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A GENERIC APPROACH TO SPATIAL INDIVIDUAL-BASED MODELLING AND SIMULATION OF PLANT COMMUNITIES

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Abstract. A general framework is proposed for the formulation and simulation of spatially explicit individual-based models of plant communities. A software implementation, *siplab*, was developed using the *R* statistical programming language. The scheme is a synthesis that encompasses many approaches from the literature, making possible to compare and combine their different components. Relationships between plant growth and various competition or assimilation indices are discussed, together with the choice of state variables and statistical issues in growth equations. Modelling is extended to deal with environmental heterogeneity, specified as a given resource distribution in the plane. Plants exert competitive pressure over resources at each point, represented by size- and distance-dependent functions that emulate or generalize similar concepts used in existing models. The partitioning of resources where these functions overlap is parameterized in a way that includes the one-sided fully asymmetric allocation of tessellation models, as well as a continuum of symmetric and asymmetric resource sharing alternatives. Finally, the plant resource uptake is integrated over space, with an optional size- and distance-dependent plant response or efficiency weighting. The framework and software permit conducting simulation studies where results are less dependent on any specific model structure.

Keywords: individual-tree, spatially explicit, growth, competition, asymmetry, *R*, *siplab*

1 Introduction

Spatially explicit individual-based models are frequently used for understanding and predicting the development of plant communities. In forestry they can be traced back to the early 1800's, when Reventlow quantified tree interactions in terms of the relative locations and sizes of neighboring trees (Reventlow 1879). Staebler (1951) introduced the idea of overlapping zones of influence widely used today. These models proliferated once electronic computers became generally available, starting with Newnham and Smith (1964). Although largely abandoned for practical forest management in favor of aspatial approaches in the 1980's (an exception is the continuing use of TASS (Mitchell 1975) in British Columbia), spatial individual-plant models (SIPMs) remain important research tools (Vanclay 1994, Weiskittel et al. 2011, Burkhart and Tomé 2012). In the ecological literature individual-based models became widespread after about 1990 (Grimm 1999), although earlier examples exist (e.g., Cormack 1979, Wyszomirski 1983). Useful reviews are provided by Cormack (1979), Stoll and Weiner (2000), Lischke (2001), Grimm and Railsback (2005), Gratzer et al. (2004), Weiskittel et al. (2011), Burkhart and Tomé (2012) and Larocque et al. (2013), among others.

Model implementation usually involves custom computer coding. In many instances this may be unavoidable, but it has adverse consequences on developing effort, transparency, reproducibility, and on the generality of simulation results. Differences in concepts and terminology hinder communication, and it can be difficult to know to what extent any conclusions are dependent on particular model details (Lorek and Sonnenschein 1999, Grimm and Railsback 2005, Sec. 1.6). Some of these challenges are addressed by packages designed specifically for individual-based simulation (Lorek and Sonnenschein 1999, Railsback et al. 2006, Petzoldt and Rinke 2007, Lytinen and Railsback 2011). Any such software must strike a compromise between the maximum generality, flexibility, and complexity of programming directly in a general-purpose computer language, and the simplicity and ease-of-use of systems restricted to a narrow class of problems. The approach described here attempts to provide a conceptual framework that includes

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a wide range of SIPMs, and a simple software implementation capable of handling different formulations in an unified way.

SIPMs usually split predictors of growth and mortality (and sometimes of recruitment potential) into a part depending on subject plant attributes, and another part representing neighbor interactions. The interactions are encapsulated into a competition, resource capture, or growth-modifier index (possibly vector-valued). The next section deals with this topic. The different indices are closely related, and the rest of the article focuses mainly on the computation of an "effective resource capture" index, called *assimilation index* for short. For simplicity, the discussion will be in terms of resource-mediated competition, the most important type of interaction among plants (Harper 1977, Cormack 1979, Tilman 1990, Ford and Sorrensen 1992, Stoll and Weiner 2000), although other kinds of interactions can be modelled by methods similar to those described.

Effective resource capture (*assimilation*) is specified on a horizontal plane projection through a sequence of 4 sub-models that combine to mimic many of the models found in the literature. The 4 components are: (1) a two-dimensional *resource map*, representing a spatial distribution of resource availability; (2) an *influence function*, representing the competitive ability of a plant at a given point; (3) an *allotment rule*, determining how the resource at any point is shared among plants according to their influence function values; and (4) an *efficiency function*, weighting the contribution of resource uptake depending on distance and plant attributes. The computed effective uptake at each point is integrated over the study region to obtain the assimilation index for each plant. In particular models some of the components are typically missing or trivial, but this general framework allows for consistent comparisons and "mix-and-match" of elements from different SIPMs.

