

## Exploring Ecological Significance of Tree Crown Plasticity through Three-dimensional Modelling

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- **Background and Aims** Morphogenetic plasticity may be as important as physiological plasticity in determining plant adaptability to changing environmental conditions. This study examines the importance of crown plasticity of trees in stands.
- **Methods** A three-dimensional forest simulator is used to explore the impact of crown shape plasticity on tree growth. Crown deformation is mediated through the local response to light and overall allometric constraints governing tree dimensions. By altering shape response parameters of *Hevea brasiliensis* the impact of increased or decreased plasticity is explored in a variety of competitive environments defined by various combinations of tree density and relative frequency of different strategies. The possible interactions between plasticity and growth rate and plasticity and below-ground competition are also explored.
- **Key Results** Crown plasticity confers competitive superiority in all cases studied. Interactions with other processes may downplay or enhance this competitive advantage.
- **Conclusions** Simulation results strongly suggest that crown plasticity does have a significant impact on tree performance in nature and that commonly observed crown shape deformation response of trees is of adaptive value.

**Key words:** Crown plasticity, 3D simulation, individual-based model, competition.

### INTRODUCTION

Morphogenetic plasticity may be as important as physiological plasticity in determining plant adaptability to changing environmental conditions. For instance, it has been shown that change in leaf life span of tropical species when seedling acclimate to light environment affects plant carbon budget, to an extent similar to the better known photosynthetic capacity adjustment (Vincent, 2006). Furthermore, because plants are sessile organisms facing spatial and temporal heterogeneity in resource distribution, their capacity to respond to such heterogeneity is likely to be of particular adaptive value (Brisson and Reynolds, 1997; Hodge, 2006). Indeed a number of experimental studies have shown that tree crowns respond to anisotropic light and space availability and that they do so in a species-specific way (Brisson, 2001; Muth and Bazzaz, 2002, 2003).

Tree photomorphogenetic response, which typically occurs at a variety of organizational levels (leaf, twig, crown, whole tree), is expected to affect tree performance by modifying different processes at different time scales (Givnish, 1988; Bloor and Grubb, 2004). This study focuses on crown deformation.

Photomorphogenetic responses of plants are complex and may imply a number of mechanisms such as:

- (1) Phytochrome-mediated shade avoidance response governing etiolation (Smith, 1982, 1995). Such a shade avoidance mechanism has been reported to be more

pronounced in light-demanding species than in shade-tolerant species (Gilbert *et al.*, 2001).

- (2) Blue light response governing phototropism (bending being triggered by a differential growth on the shaded/unshaded side of the stem (Loehle, 1986; Ballare, 1994, 1999). Such whole tree phototropism seems to be mostly associated with riverine species supposedly because of the adaptive value of such a strategy when risk of being overtopped is low (Loehle, 1986).
- (3) Local ‘passive’ proliferation in response to locally abundant light (Russell *et al.*, 1989; Stoll and Schmid, 1998). The intensity of this kind of local response is constrained by the level of physiological integration of the elementary growth units, with ‘guerilla’ growth forms being more plastic in shape than ‘phalanx’ growth form (Franco, 1986).

What specific advantage is crown photomorphogenetic plasticity likely to confer? Let us first express the relative growth rate (RGR; unit biomass increase per unit time per unit biomass) of the individual tree as the product of light use efficiency (LUE) and light capture efficiency (LCE). LUE is expressed in units of biomass increase per unit of light intercepted, i.e.  $\text{kg MJ}^{-1}$ , and LCE is expressed as unit of light intercepted per unit of biomass per unit of time, i.e.  $\text{MJ year}^{-1} \text{kg}^{-1}$ . LCE can further conveniently be broken down into the product of two terms: ‘leaf display efficiency’ (LDE) and leaf area ratio (LAR), where LDE is expressed in units of light intercepted per unit leaf area, i.e.  $\text{MJ yr}^{-1} \text{m}^{-2}$ , and LAR is the leaf area

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per unit (above-ground) biomass,  $\text{m}^2 \text{kg}^{-1}$ . Hence,

$$\text{RGR} = \text{LUE} \times \text{LCE} = \text{LUE} \times \text{LDE} \times \text{LAR}. \quad (1)$$

Crown deformation in response to uneven light distribution or strong lateral shading may affect both LUE and LCE.

