

Shedding light on plant competition: Modelling the influence of plant morphology on light capture (and vice versa)

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Abstract

A plant's morphology is both strongly influenced by local light availability and, simultaneously, strongly influences this local light availability. This reciprocal relationship is complex, but lies at the heart of understanding plant growth and competition. Here we develop a sub-individual-based simulation model, cast at the level of interacting plant components. The model explicitly simulates growth, development and competition for light at the level of leaves, branches, etc, located in 3-d space. In this way, we are able to explore the manner in which the low-level processes governing plant growth and development give rise to individual-, cohort-, and community-level phenomena. In particular, we show that individual-level tradeoffs between growing up and growing out arise naturally in the model, and robustly give rise to cohort-level phenomena such as self-thinning, and community processes such

as the effect of ecological disturbance on the maintenance of biodiversity. We conclude with a note on our methodology and how to interpret the results of simulation models such as this one.

Key words: plant morphology, simulation, individual-based, L-Systems

1 Introduction

Competition for light is a highly significant environmental influence on plants. Successful plant life-history strategies maximise light capture (amongst other things) despite the presence of competing plants (Crawley, 1986). Understanding how plant-plant competition drives population-level phenomena is made more difficult by the fact that plant structure is far more developmentally plastic than that of most animals. Above-ground plant morphological plasticity is largely the result of heterogeneity in the local light environment. Of course, just as light availability influences a plant's structure, so a plant's structure affects its ability to capture light. The intimate, reciprocal relationships between a plant's current morphology, the structure of its local environment (including competing plants), its resultant ability to capture light, and any subsequent changes to its structure are highly complex (Hutchings and de Kroon, 1994). However, it is precisely these relationships that drive plant growth and determine competitive success when light limits growth.

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In order to answer questions about the nature of competition for resources, ecologists have typically resorted to non-spatial models (Tilman, 1982). More recently, ecologists have recognised that spatial heterogeneity (Pacala and Deutschman, 1994) and asymmetry in the effects of competition on individuals can significantly effect the predictions of a model (Schwinning and Weiner, 1998). Although relationships between population-level characteristics (such as mean size or density) have been derived empirically (Westoby, 1984), constructing analytically tractable models of these population level processes is difficult. Consequently insights into the mechanisms driving such relationships have been hard to come by (Weller, 1991). Equally, modelling populations at the level of individuals (modelling competition in terms of, for instance, nearest neighbour interactions, e.g. Benjamin and Sutherland, 1992), fails to capture changes in individual performance as a result of “foraging for light” – i.e., processes of within- and between-plant competition. In order to explore the manner in which foraging for light impacts on plant morphology, plant-plant competition, and population-level phenomena, models must represent plant growth *and* light capture at a level below that of individual plants.

Sub-individual based models address the problem of modelling the structure and function of plants by dividing the structure of a plant into sub components. The rate of production of new components may be coupled to the transport and allocation of carbon, allowing the plant to grow in a morphologically plastic way (Prusinkiewicz, 2004). A variety of formalisms have been used to explicitly capture plant structure in these “functional-structural” models, a common formalism being Lindenmayer-Systems (Perttunen and Sievanen, 2005; Allen et al., 2005). An L-system is a formal grammar consisting of an initiator and a set of rules, each describing a valid substitution (Lindenmayer,

1968). When repeatedly applied in parallel, such rule-sets are capable of generating complex structures. Until recently, such models have largely been applied to problems in agricultural research (Hanan and Hearn, 2003; Ruiz-Ramos and Mínguez, 2006) and in computer graphics (Deussen et al., 1998; Lane and Prusinkiewicz, 2002).

Here we explore the manner in which low-level processes governing plant growth and development are implicated in plant competition for light, and how this competition gives rise to higher-level effects typically associated with plant populations (Takenaka, 1994; Colasanti and Hunt, 1997; Colasanti et al., 2001). As such, the model is cast at a level below that of most models of plant competition. For example, a plant's height is not encoded explicitly anywhere in the model, but arises as the result of an interplay between influences on plant growth at each of its apices. By taking this perspective we are able to explore the effects of competition without making a priori assumptions about its nature. For instance, we do not need to make assumptions concerning the degree or character of competitive asymmetry (Weiner, 1990), nor fix the scale over which plants interact competitively (Sletvold and Hestmark, 1999). By contrast with previous models, these important elements of plant competition become *dependent* rather than independent model variables. In addition, we are able to explore how morphological characteristics such as branching angle and branching frequency affect relative competitive ability and how these effects propagate up to population and community-level processes such as succession (Horn, 1971; Niklas and Kerchner, 1999). This approach allows ecologists to test the effects of low-level constraints on plant structure and the interaction between structure, light-capture and growth (Pearcy et al., 2005; Sterck et al., 2005)

In the next section we present the model in detail. The model's results at the level of the individual, the population and the community are provided in Section 3. In Section 4 we discuss these results and their relation to the major empirical findings in plant ecology, before concluding in the final section.

2 Method

In this section we describe the structure of our model and the behaviour of the component parts and their interactions. A more formal description of the model is given in Appendix A.

Plants are modelled as a list of components. Each component type is subject to one or more context-sensitive growth rules or productions. This means that the behaviour of individual components depends upon the state of components before and after them, allowing them to interact in a local manner. Each iteration, growth rules are applied to the list of components in parallel (Figure 1).

One of the most important parts of the model is the flow of photosynthate between components. Photosynthate is produced by each leaf and is transported between adjacent components along a concentration gradient at each iteration of the model. Photosynthate is consumed in the production of new internodes, the growth of leaves, and the production of new seeds by flowers.

Every plant begins life as a single seed component. A seed has a probability, each iteration, of germinating and being replaced by an internode, a leaf, and an apex. This is the basic form of a plant.

