New Phytologist

Research

Phyllotaxis: is the golden angle optimal for light capture?

Sören Strauss[1]*, Janne Lempe[1]*, Przemyslaw Prusinkiewicz[2], Miltos Tsiantis[1] and Richard S. Smith[1,3]

[1]Department of Comparative Development and Genetics, Max Planck Institute for Plant Breeding Research, Cologne 50829, Germany; [2]Department of Computer Science, University of Calgary, Calgary, AB T2N 1N4, Canada; [3]Present address: Cell and Developmental Biology Department, John Innes Centre, Norwich Research Park, Norwich, NR4 7UH, UK

Author for correspondence:
Richard S. Smith
Tel: +49 221 5062 130
Email: smith@mpipz.mpg.de

Received: *7 May 2019*
Accepted: *24 June 2019*

New Phytologist (2020) **225:** 499–510
doi: 10.1111/nph.16040

Key words: computer simulation, heteroblasty, light capture, phyllotaxis, plant fitness.

Summary

- Phyllotactic patterns are some of the most conspicuous in nature. To create these patterns plants must control the divergence angle between the appearance of successive organs, sometimes to within a fraction of a degree. The most common angle is the Fibonacci or golden angle, and its prevalence has led to the hypothesis that it has been selected by evolution as optimal for plants with respect to some fitness benefits, such as light capture.
- We explore arguments for and against this idea with computer models. We have used both idealized and scanned leaves from *Arabidopsis thaliana* and *Cardamine hirsuta* to measure the overlapping leaf area of simulated plants after varying parameters such as leaf shape, incident light angles, and other leaf traits.
- We find that other angles generated by Fibonacci-like series found in nature are equally optimal for light capture, and therefore should be under similar evolutionary pressure.
- Our findings suggest that the iterative mechanism for organ positioning itself is a more likely target for evolutionary pressure, rather than a specific divergence angle, and our model demonstrates that the heteroblastic progression of leaf shape in *A. thaliana* can provide a potential fitness benefit via light capture.

Introduction

Two key questions in biology are to understand how biological patterns emerge and what their physiological functions are. Phyllotaxis, the arrangement of plant organs around a central axis, is an example of a highly structured pattern that has fascinated biologists and mathematicians for centuries; for a review, see Adler *et al.* (1997). This fascination is largely attributable to the observation that emerging organs are often arranged into a spiral, with the divergence angle between consecutive organs close to the Fibonacci or golden angle of *c.* 137.5°. Though there has been considerable progress in understanding the morphogenetic basis of this geometrically conspicuous pattern (Reinhardt *et al.*, 2003; Jönsson *et al.*, 2006; Smith *et al.*, 2006a; Besnard *et al.*, 2014), the physiological functions or consequences of phyllotaxis, and how those might have influenced its evolution, are poorly understood. One hypothesis is that spiral phyllotaxis evolved to optimize leaf spacing on the growing apex, thereby maximizing interception of light for photosynthesis, and by implication thereby maximizing plant fitness (Niklas, 1998; Pearcy & Yang, 1998; King *et al.*, 2004).

This idea is appealing; and if true, the prevalence of the golden angle in nature could be attributed to optimal light capture. However, there are several indications that optimal light capture is unlikely to be the predominant driver for the evolution of the golden angle. First, spiral phyllotaxis can also develop from several other divergence angles associated with Fibonacci-like sequences, albeit not as prevalent, such as the Lucas angle of *c.* 99.5° and the first anomalous sequence angle of *c.* 151.14° (Jean, 1994). Additionally, other spiral patterns have been observed, where organs initiate in pairs or triplets and the divergence angle is a half or a third of the golden angle. Light harvesting is also modulated independent of organ divergence angle. Many plants exhibit substantial genetically programmed age-dependent variation in leaf shape that could conceivably influence light capture. Environmental fluctuations in light quality play a role as well, with many plants responding rapidly by altering their leaf and shoot growth to avoid shade (Novoplansky *et al.*, 1990; Smith & Whitelam, 1997; Franklin, 2008; Fankhauser & Christie, 2015). The multitude of phyllotactic patterns seen in nature, together with evidence that other factors, both genetic and environmental, can affect light capture, challenges the idea that the golden angle represents a fundamental light-harvesting optimum constraining evolution of phyllotactic patterns, as favored by Niklas (1998) and Valladares & Brites (2004). To evaluate the hypothesis that selection for maximizing light capture has underpinned the evolution of the golden or other divergence angles, we have developed a computer simulation model of plant light capture.

Several methods have been used in this context to assess the light-harvesting ability of plants with simulation models. For example, Niklas (1988, 1998) developed a model in which light arriving at different angles was simulated to account for the different positions of the sun. Although he found a global maximum

---

*These authors contributed equally to this work.

of light capture when leaves were placed at the golden angle, he argued that other morphological features not correlated with the divergence angle, such as leaf shape and petiole length, could compensate for less than ideal angles. Pearcy & Yang (1998) analyzed the light capture of *Adenocaulon bicolor*, a redwood forest understory plant. They used an elaborate method based on canopy photographs, taking into account diffuse light combined with occasional direct light coming from gaps in the forest canopy. They also found a global maximum for light capture close to the golden angle, suggesting it is optimal. King *et al.* (2004) defined a shadow function for each leaf, which was used to approximate the shading effects of upper leaves on the lower ones, taking into account a decrease in the shading effect with distance. They compared their model with the empirical results presented by Pearcy & Yang (1998) and reported a good fit to the data. They also suggested that the golden angle was selected by evolution as ideal for light capture. By contrast, Valladares & Brites (2004) suggested that the divergence angle had little influence on light capture compared with other morphological traits, except in the case of opposite phyllotaxis, where it would be detrimental by increasing leaf overlap. Sarlikioti *et al.* (2011) reported a similar result by modeling tomato plants, where leaf angle or leaf length influenced light capture but the divergence angle had little effect.

An alternative explanation for the prevalence of the golden angle might be developmental constraints, if, for example, it arises as part of a favorable mechanism for organ packing at the shoot apex (Maynard Smith *et al.*, 1985; Beldade & Brakefield, 2002). Further, though the idea that leaf spacing can help optimize light capture is intuitive, the fitness consequences of increased light capture in field conditions are not always clear. For example, excess light can cause stress by overheating or phototoxicity, suggesting that any potential beneficial effects of organ spacing on light capture are likely to be conditional rather than universal (Osmond *et al.*, 1987).

Here, we re-examine the effect of leaf divergence angle on light capture by employing a computational model to examine the efficiency of light capture for all of the common and the not-so-common angles observed in nature. We use simulations of plants bearing idealized leaves of different shapes, such as simple, lobed, and dissected, as well as leaf scans of *Arabidopsis thaliana*, which has simple leaves, and *Cardamine hirsuta*, which has dissected leaves with leaflets. With the models, we tested the interplay between leaf shape variation and light capture under different developmental and environmental circumstances.

Materials and Methods

Computer simulation model of light capture

A simulation model of plant light capture was developed using both idealized leaves and digitized *A. thaliana* and *C. hirsuta* leaves. The model was programmed in C++ using vertex–vertex systems (Smith *et al.*, 2003) within the VLAB modeling environment (Federl & Prusinkiewicz, 1999). Plant models were generated by using images of idealized or scanned leaf shapes, where successive leaves were placed at a fixed divergence angle θ around the central axis. Most of the simulations considered only direct light. The total light capture was calculated by using a parallel projection of the leaves onto a plane orthogonal to the direction of the incoming light. If the viewing direction was considered to be the position of the light source, then the resulting image gave a two-dimensional projection of the leaves as seen from the light source. The projection plane was then divided into pixels, and the pixels covered by the leaf in the frame buffer were summed up to determine the total light capture (Takenaka, 1994). This made it straightforward to calculate light capture when parameters such as divergence angle, angle between the leaf petiole and stem, leaf shape, and the angle of incoming light are changed. A further advantage of the method was visual verification, since the actual projection used for calculating the light capture model could be monitored as the simulation progressed (Fig. 1b). In our simulation, we used OPENGL (v.3.0) renderings of the images with an orthographic projection and a frame buffer resolution of 1600 × 1600.