LCE will be affected as a result of a change in both the LDE and the LAR. LDE is expected to increase if crown develops preferably towards high-luminance sectors: deploying leaves in areas of abundant incoming light will increase the average light capture per unit leaf area. This may be the main positive feedback of crown deformation. Conversely, allowing crown to stretch either vertically or laterally will tend to decrease the LAR by increasing the mean distance from root to leaf (longer xylem network, larger cost of supporting tissue) and therefore will tend to affect LCE negatively.

Light use efficiency may also be affected by change in crown shape in a number of ways. For example, LUE may be negatively affected by the change in the length of the xylem network from roots to leaves, which will affect hydraulic conductance and in turn affect photosynthesis (Schafer *et al.*, 2000; Hubbard *et al.*, 2001; Midgley, 2003; Delzon *et al.*, 2004).

The net effect of crown deformation on LCE and on the tree RGR is complex and time-dependent. The mere shape of the return function (net carbon gain in response to deformation towards light) is unknown. It may be hypothesized that the immediate feedback effect of preferential growth towards high light is predominantly positive via the increase in LDE. But as crown deformation progresses and irregularity or eccentricity of crown or slenderness of tree increases, LCE may *in fine* decrease as a result of the increase in LDE being completely offset by the decrease in LAR (notwithstanding the possible concomitant decrease in LUE due to hydraulic constraints). The optimum degree of deformation in response to a particular light field will probably depend strongly on parameters related to the architectural and physiological characteristics of the target species. However, the distribution of incoming light changes over time as the tree and its neighbouring competitors grow and/or canopy gaps are created in the vicinity of the tree (Lieffers *et al.*, 1999). Benefits of crown deformation in terms of improved carbon budget at the whole tree level will depend on the payback time of the additional structures developed to increase light capture. The structural cost associated with the preferential display of leaves in a high-light microsite is more likely to be amortized if growth is rapid and turnover rates are high. Both characteristics would indeed contribute to minimize the risk of being shaded out before the structural costs of investment into new leaves and twigs have been paid back.

The discussion above makes two important points clear, namely that: (1) both costs and benefits associated with a particular degree of morphogenetic plasticity will depend largely on tree architectural and eco-physiological characteristics; and (2) the net benefit of tree morphogenetic

plasticity is strictly contingent on the competitive environment in which the tree grows.

The latter point means that we have resorted to computer simulation experiments to evaluate the likely benefits brought about by crown plasticity. We use a forest stand growth model that simulates individual tree deformation in response to the local neighbourhood to explore the predicted effect of crown plasticity on growth performance in a variety of competitive environments.

More specifically, the model is used to test the following hypotheses:

- (H1) Ecological significance of morphological plasticity in response to light in a forest stand. In a mixed species stand, a change in plasticity of one of the component species will affect (1) performance of individual trees of that species, (2) species population-level performance and (3) whole-community performance (community resource capture rate and resource use depletion rate).
- (H2) Performance of a particular degree of morphological plasticity (a particular morphogenetic strategy) is context-dependent, and notably frequency-dependent; indeed, increased height growth or lateral gap filling is expected to generate a larger pay-off if that strategy is rare among the competing individuals.
- (H3) Fast-growing species benefit more from morphological plasticity than slow growing species, i.e. there is a positive interaction between growth rate and crown shape plasticity.
- (H4) Competition occurs simultaneously for multiple resources and notably below-ground as well as above-ground resources. Numerous observational and experimental studies (reviewed in Tilman, 1987) have shown that species performance in mixture is modified by a change in the ratio of limiting resources. As a consequence it is hypothesized that the competitive advantage of above-ground plasticity will be affected by the degree of below-ground competition.

