

REVIEW PAPER

Constraints of space in plant development

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Abstract

Like all forms in nature, plants are subject to the properties of space. On the one hand, space prevents configurations that would place more than one component in the same location at the same time. A generalization of this constraint limits proximity and density of organs. On the other hand, space provides a means for a plant to create three-dimensional forms by differentially controlling their growth. This results from a connection between the metric properties of surfaces and their Gaussian curvature. Three strategies used by plants to develop within the constraints of space are presented: expansion to another dimension, egalitarian partitioning of space, and competition for space. These strategies are illustrated with examples of curved surfaces of leaves and petals, self-similar branching structures of compound leaves and inflorescences, and tree architecture. The examples highlight the fundamental role of the constraints of space in plant development, and the complementary role of genetic regulation and space-dependent emergent phenomena in shaping a plant.

Key words: Competition for space, curvature, dimension, fractal, genetic regulation of form, leaf margin, metric, plant modelling, tree architecture.

Introduction

Constraints on form imposed by obstacles in space are fairly intuitive. For example, the border of a pool table prevents the balls from moving outside the table. Players can turn this constraint to their advantage and create an otherwise impossible path by bouncing a ball off the border. The border thus both limits and extends the range of possible paths. Even empty space, however, puts constraints on the forms embedded in it. Like the border of the pool table, these constraints play the dual role of making some forms impossible while providing a means for creating other forms. The fundamental constraint is the subject of Aristotle's exclusion principle, which states that material objects extend in space, and no two objects can be in the same place at once (Aristotle, 350 BC, Book IV; Morison, 2002). Taken literally, this principle prevents interpenetration of colliding objects competing for physical space. Interpreted more broadly, it provides a geometric abstraction of spatial interactions mediated by diverse phenomena, such as red/far red ratio signalling and

competition for spatially distributed resources including light, water, and mineral nutrients. Space itself can be viewed as a resource and an object of resource-mediated competition, since, when 'consumed' by one plant or plant organ, it becomes unavailable to other plants or organs (Stoll and Weiner, 2000).

A more subtle constraint is a consequence of Gauss's Theorema Egregium (Gauss, 1902, p. 20; Vaisman, 1984, p. 122), which relates the metric properties of surfaces—distances, areas and angles—to the surface curvature. A precise statement of the Gauss theorem is mathematically involved, but its essence can be illustrated using a simple geometric construction. Consider a regular hexagon: it is a planar figure that can be divided into six equilateral triangles (Fig. 1A). Remove one of them and glue together the free edges of the triangles on both sides of the resulting gap. The glued surface will consist of five equilateral triangles arranged around a common vertex, and will no longer be planar, but will form a cup

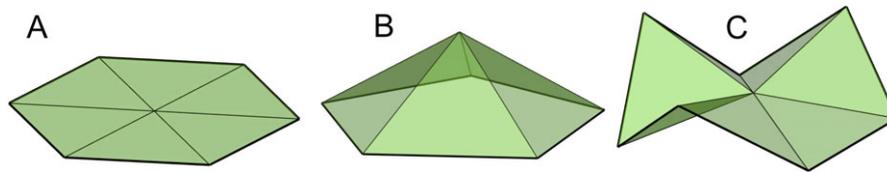


Fig. 1. Illustration of Gauss's Theorema Egregium. Change of metric in a regular hexagon (A), induced by the removal of a triangle, produces a cup-like shape (positive Gaussian curvature) (B). Conversely, insertion of a triangle produces a saddle shape (negative curvature) (C).

(Fig. 1B). Conversely, if an additional triangle is inserted, so that the resulting surface consists of seven equilateral triangles arranged around a common vertex, the resulting surface will have a saddle-like shape with a wavy border (Fig. 1C). Thus (in the presence of many assumptions implied in this example) an excess of surface area with respect to the border length will produce a cup-like shape (a surface with positive Gaussian curvature), whereas an excess in border length with respect to the area will imply a saddle form (negative curvature). The impact of these relations on natural forms was succinctly characterized by Stevens (1974, pp. 8–9): ‘No matter how we try, we cannot make a saddle from five equilateral triangles or a simple cup from seven. Nature, too, is similarly constrained: she makes cups and saddles not as she pleases but as she must, as the distribution of material dictates.’

Selected examples of the roles that Aristotle's exclusion principle and Gauss's Theorema Egregium play in shaping plants are discussed below.

Growth and form of surfaces

Relations between growth and form can be considered at different spatial scales and levels of abstraction. For example, the growing thin tissue of an organ, such as a leaf or a petal, can be viewed as an assembly of individual cells or approximated as a continuous surface. The latter approach provides a convenient framework for explaining the form of biological surfaces at macroscopic scales, where properties of individual cells can be averaged out (Coen *et al.*, 2004).

Conceptual frameworks for relating growth to form have been proposed by Rodriguez *et al.* (1994) (see also Goriely and Ben Amar, 2007) and, in the case of thin sheets, by Klein *et al.* (2007). Here we focus on the latter framework due to its emphasis on geometry. As shown in Fig. 2, growth or shrinkage changes the surface metric (distances between points). This change may induce positive or negative Gaussian surface curvature, as prescribed by the Gauss theorem. In some cases (closed convex surfaces), Gaussian curvature distribution uniquely defines the overall form of the surface (Cauchy and Alexandrov–Pogorelov theorems, Alexandrov, 2005). In general, however, the definition of a surface in terms of its metric may be under- or overconstrained, which means that there are many

solutions or none, respectively¹. Elastic properties of thin tissues are then called upon to address both problems. In the former case, elasticity introduces additional factors, such as minimization of stretching and bending energy, to reduce the number of solutions. In the latter case, it resolves contradictions present in the overconstrained systems by allowing solutions that are ‘close enough’. The final forms may have residual stresses, which implies that their actual metrics differ to some extent from the target metrics prescribed by growth.

The interplay between metric and elastic properties in the shaping of surfaces has been studied in physical experiments. Sharon *et al.* (2002, 2004) considered thin rectangular sheets of plastic that were torn by pulling from the sides. The high stresses near the propagating crack irreversibly stretched the adjacent material, with the greatest deformations occurring in the immediate proximity of the crack. After the stresses were removed and the torn sheet was free to relax, the cracked edge spontaneously buckled, forming a fractal cascade of waves built upon each other. Sharon *et al.* conjectured that a similar buckling is caused by the differential growth of biological surfaces, and supported this conjecture with many examples of biological surfaces that are strikingly similar to those obtained in their experiments (Sharon *et al.*, 2004). They concluded that ‘no genetic coding is needed to instruct pieces of a leaf to curl up and curl down. All that is required is a growth process to elongate the sheet along its edge – elasticity takes care of the rest’ (Sharon *et al.*, 2002).