Idealized *A. thaliana* leaves were composed using a rectangle as the petiole with a length of 1.0 and a width of 0.1 in arbitrary units. Attached to this rectangle was an ellipse simulating the leaf lamina. The length of the leaf was defined by the (major) radius of 0.6 and the width by the (minor) radius of 0.35. These proportions closely resemble the actual leaf shape of an adult *A. thaliana* leaf (see Fig. 1a). For the simulations we used idealized plants with up to 30 leaves. In order to simulate the developmental change in leaf size at different nodes, the size of the idealized leaves in the model increased linearly, whereas the shape remained unchanged (Fig. 1b). As the idealized leaves do not capture heteroblasty, which is the change in leaf shape over developmental time (Poethig, 1990, 2013; Willmann & Poethig, 2011), we used scanned leaves in some of our simulations.

We defined two unitless measures for quantifying light capture. To visualize the progression of light capture with increasing number of leaves, we defined the light capture area (LCA), which is the ratio of leaf area exposed to the light source to the total area of all of the leaves at the final stage of the simulation (with the maximum number of leaves). We also used the light capture efficiency (LCE), which is defined as the ratio of the leaf area exposed to the light to the current total leaf area of the plant at a given stage. Note that the two measures are the same for the full number of leaves in a given simulation.

Plant growth conditions and leaf image acquisition

We used scanned leaves of *A. thaliana* Col FRI *flc-3* (Michaels & Amasino, 1999) and *C. hirsuta* NIL_{Ox} (Cartolano *et al.*, 2015) plants as input for computer simulations. Plants were grown in Hettich ESP PRC1700 growth cabinets under short-day conditions (8 h : 16 h, light : dark cycles) at a light intensity of 180 μmol m^{-2} s^{-1}, at 20°C during day and 18°C during night.

They were harvested when they reached a comparable developmental stage with 30 ± 2 leaves visible by eye. Leaves were mounted on white paper using spray glue and digitized with an Epson V700 Photo scanner at 600 dpi (Hettich Benelux B.V.,

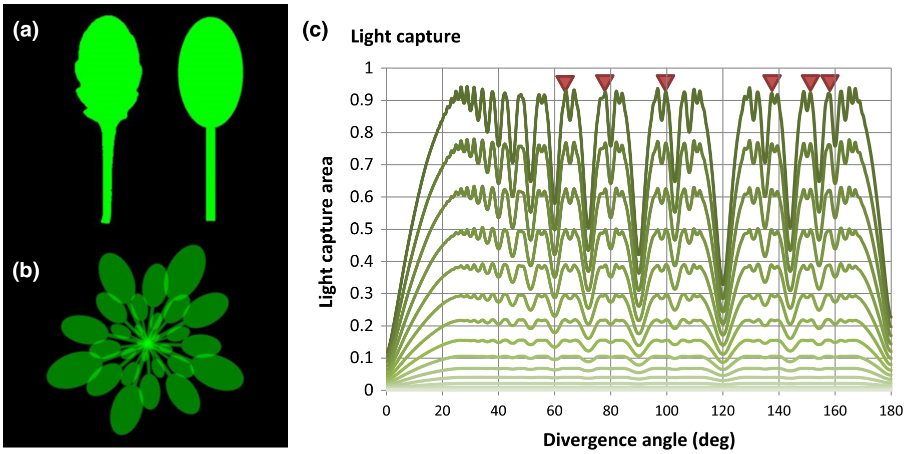


Fig. 1 (a) Scanned adult *Arabidopsis thaliana* leaf 13 compared with our idealized model leaf. (b) Simulated plant with idealized leaves. The leaves increase linearly in size and were rendered with transparency to visualize the overlapping leaf areas. (c) The light capture curve shows the light capture area (LCA) of simulated idealized plants with two (light green curve) to 30 (darkest green) leaves with different divergence angles. This measure is normalized by the total leaf area of the plant with 30 leaves; therefore, the LCA increases for plants with more leaves. The graph for angles between 180° and 360° would be a mirror image, but otherwise identical. In plants with a higher leaf number, the divergence angle becomes more important to avoid overlapping leaves and thus a loss in light capture. The graph shows very distinct minima at angles of common fractions (e.g. 120° = ⅓) and maxima at angles produced by the irrational fractions of the golden angle of 137.5° or related angles such at the Lucas angle of 99.5°, the second and third accessory angles of 77.96° and 64.08°, and the first and second anomalous angles of 151.14° and 158.14° (see red markers). For a complete overview of all maxima and minima, see Supporting Information Tables S1 and S2; see also Marzec & Kappraff (1983) and Jean (1994).

Geldermalsen, Netherlands). Obvious artifacts, like bending or ruptures in leaves, were removed from leaf images using Adobe PHOTOSHOP. One representative sample per species was used for the comparison of the computer simulations of idealized leaves with actual leaves from *Arabidopsis* and *Cardamine*. For the heteroblasty simulations, we used the leaves of all eight *Arabidopsis* replicates.

Results

Effects of phyllotaxis on light capture

To investigate the light capture potential of plants with all theoretically possible divergence angles, we developed a computational model that allows the simulation of plants with 1–30 idealized leaves (Fig. 1a,b) with divergence angles from 0° to 180° in steps of 0.25° (Supporting Information Video S1). The leaf size was linearly increased over time; and since the light source was placed directly above the plant, internode length was neglected. We next plotted the LCA of the simulated plant against the divergence angle, generating a 'light capture curve' (Fig. 1c). Note that the light capture curve only measures the leaf area exposed to the light as an approximation for the ability of different phenotypes to capture light and is not intended to express fitness in the broad sense. As leaves were added to the simulation, the graph showed an increase in LCA and also became more complex, which can also be seen when normalizing the light capture leaf area to the total area, plotted as LCE (Fig. S1A). This can be explained by a higher importance of the divergence angle in plants with higher leaf numbers, as the potential loss from a nonoptimal angle becomes higher due to an increase in leaf overlap.

The light capture curve showed that the golden angle of 137.5° indeed optimizes the LCE of the idealized plant. However, our model identified many other maxima that provide an equally good LCE. The shape of the curves in Fig. 1(c) is qualitatively similar to the effect of the divergence angle on the packing efficiency of a regular lattice (Marzec & Kappraff, 1983). The maxima correspond to divergence angles associated with other Fibonacci-like sequences generated by beginning the sequence with different starting pairs of integers. Examples are the Lucas sequence at 99.5°, which starts with (1, 3), or the first anomalous sequence of 151.14°, which begins with (2, 5) (see Table S1). Although not as common as 137.5°, the Lucas and first anomalous divergence angles do appear relatively frequently in nature (Jean, 1994). Our simulations confirm that the golden angle of 137.5° is indeed an optimal angle; however, there are many other angles that can be generated by Fibonacci-like sequences that are also optimal with respect to light capture. Note that the positions of minima in the graphs are associated with angles represented by fractions of the full angle with small denominators (less than leaf number); for example, ½ × 360° = 180° or ⅓ × 360° = 120° (Table S2). The common property of all the optimal angles is that they are not close to angles made by fractions with small denominators, which cause leaves to shade each other.

Light capture of plants with bijugate phyllotaxis Plants that show multijugate patterns of phyllotaxis initiate more than one organ at a time in whorls of equally spaced organs. In bijugate patterns, opposite pairs of organs are initiated simultaneously. The simplest example of this is decussate phyllotaxis, as is observed in the vegetative shoot of *Antirrhinum*, where successive pairs of leaves are placed in the center between the previous pair; that is, with a divergence angle of 90°. However, spiral bijugate patterns also exist, with successive whorls placed at a fixed divergence angle (< 90°) from the previous pair. The most common spiral bijugate pattern is Fibonacci spiral bijugate phyllotaxis, where pairs of organs appear at the divergence angle of *c.* 68.75°, which is approximately half the golden angle (Jean, 1994). In the subsequent series of simulations we examined how the divergence angle influences the light capture in such plants. The simulation setup was identical, but instead of placing one leaf at a time we placed a pair of opposite leaves up to the total number of 30 leaves (or 15 pairs). The light capture curve was generated by varying the divergence angle between the pairs from 0° to 90°.