Each iteration, the amount of light reaching each leaf is estimated using the technique described in Section 2.1. If the shading of a leaf is greater than a threshold value, it is shed (and removed from the model). Otherwise, the amount of photosynthate contained in the leaf is increased at a linear rate proportional to its area and inversely proportional to its shading. A proportion of the photosynthate is consumed as the leaf grows and the radius of the leaf increases. The remainder of the photosynthate is contributed to the internode subtending the leaf. Leaves increase in size up to a predefined limit which is the same for all species. A plant is considered to have died, and is removed from the model, if it has no leaves.

If the loading of an internode (the number of internode components it supports) exceeds a critical value that is proportional to its strength and radius and a function of its orientation then it breaks, and is removed from the model, along with all of its descendant components (i.e., those further up the branch). Otherwise an internode persists and increases in radius such that its radius is larger than that of the internode(s) it supports. The length of an internode remains constant: longer gaps between branches consist of larger sequences of internodes. Internodes transport photosynthate into neighbouring components at a rate proportional to the concentration gradient between the internode and the components above and below them.

At each iteration, photosynthate is transported into each apex at a rate proportional to the concentration gradient between the apex and its preceding internode. If the age of the apex exceeds the age at which the plant becomes reproductively active, then it is replaced with a flower. Otherwise, given that enough photosynthate is available, it extends the branch by producing internodes, placing them between itself and the preceding internode, finally produc-

ing a single leaf. At each iteration there is a probability that each apex will branch, dividing into two separate apices with altered orientation ¹. Flowers persist until the plant dies or until the end of the simulation. At each iteration, photosynthate is transported into the flower at a rate proportional to the concentration gradient between the flower and its preceding internode. The flower will produce new seeds at a rate proportional to the amount of photosynthate present in the flower.

Seeds disperse according to a Gaussian distribution centred on the flower producing them. At each iteration, a dormant seed will germinate with fixed probability.

Several life-history parameters govern the behaviour of the L-system described above. The probability of branching determines the rate of occurrence of stochastic branching events during plant growth. Branching frequency increases linearly with apex order. Branching events result in two apex components oriented in different directions (Figure A.1). The orientation of the apices relative to their parent is governed by two angles (branching angle 1 and branching angle 2). Low branching angles result in a small change in orientation of the apex relative to its parent branch. An internode with a branching angle of 90° grows perpendicular to its parent branch. Internode strength is determined by a parameter representing the amount of secondary compounds within each branch. Internodes which have a higher strength take more photosynthate to produce, but can support more child nodes.

¹ The production of new branches through the division of apex nodes differs from the production of new growth via sub-apical buds in biological plants, although the overall branching patterns that are produced are similar.

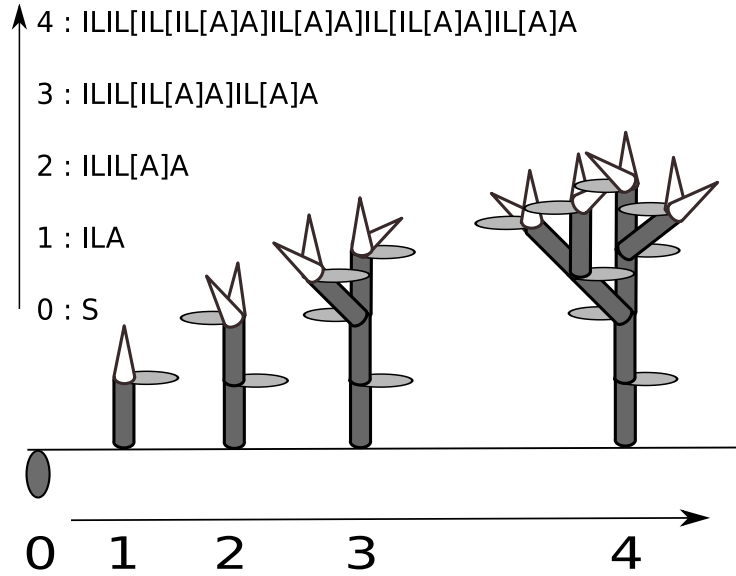


Fig. 1. A schematic figure depicting, symbolically and graphically, the development of an L-system with the following alphabet and rule-set: a seed (dark gray oval), $S \mapsto ILA$; an internode (stem or branch, dark gray cylinder), $I \mapsto I$; a leaf (light gray oval), $L \mapsto L$; an apex (tip of plant, white cone), $A \mapsto IL[A]A$; the beginning of a branch, $[\mapsto [$; the end of a branch, $] \mapsto]$.

The age at which a plant begins to produce seeds is determined by a single parameter. Since we are not particularly interested in the trade-offs associated with reproductive aspects of plant life-history strategies, we model the onset of reproduction as a plant-wide switch from vegetative to reproductive activity triggered at a particular age. At this point, growth ceases, and seed production begins. In addition, we set the probability of germination to 1.0 to avoid the complexity of introducing a seed bank into the simulations examining competition between individuals (Section 3.3).

A plant's development is modelled as a consequence of many iterations of the simple rules outlined above. Figure 2 presents an example of plant morphology generated by the model. The image was generated by translating the

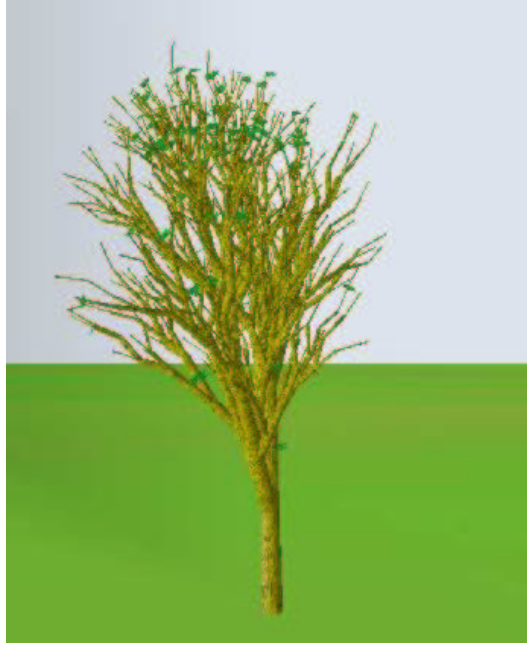


Fig. 2. Visualisation of an example plant morphology generated by the model. Life-history parameters are Branching Probability 0.3, Branching Angle 1 1.0° , Branching Angle 2 30° , Internode Strength 572 (arb units), run for 36 iterations.

formal representation of plant structure employed by the model into a 3-d visualisation.