## MATERIALS AND METHODS

### *The simulation model*

A detailed description of the SE*x*I simulator (Spatially Explicit Individual-based) and an executable version of the model is downloadable from the Web (<http://www.worldagroforestry.org/sea/Products/AFModels/SExI>). Only an outline of the algorithms most relevant to the present study is given here. The model focuses on tree–tree competition processes and notably on competition for light and space. The model was initially developed for Indonesian agroforests and simulates tree growth on an annual time step.

The STR*e*TCH (Shape Transformation Response of Trees in Crowded Habitats) module is dedicated to simulating crown deformation in response to crowding. The crown of a tree is represented as a growing deformable solid. This expanding polyhedron is defined by a set of vectors (later

referred to as ‘virtual branches’) all stemming from the crown base. The growth rate of these virtual branches (VBs) is a function of local light conditions (local response) and their relative position. The way in which VBs are affected by local light conditions or constrained by their relative position within the crown is species-dependent.

Deformations considered in the model include vertical stretching of tree (also referred to as ‘etiolation’), a global response which is triggered by lateral shading, as well as a local response by which individual VB growth rates are modified according to local light availability. Global displacement of the crown through bending of the main stem (whole tree phototropism response) is not considered in the model. Our own observations suggest that such a response is mostly important during the early stages of development of the young individuals.

The height–diameter relationship is modified according to the observed vertical light gradient while imposing mass conservation [assuming that total stem biomass scales isometrically with the product of stem cross-sectional area at breast height (derived from diameter at breast height, dbh) and tree height]. The degree of ‘stretching’ increases with intensity of the vertical light gradient and is controlled by two species-specific parameters, namely Flexi and Sensi. The Flexi parameter stands for flexibility and is a measure of maximum departure from a reference H–dbh relationship established for open grown trees, i.e. maximum etiolation. Measured values of Flexi typically range between  $>0$  and 1 (G. Vincent, unpubl. data). Practically, H–dbh allometric relationships are adjusted per light environment (typically open grown vs high-density stands) and the ratio between the first derivatives ( $\delta H/\delta dbh$ ) of those relationships are used to estimate Flexi (formally defined as 1 minus this ratio). The Sensi parameter stands for sensitivity and captures species-specific signal detection sensitivity. The higher Sensi the lower the vertical light gradient needed to trigger a given percentage change in the ratio of height growth rate to diameter growth rate. The parameter values range between 0 and 2. A value of 1 means that the alteration of the  $\delta H/\delta dbh$  ratio is simply proportional to the light vertical gradient. In practice this parameter is fairly difficult to calibrate and it is usually adjusted by expert judgement. Shade-tolerant species will typically have lower sensitivity than light-demanding species. Lateral deformation may be a consequence of anisotropic light or spatial constraints. Anisotropic light will result in preferential growth of VBs in sectors of higher illuminance as well as selective shedding of ‘branches’ if light drops below a certain threshold (Sprugel, 2002). This reallocation of growth between VBs, which leads to crown lateral deformation, is also a function of both Sensi and Flexi parameters. Crown envelope surface is further constrained by imposing a species-specific relationship between stem section and crown surface. Indeed, this relationship has been observed to be very stable and notably independent of light environment (G. Vincent, unpubl. data). Lowermost branches are shed to adjust crown envelope surface to the species maximum value given current stem diameter value.

Tree diameter increment in the model is computed as the product of tree potential growth and growth reducers as is

classically implemented in forest and crop models (Reed *et al.*, 2001). Two growth modifiers are used to capture above-ground tree–tree interactions. The first is based on crown position (CP), an index of how much light an individual tree receives. The second is based on CF (CF) an index of its photosynthetic potential (Vincent *et al.*, 2002). CP is computed in a similar way as in the simple light interception model (Vincent and Harja, 2002). Light extinction through successive canopy layers is computed using species-specific light porosity of crown envelope. A species-specific function relates CP to the growth reduction factor. A modification of the original SLIM module described in Vincent and Harja (2002) was implemented in the light interception module used here. To compute the total light interception at crown level, the incoming light from any solid angle is weighted by the corresponding relative crown surface intersected (<http://www.worldagroforestry.org/sea/Products/AFModels/SExI>). As a consequence, crown deformation into high-light microsites increases whole crown light capture.