More recently, Klein *et al.* (2007) designed experiments in which thin gel sheets shrank when temperature was increased above a threshold value. The shrinkage ratio was controlled locally by regulating the concentration of polymerizing monomers in the gel. Depending on the distribution of shrinking ratios, this process yielded a variety of

¹ Studies of the existence and uniqueness of the embeddings of surfaces with a given metric have an extensive and illustrious history (Han and Hong, 2006). The resulting theorems depend on the degree of the continuity of the metric and the surface, and—in a more abstract setting—on the number of dimensions of the surface and the ambient space. Solutions need not exist if growth specification calls for different growth rates in adjacent regions, and thus for a discontinuous resulting metric. Biologically, this case corresponds to non-symplastic growth (Priestley, 1930; Romberger *et al.*, 1993), during which cells slide with respect to each other. In the modelling practice, overconstraining may also occur while approximating curved surfaces with (straight-edge) polygon meshes.

shapes including cups and saddles with smoothly waving or fractal margins, again resembling those found in plants.

Similar results have been obtained using computer simulations. Prusinkiewicz and Streibel (1986) proposed a purely geometric method for generating surfaces by the prescription of distances, and illustrated it with examples of simple surfaces with positive and negative curvature. They also identified problems caused by the presence of multiple solutions. Dimian (1997), Matthews (2002), and Combaz and Neyret (2002, 2006) developed computational counterparts of the physical experiments on programmable gels. Changes of metric were specified interactively, by painting morphogens that induced stretching or shrinking of an elastic surface model. For example, the model by Matthews (2002) visualizes the basic properties of a physical sheet undergoing differential growth: the production of a cup-like shape when the surface expansion is not matched by the expansion of the border; the production of a saddle shape when the border expands more than the interior and the decrease of expansion rates towards the interior is slow; and the emergence of waves at the expanding border when the decrease of expansion rates towards the interior is fast (Fig. 3).

The relations between growth distribution, mechanical properties of the sheet, and the form of waves emerging at the sheet border have been the subject of several theoretical analyses (Audoly and Boudaoud, 2003; Marder *et al.*, 2003;

Sharon *et al.*, 2007). A simulation model that elucidates the factors controlling the frequency of simple waves such as found in *Asplenium australasicum* (bird's nest fern) (Fig. 4A, B) was proposed by Dimian (1997). In its essence, the model is a rectangular surface approximated by a sequence of parallel rods (Fig. 4C). At one end, the rods are attached to an axis about which they can rotate. At the other end, the rods are connected by growing edge segments (stiff linear springs), which cause the surface to buckle as their length increases. The system is complemented by two types of rotational springs. Type 1 springs are located at the axis and counter out-of-plane dislocation. Type 2 springs are located along the growing edge and counter its bending (Fig. 4D). Simulations show that if Type 1 springs are relatively weak compared with Type 2, the system settles in a configuration with a small number of large waves (Fig. 4D). Conversely, if Type 2 springs are relatively weak compared with Type 1, the final configuration consists of a larger number of small waves (Fig. 4E,F). Thus, in this model, the departure from a planar configuration is a geometric necessity imposed by the extension of the growing edge with respect to the rigid axis, while the frequency and amplitude of the emerging waves are determined by the elastic properties of the system.

The emergence of fractal cascades of waves of decreasing amplitude and increasing frequency is illustrated in Fig. 5, using kale leaves (a variety of *Brassica oleracea*, Fig. 5A, B)

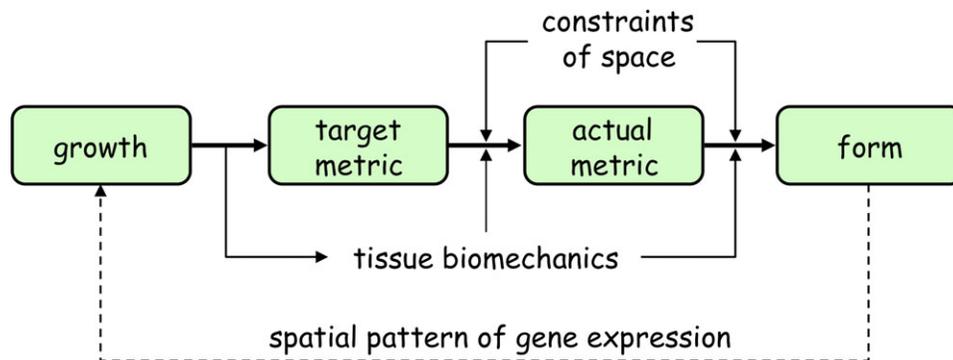


Fig. 2. Relation between growth, metric and form of surfaces according to the conceptual model of Klein *et al.* (2007).

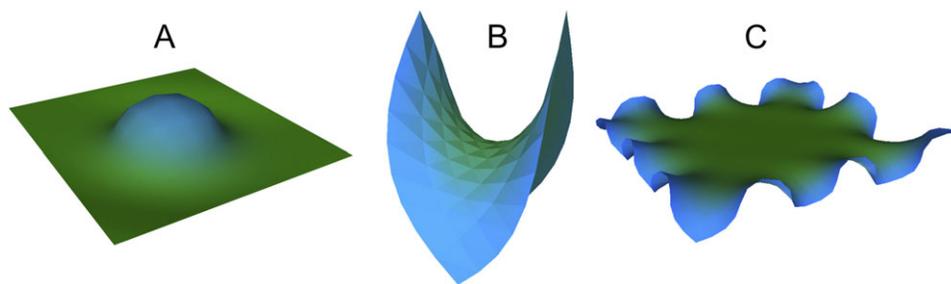


Fig. 3. Snapshots from an interactive program illustrating relations between growth, metric, and form (Matthews, 2002). The simulation begins with a relaxed square shape. Deposition of a growth-inducing morphogen (blue) in the central parts of the surface causes the formation of a cup-like shape (A). Deposition of the morphogen at the margin, with the concentrations slowly decreasing towards the centre, induces a saddle shape (B). Deposition of the morphogen along the margin, with the concentration quickly decreasing towards the centre, results in a wavy border (C).