Note that model plants only interact in terms of competition for light. Neither direct physical interference, nor below-ground competition are simulated. As such, the differential photosynthate production across a plant's leaves is a crucial determiner of plant morphology. Consequently, it is important to model the manner in which light falls across a plant. To achieve this we employed a simple, but computationally expensive, ray-tracing technique.

2.1 Estimating the Light Environment

Sophisticated light models have been developed in order to address this type of problem (Brunner, 1998; Chelle and Andrieu, 1998, 1999). Monte Carlo ray-tracing, for example, is a numerical technique that is simple and intuitive. Particles representing photons are projected into a scene that contains a number of surfaces such as leaves. The direction of the particle is based on a stochastic function. If the path of the particle intersects with a surface then the particle is either transmitted, reflected, or absorbed according to the properties of the surface and the angle of intersection. If the particle is absorbed or crosses the boundary of the simulation, then it is no longer considered. By repeated sampling, the optical properties of a scene, such as the number of photons absorbed by each leaf surface in the scene, can be estimated (Smits, 1998).

Here, we use a much simpler approach to assess the amount of light falling on each leaf, accounting for the effects of self-shading and between-plant shading. The light environment was modelled as a set of 9 point sources suspended some distance above the population. A ray (a straight line-segment in 3-D space) was projected from each of these points to the centre of each leaf in turn. Leaves were considered to be circles of varying radius parallel to the x-y plane. The degree of shading experienced by a leaf was calculated as proportional to the number of intervening leaves intersected by each ray. This technique has the advantage of explicitly calculating the light levels incident to each leaf surface, and also models shading in three dimensions. Internodes and other components were ignored in these calculations. In addition, light is modelled as straight line segments, so reflection of light is not considered in this model.

Explicitly calculating the shading for each leaf in the population is a computationally intensive task (it scales with time-complexity $O(n^2)$). In order to improve the tractability of the model, we implemented an optimisation technique that grouped the population of leaves into smaller sub-populations, allowing fast rejections of unimportant regions of space (Smits, 1998).

3 Results

3.1 Individual Level

Leaf shedding, internode strength, photosynthate transport, and the investment required in order to produce new plant structures impose significant trade-offs that constrain plant growth and development, and restrict plant life-history strategies. The interactions specified in the model were between neighbouring components, but gave rise to behaviour at the level of individual plants. We selected 4 parameters and varied them across a range of values, examining the growth rate and light capture of individual plants. All other parameters were set at the values given in Figure 2. We have defined effective leaf area as the sum of the unshaded leaf area of the plant (e.g. each leaf i has radius r_i and shading s_i , $ELA = \sum_{i=1}^n (1 - s_i) \pi r_i^2$).

As branching angles 1 and 2 were increased from 1° to 90° , the efficiency of light capture increased because self-shading was decreased. However, increasing the branching angle decreased the rate of vertical growth, leading to smaller plants. There is a direct trade-off between efficient light capture and rate of vertical growth (Figure 3).

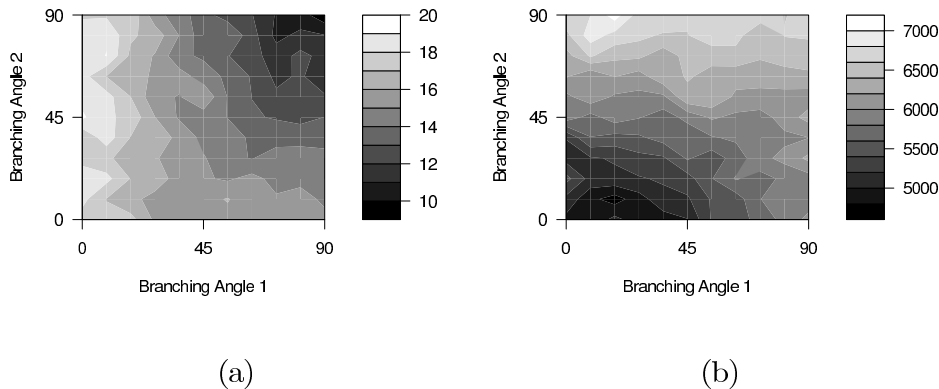


Fig. 3. Trade-offs between (a) growing up and (b) growing out for the plant pictured in Figure 3. Two contour plots depict the impact of branching angles on (a) maximum apical height (lighter contours represent taller plants) and (b) effective leaf area (lighter contours represent plants with a greater unshaded leaf area). Each contour plot comprises 121 points each representing the mean of 10 replicate simulations after 36 iterations. Plants with the lowest branching angles grow faster but capture less light.

We also varied the strength of internode components. Because strong internodes were more energetically expensive to produce, plants with strong internodes grew slowly. However, strong internodes are able to support more biomass, leading to a higher effective leaf area in the long term (Figure 4).

Finally, we varied the age at which a plant became reproductive. Plants that become reproductive later were able to produce more flowers, and were also able to produce more leaves which capture more energy to produce seeds. However, plants that become reproductive earlier were reproductive over a longer period. Consequently, for a given set of parameters and a given simulation length, there was an optimal age for plants to switch from vegetative growth to reproduction (Figure 5).

