light dynamics and short-scale photosynthetic responses in the canopy setting are scarce.

Strategies for measuring canopy movement and its physiological effects

Movement of leaf material and corresponding changes in light levels can occur over rapid timescales (sub-second) and plant 3D spatial structures are so complex that the capacity to accurately and comprehensively sense and log motion and light levels will be limited. Attention must be given to the fact that the physical presence of any sensors (such as light sensors) may influence the canopy properties. Hence the correct positioning and size of sensors will be critical and practical constraints are unavoidably imposed by the need to provide sufficient spatial resolution (high numbers of sensors) with accurately recorded positions in 3D space in order to track each leaf light history accurately. Within an experimental field plot, it is impossible to record all features of a moving canopy at all positions within that canopy with very high spatial resolution e.g. physical leaf and stem movement, leaf microenvironment, leaf light absorption. Occlusion is a particular problem for the imaging methodology. Measurements of photosynthesis during canopy movements e.g. with gas exchange or fluorescence is possible but suffers from the same self-evident limitations.

Given this, the ‘conundrum’ from the paper title should be solvable by a combination of sufficient plant and canopy measurements combined with accurate mechanical models of canopy movement, in part informed by imaging and tracking of real canopies linked with well parameterised models of photosynthesis. Validation of theories will be difficult to achieve without a means of quantifying movement in the field so that it may be meaningfully linked to yield, biomass and radiation use efficiency measurements. Whole canopy chambers such as those described in (Song *et al.*, 2016) are promising for assessing the impact of different plant properties on canopy productivity but it remains to be seen if realistic movement is achievable in a combined space. It seems possible that larger scale field-based techniques such as eddy flux, combined with computer vision techniques for tracking movement could be recruited to analyse the impact of movement on canopy photosynthesis, albeit over longer time scales (Groenendijk *et al.*, 2011).

Wind and the canopy light environment

Canopy productivity depends upon the integrated performance of photosynthetic elements, their local light environment combined with their biochemical and physiological properties (Horton, 2000; Sinoquet *et al.*, 2001; Valladares and Niinemets, 2007; Zhu *et al.*, 2010; Matloobi, 2012). Architectural features such as leaf area index and density, clumping, leaf angle and leaf dimensions determine the patterning of light within a canopy (Hirose, 2005; Song *et al.*, 2013; Burgess *et al.*, 2015, 2017*a*). In terms of whole canopy photosynthesis, the most efficient architecture is one in which all the leaves are evenly illuminated at quantum flux densities which either approach or saturate photosynthesis (Valladares and Niinemets, 2007). This is often achieved using a combination of a high leaf area index and erect leaf stature, so as to avoid light saturation at the top of the canopy but allow efficient penetration to lower canopy layers (Hirose, 2005; Zhu *et al.*, 2010; Song *et al.*, 2013; Burgess *et al.*, 2015). Such canopy principles have been applied to static canopies (e.g. (Song *et al.*, 2013; Burgess *et al.*, 2015, 2017*b*,*a*; Townsend *et al.*, 2017), but movement has not been fully or realistically addressed in this context (Burgess *et al.*, 2016). In cereal crops, movement is a highly complex behaviour determined by a multitude of factors including stem and leaf mechanical properties, height, ear size, leaf properties (e.g. stiffness, weight, shape and angle), tiller number, dry matter partitioning and planting density (Figure 1).

A small number of studies have shown that wind-induced movement is highly effective in altering the light environment within the canopy both in terms of overall amount of light but also the temporal pattern of light penetration. This principle can be visualised in Figure 2, which indicates the fate of different light rays on an idealised crop plant. (Burgess *et al.*, 2016) used 3D reconstructions of rice canopies in different configurations to reflect movement in wind. When used in combination with a ray tracing algorithm Song *et al* (2013) found that such simulated movement can increase light distribution and modelled canopy photosynthesis up to 17% above a static canopy. This is due to the movement providing more opportunities for photon penetration as the canopy shifts between different configurations. In a constantly moving canopy, it is more likely that any given leaf surface will receive an appropriate period of high light and thus be more likely to be able to maintain a higher photosynthetic induction state. This is analogous (though arguably more complex) than previous work on natural systems. A high frequency of movement of leaves in light winds, known as flutter or twisting, can result in greater penetration of light to lower layers. This can be seen in tree species such as Aspen (Roden and Pearcy, 1993*a*,*b*; Roden, 2003; de Langre, 2008). The effect of isolated leaf movement can be visualised in Figure 3, where rapid movement of a 'distributor' leaf will alter the probability that a direct ray of light will reach a 'recipient' leaf. Within tree and broadleaf species, this is predominantly caused by rotation about the petiole (Derzaph and Hamilton, 2013) and has the effect of producing very short, rapid bursts of light (sun flecks) on the sub- second scale. Visually similar movements can also be seen within cereal canopies, and we propose that this type of behaviour can be used to optimise canopy productivity. Here we will refer to them simply as isolated leaf movements rather than flutter, which is a specific term that may not refer to the type of movement capable by cereals.