The shape of the resulting light capture curve looked almost identical to the single organ, with all angles divided by 2 (Fig. S1B). Significant minima could be found at 60° and 90°, and maxima at 50.25° (approximately half of Lucas) and 68.75° (approximately half of Fibonacci). Similar to the previous simulations, the halved golden angle was just one out of many angles that maximized the LCE, and again the minima generated by low-denominator fractional angles dominated the light capture curve. Similar results were obtained with higher whorl sizes, such as for trijugate phyllotaxy, where the extrema in the divergence angles have a third of the values of the original light capture curve.

Leaf traits affecting light capture

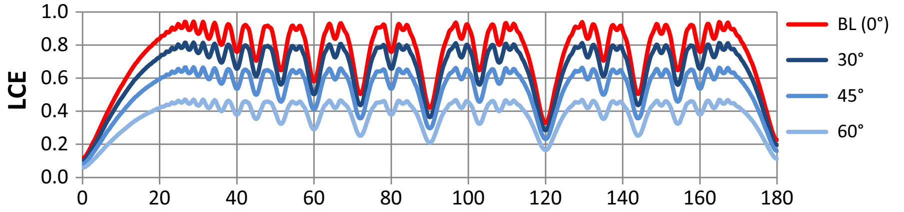
The simulations so far considered only horizontal leaves with the light source directly above the plant. In nature the angle of incident light and the angle between the leaf and the stem vary. Reorientation of leaves is also observed as a reaction to shading by competing plants (Franklin, 2008). Nevertheless, in environments with very diffuse light, plants often have horizontal leaves (Givnish, 1988) and even distichous phyllotaxis (Givnish, 1995), suggesting that these traits may be of less importance when direct light is not in abundance. The subsequent simulations explored the influence of the light angle and of traits such as leaf shape and petiole length on the light capture ability (Niklas, 1998).

Angle of incident light The sun moves across the sky during the course of a day. Hence, the area of the plant that is directly exposed to the sun changes significantly. We simulated this effect by changing the location of the light source in our model, by placing it at angles of 30°, 45° and 60° from the vertical axis. Then we simulated an idealized plant with 30 leaves and divergence angles ranging from 0° to 180° and compared the resulting light capture curves with the one from the first simulation.

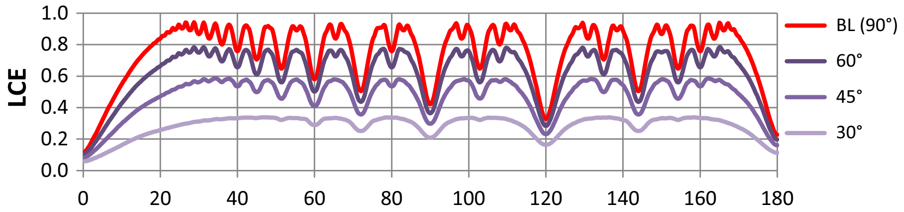
The results showed that plants received less light with higher angles but that the overall shape of the light capture curve was independent of the incident light angle (Fig. 2a). The different values for the angle of the incoming light simply act as a scaling factor for the light capture ability and efficiency and do not influence the relative optimality of the divergence angles, as all values are scaled equally by a factor < 1.

Leaf angle In addition to the angle of incident light, the angle between the leaves and the stem can vary. In previous simulations this angle was set to 90° (i.e. the leaves were placed flat around

(a) Angle of incident light



(b) Leaf angle



(c) Internode length

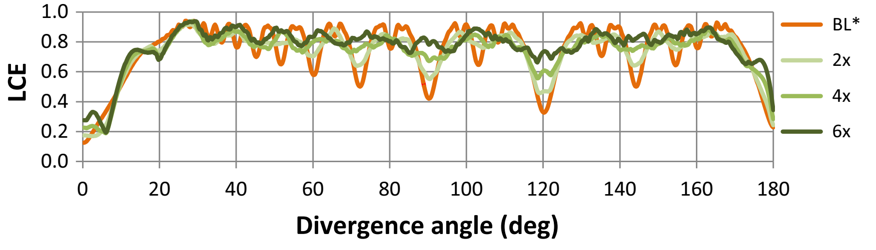


Fig. 2 The influence of geometric parameters on light capture on an idealized plant with 30 leaves. The red lines are the results from the baseline (BL) simulation of Fig. 1 using 30 leaves. (a) The influence of the angle of incoming light on light capture efficiency (LCE). The LCE decreases with increasing incident angle; however, the overall shape of the graph remains unchanged. (b) The influence of leaf angle on LCE. With decreasing angle between leaves and the stem the LCE decreases globally, becomes smoother, and shows fewer local maxima and minima. (c) The influence of internode length on the light capture curve. Here, the baseline is an idealized plant with 30 leaves and an angle of incident light of 15° and a leaf angle of 75° (BL*). The internode length was constant and equal to two, four, or six times the length of the smallest leaf, resulting in a stem size of almost two, four, or six times the length of the largest leaf, respectively. The divergence angle becomes less important with increasing internode length.

the stem). In this simulation, we tested the influence of leaf inclination by placing the leaves at angles of 60°, 45° and 30° from the stem, with the light source placed directly overhead.

The light capture curve again showed characteristics similar to when the angle of the incident light was varied. Increasing the leaf angle caused the LCE to decrease globally (Fig. 2b), confirming previous results (Falster *et al.*, 2003; Bongers *et al.*, 2014). Moreover, the curve became smoother, leading to a reduction in the number of maxima and minima for a given number of leaves. Nevertheless, the frequency and size of the optimal divergence angles with ideal light capture fitness was unaltered.

Internode length Another parameter is the length of the stem between successive leaves; that is, the internode length. With a light source placed directly above the plant, the internode length does not have an effect on the leaf area directly exposed to light. Thus, in order to test the influence of the internode length in a situation where light is not directly overhead, we set the angle of incoming light to 15° and the leaf angle to 75°. We simulated three different internode length settings between successive leaves: constant, linearly increasing, and increasing following a logistic function. The differences between the three different settings were negligible (see Fig. S2C). When the internode length was small, there was only a minor influence on the overall light capture curve, creating a curve with slightly higher minima and lower maxima (Fig. 2c). With longer internodes the light capture curve was 'equalized': minima became less deep and maxima decreased, so that the overall importance of the divergence angle decreased.

Translucency When simulating translucency by using a blending function, we found that the effect of translucent leaves was negligible and had little influence on the overall shape of the light capture curve, and the minima and maxima angles remained the same (see Fig. S2A). With the LCE normalized to the total area times the transparency factor, the LCE was increased as additional light from overlapping leaves was harvested. If the LCE was normalized to the total area assuming full light capture, then the LCE was greatly reduced except in the areas of significant overlap, where it almost approaches the nontransparent values. The former case would correspond to the situation where the photosynthetic capacity of translucent leaves is saturated, so that light passing through is not a loss, whereas in the latter case any light passing through the leaf is lost. In nature, it is likely that the plant operates somewhere between these two extremes.

Photosynthetic decrease Leaves of different ages do not necessarily contribute equally to photosynthesis and carbon gain (Thomas, 2013). We simulated the effect of aging in our model by linearly reducing the photosynthetic capacity in older leaves while keeping the youngest leaves at full capacity. We found that this had a similar effect to the plant having a smaller number of leaves, with the light capture curve becoming smoother with less minima and maxima as the contribution from older leaves is diminished (compare Figs 1c, S2B).