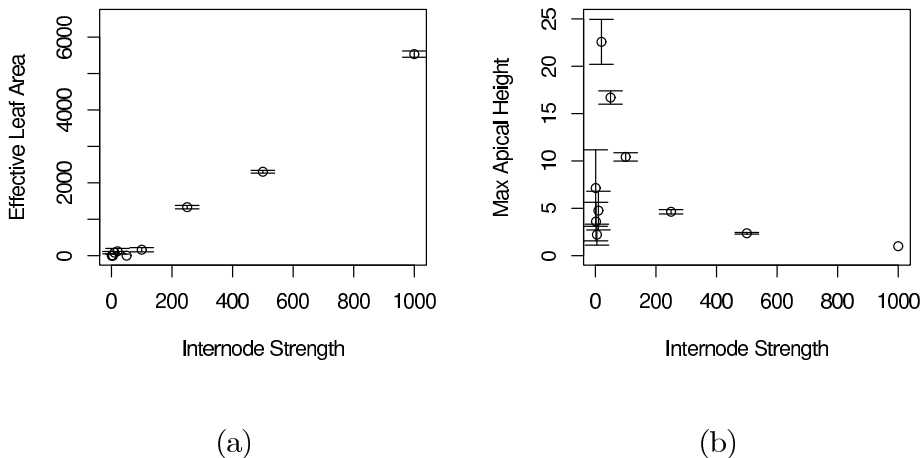


Fig. 4. Trade-offs between internode strength and (a) plant height and (b) effective leaf area. Each data point represents 10 replicate simulations (mean \pm one standard deviation). 4(a): Plants with strong stems grow slowly because stronger tissue is more energetically expensive to manufacture. 4(b): Ultimately, plants require strong tissue in order to support the biomass associated with a high effective leaf area.

Since we model growth as dependent on the local light environment of each leaf, we would expect that the same plant would exhibit a degree of morphological plasticity in the presence of varying illumination regimes. Figure 6 demonstrates that, as the source of illumination changes from a highly directional over-head spotlight to a more ambient diffuse regime, the morphology of a particular plant varies considerably. In the case of Figure 6(a), light was available from directly above the plant only. Consequently self-shading was strong and leaves towards the base of the plant were shed. In contrast, the oblique angle at which the rays intercepted leaves in Figure 6(b) resulted in relatively little self-shading and greater persistence of leaves. In addition, the larger amount of light captured by the plant resulted in more growth.

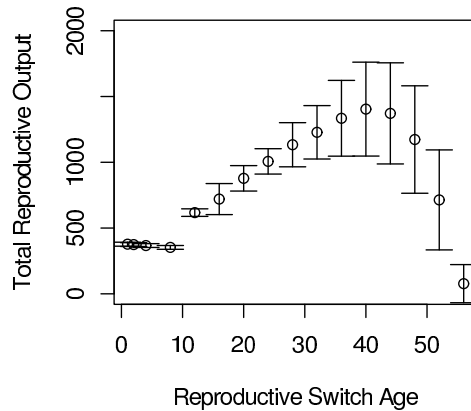


Fig. 5. There is a trade off between delaying reproduction (which results in the plant accruing more energy-producing tissue and increases its photosynthetic capacity) and reproducing early (which guarantees reproduction at a lower rate). In any given time frame, there is an optimum age at which plants should switch to reproduction. Points represent 10 replicate simulations (mean \pm one standard deviation).

At the level of the individual plant, the model exhibits many well-characterised trade-offs between different plant life-history characteristics. These relationships are not explicitly represented within the model, but arise as a result of the low-level mechanisms implemented within it.

3.2 Cohort Level

In order to explore the effects of competition between individuals with the same life-history strategy, we simulated populations of same-aged plants sharing identical life-history parameters (given in Figure 2). A simulation was initialised with 512 of seeds distributed at random across a square plot. Seeds germinated asynchronously, allowing those that germinated early the potential

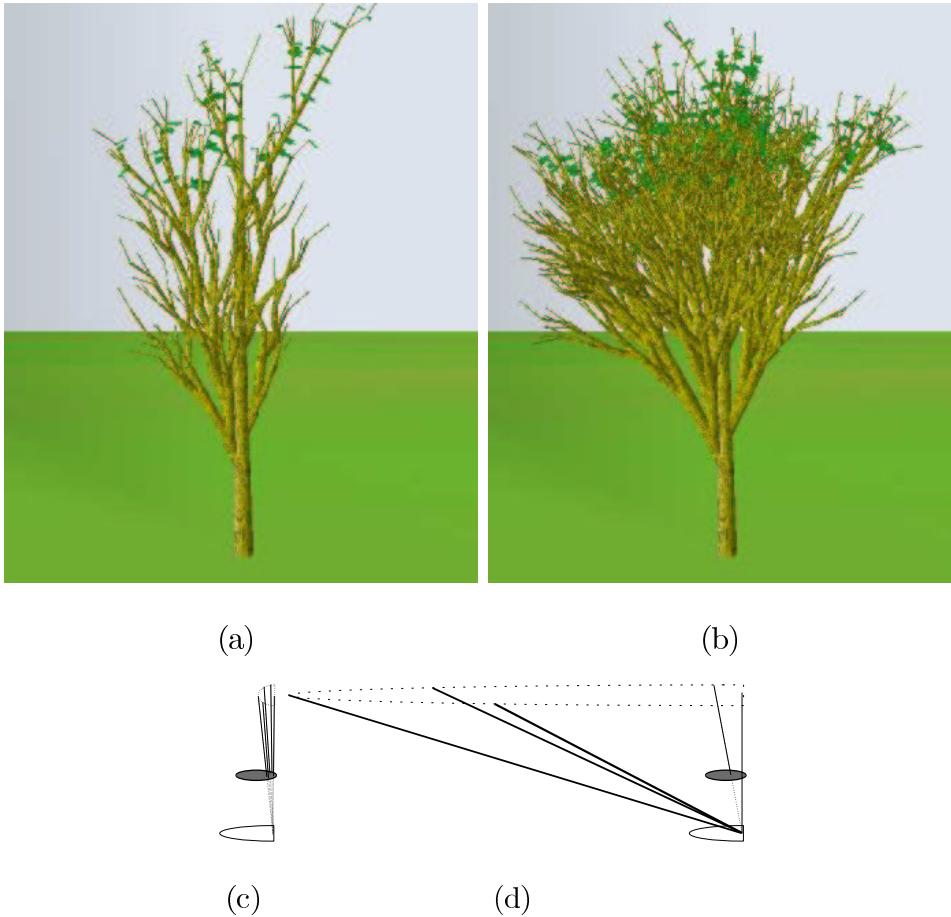


Fig. 6. Variation in plant morphology caused by different light environments. Parameters & random seed are the same as used in Figure 2, with plants grown for 36 iterations. In 6(a) the light sources are located directly above the plant. This leads to greater self-shading due to more rays intersecting the upper leaves of the plant (6(c)). In 6(b) the light sources are spread further apart, leading to fewer rays intersecting the upper leaves and less self-shading (6(d)).

to benefit from a relatively competition free environment. Each plant shared the same life-history parameters, but differed from its conspecifics as a result of the local variation in its light environment. In this section, plant reproduction is switched off. All results presented in this paper exclude plants at the periphery of the plot in order to minimise any edge effects that might arise as a result of the favourable conditions enjoyed by these plants.