The increase in light interception associated with vertical stretching due to vertical light gradient accrues from the crown shape modification (contribution of the upper crown to the global light budget is larger in more slender crowns) and also from crown rise, which occurs through shedding of the lowest branches.

Crown form is an index defined as the ratio of crown envelope surface to reference crown surface of a tree with same dbh value. Crown form degradation may result from spatial constraints (crown collision) or branch shedding following suboptimal light availability. Vertical stretching of a crown will not reduce crown surface and hence not affect CF negatively. Rather, crown rise will follow from vertical stretching as a result of imposing a maximum crown surface for a given stem section (see above). Hence, plasticity (both vertical and lateral) confers an additional indirect advantage to trees: it allows CF to recover quickly following crown degradation.

We can reformulate the way the model implements crown plastic response in the terms of the formal decomposition of RGR introduced in the previous section (eqn 1). By altering crown shape in response to light gradients, the model simulates the associated change in LDE. The change in LAR (approximated by the ratio of crown surface to total biomass) associated with increased slenderness is also explicitly modelled. The model, however, does not consider any possible change in LUE and we come back to this point in the discussion section.

An additional growth reducer is associated with below-ground competition. Below-ground competition in the model is based on a crowding index, which is itself computed on the basis of overlap of influential zones. The influential zone is set to be proportional to tree stem diameter. For a given crowding index the corresponding growth reducer will depend on the site fertility index (<http://www.worldagroforestry.org/sea/Products/AFModels/SExI>). When exploring the possible interaction between below-ground and above-ground competition, the intensity of below-ground competition was reduced by increasing the fertility index.

Below-ground competition is essentially two-sided and will tend to reduce the competitive superiority of taller trees, which results from their better access to light. Despite being two-sided, below-ground competition is not symmetric. Let us consider two trees with overlapping influential zones. The growth reduction associated with this overlapping zone is a strictly increasing function of the area of the overlapping zone relative to the tree influential zone (<http://www.worldagroforestry.org/sea/Products/AFModels/SExI>). Hence, the tree with the larger influential zone will be less affected than the tree with the smaller one. Consequently, as vertically stretched trees will have their influential root zone reduced because of a retarded diameter increment associated with their accelerated height growth, they are expected to be less competitive in mixture if below-ground competition is taken into account.

This reasoning, however, is only valid ‘on average’. Clearly, when trees are randomly located, in some cases a smaller influential zone may mean lesser below-ground interaction with neighbours and subsequently an enhanced growth rate. This kind of effect is highly dependent on the local spatial pattern and may be particularly important in the early stages of stand development, before most trees start to interact with many others.

The model was calibrated for *Hevea brasiliensis* (Willd.) Muell.Arg as the autoecology and growth dynamics of rubber, a non-pioneer light-demanding species, have been well studied. To illustrate the capacity of the model we present the results of the growth function calibration applied to a rubber density trial (Boerhedy, 1990).

After having shown that the model used is capable of simulating growth under contrasted situations we then move on to a more theoretical standpoint. Using the previously obtained parameterisation for the rubber tree, virtual tree communities are simulated by ‘planting’ together populations of trees which vary for one or more parameter, and we observe how the modified growth strategies

perform against each other. In most simulations presented mortality and regeneration modules were disabled, which admittedly resulted in simulating theoretical stand structure unlikely to be observed in reality. The point in disabling the demographic processes when studying growth is precisely to maintain stand density and stand composition constant when assessing the specific growth performance of a particular strategy. However, when exploring how below- and above-ground competition interact in affecting a particular plasticity level, we resorted to long-term simulations- which included demographic processes (and hence self-thinning). In the model mortality is directly affected by growth reducers themselves, reflecting the competitive pressure (i.e. mortality is density-dependent). Annual recruitment rate is proportional to relative abundance of trees of a particular strategy among adult trees. Adulthood was defined by a threshold dbh of 15 cm. Hence, relative abundance at which a particular strategy is maintained in the long term is a direct measure of its ecological performance. Arguably, in many cases, the use of long-term simulations focusing on relative frequency of a particular strategy as a measure of its performance is equivalent to performing growth simulations without demographic processes while focusing on growth performance. The latter option, however, is more convenient when density or relative frequency need to be controlled as they constitute the main effects being studied.