The effect of movement on plant integrated biochemical capacity

The integrated photosynthetic yields available to a plant are determined by the duration and frequency of light events across all of the photosynthetic surfaces, therefore any changes to these light dynamics can impact on productivity as previously described (Retkute *et al.*, 2015; Burgess *et al.*, 2016; Townsend *et al.*, 2017). As such, manipulating plant movement to facilitate light distribution within a canopy, or manipulating the metabolic features of plants enabling them to optimally respond to a change in light, should provide key targets for future crop improvement (see below). Work by Caldwell (1970) first predicted that changes in leaf angle brought about by wind could influence whole plant photosynthesis. Photosynthesis is a multi-component process that does not perfectly track fluctuating light and frequently presents 'lag' according to the kinetics of component processes which can limit integrated carbon gain and canopy biomass (Walters and Horton, 1994; Athanasiou *et al.*, 2010; Retkute *et al.*, 2015; Kromdijk *et al.*, 2016; Taylor and Long, 2017). The 'induction state' of photosynthesis can be thought of as the maintenance of enzyme activity, thylakoid energisation, metabolite pool sizes and stomatal aperture in a state that can support high photosynthesis. Attaining this state takes time and the leaf will revert to a lower state of induction once transferred to darkness or lower light. For example, Rubisco activation exerts strong limitation during photosynthetic induction (Pearcy, 1990) due to its slow rates of recovery from low light events (Salvucci and Anderson, 1987). Recent work has shown that the dynamics of stomatal aperture changes in response to environmental stimuli should imposes a substantial limitation on carbon gain in fluctuating light via the lag during low to high light transitions. Notably there should also be a decline in water- use efficiencies during high to low transitions as stomata remain open and transpiring whilst photosynthesis declines due to light limitation (Lawson and Blatt, 2014; McAusland *et al.*, 2016; Matthews *et al.*, 2018). The acclimation status of leaves within a canopy also determines their ability to utilise sun flecks effectively (Athanasiou *et al.*, 2010; Retkute *et al.*, 2015; Townsend *et al.*, 2017). The amplitude and frequency of switching between high and low light will determine the "drag" effect of photosynthetic induction: a higher frequency can lead to a higher integrated photosynthetic rate (Retkute *et al.*, 2015) and can be related directly to intrinsic processes such as Rubisco activation state (Roden and Pearcy, 1993*a*,*b*; Roden, 2003). This is especially important in dense canopies where it can be predicted that unless sun flecks are frequent or of sufficient duration, the induction time is too low to adequately exploit any periods of high light (Retkute *et al.*, 2015; Townsend *et al.*, 2017). Optimal productivity would require tracking changes in environmental conditions in real time and matching the biochemical capacity and physiological state to such conditions that a leaf section directly experiences (Retkute *et al.*, 2015; Kromdijk *et al.*, 2016; Ruban, 2017). As outlined below, we propose that modes of movement already seen in nature, such as aspen leaf flutter, could be transferred to crop species to provide a means of maintaining lower leaves in a higher state of induction and thus increase the integrated photosynthetic rate.

Modelling wind-induced movement

Canopy models are essential for understanding how spatio-temporal shifts in light and other environmental variables influence photosynthesis, growth and yield. One of the limitations has been the ability to accurately describe 'real' canopies in the field and to model light fluxes within them, but this is being overcome (Song *et al.*, 2013; Burgess *et al.*, 2015, 2017*a*,*b*; Townsend *et al.*, 2017). Dynamic photosynthesis is the focus of more and more studies and models even though the computational power required for its assessment is quite large. Despite this, the number of dynamic empirical and mechanistic models of photosynthesis capable of handling light fluctuations and making future predictions is increasing and it is then a case of applying these models to the light fluxes that are induced by canopy movement (Porcar-Castell and Palmroth, 2012; Retkute *et al.*, 2015; Harbinson and Yin, 2017; Townsend *et al.*, 2017; Morales *et al.*, 2018). Models of individual processes are also becoming more sophisticated e.g. for photoprotection (Zaks *et al.*, 2012). The accuracy of this may depend on sufficient model parameterisation. A recent striking example demonstrated how an earlier prediction from dynamic canopy light fluctuations (Zhu *et al.*, 2004) led to an experimental validation and improvement of crop biomass and yield through manipulation of a photosynthetic process (recovery from photoprotection) (Kromdijk *et al.*, 2016).

Whilst the mathematical infrastructure is becoming increasingly available to cope with the types of rapid dynamic shifts observed in natural and agricultural canopies described here, the limitation of accurately assessing the effects of wind movement on crop canopies seems to be in the difficulty of generating dynamic mechanical models of crop canopies and the 3D and '4D' (i.e. 3D over time and space) descriptions that are required model light dynamics. Firstly, it is important to achieve a plant description that can accurately mimic a wide range of movements. These movements can be captured, or predicted, via different methods and can be broadly split into computer vision-based approaches or biomechanical based approaches, each of which is discussed below.

Computer vision approaches to modelling movement

Two broad approaches can be used to gather a description of plant geometry. These are rule-based approaches, which apply a series of generative rules based on manual measurements of plants and image-based approaches, which use actual visual descriptions of a target plant in the form of 2D images (Remondino and El-hakim, 2006). The latter rely upon computer vision techniques and tools to extract the required information from the available image data. Image-based methods are further categorised as either active, in which some form of controlled radiation is projected onto the plant, or passive, in which only natural illumination is used. Both methods have been applied to controlled and field-based environments. Active methods are significantly more expensive and require specialist hardware. Passive techniques are typically portable and low cost, recording data using radiation already present in the scene. Light Detection and Ranging (LiDAR), also known as Laser Scanning, can be classified as active whereas Space Carving, Shape-from-Silhouette, Shape-from-Shading, Shape-from-Contour, Stereo vision and Structure from Motion are passive approaches, commonly using standard hand-held cameras to acquire data (Kender, 1981; Horn and Brooks, 1989; Cryer and Shah, 1999; Seitz, 2000; Wahl, 2001; Tan *et al.*, 2007; Pound *et al.*, 2014; Gibbs *et al.*, 2017, 2018).

Data obtained using computer vision methods, such as 2D images and 3D point clouds, can aid the detection of motion by matching features between views and tracking their position over time (Yang *et al.*, 2011). For 2D movement, features of interest (for example leaf or ear tips) can be detected for each frame within a video and matched, producing a 2D movement path for each. One such example of this is the movement of a single organ, for example a leaf. A video can be made of a moving leaf which is segmented from the background. Frames can be split and the difference between each frame (i.e. the position of the leaf in frame i subtracted from the leaf in $i+1$) will reveal the difference (i.e. the movement) in the leaf over time, in this case over two frames. Applying this principle across all frames within a video can allow a spline to be fitted and thus the path of the leaf can be described. This principle can be applied to any plant organ and even scaled up to a canopy in a field setting given the accurate detection of a given feature.