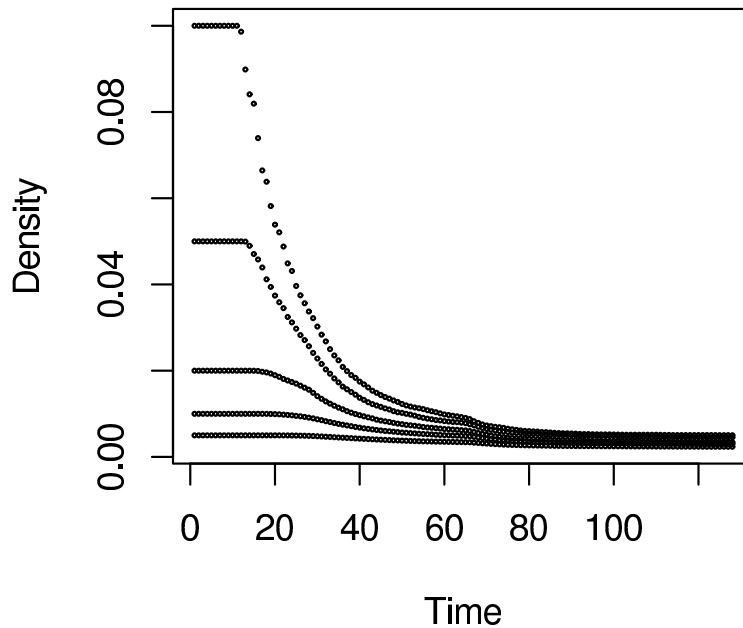


Fig. 7. Time series of simulations started at different initial densities. As time goes on they all converge to a single final density. Points are means of 10 replicate simulations.

Figure 7 shows the decay of plant density over time, demonstrating density-dependent mortality rates characteristic of natural stands. In this model, competition for light alone, ensures that increasingly dense populations suffer increased mortality. Regardless of initial plant density, populations tend to the same density at equilibrium.

Figure 8 shows that the simulated populations self-thin, although the fitted relationships deviate from the $-3/2$ exponent found in natural plant populations (Yoda et al., 1963). Once a population achieves canopy closure, mortality is directly compensated for by growth in surviving individuals, resulting in a

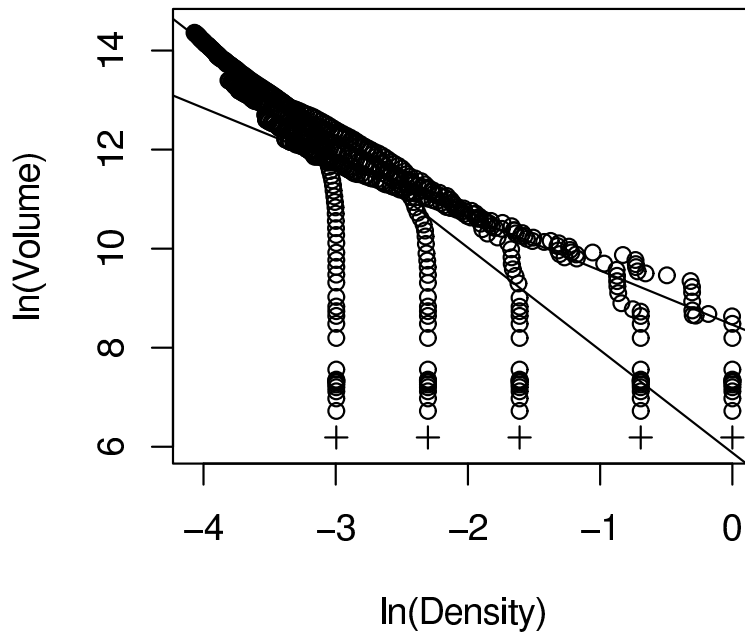


Fig. 8. Self-thinning curves for simulations started at different initial densities. Initial populations (indicated by crosses) increase in volume without suffering any mortality. Eventually the canopy closes and the smaller individuals begin to suffer mortality. The populations shown here have self-thinning exponents between -1 and -2 (shown on the graph as trend lines for the two most extreme cases). Each point is a mean of 10 replicate simulations each run for 128 iterations. Plant volume was calculated by summing the volumes of each internode for each plant in the population. Leaves, apices and flowers were assumed to have zero volume.

log-log relationship between plant density and volume with an exponent of between -1 and -2 .