To illustrate the crown model deformation and its implication on individual tree growth performance, we first use fixed light maps (fixed vertical gradient, fixed radial anisotropy) imposed upon isolated trees. Figure 1 shows the output of the calibration procedure applied to a density trial conducted in Sumatra by the Indonesian Rubber Research Institute (Boerhedy, 1990). The overall dynamics and notably the faster decrease in dbh increment in dense stands is well reproduced by the model. For all the experiments we use the default parameterization of *Hevea brasiliensis*.

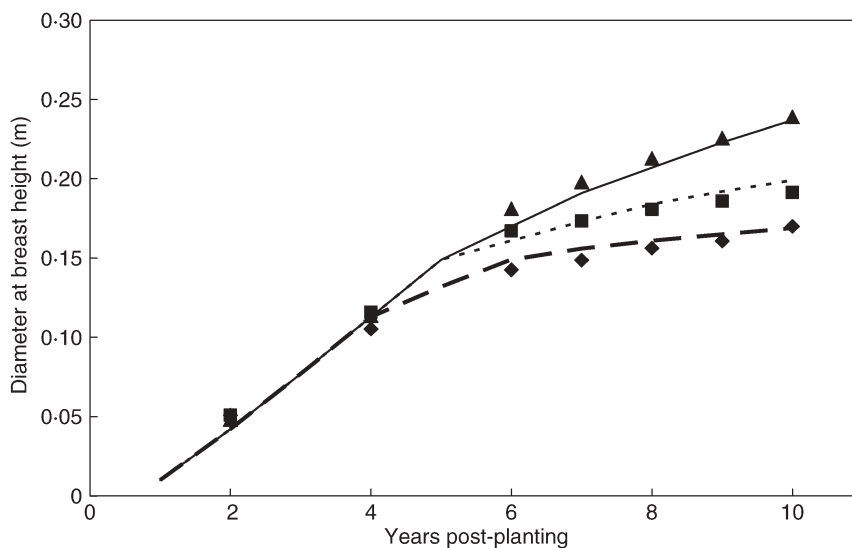


FIG. 1. Predicted (lines) and observed (symbols) dbh of rubber GT1 clone in a 10-year rubber density trial (continuous line and triangles: 6 × 6-m planting pattern; dotted line and squares: 4 × 4-m planting pattern; broken line and diamonds: 3 × 3-m planting pattern).

Preliminary test-runs were conducted on isolated trees growing in fixed light environment

A flexible tree reacts to an imposed vertical gradient by increased slenderness (Fig. 2). This has an overall *negative* impact on performance. The reduced growth rate proceeds from the reduced crown size itself being a consequence of increased growth in height (increased height growth reduces dbh increment, which constrains total crown size). No positive impact of crown rise is expected in the present case as the light map is applied at tree crown base. Note, however, that the change in crown shape in response to light vertical gradient (a local reaction and not a global etiolation response) results in an average 14 % increase in light interception. This is not sufficient to compensate for the delay due to increased height growth, and over the 30 years of simulation the plastic tree biomass index is 13 % lower than that of the strictly non-plastic control tree.

Lateral crown deformation in response to light anisotropy (Fig. 3) has a significantly *positive* impact via improved