Whilst the 2D tracking approaches described above could be used to gather a general description of movement, more accurate modelling will rely on the determination of plant geometry and motion in 3D. This can be achieved using image-based approaches by positioning, for example, multiple cameras around a target plant, or canopy. The same principle can be applied as above, but multiple frames are captured at the same point in time from different viewpoints, which can then be matched across each of the frames. By matching features in 2D across multiple frames, the 3D position of each feature can be estimated. Continuing to do this over time enables a 4D model of features to be produced which represent the motion of the full organ, plant or canopy. Such descriptions could be combined with light modelling approaches (e.g. ray tracing (Song *et al.*, 2013)) in order to assess alterations in light dynamics brought about through movement. Further applications are also possible such as the comparison of different modes of movement; modelling disease or pest spread or; predicting the effects of climate change. For more details see Burgess *et al.*(2016) and references within.

Biomechanical approaches to modelling movement

In order to accurately model movement of a crop stand, biomechanical properties of individual organs, the whole plant, and, ultimately, the whole canopy must be known (de Langre, 2008).

A number of models exist that simulate movement, ranging in complexity from simple, to more complex descriptions (e.g. Berry et al., 2003; Doaré et al., 2004; Tadrist et al., 2014; Gonzalez-Rodrigues et al., 2016; Tadrist et al., 2018). Models are often created based on vibration analysis of a single plant (de Langre, 2008; Der Loughian *et al.*, 2014). This allows the measurement of displacement, local deformation or rotation in order to determine modal frequencies and can be captured via a number of different methods, as described in de Langre (2008). Such techniques are suitable for large plants, and have commonly be applied to study movement in trees (e.g. (Sellier *et al.*, 2006; Moore and Maguire, 2008; Rodriguez *et al.*, 2008; Der Loughian *et al.*, 2014; Tadrist *et al.*, 2014; Gonzalez-Rodrigues *et al.*, 2016). We argue here that crop plants actually provide a more complex modelling scenario as the presence of plants within a community (i.e. the canopy) means that the characteristics of movement and interactions between individuals are homogenised, and reliant on the specific structure of the community as a whole. Whilst some models have been generated to cover specific aspects of movement in crops (e.g. Berry *et al.* 2003), the lighter weights of organs and softer tissues combined with contact and collisions with neighbouring vegetation mean that the methods applied to tree species are often not appropriate. Furthermore, trees often contain several orders of regular branching; a much contrasting architectural system to that present in crop species.

Obtaining a geometrical description of a plant or organ is the first step towards characterising movement and can be achieved using the computer vision- based approaches described above, although manual measurements are also required. Mechanical properties will differ depending upon the plant of study; for example, the structure of broadleaf species is highly contrasting to that of cereals. Other considerations are the mass, stiffness and damping of individual organs; all of which will vary depending upon the specific architectural properties and local conditions (de Langre, 2008). Firstly, the distortion of a leaf must be characterised. Leaves are often represented as a tapered inextensible elastic rod that is stiffer and anchored at the base. Similar representations of a fixed structure can also be applied to branches or petioles (Niklas, 1991; Vogel, 1992). The rod is subject to gravity, intrinsic curvature and drag forces in the presence of wind; the full effect of which will depend upon turbulence (Finnigan, 2000). For crops such as wheat, the leaf will be attached to a stem structure, which will have its own distinct mode of movement. Stems have often been modelled as a mono- or bi-dimensional oscillating rods, with complexity of models ranging from isolated stem movements (Farquhar *et al.*, 2000; Niklas and Speck, 2001), a set of discrete stem movements (Farquhar *et al.*, 2003), or a community of moving stems which include collisions (i.e. plant-to-plant contacts) between neighbours (Doaré *et al.*, 2004).

The influence of breeding on crop canopy movement

Selection for modern crop varieties has occurred over centuries within the field setting, thus wind is likely to have already had an influence on selection pressure. The switch in plant height from tall to small varieties in the mid 20th century (part of the ‘Green Revolution’) was brought about through the introduction of dwarfing genes (Monna *et al.*, 2002; Hedden, 2003; Pearce *et al.*, 2011). Reduced stature enabled an increase in harvest index, improved responsiveness to nitrogenous fertilisers and a reduced risk of lodging. This latter trait is a result of a reduction of the centre of gravity of the plant body, thus increasing the natural frequency of the stem movement, plus exposure to smaller drag forces (Onoda and Anten, 2011; Piñera-Chavez *et al.*, 2016; Hirano *et al.*, 2017). Selection has also been targeted at traits that permit a higher planting density, including changes in stature, leaf and tiller number (Duvick, 2005*a*,*b*). This latter feature is important because the increased proximity of neighbouring plants provides additional support to individual plant structures through elastic collisions between material (Doaré *et al.*, 2004). Whilst these alterations were not selected in order to improve movement, *per se*, they will inadvertently have altered the primary mode of movement present. In fact, it is feasible that these alterations will have selected against the optimal movement for canopy productivity. For example, it can be predicted that a flexible and elastic supporting structure will permit the greatest penetration of light to lower canopy layers and extend the period of time that lower leaves will be exposed to higher light intensities, thus increasing the ability for lower leaves to acclimate and maintain high induction rates (Athanasiou *et al.*, 2010; Retkute *et al.*, 2015; Townsend *et al.*, 2017). However, a reduction in plant height combined with an increase in the strength of structural support may have the opposite effect, leading to reduced elasticity and more rapid movements of the stem. Therefore, selection for improved movement will also probably require consideration of such conflicting considerations.

Can we improve photosynthesis and yield?

As we move further into the 21st century, photosynthesis is increasingly considered as a key limitation to achieving theoretical crop yield maxima (Long *et al.*, 2006, 2015; Murchie *et al.*, 2009; Zhu *et al.*, 2010). It has long been argued that photosynthesis per unit leaf area has not undergone genetic improvement during breeding and the improvements in photosynthesis per unit ground area over time were a result of improvements to other physiological and morphological traits such as nutrition and leaf area index. Recent research suggests that different aspects of leaf photosynthesis remain a viable target for improvement if genetic diversity is sufficient. This includes traits that are important in order to fully exploit the proposed improvements to biomechanical properties i.e. maintenance of photosynthesis induction state and optimisation of photoprotection in rapid light fluctuations. It seems then that multiple traits must be targeted in order to realise the optimal ideotype for a given environment (i.e. Figure 4: Reynolds *et al.*, 2000; Murchie *et al.*, 2009).