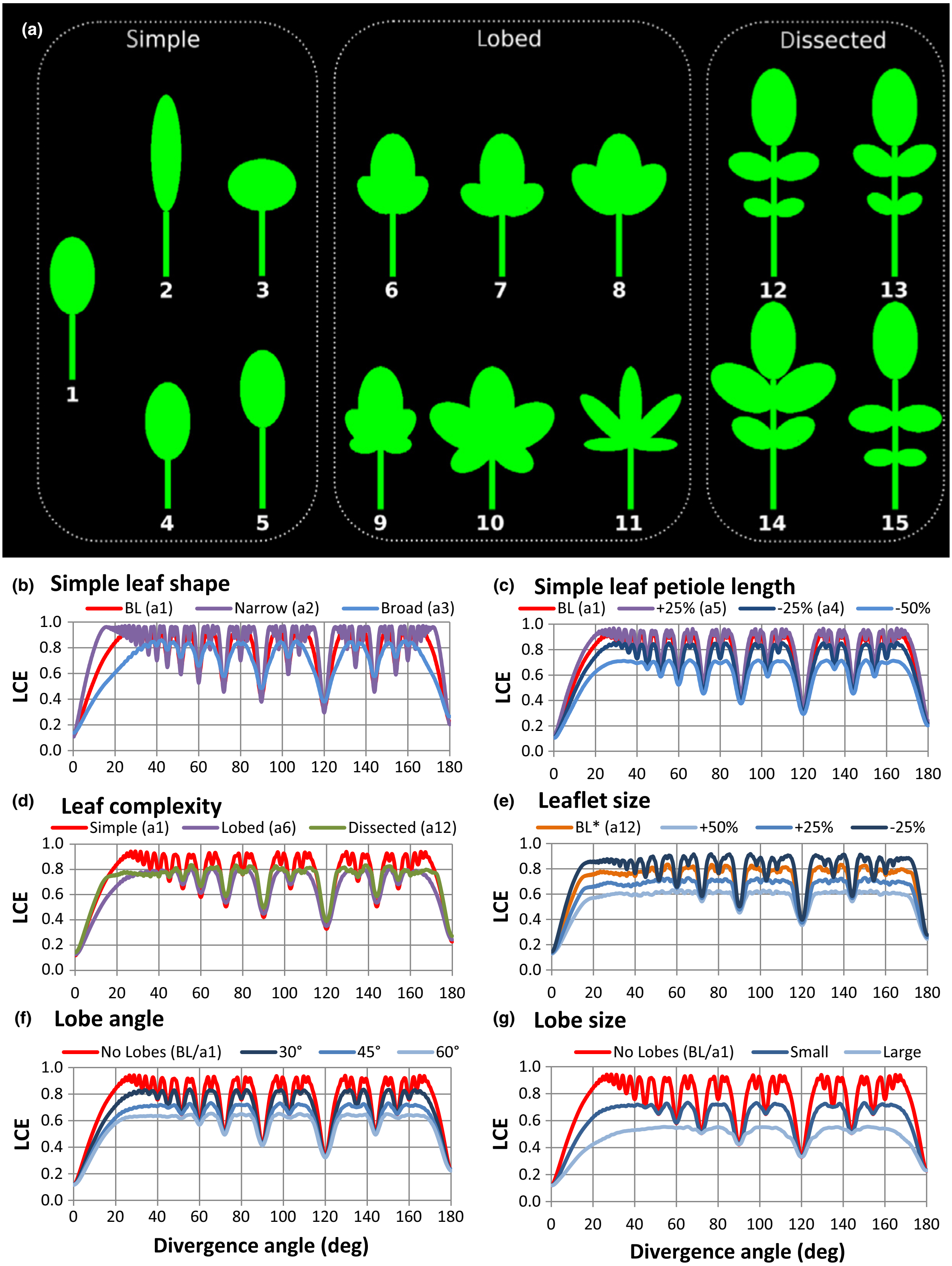
Effect of leaf shape on light capture

It is expected that leaf shape would also have an influence on the light capture ability of a plant. For instance, broader leaf blades and shorter petioles should lead to an increased leaf overlap and therefore to smaller LCE (Takenaka, 1994; Niklas, 1998). To test the influence of these traits, we simulated idealized plants with varying leaf shapes, complexity, and petiole length while other simulation parameters were unchanged.

Leaf shape and petiole length We changed the parameters of the ellipse that define the leaf blade to manipulate the overall leaf shape while keeping the leaf complexity low. Multiplying the long axis by a factor of 3/2 and the short axis by 2/3, relative to our default idealized leaf, led to elongated, slimmer leaf blades, whereas the opposite led to shorter, broader leaf blades (see Fig. 3a1–3). For the simulation with varying petiole lengths we used idealized leaves with identical simple leaf shapes as in the first simulation, and factors for the petiole lengths of 1.25, 0.75, and 0.50 (see Fig. 3a4,5).

The resulting light capture curve of simulated plants with different simple leaf shapes is again influenced mainly by the angles at small fractions, where local minima could be found (Fig. 3b). However, there are some noteworthy differences between the results produced with different leaf shapes. Slimmer leaf blades yield narrower 'valleys' in the curve. Their local minima are lower and their maxima are higher than the standard leaf, and they show a lower total overlapping area. This suggests that plants with slimmer leaf blades have a potential gain due to a leaf shape that prevents overlap. By contrast, plants with broader leaf blades have an overall lower curve, but it is much smoother as it increases the minima and decreases the maxima. For such plants, the light capture stays more or less stable around their maxima.

The results for different petiole lengths were comparable to the previous simulation that varied leaf shape. A longer petiole led to lower overall overlapping area and more pronounced maxima and minima (Fig. 3c). By contrast, simulations with a shorter petiole showed a smoother light capture curve with fewer local maxima and minima and strongly increased overlap; thus, it is not surprising that this trait is strongly regulated by the light environment in many species (Bongers *et al.*, 2014; Pierik & de Wit, 2014). In contrast to simulations with varying simple leaf shapes, a longer petiole was always beneficial in terms of LCE, when compared with a shorter petiole, as the leaf is placed further away from the stem and is less likely to overlap with other leaves. An interesting comparison with the leaf angle simulations can be made. A change in the leaf angle 'virtually' decreases the petiole length and changes the aspect ratio of the leaf. Thus, the results from the leaf angle simulation can be explained by a combination of these two factors.



Although it might be beneficial for LCE to increase petiole length and decrease leaf width, both traits could affect the overall plant fitness in a negative way. For instance, an excessively long petiole might reduce mechanical stability, and a too narrow leaf might negatively influence photosynthetic surface area. Nevertheless, overall, it is reasonable to expect that diversification of these leaf traits in natural environments might have conditionally contributed to plant fitness (Takenaka, 1994).

Fig. 3 The influence of leaf shape on light capture. (a) Examples of model leaves used in the simulation. In comparison with the baseline leaf from Fig. 1 (a1, red line in all graphs), we altered leaf length and width (a2, a3) and petiole length (a4, a5). To produce more complex leaf shapes we added one pair of lobes (a6–a8), two pairs of lobes (a9–a11), and leaflets (a12–a15) with different sizes and angles. (b) When changing the simple leaf shape, the light capture efficiency (LCE) plot for a narrower leaf (a2) shows more detail and lower minima but higher maxima, whereas for a broader leaf (a3) the opposite was observed. (c) Longer petioles (a5) globally improved the LCE, whereas a shorter petiole (a4) significantly increased the overlapping leaf area, and the curve becomes smoother. (d) Comparison of leaves with different complexity: simple (a1), lobed (a6), and dissected (a12). Leaf complexity itself had only a minor effect on the light capture curve. (e) Effect of leaflet size on dissected leaves. Indicated values are changes in the ellipse axes lengths of the leaflets. Larger leaflets lower the achievable maximum LCE and also equalize the maxima, whereas the minima are not affected. (f) The effect of the lobe angle of a leaf with two pairs of lobes which had sizes of 60% and 40% of the size of the central ellipse. Indicated angles are the ones of the first lobe pair with double the value for the second lobe pair. With increasing angle, the LCE is decreased and maximum values are smoothed out. (g) Here, the angles were held constant (at 45°) and the sizes of the lobes varied (small: similar to (f); large: + 50% ellipse axes of lobes). This had a similar effect as increasing the angles: larger lobes decreased and smoothed the LCE curve.