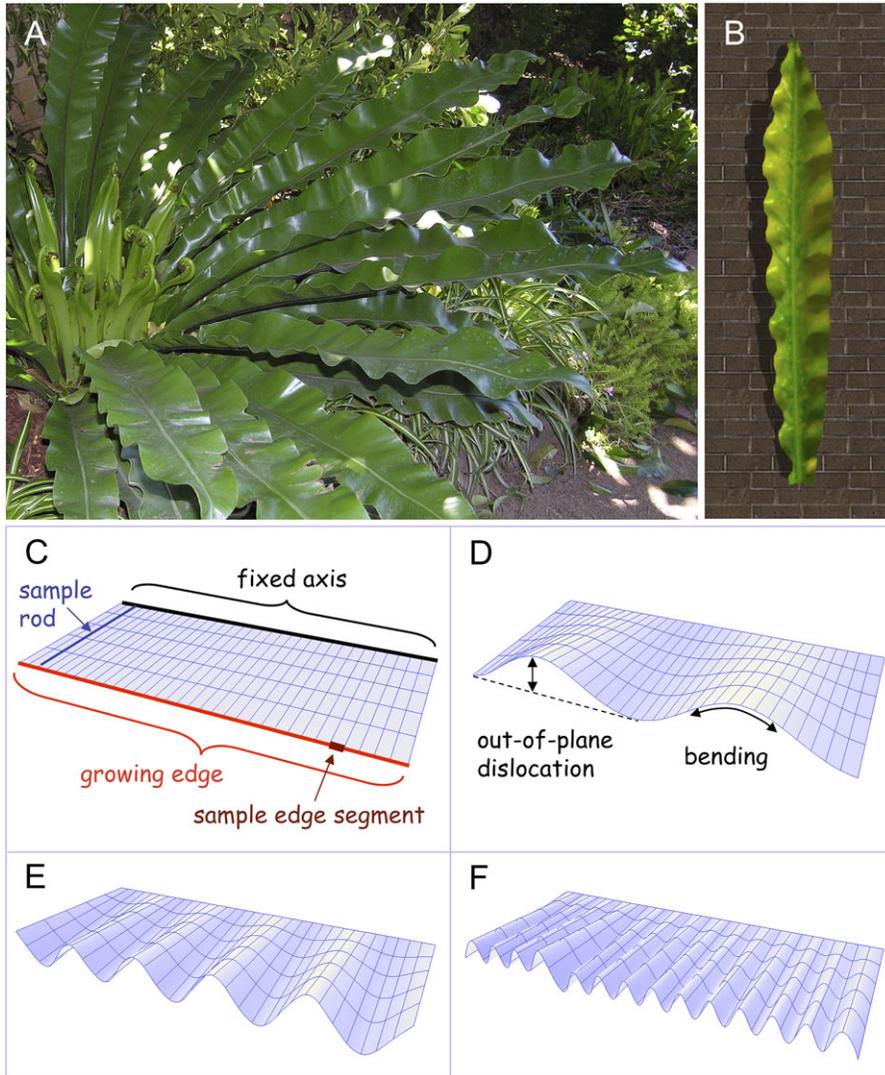


Fig. 4. Simulation study of wavy leaves. A photograph (A) and a simulation model (B) of *Asplenium australasicum* leaves showing simple waves along the margin. The model was constructed by joining surface models representing the left and right parts of the blade along the midrib. Each surface was represented as a sequence of rods spanning the area between a fixed axis and a growing edge (C). An increase in the growing edge length causes buckling, which is controlled by the relative strength of springs that counter out-of-plane dislocation and springs that counter bending of the growing edge (D). Simulations show that increasing the strength of the former type of springs compared to the latter type decreases the wavelength and amplitude of the waves (E). This effect is amplified as the ratio of spring strengths increases (F). In the leaf model (B), waves are an emergent property of the surface metric and the buckling process, while the overall leaf shape, tapered towards the base and near the tip, was specified explicitly. Image (B) from Dimian (1997) courtesy of Daniel Dimian, (C–F) courtesy of Steven Longay.

as a reference. In the model, a square surface is divided into rows of geometrically similar rectangles, each of which is further subdivided into three triangles (Fig. 5C). Beginning with a single rectangle at the top, the number of rectangles in each row increases by a factor $N=2$. Initially the structure is embedded in a plane, which requires that the length of the horizontal edges of the rectangles decrease by the scaling ratio $r = \frac{s_{i+1}}{s_i} = 0.5$ between consecutive rows. Growth is modelled as a change of metric such that $r > 0.5$. A geometric construction shows that cross-sections of the resulting surface then form a cascade of wedges of decreasing size, each supported by the previous wedge (Fig. 5D). The length of the polygonal lines representing

consecutive sections is equal to $s_0(2r)^i$, and thus increases exponentially with i for $r > 0.5$. The fractal dimension D of these lines can be calculated by solving the equation $Nr^D=1$ (Falconer, 1990, p. 117) and is greater than 1 for r between 0.5 and 1, indicating that the cross-sections are indeed fractal. The scaling ratio $r = \frac{\sqrt{2}}{2} \approx 0.707$ represents the limit case for which the fractal dimension D is equal to 2. With $i \rightarrow \infty$, the margin of the surface would then fill a portion of the plane within gaps. To avoid self-intersections of the surface, buckling directions have been imposed corresponding to the space-filling dragon curve (Mandelbrot, 1982, p. 66) (Fig. 5E) on the model. The resulting surface (Fig. 5F) resembles kale leaves. Other changes of metric