The integration of photosynthetic properties of individual leaves into a 3D canopy is thought to be suboptimal for a number of reasons that are related to the efficiency with which radiation is distributed vertically. The number of approaches to improve this is expanding rapidly, with optimality dependent upon changes in multiple interacting traits. Vertical leaf orientations improve penetration while optimising photosynthetic saturation (Long *et al.*, 2006); reduced chlorophyll content e.g. via reducing antenna size aids penetration while not affecting saturation levels (Slattery *et al.*, 2017; Song *et al.*, 2017; Walker *et al.*, 2018); dynamic responses of photosynthesis and photoprotection to light reduces the time lag in response to change (Kromdijk *et al.*, 2016); and optimising nitrogen distribution matches photosynthetic capacity to the available light levels (Hikosaka, 2016; Hikosaka *et al.*, 2016; Muryono *et al.*, 2017; Townsend *et al.*, 2017). Here we propose the addition of canopy movement properties to this list, which may provide a simple way to extend and modify the light distribution in a canopy by using existing biomechanical variation in major crops that has not previously been considered in this context (e.g. (Wang and Li, 2006; Berry *et al.*, 2007; Burgess *et al.*, 2016; Piñera-Chavez *et al.*, 2016*b*). Maximum canopy productivity could be achieved by altering plant mechanical properties to favour beneficial responsiveness in low wind, which is likely to be commonplace even if not continuous. Biomechanical properties that allow small but rapid movement could include altered stem and leaf strength, sheath or petiole flexibility, leaf blade width and length. The ideal plant type for a cereal crop could be viewed as having rapidly moving leaves at the top of the canopy, perhaps similar to the flutter type, and reduced movement lower in the canopy. It can be predicted that increased stem and leaf stiffness is likely to increase the frequency of motion, which in turn will shorten the duration of light periods (i.e. sun flecks). The type of movement beneficial to a plant will depend upon multiple factors including the crop chosen and its physiology; the range of movement available dependent upon existing architectural constraints; and other negative impacts to yield (see above). Substantial variation for morphological and biomechanical properties exists in crop plants for traits including stem strength, leaf size and leaf angle (Falster and Westoby, 2003; Wang and Li, 2006; Kashiwagi *et al.*, 2008*a*). The impact of such movement may be affected by the way that the leaf boundary layer and stomatal conductance are affected.

Furthermore, optimal movement will require balance between different traits and their perceived conflicts. For example, resistance against failure (such as lodging), requires a trade-off between stem properties. Increasing the strength of the stem cross section may reduce the risk of stem buckling or splitting but increase the risk of anchorage failure (Farquhar and Meyer-Phillips, 2001). A second example is leaf size and thickness: an increase in both parameters has been considered beneficial in the improvement of rice photosynthesis, especially at high leaf angles (Horton, 2000; Wang *et al.*, 2012). However, this trend could reduce frequency and responsiveness to light winds unless successfully compensated for by alternative traits such as increased leaf number or an altered mechanical property that permits greater rotation around the ligule region. It may be easier to replicate flutter-like movement in smaller leaves at the top of the canopy and thus shift larger leaves to mid and lower regions where less movement is required. The uppermost leaves then have a dual role as effective distributors of light in addition to photosynthesising at high rates (Figure 3). Such compensation seems feasible because optimal light distribution is predicted to be a major limitation to crop yield (see above). A flexible and elastic supporting structure may permit the greatest penetration of light to lower canopy layers and extend the period of time that lower leaves will be exposed to higher light intensities, thus increasing the ability of lower leaves to acclimate and maintain high induction rates (Athanasiou *et al.*, 2010; Retkute *et al.*, 2015; Townsend *et al.*, 2017). However, a reduction in plant height combined with an increase in the strength of structural support, which are desirable properties to prevent yield loss through lodging, will have the opposite effect, leading to reduced elasticity and more rapid movements of the stem.

Geographic location and growing season are other important considerations when selecting the optimal plant ideotype, with climatic conditions, including wind speed and direction, plus light conditions being dependent upon latitude, altitude and the topography/exposure of the growing site. This means that an optimised structure will not be suitable for all environments, and thus an understanding of the local conditions combined with how they will influence canopy movement will be required. For example, in environments with high wind speeds, and thus at increased risk of lodging, improvements to cereals or other lodging- susceptible plants can be achieved by biomechanical changes to the upper part of the canopy alone.

It can be predicted that the optimal response to movement will be linked to the photosynthetic capacity and kinetic properties of a plant. For example, we anticipate that faster movement in the upper layers of the canopy will lead to an overall higher state of photosynthetic induction. (Roden and Pearcy, 1993*a*,*b*; Roden, 2003). This characteristic of frequent but high amplitude shifts may alter photoprotective requirements and demand even higher capacity and more rapid relaxation kinetics of non-photochemical quenching which has recently been shown to be achievable (Kromdijk *et al.*, 2016; Hubbart *et al.*, 2018). Such traits could also provide initial lines from which to improve; with altered movement targeted at lines that will be most able to utilise and exploit the new light environment. Genetic variation in photosynthetic induction rates is likely to be present to provide this platform.

This also raises the intriguing question as to whether the evolution of mechanical properties might have coincided with the evolution of dynamic photosynthetic efficiency. A dense canopy with steep light extinction and severe light limitation at the base will require a certain amount of movement to act as an efficient distributor of light and maintain photosynthetic induction states. Hence optimal responsiveness of photosynthesis to the type of fluctuating light dynamics caused by movement may have co-evolved and become mutually dependent. The high leaf area index in post-green revolution types compared pre-green revolution may provide an agricultural analogy. As long as the constraints of any given environment are fully characterised and considered, manipulation of biomechanical properties of plants, combined with improved biochemical responses to changes in light levels, can be used as a means to improve whole canopy productivity and thus provide a route for future crop improvement.