Complex leaf shapes The leaf blade of simple leaf shapes can be approximated with a single ellipse; however, in nature, more complex leaf shapes with serrations, lobes, and leaflets are common. To test whether our previous simulation results were representative for such leaf shapes, we studied more complex idealized leaf shapes composed of several ellipses that were acting as lobes when attached at the base of the leaf blade and overlapping with the central ellipse, thus forming a larger lobed leaf. Dissected leaves were created by extending the petiole and adding leaflets by attaching additional ellipses further down the petiole not connected to the central ellipse. By varying these ellipses in number, size, and angle we were able to cover a large range of possible leaf shapes from complex to dissected leaves (see Fig. 3a). Since the LCE and LCA are normalized by total area, and the increase in leaf size in the simulations is linear, differences in leaf area for the various shapes do not affect the results. Note that the simulated dissected leaf shapes closely resemble the leaf shape of *C. hirsuta*, a relative of *A. thaliana* that is an attractive model for comparative development studies (Fig. 3a12; Hay & Tsiantis, 2006; Vlad *et al.*, 2014; Gan *et al.*, 2016).

The results of the simulations are shown in Figs 3 and S3. Complex leaves with larger lobes or leaflets broaden the leaf, which leads to an increase in overlap and a significantly lower achievable LCE, similar to the effect observed in simple broad leaves (Fig. 3d). For leaves with large lobes, the light capture curve was smoothened for angles that are close to a maximum, but minima were unaffected (Fig. 3g). We observed a similar effect when the angle between main axis of the leaf and the axis of the lobe ellipse (‘lobe angle’, Fig. 3f) was increased. These results were slightly more pronounced when two pairs of ellipses were added than for a simpler leaf shape with only one pair of ellipses (Fig. S3A,B). If the width of all leaf ellipses was scaled by a factor of 0.5 (‘slim lobes’) the pattern in the light capture curve was more noisy for different sizes and angles of lobes (Fig. S3C,D).

In dissected leaves, we also explored the effect of leaflet size, angle, and position. Increasing the leaflet size yielded a smoothened light capture curve around maxima but did not affect minima (Fig. 3e). Changing the angle of the petiole or the position of the leaflets along the petiole had very minor effects (Fig. S3E,F). Notably, leaflet placement further away from the center of the plant appeared to positively influence LCE.

Overall, we concluded that variation in leaf shape from lobes or leaflets did not play a significant role in optimizing the divergence angle for light capture.

Examining the effect of leaf heteroblasty

The idealized simple leaves used thus far in our models were designed to look similar to adult *A. thaliana* leaves, with a simple linear size scaling. Though these capture the simple geometric leaf shape of *A. thaliana* well, they do not take into account the leaf shape change due to heteroblasty. To assess how heteroblastic shape changes affect light capture, we used scans of entire sets of leaves of *A. thaliana* as input for our model (see Fig. 4a; Video S2).

We compared the LCE of a simulated plant without shape change and continuous increase in leaf size with digitized leaves with heteroblastic shape and size change (Figs 1b, 4b). For both models, we used the same number of leaves. The light capture curve with digitized leaves was almost the same as for idealized leaves (Fig. S4A). This supports the idea that the general shape of the graph – more specifically, the locations of the minima and maxima – is not sensitive to heteroblastic changes in leaf shape. However, one difference was that the idealized plant reached higher LCE values for optimal divergence angles, which was caused by its linearly increasing leaf size. In comparison the later leaves from the scans were smaller as they were not fully expanded. This was also true when comparing idealized dissected leaves (Fig. 3a12) with scanned leaves of *C. hirsuta* (Fig. S4b,c).

In the heteroblastic shape, the first leaves referred to as juvenile are smaller and rounder than later adult leaves (Fig. 4a; Willmann & Poethig, 2011). The physiological relevance of these leaf form differences is unclear, but one possibility is that they help to maximize light capture at different stages of the plant’s development. Motivated by this hypothesis, we explored how the shapes observed at different developmental times might influence light capture in our computational framework. Using scanned leaf images of eight biological replicates, we simulated plants by taking the leaf shape of one particular leaf, replicated it 30 times, and scaled it to the actual leaf length. An example is shown in Fig. 4(c) for leaf 3. This scenario would be equivalent to a plant regulating only the size of the leaf and not the shape. Comparing those simulated plants, we found that plants that are entirely made of juvenile leaves or very late leaves have a poor LCE compared with plants with mature leaves. Plants composed of adult

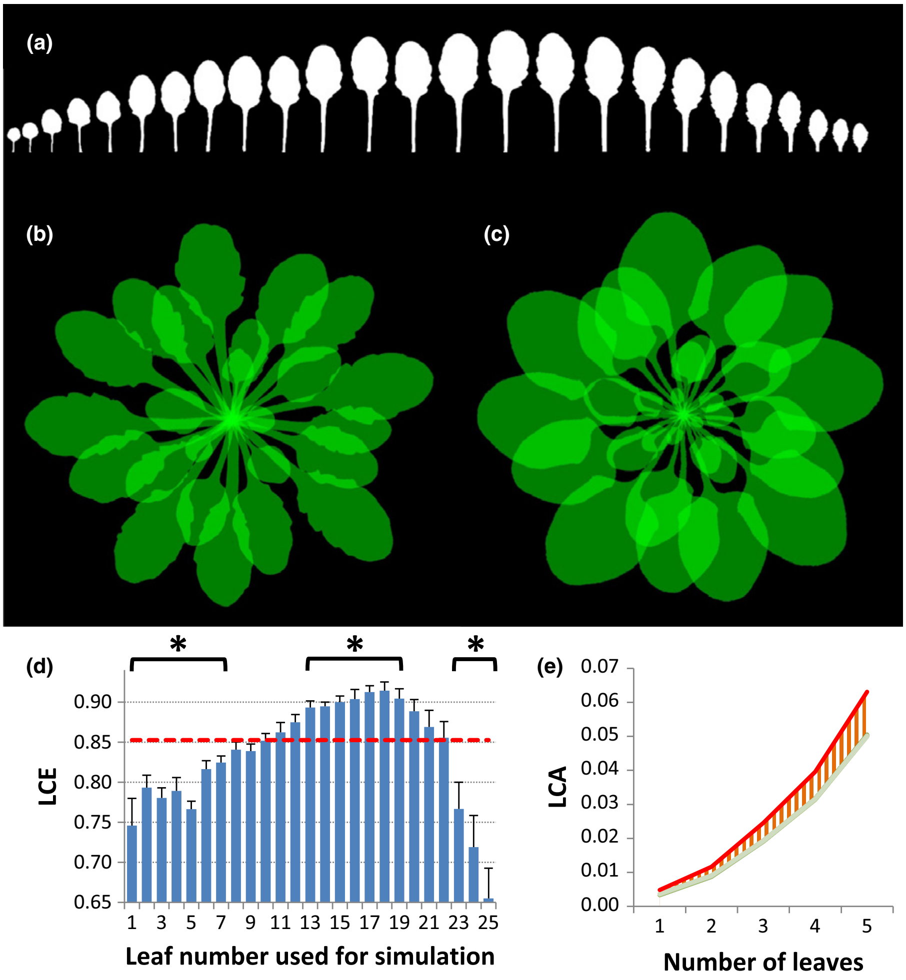


Fig. 4 The influence of heteroblasty on the light capture efficiency (LCE) of *Arabidopsis thaliana*. (a) Digitized leaves of an *A. thaliana* plant used for light capture simulation. (b) Model output using digitized *A. thaliana* leaves placed at a divergence angle of 137.5°. The simulated plant is shown with transparent leaves in order to highlight the overlapping area. (c) Simulated plant consisting of leaves with the shape of digitized leaf 3 from the same plant scaled to the actual leaf length. (d) LCE of simulated *A. thaliana* plants consisting of only one leaf type (blue bars represent average values of eight plants with their SE) compared with the average value of the same wild-type plants with heteroblasty (dashed red line). The single-leaf-type plants show reduced LCE for juvenile and very late leaves, but improved light capture for adult leaves 13–19 (*, $P < 0.05$ using a *t*-test comparing the results of the single-leaf-type plants and the wild-type plants). (e) The heteroblasty yielded a larger light capture area (LCA) for the first few leaves (red line) compared with the single-leaf-type plants (green line, difference in orange), possibly giving the young plants an advantage.

leaves (leaves 10–22), however, show similar or improved light capture compared with the full heteroblastic series (Fig. 4d). Juvenile leaves are rounder and very late leaves have a short petiole, both traits that increase the overlap (as also confirmed in the earlier simulations). By contrast, the shape of adult leaves yields excellent LCE, with later leaves fitting almost perfectly into the gaps in between earlier leaves, which shows that there is a high variability in LCE between the different leaf shapes of the heteroblastic series of *A. thaliana*.