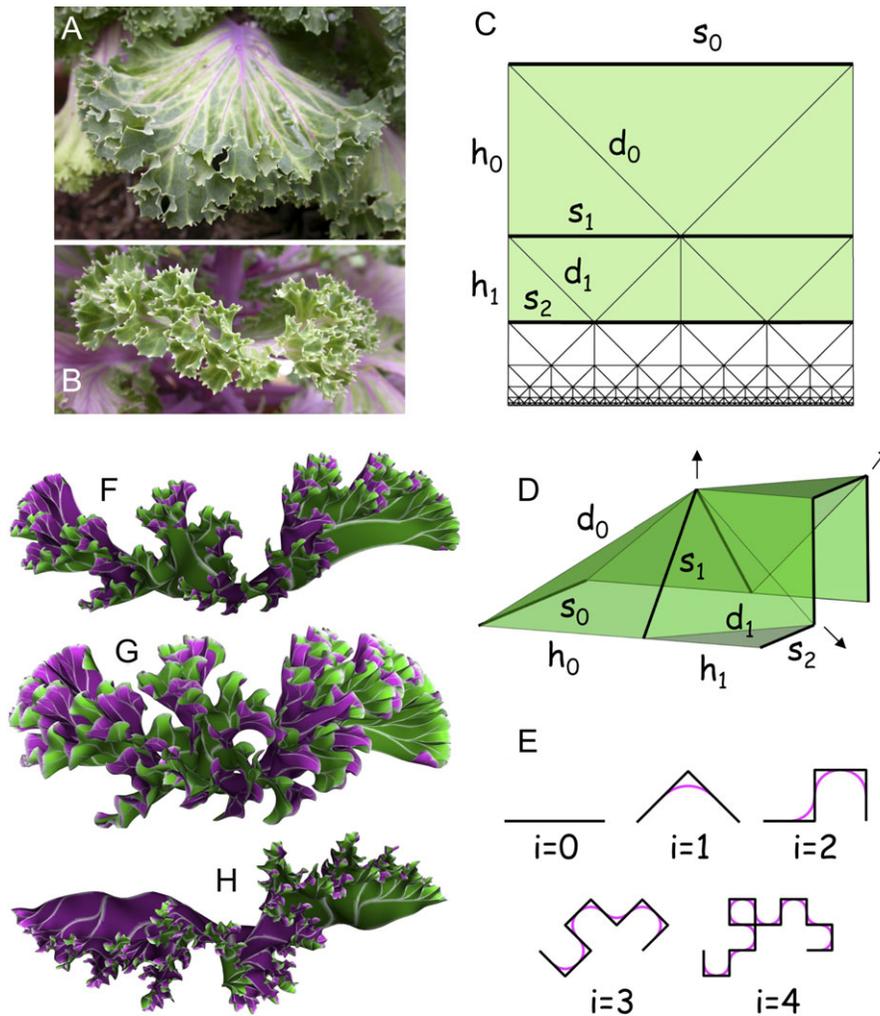


Fig. 5. Simulation study of surfaces with a fractal cascade of waves at the margin. (A) A kale (a variety of *Brassica oleracea*) leaf showing a superposition of waves with a decreasing amplitude and wavelength towards the leaf margin. (B) The fractal character of the leaf margin. (C) A computational representation of a leaf. The surface is divided into rows of geometrically similar rectangles, each row with twice the number of rectangles as its predecessor. The first two rows are highlighted in green. Each rectangle is further subdivided into three triangles. Proportions are controlled by the scaling ratio r , initially set to $\frac{1}{2}$, such that $s_{i+1}=h_i=rs_i$ and $d_i=r\sqrt{2}s_i$ for $i=0,1,2,\dots$ (D) The highlighted portion of the surface (C) after increasing the scaling ratio to $r=\frac{\sqrt{2}}{2}$. Arrows indicate buckling directions imposed on the surface to avoid self-intersections. The resulting cross-sections (bold lines) correspond to consecutive generations of the dragon curve (Mandelbrot, 1982, p. 66). (E) Several generations of the dragon curve (black lines) and their smooth approximations (magenta lines). (F) The model of a kale leaf, generated using 10 rows of smoothed rectangles with $r=\frac{\sqrt{2}}{2}$. (G) The surface obtained by increasing the scaling ratio r to 0.8. (H) The surface generated with $r=\frac{\sqrt{2}}{2}$ and $d_i=rs_i$. In the simulations, all edges were represented as springs with the rest lengths defined by the target metric. The final forms exhibit no residual stresses.

produce surfaces with a larger amplitude of waves (Fig. 5G) or with serrated margins (Fig. 5H).

The uses of the dragon curve to resolve buckling directions may appear to be a purely heuristic technique for creating non-self-intersecting fractal surfaces and surface margins. It raises, however, interesting questions regarding physical and biological mechanisms that create such forms. One possibility is that non-self-intersecting fractal surfaces may represent a minimum-energy state of buckling elastic plates. Such plates might have non-uniform mechanical properties, reflecting, for example, the presence of veins in a leaf. Another possibility, applicable to leaves that develop within buds (Couturier *et al.*, 2009), is that buckling

directions are predetermined by the pattern in which young leaves are folded in the buds. The fractal character of repetitive folding has been revealed in previous mathematical studies (Dekking *et al.*, 1982).

The above examples support the two-stage model of plant surface development, according to which the form of some biological surfaces is not genetically programmed in detail, but results from a coarse genetic control of growth rates, complemented by emergent processes induced by geometric constraints of space and elasticity (Green 1996, 1999). The plausibility of this model is further corroborated by recent genetic experiments. Nath *et al.* (2003) explained the difference between the flat leaves of wild type *Antirrhinum*

majus (snapdragon) (Fig. 6A) and the negative-curvature leaves of its *cincinnata* mutant (Fig. 6B–D) in terms of delayed growth arrest on the margin of mutant leaves causing their excessive expansion. Efroni *et al.* (2008) analysed and provided a similar explanation for the wrinkled form of *Arabidopsis* leaves with a reduced activity of *CINCINNATA-TCP* growth regulators (Fig. 6E). Some of these leaves resemble kale (Fig. 6F), which suggests a general mechanism involved in producing wrinkled leaf shapes across different taxa. The distinction between saddle surfaces (Fig. 6B, C), simple waves (Figs 4A, 6D) and fractal cascades of waves at the margin (Figs 5A, B, 6E, F) can be attributed to the different distributions of growth rates. Simulations show that a slow increase of growth rates

towards a margin transforms a flat surface into a saddle (Fig. 3B), a faster increase localized near the margin produces simple waves (Figs 3C, 4D–F), and exponential expansion towards the margin produces fractal cascades of waves (Fig. 5F–H) (see also Sharon *et al.*, 2007, Fig. 2).

Space constraints and branching forms

The constraints of space discussed in the previous section manifest themselves by expanding flat surfaces into a third dimension and result in surfaces with negative when the Gauss theorem does not allow them to remain flat. Constraints of space are not limited to surfaces, however.