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Figure Legends

Figure 1: Schematic representation of movement in a theoretical plant and properties determining the mode of movement.

Figure 2: The fate of light rays in a simplified plant canopy subject to wind- induced perturbation. Three configurations are shown and colours represent alternate penetration patterns according to these configurations: blue rays penetrate lower in the canopy, red rays do not reach as far and black rays reach the same position, relative to the static configuration. In this example, movement presents incident photons with more opportunities to pass through the canopy making it more likely that any given leaf surface area will receive a period of high light.

Figure 3: The fate of light ray distribution between a distributor and recipient leaf as a result of movement in a broadleaf versus a cereal canopy. Different configurations are shown for each canopy type and colours represent alternate penetration patterns according to these configurations: blue rays penetrate lower in the canopy, red rays do not reach as far and black rays reach the same position, relative to the static configuration. In this example, movement presents incident photons with more opportunities to move past the distributor leaf making it more likely that a recipient leaf will receive a period of high light.

Figure 4: Summary of possible traits that could be targeted to improve light absorption and conversion in canopies.

Figure 1

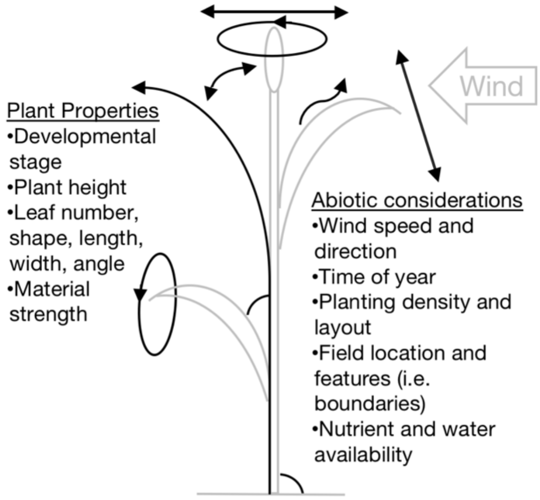

Figure 1: Schematic representation of movement in a theoretical plant and properties determining the mode of movement.

Figure 2

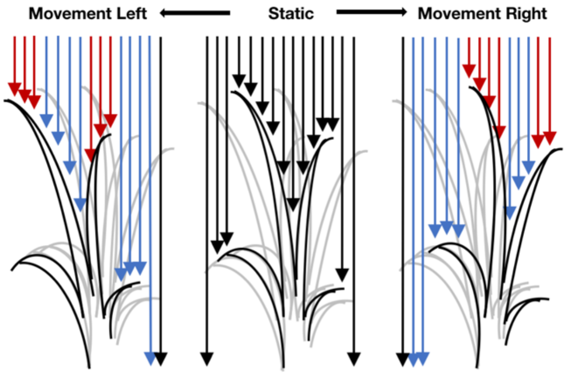

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Figure 3

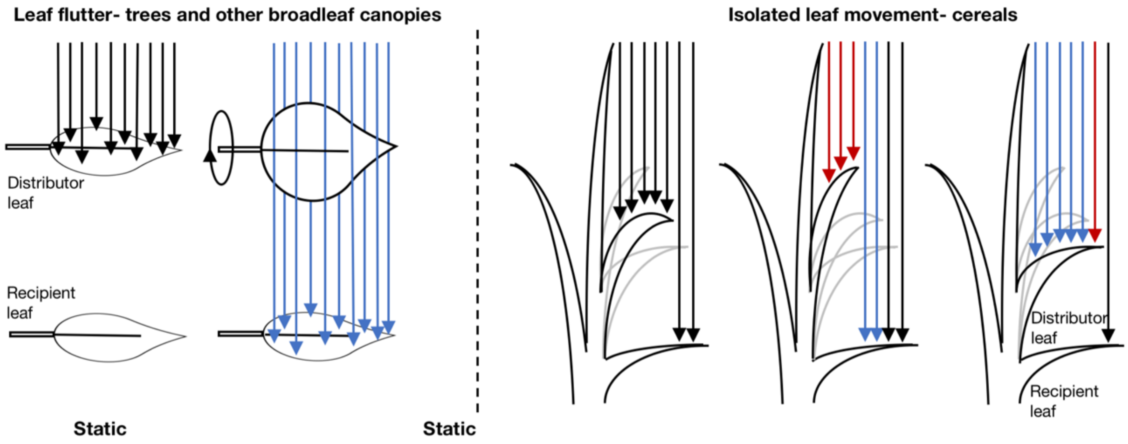

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Figure 4

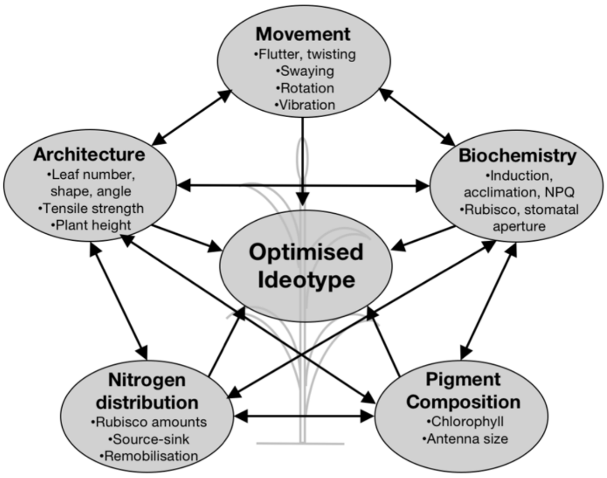

Figure 4: Summary of possible traits that could be targeted to improve light absorption and conversion in canopies.

References

Athanasiou K, Dyson B, Webster R, Johnson G. 2010. Dynamic Acclimation of Photosynthesis Increases Plant Fitness in Changing Environments. Plant Physiology **152**, 366–373.