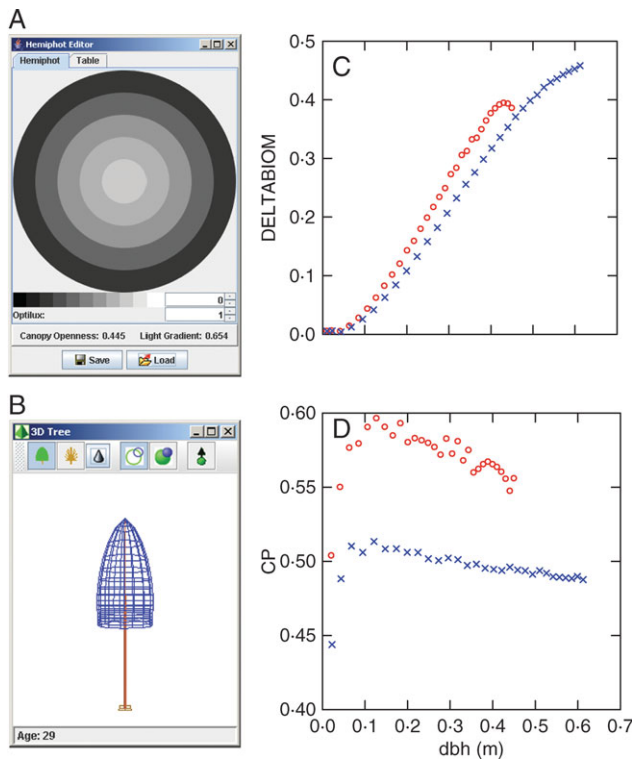


FIG. 2. Shape, growth rate and light capture of an isolated tree exposed to a fixed vertical light gradient. (A) Hemispherical photograph showing vertical gradient imposed. The lighter the ring the more incoming light from the corresponding inclination. (B) Predicted tree shape developed in response to vertical light gradient shown in A. (C) Predicted annual biomass index increment (DELTABIOM, unitless) at a given dbh (m) is larger for a responsive tree (circles) than a non-responsive control tree (crosses). Growth of responsive trees is nevertheless delayed due to increased biomass allocation to non-productive stem growth. (D) Light capture index (CP, proportion of available light as compared with an open-grown tree) as a function of dbh (m) showing that light capture is improved following crown deformation even when imposing a fixed light map. Here benefits accrue from a change in crown shape not crown rise. Symbols are as in (C).

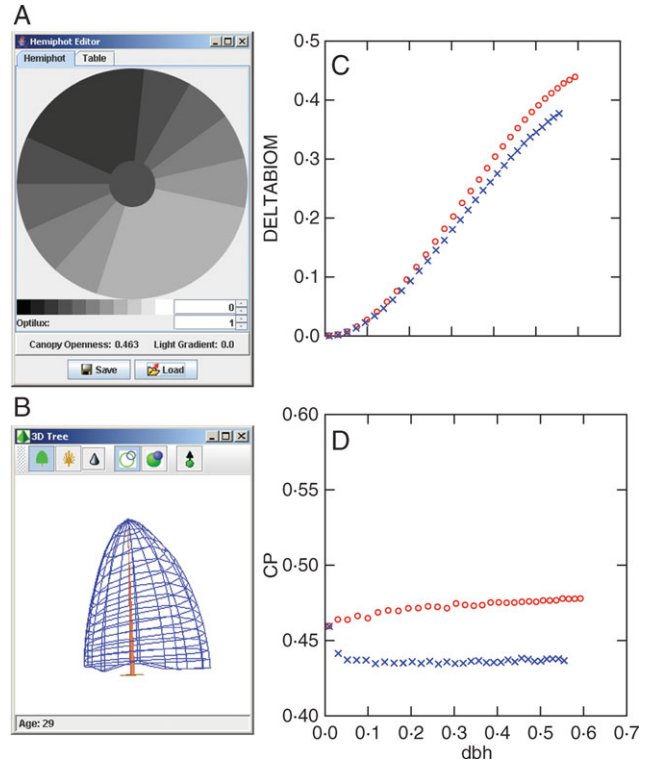


FIG. 3. Shape, growth rate and light capture of an isolated tree exposed to a fixed anisotropic light field. (A) Hemispherical photograph showing lateral anisotropy of the light field. The lighter the sector the more incoming light from the corresponding azimuth. (B) Predicted tree shape of tree exposed to lateral anisotropy of light shown in A. (C) Predicted annual biomass index increment (DELTABIOM, unitless) at given dbh (m) for a responsive tree (circles) or non-responsive tree (crosses) under anisotropic light. Growth rate is significantly improved by crown deformation towards light. (D) Light capture index (CP, proportion of available light as compared to an open-grown tree) as a function of dbh (in m) showing that light capture under anisotropic light field is improved by crown deformation. Symbols as in (C).

light interception (CP index is increased by an average 8 %) and, consequently, accelerated growth rate (final biomass is increased by 21 %).