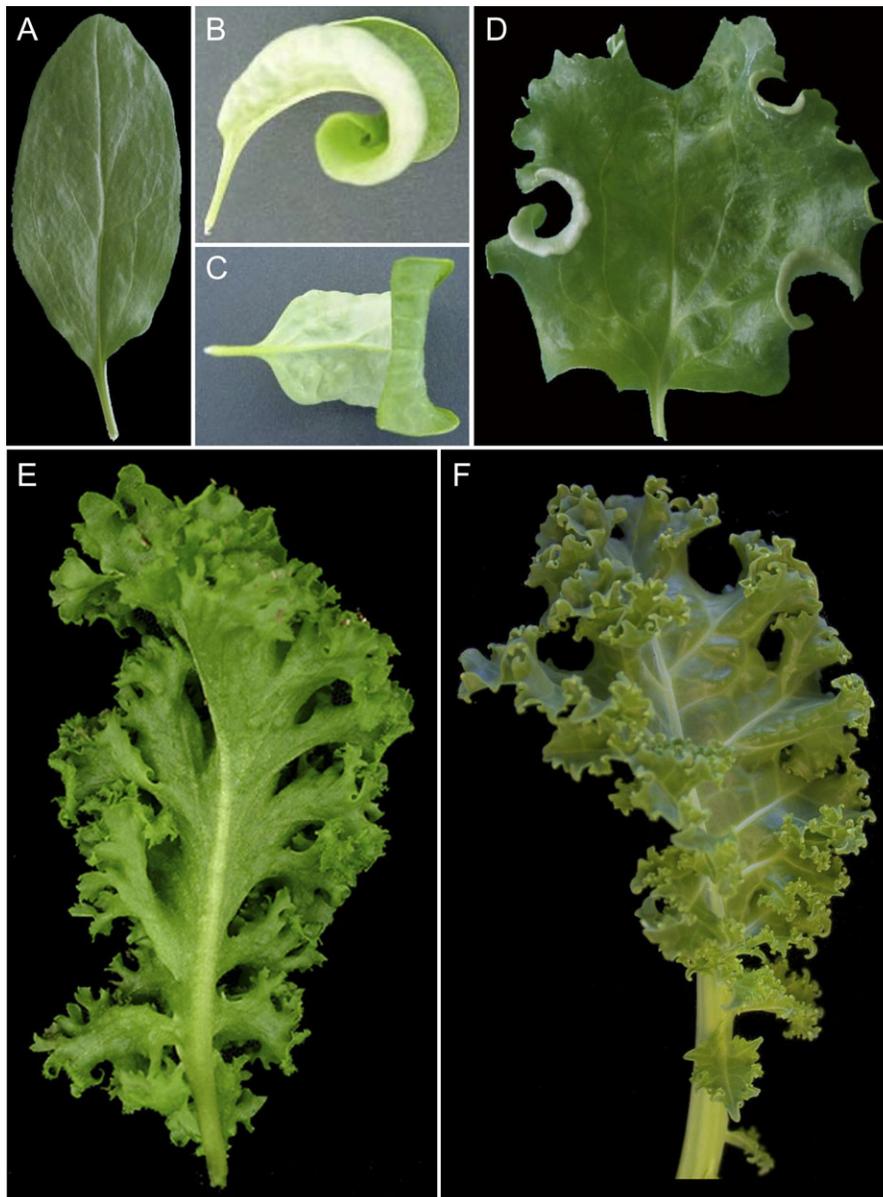


Fig. 6. Genetic basis of the emergence of negative curvature in leaves. (A–D) Sample leaves of wild type (A) and *cincinnata* mutants (B–D) of *Antirrhinum majus*. (E) Leaf of *Arabidopsis thaliana* with reduced *CIN-TCP* levels. (F) A young kale leaf. Images (A) and D courtesy of Enrico Coen and John Innes Centre; (B, C) courtesy of Utpal Nath, (E) from (Efroni *et al.*, 2009) courtesy of Yuval Eshed, copyright American Society of Plant Biologists, reprinted with permission.

In particular, they also play an important role in the development of branching structures.

The relations between branching angles, branch segment lengths, and the occupancy of space by small branching structures with a fixed topology were examined in the pioneering studies by Honda and Fisher (1978, 1979). Using simulation models, they found that the values of these parameters observed in nature approximately maximize the coverage of space. Further insights into the interplay between branching structures and space can be obtained by considering compound forms with a more repetitive structure (Fig. 7A–D).

Regular arrangements of modules of the same size along an axis extending in one dimension can be characterized by the symmetries of the pattern. A single translational symmetry underlies monopodial structures, which extend in one spatial dimension (Fig. 7A, E). Additional translational symmetries of the lateral axes produce double-compound structures that occupy a portion of the plane (Fig. 7B, F). Likewise, triple-compound structures may fill a three-dimensional volume (not shown). However, if the branch order is not limited, the resulting branching pattern no

longer fits in the available space: the modules intersect and overlap (Fig. 7G).

The following reasoning (Borchert and Slade, 1981) shows that the impossibility of embedding an indeterminate recursively-branching structure with equally-sized branch segments is a consequence of the properties of space. Consider a rhythmically developing tree that, in each season, creates two new branches at each terminal node. After n seasons, this structure would have $N=2^n$ terminal nodes. Assume that all branch segments are of approximately equal length l , such that all terminal nodes, and leaves that they may bear, are arranged in a hemisphere. After n seasons, this hemisphere will have radius nl and surface area $A=2\pi(nl)^2$. As age n increases, the area allocated to a leaf, $A_L=A/N$, will thus asymptotically decrease to 0. This decrease is caused by a disparity between the exponentially growing number of elements to be placed and the much more slowly growing available space. A similar disparity would occur if the distribution of internodes and leaves was considered throughout the volume of a tree crown, or if the discussion was restricted to planar branching patterns.