This observation begs the question as to why, from a light capture perspective, *A. thaliana* does not just make adult-shaped leaves from the start. To explore this issue, we considered how the light capture ability changes over developmental time. We analyzed the LCA of the previously simulated plants consisting of only a single leaf shape of the heteroblastic series. We observed that differences between the simulated plants only occurred for *c.* 15 or more leaves (Fig. S5), as with fewer leaves there was almost no overlapping leaf area. Moreover, we found that the last leaves to be added did not contribute much to the total LCA, as these latest leaves almost entirely overlapped earlier leaves. This was particularly noticeable for the leaf shapes with the lowest LCE (juvenile and very late). Fig. 4(e) shows the graph zoomed in on the first five leaves and shows that plants consisting of only one leaf type have practically identical values of LCA, which is a result of the scaling of those leaves and the absence of leaf overlap. The values for the full heteroblastic series are considerably higher, showing an average increase of 32% in LCA for the first five leaves and 24% for the first 10 leaves.

The effects of heteroblastic progression for *A. thaliana* light capture appear to be two-fold: First, the broader, rounder juvenile leaves fill up available space quicker than their adult counterparts, thus increasing light capture at early stages of plant development. Second, as leaf number increases, the progression towards the narrower and more elongate adult shape helps *A. thaliana* to reduce leaf overlap and consequent self-shading. Later in development, leaves become smaller as the plant transitions to flowering (Willmann & Poethig, 2011), although a portion of the effect in the later leaves shown in Fig. 4(a) is due to the staging of the samples.

Effect of noise in phyllotactic patterns on light capture

In nature, the mechanisms generating leaf phyllotaxis are subject to noise from a variety of sources. For example, in *A. thaliana*, *c.* 20% of the leaves deviate at least 15° from the default divergence

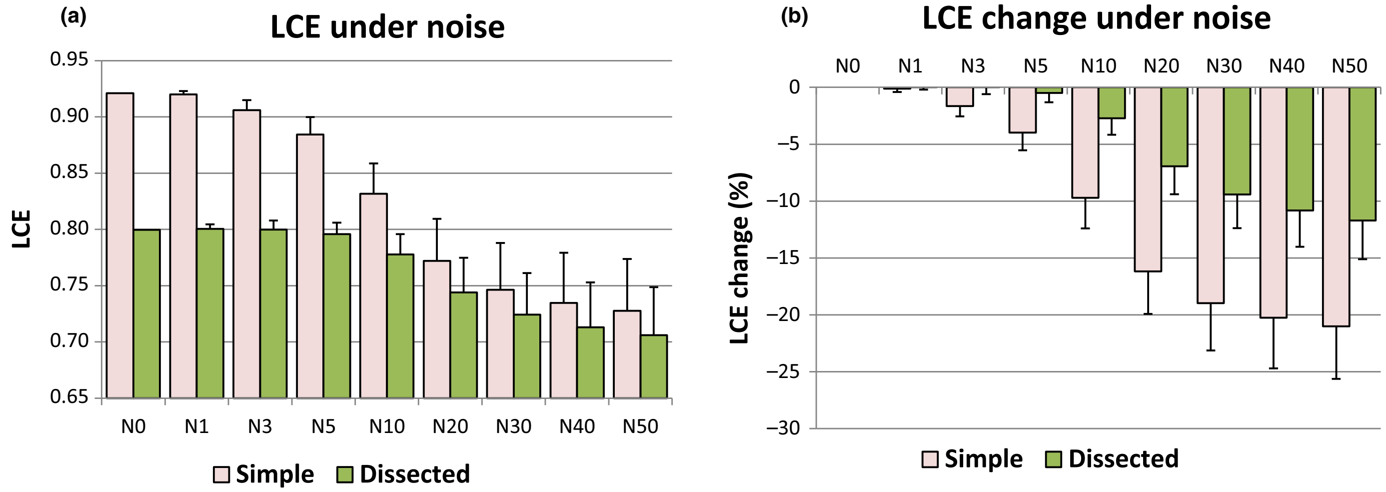


Fig. 5 The influence of noise in the divergence angle on the light capture efficiency (LCE) of the idealized simple-leaved plant (light red bars, leaf from Fig 3a1) compared with the idealized dissected-leaved plant (dark green, leaf from Fig. 3a12). (a) The results in the different conditions. (b) The difference to the no noise condition. The different simulations are named N*x*, where *x* stands for the SD of the normally distributed noise that was added to the divergence angle of 137.5°. We simulated 1000 plants in each condition, and the mean results and their SDs are displayed.

angle of 137.5° (Peaucelle *et al.*, 2007). Consequently, in our next simulation, we tested how noise affects leaf overlap.

We simulated plants consisting of the previously tested simple, lobed and dissected leaf shapes (see Fig. 3a) for their sensitivity towards noise. In each condition we conducted 1000 simulations using the golden angle (137.5°) and applied normally distributed noise with a mean of zero and different standard deviations (up to 50), which was added as deviation from the default final divergence angle for each leaf. All of the leaf positions in a simulation were first calculated and then noise applied, so that noise in the divergence for one leaf did not affect subsequent leaves. In our comparison of simple (Fig. 3a1) vs dissected (Fig. 3a12) leaf blades, we also tested the most common divergence angles other than the golden angle (99.5° and 151.1°). We found that the different angles had no effect, so we only show the results for the golden angle of 137.5°.

Overall, increasing noise resulted in a worse LCE across all the different conditions. The results showed only a small influence for most leaf parameters (see Fig. S6A,B) except simple vs dissected leaves, which showed a substantial difference (Fig. 5). Moreover, we found similar results for simulations using scanned leaves of *A. thaliana* and *C. hirsuta* (see Fig. S6C,D). Within our parameter space tested, we found only minor differences in how plants with different simple leaves are affected by noise. Plants with broader leaf blades showed a lower loss for small values of noise, which might be due to the fact that in those plants leaves already show significant overlap without noise and their light capture curve is smoother around maxima. Plants with narrower leaf blades or longer petioles showed slightly less relative LCE loss in the high noise conditions.

Plants with lobed and dissected leaves were more resistant to noise, with only minor losses up to the N10 condition, whereas plants with simple leaves showed higher losses as soon as at N5 (Fig. 5b). Plants with simple leaves showed significantly more leaf overlap than their dissected leaf counterparts under the influence of noise and subsequently lost more LCE in high noise conditions. However, the simple-leaved plant has a much higher LCE under the no noise condition (Fig. 5a).

It is likely that the high resistance to noise observed in dissected leaves is caused by the overall smoother light capture curve that they showed compared with simple leaves (Fig. 3d). This smoother curve has two effects. First, it leads to a reduced effect of angle deviations on LCE. Second, there is a lower potential to lose light capture since the distance between maxima and minima is smaller than the one found in LCE curves of simple leaves.

Conclusion

In our first simulations we used virtual rosette plants with a leaf shape idealized from *A. thaliana* to gain insight into the nature of the light capture ability of plants in relation to the divergence angle and leaf shape. Our simulations confirmed previous results by showing that the golden angle of 137.5° is indeed optimal for light capture and that morphological traits can influence the light capture curve. However, with a finer sampling of angles from 0° to 180° (resolution of 0.25°) our results also showed that there are many other divergence angles with comparable fitness based on light capture ability. Thus, the golden angle cannot really be seen as 'the' global maximum in terms of LCE, but is rather one of many optimal angles.

Traits such as petiole length, leaf shape, leaf complexity, and leaf angle all quantitatively change the effective light capture; however, the overall shape of the curve largely remains unchanged. This is also true for varying environmental conditions, such as the angle of incident light. A notable exception is the internode length. Long internodes can substantially alter the light capture curve and enable plants to achieve little leaf overlap with nonoptimal angles, such as those associated with smaller fractions, such as ½ = 90° or ⅓ = 120°. The low LCE of those angles for plants with short internodes, however, might explain the scarcity of rosette plants with decussate patterns. Hence, our results for the divergence angle remain valid mainly for rosette plants, such as *A. thaliana*, or plants with short stems (Bell & Bryan, 1991).