An implementation of the scheme in *R* (R Development Core Team 2009) is available in the package *siplab* from *The Comprehensive R Archive Network* (CRAN, `http://CRAN.R-project.org`). A detailed software manual and source code for the latest version can be downloaded from CRAN (`http://cran.r-project.org/web/packages/siplab`) or from `http://forestgrowth.unbc.ca/siplab`. The Supplementary Data at `http://mcfns.com/index.php/Journal/article/view/6_36/data` includes listings for the version described here.

An important class of SIPMs greatly simplifies computation by including only pair-wise interactions between a plant and each of its neighbors, ignoring the more detailed spatial configuration (e.g., Staebler 1951, Newnham and Smith 1964, Schneider et al. 2006, Stadt et al. 2007, Coates et al. 2009). A flexible version of that approach is also included in *siplab*, but it will not be discussed further here.

2 SPATIAL INDIVIDUAL-PLANT MODELS

2.1 Indices. In a SIPM, a plant's growth rate is a function of the sizes and positions of all plants in some neighborhood:

$$\Delta s_i = f_i(s_1, p_1, s_2, p_2, \ldots, s_n, p_n) \; ,$$

where s_i and p_i denote size and position for plant i, respectively. The "size" s could be a scalar or a multivariate vector (see below), and p may be a vector of coordinates specifying the plant location in 2- or 3-dimensional space. Without loss of generality, the modelling is commonly factorized into two components, by expressing growth in terms of the size and position of the subject plant and of a resource capture or competition index C_i that represents interactions:

$$\Delta s_i = g_i(s_i, p_i, C_i) \tag{1}$$

$$C_i = h_i(s_1, p_1, s_2, p_2, \ldots, s_n, p_n) \; . \tag{2}$$

Similar relationships for death or recruitment probabilities are often used. In most models g_i is the same for all i (possibly with species-dependent parameters), size is represented by a simple scalar such as plant biomass or tree diameter, C_i is a scalar, and the models are isotropic, with relative positions represented by inter-plant distances. We allow for more general situations.

C_i can be a competition index, a phenomenological expression reflecting the direct effect of competitors on growth or mortality of plant i. Alternatively, C_i may represent competition-dependent resource capture or assimilation, possibly from a more mechanistic point of view. Both indices are closely related, a competition index generally measuring the loss of growth or of resource capture compared to that under free-growing conditions. It can be seen as equal, or as functionally related, to the difference between the value of an assimilation index and the same assimilation index computed in the absence of competitors (e.g., setting competitor sizes equal to 0 or inter-plant distances equal to infinity).

Another popular approach writes growth as the product of a potential growth rate in the absence of competitors, and a competition-dependent modifier (e.g., Pretzsch 2009, Sec. 11.5.22; Coates et al. 2009, Weiskittel et al. 2011, Sec. 6.2.1). If C_i^0 is the free-growing competition or assimilation index, equation (1) can always be written in potential/modifier form as

$$\Delta s_i = g_i(s_i, p_i, C_i^0) \times \frac{g_i(s_i, p_i, C_i)}{g_i(s_i, p_i, C_i^0)} \; .$$

Again, there are no essential differences between the formulations.

Competition patterns can differ among resources. In particular there may be differences between above-ground competition for light and physical space, and below-ground competition for water and nutrients (Cormack 1979, Wixley 1984, Tilman 1990, Stoll and Weiner 2000, Coates et al. 2009). Therefore, the index C_i could be a vector, although it is more common to model only the resource believed to be most limiting, or to use a combined over-all scalar value. We show how to compute a real-valued assimilation index, which might possibly correspond to a resource vector component.

2.2 Which size? For many annual plants a scalar size measure such as width or biomass is sufficient. This is less satisfactory with trees, where allometry can change substantially with growing conditions, including competition. Most SIPMs have described the state of a tree solely by its stem diameter or basal area, but height and possibly crown dimensions can also be important. With a multivariate "size" vector, a complete dynamic model must include a rate of change equation for each of the vector elements (García 2013). In particular, if crown dimensions are used, then equations predicting the rate of change in these dimensions are needed.

When studying tree competition, there is often discussion on whether one should use tree diameter or tree basal area on the left-hand side of eq. (1) (e.g., Burkhart and Tomé 2012, Sec. 14.3). The choice is sometimes based on the regression r-square, but such comparison for different dependent variables is not valid. More importantly, the increment variable affects which variables and in what form they appear on the right-hand side. For instance, the instantaneous increments in diameter (d_i) and in tree basal area ($b_i = kd_i^2$) are related by $\mathrm{d}b_i/\mathrm{d}t = 2kd_i\,\mathrm{d}d_i/\mathrm{d}t$. If the diameter increment were independent of size, the basal area increment would not be, and vice-versa.