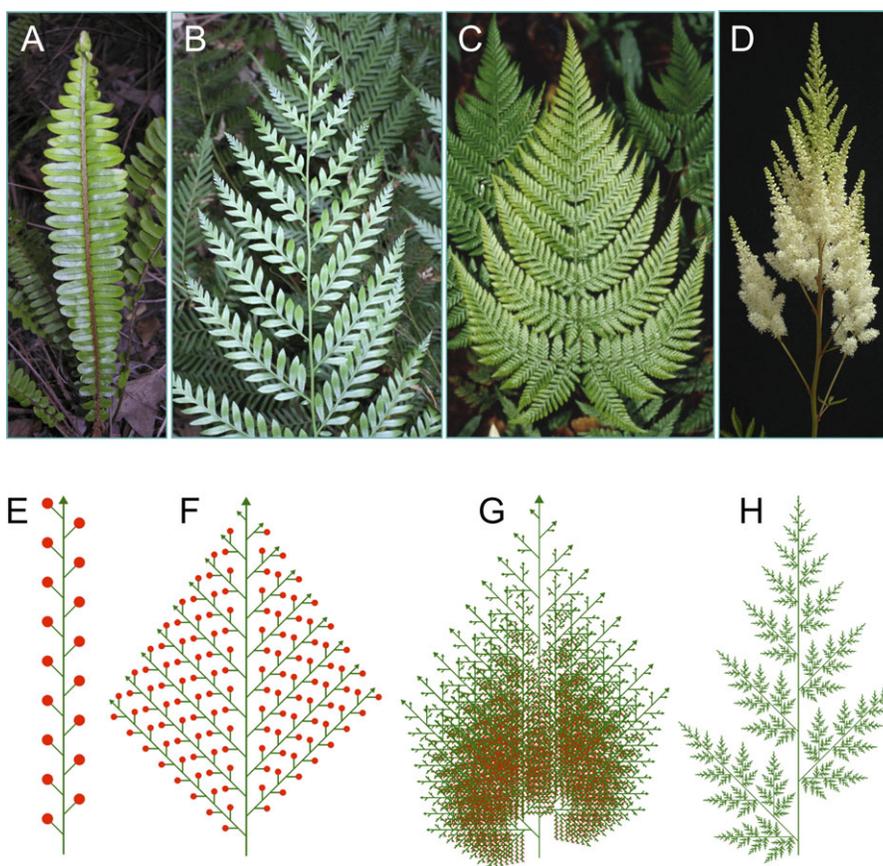


Fig. 7. Selected branching patterns (A–D) and their idealizations (E–H). Pinnate (A), bi-pinnate (B), and recursively compound (C) fern fronds. (D) An approximately self-similar inflorescence of *Astilbe* sp. with a spiral phyllotaxis. This inflorescence can be viewed as a three-dimensional counterpart of the planar frond (C). (E) Single-compound monopodial structure. Red circles denote organs, e.g. pinnae, leaves or flowers, and the triangle denotes an apical meristem. (F) A double-compound structure. (G) A hypothetical structure with indeterminate recursive branching and all segments of the same order having the same size. Note intersecting and overlapping segments in the basal part of the structure. (H) Self-similar branching structure with the same topology as (G), but with the branch segment size decreasing exponentially towards the extremities.

There are two ways in which this disparity can be resolved: a gradual decrease in the size of elements or in their number. The first strategy can be analysed most easily assuming shortening of child internodes with respect to their parent internode by a constant factor $r < 1$. The structure obtained for $r_{2D} = \frac{\sqrt{2}}{2}$ and a branching angle of 90° describes the limit case, in which a rectangular area is uniformly filled by a branching structure without collisions and intersections (Fig. 8A) (Mandelbrot 1982, pp. 164–165; MacDonald, 1983, pp. 140–143). Likewise, the structure obtained for $r_{3D} = 2^{-\frac{1}{3}}$ describes the limit case of a repetitive branching pattern filling a volume (Fig. 8B). The ratios r_{2D} and r_{3D} are the solutions to the equation $Nr^D=1$, discussed in the previous section. In this case, $N=2$ is the number of child segments produced in one generation, and D is the dimension of space: either 2 or 3. The formula $Nr^D=1$ can be generalized to the case where the daughter branch segments are shortened by different ratios, r_1 and r_2 , then adopting the form $\sum_{k=1}^N r_k^D = 1$ (Mandelbrot, 1982, pp. 56–57; Falconer, 1990, Chapter 9.2). Approximating this equation for $D=2$ and various values of rates r_1 and r_2 creates—for suitably chosen branching angles—fractal structures (Fig. 7H) that resemble highly compound fern leaves (Fig. 7C). While the possibility of generating fern-like structures using fractal methods is well known (Barnsley, 1988; Prusinkiewicz and Lindenmayer, 1990), the above analysis puts it in the context of strategies that plants employ to deal with the constraints of space. We can call this strategy egalitarian, as it treats equally all segments: they support smaller child branches unless their size falls below a threshold value.

Observations and models of highly compound inflorescences suggest that the egalitarian strategy can also explain the form of some three-dimensional branching structures (Figs 7D, 9A–D). In both the planar and three-dimensional cases, the constraints of space manifest themselves in the shortening of the child segments with respect to the parent segment that subtends them. It is an interesting question, however, whether a similar analysis applies to the branching structure of trees. Such an hypothesis was first advanced by Honda (1971), and subsequently pursued in many tree models developed for computer graphics purposes, for instance (Oppenheimer 1986). Examples of trees created

using Honda's model are shown in Fig. 10. Although resembling trees at first sight, they exhibit a highly repetitive, self-similar structure that is significantly different from the branching pattern of typical temperate-climate trees.

To provide a more realistic explanation of tree form, Sachs and Novoplansky (1995) (see also Sachs, 2004) proposed a different strategy for accommodating the constraints of space, in which competition between branches is the key. The idea of competition for space as a driving force defining trees was also the cornerstone of early computer models by Ulam (1962) and Cohen (1967), but its significance was obscured by the limited power of the computational models of the time and the restriction of the models to two dimensions. It was recently re-examined by Runions *et al.* (2007) and Pałubicki *et al.* (2009).

In the space-colonization model of Runions *et al.* (2007), the available space is represented as a set of attraction points for which developing branches compete. The Aristotelian exclusion principle is reflected in the assumption that each attractor can be allocated to at most one branch. The tree structure is generated in an iterative growth simulation. In each iteration, attractors are assigned to the branch segments that are closest to them (Fig. 11A). Each segment that is associated with at least one attractor then produces a new segment in the average direction of all attractors assigned to it (Fig. 11B). A new segment may extend an existing axis at its tip, or initiate a new branch (Fig. 11C). An attractor is removed once a tree node comes too close to it: the space associated with this attractor is then consumed and is no longer available for other branches (Fig. 11D, E). With the attraction points distributed in three dimensions, the above process results in a gradual occupation of the free space, represented by attractors, by an emergent tree structure (Fig. 11F–H). In spite of its extreme simplicity, this model appears to capture the irregular yet harmonious structures of temperate-climate trees (Fig. 11I, J).

Extensions of the above model were studied by Pałubicki *et al.* (2009). The modified model introduces an explicit representation of buds and simulates apical control of development as a competitive advantage of some buds with respect to others. Furthermore, the model makes use of light as a spatially distributed resource for which the buds

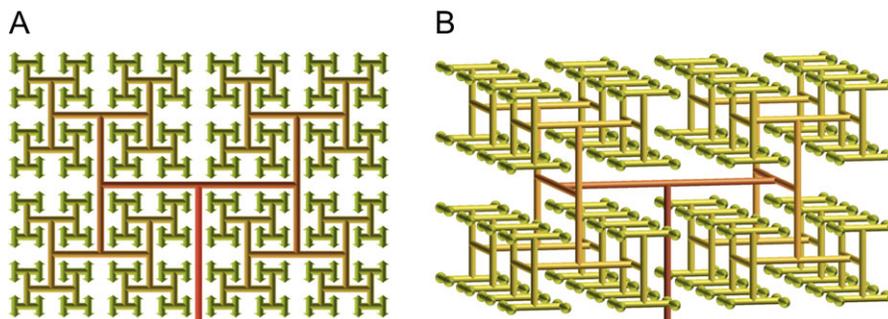


Fig. 8. Self-similar branching patterns optimally filling an area (A) and a volume (B).