Aylor D. 1990. The role of intermittent wind in the dispersal of fungal pathogens. Annual Review of Phytopathology **23**, 73–92.

Baker C, Berry P, Spink J, Sylvester-Bradley R, Griffin J, Scott R, Clare R. 1998. A method for the assessment of the risk of wheat lodging. Journal of Theoretical Biology **194**, 587–603.

Berry PM, Spink J. 2012. Predicting yield losses caused by lodging in wheat. Field Crops Research **137**, 19–26.

Berry P, Spink J, Foulkes M, Wade A. 2003. Quantifying the contributions and losses of dry matter from non-surviving shoots in four cultivars of winter wheat. Field Crops Research **80**, 111–121.

Berry P, Sylvester-Bradley R, Berry S. 2007. Ideotype design for lodging-resistant wheat. Euphytica **154**, 165–179.

Buchmann N, Ehleringer JR. 1998. *AGRICULTURAL AND FOREST METEOROLOGY CO 2 concentration profiles, and carbon and oxygen isotopes in C 3 and C 4 crop canopies*.

Burgess A, Retkute R, Herman T, Murchie E. 2017*a*. Exploring relationships between canopy architecture, light distribution, and photosynthesis in contrasting rice genotypes using 3D canopy reconstruction. Frontiers in Plant Science **8**, 734.

Burgess A, Retkute R, Pound M, Mayes S, Murchie E. 2017*b*. Image-based 3D canopy reconstruction to determine potential productivity in complex multi-species crop systems. Annals of botany **119**, 517–532.

Burgess A, Retkute R, Pound M, Preston S, Pridmore T, Foulkes M, Jensen O, Murchie E. 2015. High-resolution 3D structural data quantifies the impact of photoinhibition on long term carbon gain in wheat canopies in the field. Plant Physiology, pp.15.00722v1-00722.2015.

Burgess A, Retkute R, Preston S, Jensen O, Pound M, Pridmore T, Murchie E. 2016. The 4-Dimensional Plant: Effects of Wind-Induced Canopy Movement on Light Fluctuations and Photosynthesis. Frontiers in Plant Science **7**.

Caldwell M. 1970. Plant gas exchange at high wind speeds. Plant physiology.

Cleugh H, Miller J, Böhm M. 1998. Direct mechanical effects of wind on crops. Agroforestry Systems **41**, 85–112.

Cryer JE, Shah M. 1999. Shape-from-shading: a survey. IEEE Transactions on Pattern Analysis and Machine Intelligence **21**, 690–706.

Derzaph T, Hamilton H. 2013. Effects of wind on virtual plants in animation. International Journal of Computer Games Technology **2013**, 674848.

Doaré O, Moulia B, de Langre E. 2004. Effect of Plant Interaction on Wind-Induced Crop Motion. Journal of Biomechanical Engineering **126**, 146.

Downs R, Krizek D. 1997. Air movement. In: Langhans R,, In: Tibbitts T, eds. Plant Growth Chamber Handbook. Iowa: Ames, 87–104.

Ennos A. 1997. Wind as an ecological factor. Trends in Ecology and Evolution **12**, 108–111.

Falster D, Westoby M. 2003. Leaf size and angle vary widely across species: What consequences for light interception? New Phytologist **158**, 509–525.

Farquhar T, Meyer-Phillips H. 2001. Relative safety factors against global buckling, anchorage rotation, and tissue rupture in wheat. Journal of Theoretical Biology **211**, 55–65.

Farquhar T, Wood J, Van Beem J. 2000. The kinematics of wheat struck by a wind gust. Journal of Applied Mechanics, Transactions ASME **67**, 496–502.

Farquhar T, Zhou J, Haslach H. 2003. A possible mechanism for sensing crop canopy ventilation. In: Barth F,, In: Humphrey J,, In: Secomb T, eds. Sensors and sensing in biology and engineering. Wien/ New York: Springer Press, .

Finnigan J. 2000. Turbulence in Plant Canopies. Annual Review of Fluid Mechanics **32**, 519–571.

Gibbs J, Pound M, French A, Wells D, Murchie E, Pridmore T. 2017. Approaches to three-dimensional reconstruction of plant shoot topology and geometry. Functional Plant Biology **44**, 62–75.

Gibbs J, Pound M, French A, Wells D, Murchie E, Pridmore T. 2018. Plant Phenotyping: An Active Vision Cell for Three-Dimensional Plant Shoot Reconstruction. Plant Physiology, pp-00664.

Gonzalez-Rodrigues D, Cournède P-H, de Langre E. 2016. Turgidity-dependent petiole flexibility enables efficient water use by a tree subjected to water stress. Journal of Theoretical

Biology **398**, 20–31.

Grace J. 1977. *Plant responses to wind*. New York: Academic Press Limited.

Grace J. 1988. Plant response to wind. Agriculture, Ecosystems and Environment **22–23**, 71–88.

Groenendijk M, Dolman A, van der Molen M, Al E. 2011. Assessing parameter variability in a photosynthesis model within and between plant functional types using global Fluxnet eddy covariance data. Agricultural and Forest Meteorology **151**, 22–38.

Harbinson J, Yin X. 2017. A model for the irradiance responses of photosynthesis. Physiologia Plantarum **161**, 109–123.

Hikosaka K. 2016. Optimality of nitrogen distribution among leaves in plant canopies. Journal of Plant Research **129**, 299–311.

Hikosaka K, Anten N, Borjigidai A, *et al.* 2016. A meta-analysis of leaf nitrogen distribution within plant canopies. Annals of Botany **118**, 239–247.

Hirose T. 2005. Development of the Monsi-Saeki theory on canopy structure and function. Annals of botany **95**, 483–494.

Horn B, Brooks M. 1989. *Shape from shading*. MIT Press.

Horton P. 2000. Prospects for crop improvement through the genetic manipulation of photosynthesis: morphological and biochemical aspects of light capture. Journal of experimental botany **51 Spec No**, 475–485.