From a mechanistic point of view, it may be more meaningful to consider increments in biomass, or in some proxy like stem volume or the product of basal area and height, and to avoid diameter or basal area as drivers on the right-hand side. Diameter and basal area reflect the accumulation of (mostly dead) xylem on the stem, which is unlikely to play a significant physiological role (García et al. 2011). Such relationship would also lessen some of the statistical difficulties discussed in the next section.

2.3 Statistics of growth equations. There are statistical and conceptual problems in relating growth to size that do not seem to have received much attention. Consider a typical individual-based growth model (1), where s_i is a scalar size like stem diameter or biomass. The current size s_i is an accumulation of past increments Δs_i. In addition, growth rates vary among trees due to genetic or micro-site factors specific to each individual. Clearly, faster-growing plants tend to be larger, and a positive correlation between growth and size is to be expected. Therefore, a positive correlation in fitting equation (1) does not necessarily imply that large size causes faster growth. Paradoxically, a "wrong" model can produce the best predictions (Appendix A). The situation is further complicated by error-in-variables issues that act in the opposite direction, lowering correlations (Blomqvist 1977).

The consequences of the circularity implicit in growth equations might be less serious with a choice of variables like the one suggested in the previous section, e.g., $\Delta w_i = g(h_i, C_i)$, with h_i being height and $w_i = d_i^2 h_i$. A similar equation for Δh_i is also needed. Apart from biological interpretations, spurious correlations should be weaker, and height growth is much less affected by density and competition than growth in diameter or biomass. The difficulties are however still present to some extent.

If a number of increment periods are available for each plant, path analysis techniques may possibly be used to disentangle causality relationships (Mitchell-Olds 1987, Bollen 2005a), and individual variability can be handled by hierarchical mixed-effects models. Structural equation software that combines path analysis and hierarchical modelling could be useful (Bollen 2005b, Lamb et al. 2011, Boker et al. 2011). These issues are not pursued further here, we focus on the computation of the indices, eq. (2).

3 MODELLING COMPETITION

I describe how to compute a single scalar assimilation index for each plant. This index may represent the combined effect of above- and below-ground competition, or indices associated to different resources may be computed separately. A horizontal plane projection is used, excluding more complex three-dimensional approaches (e.g., Mitchell 1975, Pretzsch 2009), although the essential characteristics of these are sometimes adequately approximated in a 2-D projection (Mitchell's model is discussed later).

The software implementation, *siplab*, is built on top of *spatstat*, an *R* library for the statistical analysis of spatial data (Baddeley and Turner 2005). Besides analysis of marked or unmarked point patterns and related models, the library provides general data handling facilities for spatially structured data. The main function in *siplab* takes as input a *spatstat* point pattern object, and competition model components specified as described below. The point pattern object contains the plants x and y coordinates, a vector or data frame of *marks* with size variables and possibly species identification or other attributes, and a window object describing the region in which the plants are observed.

3.1 Resource map. Current SIPMs assume a homogeneous environment, equating resource availability to growing space. However, more realistic heterogeneous resource distributions could be used to study the effects of, for instance, local variation in soil quality (Cormack 1979, Mitchell-Olds 1987, Stoll and Weiner 2000, Law et al. 2002, García 2006).

Computations are performed on a rectangular grid enclosing the study region, with a given spatial resolution (pixel size). By default, the grid is generated with 1 unit of resource per unit area in every pixel, corresponding to a uniform resource distribution. Alternatively, an arbitrary pixel map can be supplied; the map size and resolution are adjusted as necessary. Functional representations, e.g., gradients or randomly generated surfaces, are also accepted.

3.2 Influence function. The competitive strength of a plant, its resource capture ability or pressure exerted at some point, normally increases with the plant size and decreases with distance. We represent this by an *influence function*, which can be specified by the user in terms of the plant mark values and of the plant-to-point vector distance. A zero value implies no resource capture at that point. Pre-programmed versions for some functions described below are provided.

Most SIPMs include implicitly or explicitly some equivalent of the influence function. Although the function is usually radially symmetric, we allow more general forms by passing as an argument the vector distance. For instance, the inclination of incident light in the Northern Hemisphere may cause shading to be stronger toward the south. Other anisotropies may be more easily handled through coordinate transformations or resource gradients. Influence is considered as translation-invariant, any spatial heterogeneity can be expressed through the resource map. A plant's influence function may vary depending on species, individual genetic traits, or other attributes included in its marks.