The asymmetric nature of competition for light ensures that the size distributions of plant populations become increasingly skewed over time. Figure 9

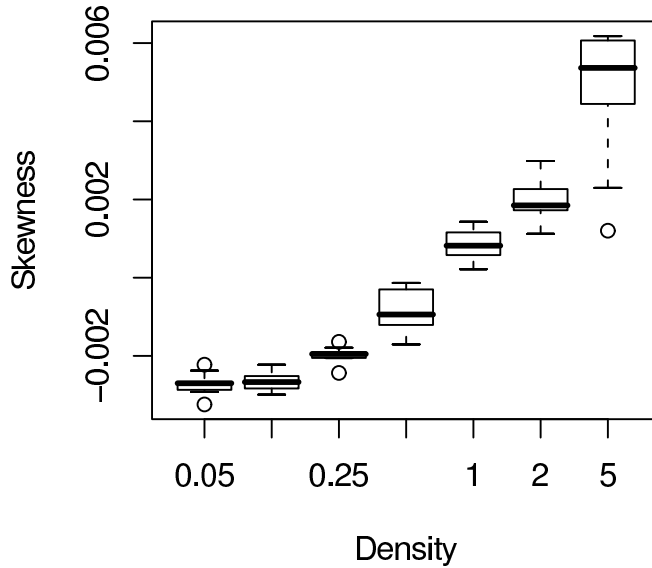


Fig. 9. Skewness in the height distribution of the population increases with the initial density. Low density populations have many tall plants and few small plants. High density populations have many small plants and a few tall plants. At each density, the sample skewness for 10 replicates is plotted, where skewness for a sample of N values is $g_1 = \sqrt{n} \sum_{i=1}^N (x_i - \bar{x})^3 / \left(\sum_{i=1}^N (x_i - \bar{x})^2 \right)^{\frac{3}{2}}$ (Sokal and Rohlf, 1995, page 111). In the boxplot, the central bar shows the median while the box denotes the first and third quartile, and the error bars denote the 95% confidence interval. Circles represent outliers.

demonstrates that, in accordance with empirical studies (Thomas and Weiner, 1989), increasing initial plant density results in final size distributions that are increasingly positively skewed towards the tallest plants.

As a result of the competition for light arising in the model, simulated populations exhibit several important population-level relationships. Despite not explicitly specifying competitive asymmetry, density-dependent mortality, etc.,

these phenomena arise naturally in the model as a result of low-level competitive processes.

3.3 *Community Level*

Morphological differences between species have long been thought to contribute to differences in their competitive ability for light (Horn, 1971). In order to explore this class of question, we simulated two stereotypical life-history strategies—one modelled on an r -selected species (strategy r), the other modelled on a K -selected species (strategy K). Figure 10 depicts visualisations of the two strategies.

Both strategies had a positive growth rate in isolation and were capable of sustaining a population in the long term. In order to further quantify whether one strategy is more “competitive” than the other we examined whether either strategy can have a positive rate of growth and reproduction when rare in an environment dominated by the other strategy. By seeding the initial population with individuals of mainly one strategy or the other, distributed at random, we modelled the growth and development of a mixed community of plants where one species was rare. If a strategy is a poor competitor we would expect it to be unable to establish itself in an environment dominated by the other strategy. If both strategies are able to establish themselves in environments dominated by the other strategy then they will be able to coexist in the long term. Figure 11 shows that while K can successfully invade an established population of r , the converse is not true.

In summary, competition between simulated plants with different life-history



(a) “r-selected”

(b) “K-selected”

Fig. 10. The morphology of the “r-selected” strategy (r) and the “K-selected” strategy (K). Life-history parameters for r are: Branching Probability 0.3, Branching Angle 1 30.0 °, Branching Angle 2 30.0°, Internode Strength 500 (arb units), Seed Energy 1.0 (arb units), Age at Maturity 10 (iterations). Life-history parameters for K are: Branching Probability 0.3, Branching Angle 1 30.0, Branching Angle 2 30.0°, Internode Strength 500 (arb units), Seed Energy 4.0 (arb units), Age at Maturity 36 (iterations). Both plants were grown until they were mature.

strategies reproduced results derived from theoretical and empirical plant ecology. The overall results of the simulations show that a simple model cast at the level of sub-individual processes can capture ecological phenomena across many levels of description.

4 Discussion

In this section, we relate the results presented above to previous models of plant competition. Since the methods used here are relatively new, we also

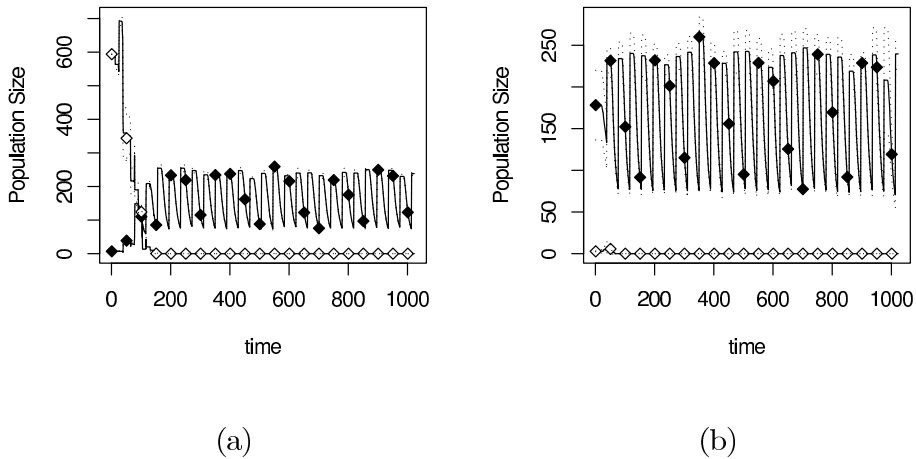


Fig. 11. Invasion time series for K (filled diamonds) and r (open diamonds) averaged over 10 replicate simulations. 11(a): Strategy K exhibits a positive growth rate as an established population of r is invaded. 11(b): Strategy r does not increase as K successfully resists an invasion.

address some of the methodological issues that surround the use of individual-based models in ecology. In particular, we suggest valid ways of interpreting results from models such as the one presented here. Finally, we review the potential for further theoretical research involving this modelling approach.

4.1 Implications

The results presented in the previous section demonstrate that the high-level behaviour of the model conforms with existing notions regarding plant population ecology. As such, these results will not surprise plant ecologists. However, they were achieved without making the simplifying assumptions regarding plant-plant competition that are typical of higher-level models. Rather, we allowed this competition to arise naturally from the interplay between the

low-level constraints and mechanisms implemented explicitly in the model.