Hubbart S, Smillie I, Heatley M, Swarup R, Foo C, Zhao L, Murchie E. 2018. Enhanced thylakoid photoprotection can increase yield and canopy radiation use efficiency in rice. Communications Biology **1**, 22.

Kashiwagi T, Togawa E, Hirotsu N, Ishimaru K. 2008*a*. Improvement of lodging resistance with QTLs for stem diameter in rice (Oryza sativa L.). Theoretical and Applied Genetics **117**, 749–757.

Kashiwagi T, Togawa E, Hirotsu N, Ishimaru K. 2008*b*. Improvement of lodging resistance with QTLs for stem diameter in rice (Oryza sativa L.). Theoretical and Applied Genetics **117**, 749–757.

Kender JR. 1981. Shape from texture.

Kromdijk J, Głowacka K, Leonelli L, Gabilly S, Iwai M, Niyogi K, Long S. 2016. Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. Science **354**, 857–861.

de Langre E. 2008. Effects of Wind on Plants. Annual Review of Fluid Mechanics **40**, 141–168.

Lawson T, Blatt M. 2014. Stomatal Size, Speed, and Responsiveness Impact on Photosynthesis and Water Use Efficiency. Plant Physiology **164**, 1556–1570.

Long SP, Marshall-Colon A, Zhu XG. 2015. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell **161**, 56–66.

Long SP, Zhu XG, Naidu SL, Ort DR. 2006. Can improvement in photosynthesis increase crop yields? Plant, Cell and Environment **29**, 315–330.

Der Loughian C, Tadrist L, Allain J, Diener J, Moulia B, De Langre E. 2014. Measuring local and global vibration modes in model plants. Comptes Rendus - Mecanique **342**, 1–7.

Matloobi M. 2012. Light Harvesting and Photosynthesis by the Canopy. In: Najafpour M, ed. Advances in Photosynthesis- Fundamental Aspects.Chapter 12.

Matthews J, Vialet-Chabrand S, Lawson T. 2018. Acclimation to fluctuating light impacts the rapidity and diurnal rhythm of stomatal conductance. Plant Physiology, pp.01809.2017.

McAusland L, Vialet-Chabrand S, Davey P, Baker N, Brendel O, Lawson T. 2016. Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. The New phytologist **211**, 1209–1220.

Moore J, Maguire D. 2008. Simulating the dynamic behavior of Douglas-fir trees under applied loads by the finite element method. Tree Physiology **28**, 75–83.

Morales A, Kaiser E, Yin X, Harbinson J, Molenaar J, Driever S, Struik P. 2018. Dynamic modelling of limitations on improving leaf CO2 assimilation under fluctuating irradiance. Plant, Cell & Environment **41**, 589–604.

Moser D, Drapela T, Zaller J, Frank T. 2009. Interacting effects of wind direction and resource distribution on insect pest densities. Basic and Applied Ecology **10**, 208–215.

Murchie EH, Pinto M, Horton P. 2009. Agriculture and the new challenges for photosynthesis research. New Phytologist **181**, 532–552.

Muryono M, Chen C, Sakai H, Tokida T, Hasegawa T, Usui Y, Nakamura H, Hikosaka K. 2017. Nitrogen distribution in leaf canopies of high-yielding rice cultivar Takanari. Crop Science **57**, 2080–2088.

Niklas K. 1991. The elastic moduli and mechanics of populus tremuloides (Salicaceae).

American Journal of Botany **78**, 989–996.

Niklas K, Speck T. 2001. Evolutionary trends in safety factors against wind-induced stem failure. American Journal of Botany **88**, 1266–1278.

Nuberg I, Bennell M. 2009. Trees protecting dryland crops and soil. In: Nuberg I,, In: George B,, In: Reid R, eds. Agroforestry for Natural Resource Management. Collingwood, Australia: CSIRO Publishing, 69–85.

Onoda Y, Anten N. 2011. Challenges to understand plant responses to wind. Plant Signaling and Behavior **6**, 139–141.

Pearcy R. 1990. Sunflecks and Photosynthesis in Plant Canopies. Annual Review of Plant Physiology and Plant Molecular Biology **41**, 421–453.

Piñera-Chavez FJ, Berry PM, Foulkes MJ, Jesson MA, Reynolds MP. 2016*a*. Avoiding lodging in irrigated spring wheat. I. Stem and root structural requirements. Field Crops Research **196**, 325–336.

Piñera-Chavez F, Berry P, Foulkes M, Molero G, Reynolds M. 2016*b*. Avoiding lodging in irrigated spring wheat. II. Genetic variation of stem and root structural properties. Field Crops Research **196**, 64–74.

Porcar-Castell A, Palmroth S. 2012. Modelling photosynthesis in highly dynamic environments: the case of sunflecks. Tree Physiology **32**, 1062–1065.

Pound MP, French AP, Murchie EH, Pridmore TP. 2014. Automated recovery of three-dimensional models of plant shoots from multiple color images. Plant physiology **166**, 1688–98.

Remondino F, El-hakim S. 2006. Image-based 3D modelling: A review. Photogrammetric Record **21**, 269–291.

Retkute R, Smith-Unna S, Smith R, Burgess A, Jensen O, Johnson G, Preston S, Murchie E. 2015. Exploiting heterogeneous environments: Does photosynthetic acclimation optimize carbon gain in fluctuating light? Journal of Experimental Botany **66**, 2437–2447.

Roden J. 2003. Modeling the light interception and carbon gain of individual fluttering aspen (Populus tremuloides Michx) leaves. Trees - Structure and Function **17**, 117–126.

Roden J, Pearcy R. 1993*a*. Photosynthetic gas exchange response of poplars to steady-state and dynamic light environments. Oecologia **93**, 208–214.

Roden J, Pearcy R. 1993*b*. Effect of leaf flutter on the light environment of poplars. Oecologia

93, 201–207.

Rodriguez M, De Langre E, Moulia B. 2008. A scaling law for the effects of architecture and allometry on tree vibration modes suggests a biological tuning to modal compartmentalization. American Journal of Botany **95**, 1523–1537.