The simplest example of influence function is that of fixed-radius neighborhood models (Grimm and Railsback 2005, Sec. 6.7.1), where the function is constant up to a certain distance and 0 beyond that. More generally, the radius can depend on some measure of plant size, defining a *zone of influence* (ZOI, Fig. 1a, Grimm and Railsback 2005, Sec. 6.7.2).

Perhaps the most easily-visualized example of a more general influence function is the one implicit in the TASS forest growth model (Mitchell 1969, 1975). There, trees are assumed to have equal-shaped potential free-growing crowns that move upwards with height growth. Radial crown growth stops at the points of contact between neighboring trees, producing a tessellation on the horizontal plane. Crowns are hollow, with 5 annual layers of surviving foliage. Therefore, except for some tapering of the foliage depth near free edges at the base of the crown, growth is related to the area allocated to the tree in the tessellation (see also García 2005, Weiskittel et al. 2011, Sec. 5.2.1.1). The influence function can be taken as the height of the surface of the crown, and the tree with the highest value grabs all the resource at each point. In TASS the crown radius at a distance L from the top is $R = b\log[(L/c)+1]$, where b and c are parameters. Therefore, if the height of the green canopy base is B ($B = 0$ in young or open stands), an influence value at distance R for a tree of height H can be written as

$$\varphi = \max\{0, H - B - c[\exp(R/b) - 1]\} \qquad (3)$$

(Fig. 1b). The influence is positive within a ZOI $R < b\log\{[(H-B)/c]+1\}$.

The crown contacts assumed by TASS are not always observed, perhaps because of the inclination of incident light radiation at higher latitudes, or for other reasons (Goudie et al. 2009). However, a more abstract interpretation of the influence function as a shading potential is possible, maybe with parameter values giving a wider horizontal reach than in Mitchell (1975). Instead of the all-or-nothing resource partitioning among plants in that model, where ZOIs overlap the resources may be shared in other ways, as discussed in the next section.

As pointed out by Gates et al. (1979), there is a close connection between influence functions and models in which horizontal space is sub-divided among plants. The simplest such model is the Voronoi diagram or Dirichlet tessellation, where points on the plane are allocated to the closest plant (Brown 1965, Mead 1966). It is known that the Voronoi diagram can be obtained from the intersections of paraboloids bR^2, where R is the distance from a plant location (Aurenhammer and Klein 1999, Sec. 3.5; in this instance the value of the common scale parameter b is immaterial). Equivalently, ground points are assigned to the plant for which their inverted paraboloid $h - bR^2$ is highest, with h being an arbitrarily chosen height. This parabolic surface acts as an influence function in the same way as the crown profile in TASS. Letting the paraboloid size vary with plant size, and/or using shapes other than paraboloid, generates other tessellations that appear in the literature (Appendix B). Truncating the influence function at 0, or at some other level, gives ZOIs outside of which resources may remain unallocated (Gates et al. 1979, Wixley 1984, Nance et al. 1988).

Gates et al. (1979) state a number of conditions that a reasonably space allocation should fulfill. If in addi-