In nature, the divergence angle in plants is prone to noise (Besnard *et al.*, 2014). Our results demonstrate that this noise affects the leaf overlap, and therefore the light capture ability. We also showed that leaf shape can influence a plant's robustness to noise. Plants with simple leaves, like *A. thaliana*, that produce very little overlap and show very distinct maxima in the light capture curve need better control of the divergence angle or any advantage is lost. By contrast, dissected leaves, such as in *C. hirsuta*, have a higher leaf overlap but were more robust to noise.

The similarity in the light capture curve between a real *A. thaliana* plant and our idealized model plant suggests that minor differences in leaf shape have little impact on overall light capture. Nonetheless, we found that the heteroblastic leaf shape change in *A. thaliana* has an effect on the LCE. It appears to be beneficial for *A. thaliana* to make initial leaves broader, rounder in shape, and with a shorter petiole in order to quickly achieve a large leaf area as the plant is being established. Later in development the leaf shape progresses to an elongated form with longer petioles, likely in order to minimize the overlapping leaf area and thus maximize light capture. Similar observations were made by Zotz *et al.* (2002) with the tropical plant *Vriesea sanguinolenta.* Their simulations of adult plants with juvenile leaves also led to an increased leaf overlap. These results are not specific to the particular divergence angle that is typical for *A. thaliana*, and this also holds for other optimal angles related to other Fibonacci-like sequences.

Previous studies explored the question of whether the golden angle was optimal for light capture (Jean, 1994; Niklas, 1998; King *et al.*, 2004). However, most previous studies and simulations did not cover the whole range of possible divergence angles, so their conclusions are in that sense incomplete (e.g. Takenaka, 1994; Niklas, 1998; Pearcy & Yang, 1998). Here, we have shown that many divergence angles are just as efficient for light capture; for example, the relatively common Lucas angle of 99.5° or the angle associated with the anomalous sequence of 151.14° (Jean, 1994). For LCE, the most important characteristic of the divergence angle seems to be to simply avoid suboptimal regions, such as the minima around angles generated by low denominator fractions, such as 90° or 120°. Although this might explain why different plants have different divergence angles, the appearance of different angles on the same plant raises the question as to how *any* specific angle could be optimized in response to selective pressures. To answer this question, it is important to consider how phyllotactic patterns are formed.

Theories for how phyllotaxis patterning occurs date back to Hofmeister (1868), who proposed that new plant organ primordia appear as far away as possible from the boundaries of existing primordia. Since then, numerous simulation models of phyllotaxis have been proposed that are based on different levels of abstraction of this idea. These models range from very general inhibition models (Douady & Couder, 1992; Smith *et al.*, 2006b) to more mechanistic models based on diffusible morphogens (Thornley, 1975; Veen & Lindenmayer, 1977; Mitchison, 1981), contact pressure (Adler, 1974), or polar auxin transport (Jönsson *et al.*, 2006; Smith *et al.*, 2006a; Heisler *et al.*, 2010). All of these models share the central principle that spiral phyllotaxis results from a spacing mechanism superimposed on a radially symmetric growing domain (Heisler & Jönsson, 2006). This simple idea, along with a few variations, is able to produce almost all of the phyllotactic patterns observed in nature (Douady & Couder, 1992; Yotsumoto, 1993; Smith *et al.*, 2006b).

Since phyllotaxis results from spacing organs on a growing domain, the patterning process is intimately connected to the dynamic nature of plant organ development. As plants are sessile, they must adapt their body plan to their surroundings. Instead of specifying the body plan in the embryo, plants are producing organs from growing shoot tips throughout their life. Operating on this domain, a simple spacing mechanism often self-organizes organ positioning into phyllotactic spirals, with the specific angle chosen likely related to conditions when the pattern is first established (Douady & Couder, 1992; Smith *et al.*, 2006b). Thus, a more appropriate way to frame the question of what evolutionary forces shape phyllotaxis might be to focus on why spiral phyllotaxis rather than on the particular case of why 137.5°. One possibility is that the mechanism under selection is able to produce approximately optimal light capture (or packing) with a simple spacing mechanism from a growing plant tip. Even though this may lead to several possibilities for the divergence angle, the fitness outcome is similar, as simulations with the various spiral phyllotaxis angles all had relatively equal light capture. Thus, our data are consistent with the idea that the mechanism of iterative organ initiation, which yields spiral phyllotaxis, might be prevalent owing to developmental accessibility and stability rather than reflecting optimization of a particular divergence angle (Goodwin, 2009). Overall, our findings highlight the importance of considering the interplay of developmental constraints and potential fitness benefits for the emergence of developmental patterns or complex traits (Gould, 2002; Sorrells *et al.*, 2015).

Acknowledgements

We thank Adam Runions, Burghard Herrmann, and Sheila McCormick for discussions and critical reading and comments on the manuscript. Funding for this research is gratefully acknowledged from the Swiss National Science Foundation Interdisciplinary Grant CR3213_143833 and SystemsX.ch 'Plant Growth' Research and Technology Development Grant to RSS, Human Frontier Science Program grant RGP0008/2013 to RSS, Natural Sciences and Engineering Research Council of Canada Discovery Grant RGPIN-2014-05325 to PP, and a core grant by the Max Planck Society to MT.

Author contributions

PP, MT, and RSS planned and designed the research. JL performed experiments. SS performed computational simulations. SS, JL, and RSS wrote the manuscript with input from the other authors. SS and JL contributed equally to this work.

ORCID

Janne Lempe https://orcid.org/0000-0002-3890-6997
Richard S. Smith https://orcid.org/0000-0001-9220-0787
Sören Strauss https://orcid.org/0000-0002-1825-0097

References

Adler I. 1974. A model of contact pressure in phyllotaxis. *Journal of Theoretical Biology* **45**: 1–79.

Adler I, Barabé D, Jean RV. 1997. A history of the study of phyllotaxis. *Annals of Botany* **80**: 231–244.

Beldade P, Brakefield PM. 2002. The genetics and evo–devo of butterfly wing patterns. *Nature* **3**: 442–452.

Bell AD, Bryan A. 1991. *Plant form: an illustrated guide to flowering plant morphology.* New York, NY, USA: Oxford University Press.

Besnard F, Refahi Y, Morin V, Marteaux B, Brunoud G, Chambrier P, Rozier F, Mirabet V, Legrand J, Lainé S *et al.* 2014. Cytokinin signalling inhibitory fields provide robustness to phyllotaxis. *Nature* **505**: 417–421.

Bongers FJ, Evers JB, Anten NPR, Pierik R. 2014. From shade avoidance responses to plant performance at vegetation level: using virtual plant modelling as a tool. *New Phytologist* **204**: 268–272.

Cartolano M, Pieper B, Lempe J, Tattersall A, Huijser P, Tresch A, Darrah PR, Hay A, Tsiantis M. 2015. Heterochrony underpins natural variation in *Cardamine hirsuta* leaf form. *Proceedings of the National Academy of Sciences, USA* **112**: 10539–10544.

Douady S, Couder Y. 1992. Phyllotaxis as a physical self-organized growth process. *Physical Review Letters* **68**: 2098.

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

Fankhauser C, Christie JM. 2015. Plant phototropic growth. *Current Biology* **25**: R384–R389.

Federl P, Prusinkiewicz P. 1999. VIRTUAL LABORATORY: an interactive software environment for computer graphics. *Proceedings of Computer Graphics International* **242**: 93–100.

Franklin KA. 2008. Shade avoidance. *New Phytologist* **179**: 930–944.

Gan X, Hay A, Kwantes M, Haberer G, Hallab A, Dello Ioio R, Hofhuis H, Pieper B, Cartolano M, Neumann U *et al.* 2016. The *Cardamine hirsuta* genome offers insight into the evolution of morphological diversity. *Nature Plants* **2**: 16167.

Givnish TJ. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* **15**: 63–92.

Givnish TJ. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species. In: Gartner BL, ed. *Plant stems: physiology and functional morphology.* San Diego, CA, USA: Academic Press, 3–49.