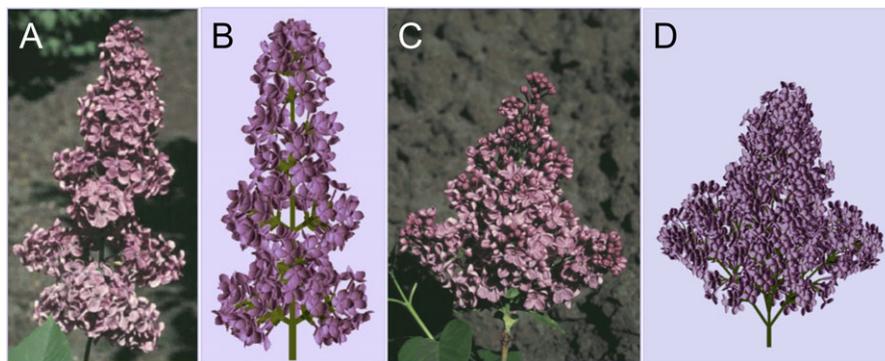


Fig. 9. Approximately self-similar 3D structure of *Syringa vulgaris* inflorescences. (A, B) A photograph and a simulation model of *S. vulgaris* cv. Congo. (C, D) A photograph and a simulation model of *S. vulgaris* cv. Etna. The difference in the form of these cultivars is due to different scaling ratios along the main and lateral branches.

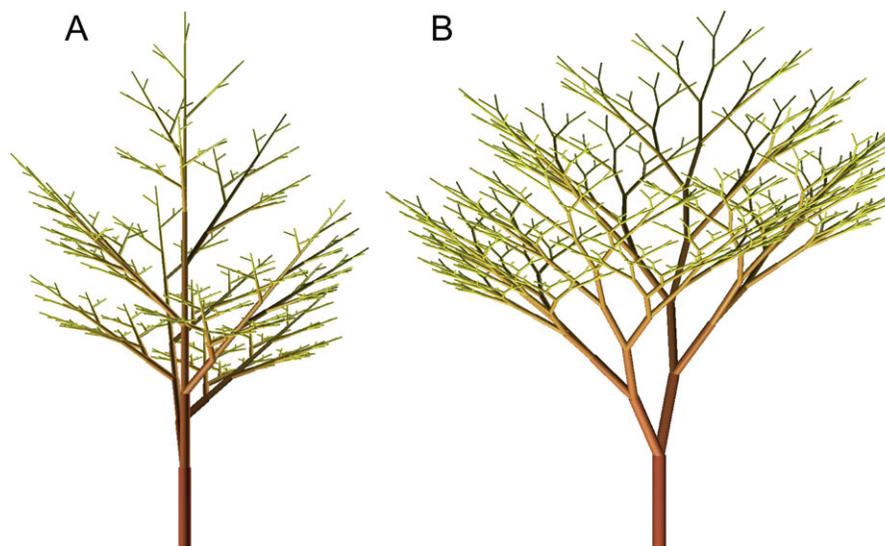


Fig. 10. Sample structures generated using Honda's (1971) self-similar tree model, assuming monopodial (A) and sympodial (B) branching.

and branches compete; this facilitates the simulation of the shedding of branches that are no longer beneficial to the tree. A wide range of plausible temperate-tree forms can be obtained by changing parameters of this model (Fig. 12).

These results support the conjecture of Sachs and Novoplansky that, as in the case of the wavy surfaces of leaves and petals, genetic mechanisms do not control tree form in detail. Instead, they set the stage for a competitive, self-organizing process through which branching forms emerge. In their own words, 'The form of a tree of a given species is generated by self-organization in which alternative branches inhibit or compete with one another following no strict plan or pre-pattern' (Sachs 2004). This perspective differs from the widely known notion of architectural tree models (Hallé *et al.*, 1978), according to which, 'Organization in plants reflects the precisely controlled genetic program which determines their development. [...] Precise growth patterns of trees are much disrupted by exogenous, environmental factors' (Hallé *et al.*, 1978, p. 74). The recognition of spatial constraints has thus a profound impact on the conceptual models of trees and their development.

Discussion

According to Aristotle's exclusion principle, two objects cannot occupy the same space. As long as this constraint is satisfied, developing plants may, however, maximize the usage of space. The first strategy is to acquire more space by extending the structure to another dimension. In the case of surfaces, the underlying relationship between growth and form is a consequence of the Gauss theorem, which implies that a flat object must extend to the third Euclidean dimension if it grows disproportionately fast near the centre or at the margin of the surface. Growth at the margin is often associated with the breaking of symmetry, as a wavy margin may no longer have the radial symmetry of an initial flat disc. When growth rates increase exponentially towards the margin, the waves acquire a fractal character.

The second strategy is an egalitarian partitioning of space between components. Considered in the context of repetitive branching patterns of unlimited order, it also leads to the formation of fractal patterns, best exemplified in nature by self-similar compound leaves and inflorescences. In this