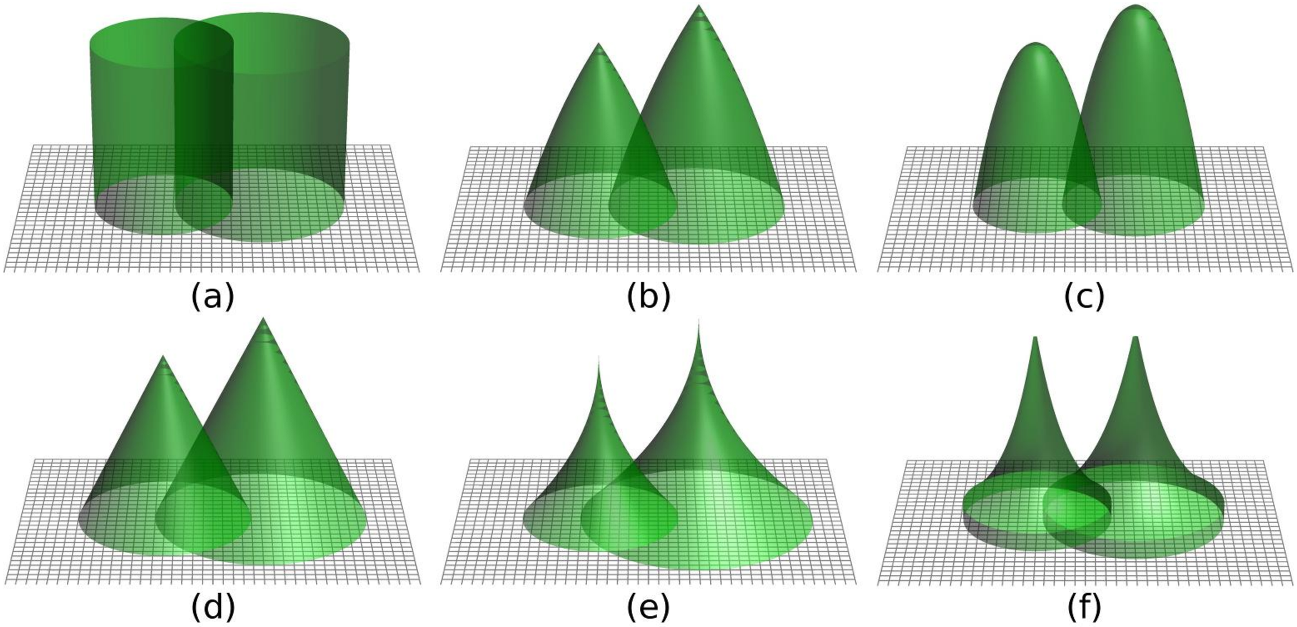

Figure 1: Some influence functions. (a) ZOI. (b) TASS, eq. (3). (c) Parabolic (gnomonic). (d) Cone. (e) Gnomonic eq. (4) with $a = 0.5$. (f) Berger and Hildenbrandt (2000)

tion the influence function has the same shape for all plants, differing only by a plant size-dependent factor, they prove that the only function compatible with those conditions is

$$\varphi = b(R_0^a - R^a)^{1/a} , \tag{4}$$

where a and b are positive constants and R_0 depends on plant size (Appendix B). With monocultures the proportionality factor b is immaterial and can be ignored, but otherwise the parameters can differ among species.

An alternative to the similarity scaling hypothesis that might make more sense, at least for above-ground competition, is to assume as in TASS a common function that moves upwards with plant size, perhaps following the growth in height. We call this *gnomonic* scaling, one meaning of gnomon being "that which, added to an entity (number or shape), makes a new entity similar to the starting entity" (Wikipedia 2013). With gnomonic instead of similarity scaling, it is found that the only function compatible with the other conditions of Gates et al. (1979) is

$$\varphi = \varphi_0 - bR^a \tag{5}$$

(Appendix B). The size-dependent parameter φ_0 is the value of the influence function at the origin, and might be taken as proportional to height or crown length, for instance. These influence functions include parabolic ($a = 2$, Fig. 1c), cone ($a = 1$, Fig. 1d), and concave shapes ($a < 1$, Fig. 1e). ZOI models correspond to $a = 0$, if the function is truncated to 0 beyond a maximum radius.

In an approach called Ecological Field Theory, Wu et al. (1985) and Walker et al. (1989) represented the effects of canopy, stems and roots through influence functions, including truncated negative exponentials and truncated Gaussians. Berger and Hildenbrandt (2000) used a function that is constant within the area of a tree stem, decreases exponentially between the stem radius and a ZOI radius proportional to stem diameter, and is 0 outside the ZOI (Fig. 1f, see also Berger et al. 2002, Grimm and Railsback 2005, Sec. 6.7.3). Truncated influence functions are commonly defined through a two-stage procedure, where first competitors are selected by some rule such as overlapping ZOIs, and then smooth interaction functions are specified for the competitors (e.g., Wu et al. 1985, Weiskittel et al. 2011, Sec.2.3.2; Burkhart and Tomé 2012, Sec. 9.2.1).

3.3 Allotment.

In tessellation models, the plant with the highest influence value φ takes all the space or resource available at a point (or pixel). An alternative is to assume that the resource at any location is shared or partitioned among the plants in some other way related to their influence values. For instance, between two competing plants i and j, plant i might capture a part proportional to φ_i:

$$\frac{\varphi_i}{\varphi_i + \varphi_j} .$$

More generally, we use a partition or allotment function

$$\frac{\varphi_i^\alpha}{\sum_j \varphi_j^\alpha}\ , \tag{6}$$

where α is a non-negative asymmetry parameter, and the sum is over all the plants (or all plants with non-zero influence). If the denominator is 0, the undetermined ratio 0/0 is taken as 0.