Goodwin B. 2009. Beyond the Darwinian paradigm: understanding biological forms. In: Ruse M, Travis J, eds. *Evolution: the first four billion years.* Cambridge, MA, USA: Harvard University Press, 299–312.

Gould SJ. 2002. *The structure of evolutionary theory.* Cambridge, MA, USA: Harvard University Press.

Hay A, Tsiantis M. 2006. The genetic basis for differences in leaf form between *Arabidopsis thaliana* and its wild relative *Cardamine hirsuta. Nature Genetics* **38**: 942–947.

Heisler MG, Hamant O, Krupinski P, Uyttewaal M, Ohno C. 2010. Alignment between PIN1 polarity and microtubule orientation in the shoot apical meristem reveals a tight coupling between morphogenesis and auxin transport. *PLoS Biology* **8**: e1000516.

Heisler MG, Jönsson H. 2006. Modeling auxin transport and plant development. *Journal of Plant Growth Regulation* **25**: 302–312.

Hofmeister WFB. 1868. *Allgemeine Morphologie der Gewächse, Handbuch der Physiologischen Botanik (W Engelmann, Ed.).* Leipzig, Germany: W. Engelmann.

Jean RV. 1994. *Phyllotaxis: a systemic study in plant morphogenesis.* Cambridge, UK: Cambridge University Press.

Jönsson H, Heisler MG, Shapiro BE, Meyerowitz EM, Mjolsness E. 2006. An auxin-driven polarized transport model for phyllotaxis. *Proceedings of the National Academy of Sciences, USA* **103**: 1633–1638.

King S, Beck F, Lüttge U. 2004. On the mystery of the golden angle in phyllotaxis. *Plant, Cell & Environment* **27**: 685–695.

Marzec C, Kappraff J. 1983. Properties of maximal spacing on a circle related to phyllotaxis and to the golden mean. *Journal of Theoretical Biology* **103**: 201–226.

Maynard Smith J, Burian R, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L. 1985. Developmental constraints and evolution: a perspective from the Mountain Lake Conference on Development and Evolution. *Quarterly Review of Biology* **60**: 265–287.

Michaels SD, Amasino RM. 1999. *FLOWERING LOCUS C* encodes a novel MADS domain protein that acts as a repressor of flowering. *Plant Cell* **11**: 949–956.

Mitchison GJ. 1981. Theories of biological pattern formation – the polar transport of auxin and vein patterns in plants. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **295**: 461–471.

Niklas KJ. 1988. The role of phyllotactic pattern as a ‘developmental constraint’ on the interception of light by leaf surfaces. *Evolution* **42**: 1–16.

Niklas KJ. 1998. *Light harvesting ‘fitness landscapes’ for vertical shoots with different phyllotactic patterns.* In: Jean RV, Barabé D, eds. *Symmetry in plants.* Singapore: World Scientific Publishing, 759–773.

Novoplansky A, Cohen D, Sachs T. 1990. How portulaca seedlings avoid their neighbours. *Oecologia* **82**: 490–493.

Osmond CB, Austin MP, Berry JA, Billings WD, Boyer JS, Dacey JWH, Nobel PS, Smith SD, Winner WE. 1987. Stress physiology and the distribution of plants. *BioScience* **37**: 38–48.

Pearcy RW, Yang W. 1998. The functional morphology of light capture and carbon gain in the redwood forest understorey plant, *Adenocaulon bicolor* Hook. *Functional Ecology* **12**: 543–552.

Peaucelle A, Morin H, Traas J, Laufs P. 2007. Plants expressing a *miR164*-resistant *CUC2* gene reveal the importance of post-meristematic maintenance of phyllotaxy in *Arabidopsis. Development* **134**: 1045–1050.

Pierik R, de Wit M. 2014. Shade avoidance: phytochrome signalling and other aboveground neighbour detection cues. *Journal of Experimental Biology* **65**: 2815–2824.

Poethig RS. 1990. Phase change and the regulation of shoot morphogenesis in plants. *Science* **250**: 923–930.

Poethig RS. 2013. Vegetative phase change and shoot maturation in plants. *Current Topics in Developmental Biology* **105**: 125–152.

Reinhardt D, Pesce E-R, Stieger P, Mandel T, Baltensperger K, Bennett M, Traas J, Friml J, Kuhlemeier C. 2003. Regulation of phyllotaxis by polar auxin transport. *Nature* **426**: 255–260.

Sarlikioti V, De Visser PHB, Marcelis LFM. 2011. How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional–structural plant model. *Annals of Botany* **108**: 1065–1073.

Smith C, Prusinkiewicz P, Samavati F. 2003. Local specification of surface subdivision algorithms. Applications of Graph Transformations with Industrial Relevance: Second International Workshop, AGTIVE 2003, vol. 3062 of Lecture Notes in Computer Science. Berlin, Germany: Springer-Verlag, 313–327.

Smith H, Whitelam GC. 1997. The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant, Cell & Environment* **20**: 840–844.

Smith RS, Guyomarc’h S, Mandel T, Reinhardt D, Kuhlemeier C, Prusinkiewicz P. 2006a. A plausible model of phyllotaxis. *Proceedings of the National Academy of Sciences, USA* **103**: 1301–1306.

Smith RS, Kuhlemeier C, Prusinkiewicz P. 2006b. Inhibition fields for phyllotactic pattern formation: a simulation study. *Canadian Journal of Botany* **84**: 1635–1649.

Sorrells TR, Booth LN, Tuch BB, Johnson AD. 2015. Intersecting transcription networks constrain gene regulatory evolution. *Nature* **523**: 361.

Takenaka A. 1994. Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. *Ecological Research* **9**: 109–114.

Thomas H. 2013. Senescence, ageing and death of the whole plant. *New Phytologist* **197**: 696–711.

Thornley JHM. 1975. Phyllotaxis. I. A mechanistic model. *Annals of Botany* **39**: 491–507.

Valladares F, Brites D. 2004. Leaf phyllotaxis: does it really affect light capture? *Plant Ecology* **174**: 11–17.

Veen AH, Lindenmayer A. 1977. Diffusion mechanism for phyllotaxy. *Plant Physiology* **60**: 127–139.

Vlad D, Kierzkowski D, Rast MI, Vuolo F, Dello Ioio R, Galinha C, Gan X, Hajheidari M, Hay A, Smith RS *et al.* 2014. Leaf shape evolution through duplication, regulatory diversification, and loss of a homeobox gene. *Science* **780**: 780–783.

Willmann MR, Poethig RS. 2011. The effect of the floral repressor *FLC* on the timing and progression of vegetative phase change in *Arabidopsis*. *Development* **138**: 677–685.

Yotsumoto A. 1993. A diffusion model for phyllotaxis. *Journal of Theoretical Biology* **162**: 131–151.

Zotz G, Reichling P, Valladares F. 2002. A simulation study on the importance of size-related changes in leaf morphology and physiology for carbon gain in an epiphytic bromeliad. *Annals of Botany* **90**: 437–443.

Supporting Information

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

Fig. S1 Light capture curves normalized to the respective total leaf area of the idealized plants and for bijugate plants.

Fig. S2 Further simulation results for the variation of different leaf traits (translucency, photosynthetic decrease & internode type).

Fig. S3 Further simulation results for the variation of different leaf traits (lobe angle, size and width for lobed leaves as well as leaflet angle and position for dissected leaves).

Fig. S4 Light capture curve of real plants using the scanned leaves compared with plants consisting of idealized leaves (*A. thaliana* vs simple leaves & *C. hirsuta* vs dissected leaves).

Fig. S5 Light capture area plot of plants with different leaf numbers consisting of a single shape of *A. thaliana* leaves compared with the wild type plant.

Fig. S6 The influence of noise in the divergence angle on the Light Capture Efficiency.

Table S1 Observed light capture maxima divergence angles and their corresponding generating sequences.

Table S2 Observed light capture minima and their corresponding divergence angles.

Video S1 Model simulation using 30 idealized leaves while increasing the divergence angle from 0° to 120°.

Video S2 Model simulation using scanned *A. thaliana* leaves while increasing the divergence angle from 0° to 180°.

See also the Commentary on this article by Sicard, **225**: 13–15.