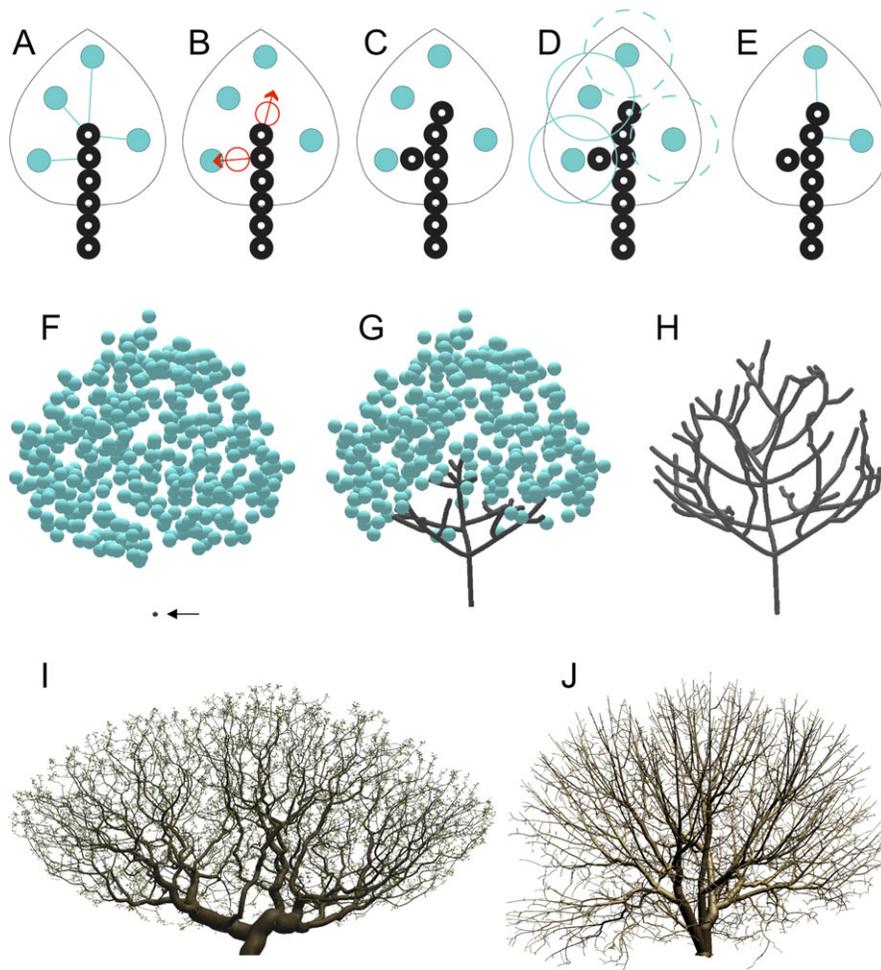


Fig. 11. The space-colonization model of tree development (Runions *et al.*, 2007). (A–E) One iteration of the generative algorithm. (A) Attractors representing available space (blue circles) are associated (blue lines) with the segments of the growing tree (black circles) that are closest to them. (B) Average directions towards the attraction points (red lines) are then calculated, defining positions of new segments (red circles). (C) The growing tree after the addition of new segments. (D) Calculation of the proximity of the tree to the attraction points. Continuous-line blue circles surround attraction points that are closer to the growing tree than the threshold distance (the circle radius), dashed circles surround attraction points that are farther than the threshold. (E) Attraction points closer than the threshold distance are removed, and the remaining attraction points are associated with tree segments, thus initiating next iteration of the algorithm in the state corresponding to (A). (F–H) Example of tree generation. Beginning with an initial segment representing the trunk base (arrow) and a cloud of attraction points (F), the tree grows through an iterative application of steps (A–E). As the tree grows, the attraction points are consumed (G) until the final form is reached (H). (I, J) Examples of trees generated using this model for different parameter values. Images (A–H, J) from (Runions *et al.*, 2007), all images courtesy of Adam Runions.

case, the constraints of space are manifest in the ratios of branch segment lengths formed in consecutive generations, beyond which the structures become too dense to fit in the available space.

Finally, the third strategy is the competitive partitioning of space. It satisfies the constraints of space by bringing into existence or maintaining only some of the potential elements of the structure. This strategy appears to play an important role in the development of temperate-climate trees.

Examples of processes and forms induced or constrained by the properties of space appear at various spatial scales. In addition to those discussed above, they encompass the shaping of single-cell organisms (Dervaux and Ben Amar, 2008), the emergence of fruit forms (Yin *et al.*, 2008), the

development of phyllotactic patterns (Dosio *et al.*, 2006; Hotton *et al.*, 2006), the differentiation of ray florets at the boundary of a capitulum (Battjes and Prusinkiewicz, 1998), the development of leaf venation patterns (Runions *et al.*, 2005), the self-thinning patterns of plant distribution (Firbank and Watkinson, 1985), and the shapes of vegetation boundaries in plant ecosystems (Gastner *et al.*, 2009). A further synthesis of these diverse examples is possible due to an extension of the notion of curvature to discrete objects, such as trees, which makes it possible to consider both wrinkled surfaces and branching structures as manifestations of negative curvature (Cannon *et al.*, 2000). This wide range of forms and scales points to the pervasive role of space constraints in plant development. In particular, space



Fig. 12. Sample models generated using an improved model of branch competition for space (Pałubicki *et al.* 2009). All images from Pałubicki *et al.* (2009), courtesy of Wojciech Pałubicki, Kipp Horel, and Steven Longay.

constraints provide a mechanism through which details of form can be elaborated in an emergent fashion on the basis of a relatively coarse genetic-level specification of growth. This mechanism can be further extended to include a feedback through which geometric or mechanical clues provide input to the molecular level processes of morphogenesis (Green, 1996, 1999; Hamant *et al.*, 2008; Newell *et al.*, 2008). The resulting forms are sensitive to changes in temporal growth co-ordination and growth rates (heterochronic changes of developmental processes, Li and Johnston, 2000), which suggests a mechanism through which relatively small genetic modifications may induce evolutionary novelties.

Given their importance, why are the properties of space, subject of philosophical and mathematical thought for millennia, only now attracting considerable attention in plant biology? The reasons may be technical. Emergent phenomena, such as fractal wrinkling or competition for space, are difficult to conceptualize without the aid of computer models, a relatively new addition to the repertoire of biological research tools. The acquisition of spatial data, such as the distribution of light, water or nutrients, may require complex experimental techniques. The incorporation of spatial phenomena, even as intuitive as the detection of

mechanical collisions and prevention of component intersections, complicates computational models, and therefore has often been avoided. Finally, the mathematical apparatus of differential geometry needed to describe and analyse curved surfaces is considered to be ‘among the most complicated and inaccessible of all the formal systems in mathematics’ (Henderson, 1998, p. xv). In particular, the relation between the curvature of surfaces, the discrete structure of surfaces and trees, and their fractal character is a very recent object of advanced mathematical investigations (Cannon *et al.*, 2000). The discrepancies between what is easy for nature to do and what is easy for us to conceptualize, measure, model, and analyse, may have concurred in turning the research focus away from considerations of space. Further progress in developmental plant biology requires, however, taking into account that ‘of all the constraints of nature, the most far-reaching are imposed by space’ (Stevens, 1974, p. 5).

Materials and methods

Figures 1 and 5C, D, F–H were generated using the tissue-modelling program VVE, based on the earlier program VV (Smith and Prusinkiewicz, 2004; Smith *et al.*, 2004). The leaf surface

models shown in Fig. 5F–H were obtained by smoothing a polygon mesh generated by a mass-spring model with two iterations of Loop subdivision (Loop, 1987; Smith *et al.*, 2004), modified to preserve the course of the main veins. Figure 3 was generated with Canvas, an interactive program for visualizing growing surfaces (Matthews, 2002). Figure 4B–F were obtained using special-purpose programs as described by Dimian (1997). Figures 5E, 7E–H, 8, 9B, D, and 10 were generated with the L-system-based modelling software L-studio and vlab (Prusinkiewicz, 2004), using L-systems and modeling methods described by Prusinkiewicz and Lindenmayer (1990). Figure 9B and D were synthesized with L-systems using methods described by Prusinkiewicz *et al.* (2001). Figures 11F–J were obtained using VV (Smith *et al.*, 2004), and Fig. 12 was generated using special-purpose programs described by Pałubicki *et al.* (2009); these results were also reproduced with L-systems.

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