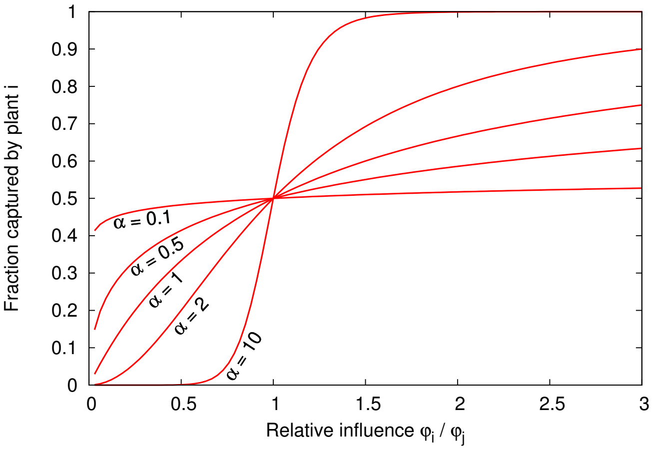

Figure 2: Resource partitioning (allotment) between two competing plants

With this function, if $\alpha = 1$ resource allotment is proportional to influence. Allotment is more than proportional if $\alpha > 1$, and less than proportional if $\alpha < 1$ (Fig. 2). In the limit as $\alpha \to \infty$, (6) tends to the one-sided all-or-none allotment rule of tessellation models: 1 if $\varphi_i = \max_j\{\varphi_j\}$, or 0 otherwise. In the limit $\alpha \to 0$ the resource is shared equally among all plants whose ZOI cover the point (Wyszomirski 1983). The software accepts $\alpha = \infty$ (`Inf` in *R*) and $\alpha = 0$ to specify those alternatives. The most appropriate allotment may differ for above- or below-ground competition.

The parameter α is related to Weiner's (1990) concept of competition asymmetry, but applied to the pressure on individual points on the plane rather than to the size of whole plants. Schneider et al. (2006) represented asymmetry for a pair of competing plants with logarithmic sizes y_i and y_j by a multiplier

$$1 + \tanh[k(y_j - y_i)]\ .$$

Substituting $y = \log\varphi$, this simplifies to twice the value of (6), with $\alpha = 2k$.

As previously indicated, only the relative values of the influence functions are relevant, multiplying all the functions by the same positive constant has no effect. With one-sided allotment ($\alpha \to \infty$), any monotonic transformation of φ produces the same results. It is also clear from eq. (6) that asymmetry and influence are mathematically indistinguishable, in the sense that any degree of asymmetry could be achieved by altering the shape of the influence functions through a power transformation. We keep them separate for convenience, flexibility, and perhaps conceptual clarity.

3.4 Efficiency and assimilation index. Multiplying the initial resource availability and the allotment function gives the amount of resource available to the plant at each point (or pixel). Many models integrate or add up this to obtain an index representative of the plant's growth capacity or competitive position. However, points may be more or less accessible to the plant depending on distance (Mead 1966, Cormack 1979), and the resource uptake, utilization efficiency, or plant response may vary (Goldberg 1990, Ford and Sorrensen 1992, García 1990, Stoll and Weiner 2000). This can be modelled by weighting by an *efficiency function*.

In the software implementation the efficiency function may be constant, but more generally it can be any user-supplied function of (vector) distance and plant attributes, specified in the same way as the influence function. It might be reasonable to use an efficiency function related to the influence function, e.g., φ/φ_0.

Some models assume direct plant-to-plant effects that may be appropriate for interactions that are not mediated by resources. These can be simulated by an efficiency with a spike at the plant location, approximated by a function that is a positive constant within a short distance and 0 elsewhere.

The product of resource map, allotment function and efficiency function is integrated over the study region to compute the assimilation index for each plant. Optionally, a free-growing assimilation index can be computed by omitting the allotment function. A competition index can be obtained as the difference between these two, or a growth modifier factor as their ratio (Sec. 2.1).

As in most SIPMs, in this formulation the effect of competitors is additive. Multiplicative influences, as in Wu et al. (1985), can be made additive with a logarithmic transformation.

Indices near the edges of the study region are distorted because of the absence of resources and competitors on the outside. Common solutions to this problem are not to use to use indices computed for plants near the edges, or (with rectangular regions) to attach translated copies, thus changing the topology into a torus. Both methods have been implemented in *siplab*.

3.5 Programming. An *R* function implementing the procedure just described has been written, in two slightly different versions. In both there is a first loop over the plants, accumulating the common denominator of the allotment function (6) into a pixel image. Then, a second loop divides the allotment numerator for each plant by the denominator, multiplies by the efficiency and resource maps, and integrates (sum of pixel values times pixel area). One version of this function makes a straightforward use of *spatstat* pixel images, and may be useful as documentation and as a basis for modifications. The other version is somewhat more opaque but several times faster, taking advantage of *R* array operation on pixel matrices.