Ruban A. 2017. Quantifying the efficiency of photoprotection. Philosophical Transactions of the Royal Society B: Biological Sciences **372**, 20160393.

Rudnicki M, Silins U, Lieffers V, Josi. 2001. Measure of simultaneous tree sways and estimation of crown interactions among a group of trees. Trees - Structure and Function **15**, 83–90.

Salvucci M, Anderson J. 1987. Factors affecting the activation state and the level of total activity of ribulose bisphosphate carboxylase in tobacco protoplasts. Plant physiology **85**, 66–71.

Seitz SM. 2000. A Theory of Shape by Space Carving. International Journal of Computer Vision **38**, 199–218.

Sellier D, Fourcaud T, Lac P. 2006. A finite element model for investigating effects of aerial architecture on tree oscillations. Tree Physiology **26**, 799–806.

Shaw R. 2012. Wind movement within canopies. In: Hatfield J, ed. Biometeorology in Integrated Pest Management. London, New York: Elsevier, 17–41.

Sinoquet H, Le Roux X, Adam B, Ameglio T, Daudet F. 2001. RATP: A model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: Application to an isolated tree crown. Plant, Cell and Environment **24**, 395–406.

Slattery RA, VanLoocke A, Bernacchi CJ, Zhu X-G, Ort DR. 2017. Photosynthesis, Light Use Efficiency, and Yield of Reduced-Chlorophyll Soybean Mutants in Field Conditions. Frontiers in Plant Science **8**, 549.

Smith V, Ennos A. 2003. The effects of air flow and stem flexure on the mechanical and hydraulic properties of the stems of sunflowers Helianthus annuus l. Journal of Experimental Botany **54**, 845–849.

Song Q, Wang Y, Qu M, Ort D, Zhu X-G. 2017. The impact of modifying photosystem antenna size on canopy photosynthetic efficiency—Development of a new canopy photosynthesis model scaling from metabolism to canopy level processes. Plant Cell and Environment **40**, 2946–2957.

Song Q, Xiao H, Xiao X, Zhu X-G. 2016. A new canopy photosynthesis and transpiration measurement system (CAPTS) for canopy gas exchange research. Agricultural and Forest Meteorology **217**, 101–107.

Song Q, Zhang G, Zhu X-G. 2013. Optimal crop canopy architecture to maximise canopy photosynthetic CO2 uptake under elevated CO2 – a theoretical study using a mechanistic model of canopy photosynthesis. Functional Plant Biology **40**, 109–124.

Speck O. 2003. Field measurements of wind speed and reconfiguration in Arundo donax (Poaceae) with estimates of drag forces. American Journal of Botany **90**, 1253–1256.

Tadrist L, Saudreau M, Hémon P, Amandolese X, Marquier A, Leclercq T, de Langre E. 2018. Foliage motion under wind, from leaf flutter to branch buffeting. Journal of The Royal Society Interface **15**.

Tadrist L, Saudreau M, de Langre E. 2014. Wind and gravity mechanical effects on leaf inclination angles. Journal of Theoretical Biology **341**, 9–16.

Tan P, Zeng G, Wang J, Kang SB, Quan L. 2007. Image-based tree modeling. ACM Transactions on Graphics **26**, 87.

Taylor SH, Long SP. 2017. Slow induction of photosynthesis on shade to sun transitions in wheat may cost at least 21% of productivity. Philosophical Transactions of the Royal Society B: Biological Sciences **372**, 20160543.

Townsend A, Retkute R, Chinnathambi K, Randall J, Foulkes J, Carmo-Silva E, Murchie E. 2017. Suboptimal acclimation of photosynthesis to light in wheat canopies. Plant Physiology, pp.01213.2017.

Valladares F, Niinemets U. 2007. The Architecture of Plant Crowns: From Design Rules to Light Capture and Performance. Functional plant Ecology.101–150.

Vogel S. 1992. Twist-to-bend ratios and cross-sectional shapes of petioles and stems. Journal of Experimental Botany **43**, 1527–1532.

Wahl SW and FM. 2001. Shape from 2D Edge Gradients. Pattern recognition, 377–384.

Walker B, Drewry D, Slattery R, VanLoocke A, Cho Y, Ort D. 2018. Chlorophyll Can Be Reduced in Crop Canopies with Little Penalty to Photosynthesis. Plant Physiology **176**, 1215 LP-1232.

Walters R, Horton P. 1994. Acclimation of Arabidopsis thaliana to the light environment - changes in composition of the photosynthetic apparatus. Planta **195**, 248–256.

Wang G, Ji M, Deng J, Wang Z, Fan Z, Liu J, Brown JH, Ran J, Wang Y. 2012. From the Cover: Models and tests of optimal density and maximal yield for crop plants. Proceedings of the National Academy of Sciences **109**, 15823–15828.

Wang Y, Li J. 2006. Genes controlling plant architecture. Current Opinion in Biotechnology **17**, 123–129.

Wu Y, Dalmacio R. 1991. Energy balance, water use and wheat yield in a Paulownia-wheat intercropped field. In: Zhu Z, ed. Agroforestry Systems in China. CAF/IFDC, 54–65.

Yang H, Shao L, Zheng F, Wang L, Song Z. 2011. Recent advances and trends in visual tracking: A review. Neurocomputing **74**, 3823–3831.

Zaks J, Amarnath K, Kramer D, Niyogi K, Fleming G. 2012. A kinetic model of rapidly reversible nonphotochemical quenching. PNAS **109**, 15757–15762.

Zhu X-G, Long S, Ort D. 2010. Improving photosynthetic efficiency for greater yield. Annual review of plant biology **61**, 235–261.

Zhu X-G, Ort D, Whitmarsh J, Long S. 2004. The slow reversibility of photosystem II thermal energy dissipation on transfer from high to low light may cause large losses in carbon gain by crop canopies: a theoretical analysis. Journal of Experimental Botany **55**, 1167–1175.