While the character of competition within the model is doubtless not identical to that experienced by real plants, the fact that there is a close agreement between the model's results and general findings from empirical plant ecology suggest that the model is capturing elements fundamental to plant competition. Many of the relationships modelled are very simple, especially in comparison with more detailed structural-functional models, parameterised from natural plants (such as LIGNUM or ALMEDA; Perttunen et al., 1990; Ruiz-Ramos and Mínguez, 2006), and we would anticipate that a more rigorous modelling approach would be necessary if our aim was to obtain results that could be directly compared with empirical data.

These results were obtained despite modelling plant growth and the physics of light capture in a very simple manner. The former was modelled as a handful of growth rules, with, for instance, no role for global co-ordination mechanisms such as plant hormones, while the latter was modelled as merely the capacity to position leaves such that they intersect individual rays of light.

It is important to stress that these results were achieved for a relatively arbitrary set of model parameters. They are not the result of fine-tuning the model, but appear to be robust features of almost any model sharing this basic form. As such, the strength of this model lies in its ability to answer questions about constraints universal to all plants.

The model presented here should not be regarded as somehow competing with models cast at higher levels of description. By contrast, in some sense it can be understood to underwrite these models by supporting the simplifying assumptions upon which they rely, for instance, those concerning the character

of competitive asymmetry. This type of support for higher-level models is important. Since the simplifying assumptions that drive these models enable them to achieve a level of simplicity that keeps them mathematically tractable and comprehensible, it is critical that we have evidence that these assumptions are valid.

4.2 Methodology

The style of model presented here is relatively novel. While the last two decades have seen an increase in the publication of individual-based models such as this one, a consistent methodology guiding their use remains elusive (Grimm, 1999; Di Paolo et al., 2000). As a result, the way in which these models are interpreted varies widely.

Those familiar with more traditional equational models, may have developed certain expectations of models in general. To some extent, individual-based models do not conform to these expectations. Rather than yielding simple relationships between explicitly defined model variables (e.g., “ A must be larger than B in order for behaviour C to be stable”), these models merely generate observable behaviour under different conditions. Deriving equivalently simple statements describing model behaviour in terms of model parameters is an additional task, and one which may be very difficult.

This difficulty stems from the relatively opaque relationship between the low level at which the model is implemented and the higher level at which the model’s results are collected. Individual-based models involve at least two levels of description, the explicitly represented individuals, and the “emergent”

population-level behaviour. Casting our model at the *sub-individual* level introduced added complexity. The model's atomic entities, components, interact in complicated and highly non-linear ways in order to generate both plant-*and* population-level behaviour.

The complexity that often results from this type of model is sometimes regarded as a strength, allowing the exploration of subtle relationships between different levels of description (Parrott and Kok, 2000). However, there is sometimes a temptation to add complexity to such models in an attempt to increase their realism. This can make them difficult to understand, and as a result can lead modellers to treat their exploration as some kind of empirical enquiry (Di Paolo et al., 2000).

A more successful strategy is to search for the minimal model capable of exhibiting the behaviour of interest (Grimm et al., 2005). Such models are often simpler than their complex behaviour would lead an observer to infer (Braitenberg, 1984). An important class of result that can be validly drawn from simulation models of this kind has the following form:

“Theory suggests that phenomenon P requires mechanisms A , B , & C , but an individual-based model exhibits behaviour akin to P through the action of A & B alone.”

This type of “existence proof” often reveals that co-ordinated high-level behaviour can arise from low-level mechanisms without the need for central control (e.g. flocking behaviour in birds, Reynolds, 1987). In the case of plant growth and development, given the lack of a central nervous system, one would expect many examples of this type of reasoning to hold. Considerations of parsimony demand that we entertain these simpler models before complicating

them further by adding centralised control mechanisms.

4.3 Further Work

One area in which physiological mechanisms achieve apparently high-level co-ordinated control of plant behaviour concerns the role of plant hormones in the coordination of reproduction and branching (Ward and Leyser, 2004; Thomas et al., 2005). Extensions to the model considered here could explore how such mechanisms interact with the resource-based mechanism of control to determine the growth and structure of individual plants.

At the level of plant-plant competition we identify two areas worthy of further exploration. First, the spatial range over which competition takes place could be assessed for different general classes of plant morphology (Purves and Law, 2002). Second, the significance of differences between morphological characteristics of life-history strategy could be assessed directly through competitive simulation. To what extent must branching angles differ before there is support for the conjecture by Horn (1971), that plants with narrow branching angles are favoured early in succession while those with wide-angled branches dominate at equilibrium?

At the level of interspecific competition, by wrapping a simple steady-state genetic algorithm (Ochoa, 1998) around the model, the coevolution of plant life-history strategies could be explored under various regimes. In the model, successful plants generate more seeds than their competitors. If each offspring's life-history parameters were to differ slightly from those of their parents, mutants with better-adapted life-history strategies would tend to dominate the

population at the expense of their competitors—coevolution would result. Simulations such as these would allow the dynamics of life-history strategy coevolution to be explored in the context of a plant community.

5 Conclusion

We have presented a model of plant growth, development and competition for light in three dimensions, making use of a simple L-system and ray tracing algorithms. Although the model is cast at the level of plant components, individual-, cohort- and community-level phenomena were robustly exhibited. We use the model to support assumptions frequently made in the plant ecology literature concerning the nature of plant-plant competition, and suggest avenues of future research in a similar vein.