Apart from the plant assimilation indices and the optional free-growing indices mentioned before, the allotment denominator pixel image is also available. It can be useful for visualizing the distribution of competitive pressure. Other optional output is the centroid of the assimilation map for each plant. It was included for a study of the effects of plasticity, where plants "move" into less contested spaces by leaning or redistributing foliage density (Umeki 1995a,b, Strigul et al. 2008).

4 Discussion and Conclusions

The characteristics of above- and below-ground competition are likely to differ. Gnomonic scaling and one-sided allotment may be reasonable approximations above-ground. Below-ground competition is more diffuse, Cormack (1979) citing a case where roots from 32 corn plants were found at a point. Similarity or radial scaling, and resource sharing, may then be more appropriate. Above- and below-ground indices could be combined as

$$\left\{[pC_a]^{-q} + [(1-p)C_b]^{-q}]\right\}^{-1/q} \ , \tag{7}$$

with p and q being positive parameters. The importance of C_a relative to C_b depends on the value of p, while q determines the shape of the response surface; the function tends to a strict limiting factor response for large q.

The proposed scheme seems to be flexible enough to reflect the main characteristics of many existing models in a unified way. It is a step in addressing for SIPMs some of the challenges that individual-based models have faced in ecology (Grimm and Railsback 2005): long time needed to develop the model, difficulty in analyzing results, lack of common language to communicate model and results, lack of generality, lack of standards. The motivations for generic computer software implementing such models are similar to those of Petzoldt and Rinke (2007), although our scope is much more limited.

The *siplab* package is a convenient platform for SIPM experimentation. *R* is a widely used free and open source software system with which many potential users are already familiar, and it permits leveraging the *spatstat* spatial data handling facilities, as well as more general statistical analysis functions. Some early testing was done with *NetLogo* (Wilensky 1999) that may also be suitable, with some advantages and disadvantages compared to *R* (Railsback et al. 2006, Lytinen and Railsback 2011). Software design prioritized ease-of-use, and being able to mimic components of known models with little or no programming by the user. However, it is easy to modify the code to adapt it to more general approaches. Discretizing space on a grid makes for model-independent and easily understandable computations, even though more accurate or efficient methods exist in special instances, e.g., for power diagrams (Appendix B).

Perhaps surprisingly, it is commonly reported that the predictive power of SIPMs is low, and non-spatial models have largely replaced them in forest management (e.g., Cormack 1979, Ford and Sorrensen 1992, Stoll and Weiner 2000, Schneider et al. 2006, Weiskittel et al. 2011, Burkhart and Tomé 2012, and references therein). Some possible reasons are:

1. Variables that summarize past growth, and that reflect individual genetic and micro-site characteristics, are good predictors of future performance in the absence of major disturbances (Sec. 2.3). Similarly to findings in time series forecasting (Makridakis and Hibon 2000), simple extrapolation techniques often outperform complex statistical or mechanistic models. The distinction between models for prediction and models for understanding is important; mechanistic models can still be useful as research tools, and possibly for prediction under drastically changed conditions.

2. Stoll and Weiner (2000) point out that "in many studies, environmental heterogeneity, such as local variation in soil quality . . . , seems to be more important than the local abundance of competing plants (Mitchell-Olds 1987)". See also Cormack (1979) and Law et al. (2002). Neighbor-to-neighbor size correlations are frequently positive, instead of negative as predicted by SIPMs (García 2006).

3. Plants exhibit plasticity in occupying available growing space, being able to lean or to redistribute foliage into canopy gaps (Umeki 1995a,b). Seemingly related to this, in tree plantations it is found that spacing rectangularity has remarkably little effect on yield per unit area or on tree size (Amateis et al. 2004). In the limit, under the *perfect plasticity approximation* of Strigul et al. (2008) plant coordinates become irrelevant.

The investigation of these issues can be assisted by simulation studies. With *siplab* it is possible to try different assumptions in a consistent framework, so that results are less depend on any specific model structure.

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Appendices

A Better predictions with the wrong model: an example.

A simple simulation illustrates some growth modelling and estimation issues. Assume that trees grow in diameter at a size- and time-independent annual rate, which varies from tree to tree due to genetic and/or local microsite differences. Generate a list of 30 such increment rates, for instance using normal random numbers with mean 0.5 cm/yr and standard deviation 0.1. Accumulate the increments over 10 years to obtain the diameters at age 10 (or simply multiply the increments by 10). Then, to estimate the growth rate at age 10, graph the increments over the diameters, and fit a linear regression.

It is seen that a regression of increment over current diameter predicts tree growth exactly, with no error. But the true model asserts that growth rate is independent of size. Using the true model, tree growth can be predicted by the mean of the 30 increments, with a standard error of $0.1 \times \sqrt{1 + 1/30} = 0.102$ cm/yr.

One could add random deviations, or use other growth functions to make the example more realistic. If diameters for several years were available, mixed-effects methods could take into account the between-tree variability. The fact remains, however, that a "wrong" empirical model can produce better predictions than the true causal relationships.

B Space allocation and influence functions

B.1 Results from Gates et al. (1979). Gates et al. (1979) considered the problem of subdividing among plants the union of their competition disks (ZOIs). They formulated a number of properties or rules for the one-sided fully asymmetric space partitioning process, and proved results for various combinations of these rules. First, they found feasible equation forms for the boundaries separating regions allocated to neighboring plants, subject to increasingly restrictive sets of rules. Then it was proven that a partition implies the existence of three-dimensional regions that are such that the projection on the plane of their exposed upper surface yields the partition. Following Mitchell (1969, 1975), these were interpreted mainly as physical crown shapes, although the authors pointed out that one could also regard the upper surface height "as the absorbed intensity (vertical flux per unit of horizontal area) of light."

Under some natural assumptions, for a single plant species it was shown that, in our notation, the crown surface or influence function must be of the form

$$\varphi = f(R_0^\alpha - R^\alpha) \;, \tag{8}$$

where $f(t)$ is some function defined for $0 \leq t < \infty$, R_0 is the basal ZOI radius, and α is a positive constant. If, in addition, it is assumed that the crown shapes are similar (i.e., differing only in scale), then $f(t)$ must be proportional to $t^{1/\alpha}$. Therefore, under the hypothesis of similarity,

$$\varphi = \beta(R_0^\alpha - R^\alpha)^{1/\alpha} \;, \tag{9}$$

with β being some proportionality constant. With several competing species the results are the same, except that the parameters α and β can vary among species.

Actually, Gates et al. (1979) proved all this only under an assumption, *Rule E*, which says that a plant whose ZOI is entirely contained inside the ZOI of another plant is completely suppressed and cannot be allocated any space. That implies $\alpha \geq 1$. They conjectured, but did not prove, that the results are also true without Rule E, for any non-negative α. For $\alpha < 1$ the influence functions are pointed like in Fig. 1e, and it is possible for a plant enclosed within another ZOI to "punch through" the upper surface (Fig. 4 of Gates et al. (1979)).

B.2 Gnomonic scaling. Instead of the crowns or influence functions for different sized plants being similar, assume that they differ in height, what we called gnomonic scaling. Then, it is found that the function f in (8) must be linear, and

$$\varphi = \beta(R_0^\alpha - R^\alpha) = \varphi_0 - \beta R^\alpha \;, \tag{10}$$

where φ_0 is the height at the origin. The parameters α and β are constants, possibly varying with species, while φ_0 depends on plant size.

B.3 Special cases. Gates et al. (1979) discussed interesting special cases of (9). For $\alpha = 1$ the influence function is a cone (Fig. 1d), and the partitioning is equivalent to the Johnson-Mehl construction for crystal growth, which has been applied to SIPMs by Cormack (1979) and Kenkel (1991). The same is true in the gnomonic case (10). For $\alpha = 2$, (9) is an ellipsoid of revolution, while (10) is a paraboloid of revolution (Fig. 1e). In both cases the boundaries between competing plants are straight lines, corresponding to the common chord of the intersecting ZOIs (Cormack 1979, Wixley 1984, Nance et al. 1988, Kenkel 1991). If all the

ZOIs are the same size, and they completely cover the plane, one obtains the Voronoi diagram or Dirichlet tessellation (Brown 1965, Mead 1966). In the limit $\alpha \to \infty$, equation (9) gives cylinders or umbrellas, with the larger plant capturing the whole of the intersection. If Rule E is relaxed and $\alpha < 1$, the smaller plant takes the larger portion of the overlap area, which Gates et al. (1979) thought unrealistic.

The gnomonic case $\alpha = 2$, the paraboloid, generates a space partition that is a generalization of the Voronoi diagram, known as a *power diagram* or *Laguerre-Voronoi diagram* (Aurenhammer 1987, Aurenhammer and Klein 1999, Okabe et al. 2000, Sec. 3.1.4). These structures have been extensively studied in computational geometry, and efficient algorithms for obtaining them have been proposed by Aurenhammer (1987) and by Gavrilova et al. (1996).

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