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References

- Allen, M. T., Prusinkiewicz, P., DeJong, T. M., 2005. Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. *New Phytologist* 166 (3), 869–880.
- Benjamin, L. R., Sutherland, R. A., 1992. A comparison of models to simulate the competitive interactions between plants in even-aged monocultures. In:

- de Angelis, D. L., Gross, L. J. (Eds.), *Individual-Based Models and Approaches in Ecology*. Chapman & Hall, pp. 455–471.
- Braitenberg, V., 1984. *Vehicles: Experiments in Synthetic Psychology*. MIT Press, Cambridge, MA.
- Brunner, A., 1998. A light model for spatially explicit forest stand models. *Forest Ecology and Management* 107 (1-3), 19–46.
- Chelle, M., Andrieu, B., 1998. The nested radiosity model for the distribution of light within plant canopies. *Ecological Modelling* 111 (1), 75–91.
- Chelle, M., Andrieu, B., 1999. Radiative models for architectural modeling. *Agronomie* 19 (3-4), 225–240.
- Colasanti, R. L., Hunt, R., 1997. Resource dynamics and plant growth: A self-assembling model for individuals, populations and communities. *Functional Ecology* 11 (2), 133–145.
- Colasanti, R. L., Hunt, R., Askew, A. P., 2001. A self-assembling model of resource dynamics and plant growth incorporating plant functional types. *Functional Ecology* 15 (5), 676–687.
- Crawley, M. J. (Ed.), 1986. *Plant Ecology*. Blackwell Scientific Publication, Oxford, Ch. 4. Life History and Environment, pp. 73–131.
- Deussen, O., Hanrahan, P., Lintermann, B., Měch, R., Pharr, M., Prusinkiewicz, P., July 1998. Realistic modelling and rendering of plant ecosystems. In: *Proceeding of SIGGRAPH 98*. Orlando, Florida, pp. 275–286.
- Di Paolo, E. A., Noble, J., Bullock, S., 2000. Simulation models as opaque thought experiments. In: Bedau, M. A., McCaskill, J. S., Packard, N. H., Rasmussen, S. (Eds.), *Artificial Life VII: Proceedings of the Seventh International Conference on Artificial Life*. MIT Press, Cambridge, MA, pp. 497–506.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: What

- have we learned, and what could we learn in the future? *Ecological Modelling* 115, 129–148.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D., 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science* 310 (5750), 987–991.
- Hanan, J. S., Hearn, A. B., 2003. Linking physiological and architectural models of cotton. *Agricultural Systems* 75 (1), 47–77.
- Horn, H. S., 1971. *The Adaptive Geometry of Trees*. Princeton University Press.
- Hutchings, M. J., de Kroon, H., 1994. Foraging in plants: The role of morphological plasticity in resource allocation. *Advances in Ecological Research* 25, 159–238.
- Lane, B., Prusinkiewicz, P., May 2002. Generating spatial distributions for multilevel models of plant communities. In: *Proceedings of Graphics Interface 2002*. Calgary, Alberta, pp. 69–80.
- Lindenmayer, A., 1968. Mathematical models for cellular interaction in development: Parts I and II. *Journal of Theoretical Biology* 18, 280–315.
- Niklas, K. J., Kerchner, V., 1999. Evolutionary walks through a land plant morphospace. *Journal of Experimental Botany* 50, 39–52.
- Ochoa, G., 1998. On genetic algorithms and lindenmayer systems. In: Eiben, A. E., Bäck, T., Schoenauer, M., Schwefel, H.-P. (Eds.), *Parallel Problem Solving from Nature – PPSN V*. Springer, Berlin, pp. 335–344.
- Pacala, S. W., Deutschman, D. H., 1994. Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos* 74 (3), 357–365.
- Parrott, L., Kok, R., 2000. Incorporating complexity in ecosystem modelling.

- Complexity International 7.
- Pearcy, R. W., Muraoka, H., Valladares, F., 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytologist* 166 (3), 791–800.
- Perttunen, J., Sievanen, R., 2005. Incorporating lindenmayer systems for architectural development in a functional-structural tree model. *Ecological Modelling* 181 (4), 479–491.
- Perttunen, J., Sievanen, R., Nikinmaa, E., 1990. LIGNUM: A model combining the structure and the functioning of trees. *Ecological Modelling* 108 (1-3), 189–198.
- Prusinkiewicz, P., 2004. Modeling plant growth development. *Current Opinion in Plant Biology* 7 (1), 79–83.
- Purves, D. W., Law, R., 2002. Experimental derivation of functions relating growth of *Arabidopsis thaliana* to neighbour size and distance. *Journal of Ecology* 90 (5), 882–894.
- Reynolds, C. W., 1987. Flocks, herds, and schools: A distributed behavioral model. *Computer Graphics* 21 (4), 25–34.
- Ruiz-Ramos, M., Mínguez, M. I., 2006. ALAMEDA, a structural-functional model for faba bean crops: Morphological parameterization and verification. *Annals of Botany* 97 (3), 377–388.
- Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113 (4), 447–455.
- Sletvold, N., Hestmark, G., 1999. A comparative test of the predictive power of neighbourhood models in natural populations of *Lasallia pustulata*. *Canadian Journal of Botany* 77 (11), 1655–1661.
- Smits, B., 1998. Efficiency issues for ray tracing. *Journal of Graphics Tools* 3 (2), 1–14.

- Sokal, R. R., Rohlf, F. J., 1995. Biometry, 3rd Edition. W. H. Freeman and Company, New York.
- Sterck, F. J., Schieving, F., Lemmens, A., Pons, T. L., 2005. Performance of trees in forest canopies: explorations with a bottom-up functional-structural plant growth model. *New Phytologist* 166 (3), 827–843.
- Takenaka, A., 1994. A simulation-model of tree architecture development based on growth-response to local light environment. *Journal of Plant Research* 107 (1087), 321–330.
- Thomas, S. C., Weiner, J., 1989. Growth, death and size distribution change in *Animpatiens pallida* population. *Journal of Ecology* 77, 524–536.
- Thomas, S. G., Rieu, I., Steber, C. M., 2005. Gibberellin metabolism and signaling. *Plant Hormones: Vitamins And Hormones - Advances In Research and Applications* 72, 289–338.
- Tilman, D., 1982. Resource competition and community structure. Vol. 17 of *Monographs in Population Biology*. Princeton University Press, Princeton, New Jersey.
- Ward, S. P., Leyser, O., 2004. Shoot branching. *Current Opinion in Plant Biology* 7 (1), 73–78.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* 5, 360–364.
- Weller, D. E., 1991. The self-thinning rule: Dead or unsupported? – A reply to Lonsdale. *Ecology* 72, 747–750.
- Westoby, M., 1984. The self-thinning rule. *Advances in Ecological Research* 14, 167–225.
- Yoda, K., Kira, T., Ogawa, H., Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Theoretical Biology* 14, 107–129.