### The computer experiments conducted

In the remainder of this study the product of diameter square and height, which is assumed to scale isometrically with total biomass, is used as a proxy for whole tree biomass.

In all the simulations a toric plot was assumed in order to avoid border effects: trees from one side of the plot acted as neighbours for the trees on the opposite side. Unless otherwise stated, mortality and recruitment options of the simulator were disabled. The default simulation time was 30 years.

### Plasticity × relative frequency

In this first experiment three ‘growth strategies’ were compared, i.e. three levels of plasticity grown in a

mixture in four different stand compositions. In the balanced composition all three strategies had the same frequency (33 %). In the other three stand compositions one strategy was dominant, representing 80 % of the total population while each of the other two strategies accounted for 10 % of the total population. Hence, each strategy was evaluated at three relative frequencies (80, 33 and 10 %).

Each strategy was defined by a particular combination of the Flexi and Sensi parameters. In the series of simulations presented here, Flexi was varied while Sensi value was held constant. The estimated value of Flexi for *H. brasiliensis* is 0.4 and served as the reference value. A Flexi value of 0.4 means that a tree subjected to strong lateral shading would reach a height 40 % larger than a tree of the same diameter growing in the open. In the least flexible strategy Flexi was set to 0.3, whereas in the most flexible strategy Flexi was set to 0.5. In every other respect the strategies were strictly identical and notably shared the same growth function, the same allometric relationships (applicable to the open grown tree) and the same growth reduction at a given CP index value (i.e. the same LUE).

Trees were randomly located on a 2500-m<sup>2</sup> plot. Sixty replicate runs were conducted for each stand composition totalling 240 simulated stands.

#### *Plasticity × density*

It may be expected that crown flexibility will provide more benefits in crowded situations. To test this assumption we compared the same three growth strategies (defined by varying the default Flexi parameter value by  $\pm 0.1$  unit) competing in a balanced mixture at three densities (300, 600, 900 trees ha<sup>-1</sup>).

Again trees were randomly located on a 2500-m<sup>2</sup> plot. Ninety virtual stands were simulated.

#### *Plasticity × growth rate*

In this third experiment two levels of growth rates were crossed with three levels of plasticity (the range of variation of the Flexi parameter was still  $\pm 25$  % of the reference). Annual growth rate was either increased by 10 % or left unchanged. Thus, six strategies were examined (two growth rates × three plasticity levels) grown in a mixture (25 trees per strategy, 150 trees per stand). Sixty replicate stands were simulated.

#### *Above × below-ground competition*

The objective of this fourth experiment was to test whether modifying below-ground competition intensity would significantly affect the competitive advantage associated with a particular strategy. To address this question long-term experiments were conducted (300 years simulated) comparing two levels of overall site fertility starting with an initially balanced composition of three growth strategies differing only by the flexi parameter, which ranged from 0.3 to 0.5 as in the previous experiments. For these long-term experiments, mortality and recruitment modules were enabled and the variable used

to measure performance in such simulations was population number at the end of the simulation time (under different levels of site fertility) instead of a biomass index. Five replicate simulations were run for each of the two fertility levels considered.

#### *Data analysis*

Growth performance of the various strategies in the various competitive ‘contexts’ explored was assessed by ANOVA. The response variable, i.e. mean biomass index per tree, was systematically analysed after 30 simulated years.

Depending on the experiment, stand density, stand composition or growth rate were the main factors considered alongside plasticity. Those factors and their interaction were treated as fixed effects. The random seed used, which served as a simulation identifier, was included as a random effect. This was done because a significant amount of the variance in mean tree performance appeared to be accounted for by this grouping factor (Fox *et al.*, 2001). This strong nested stochastic structure reflected the fact that the random spatial distribution of trees significantly affected the growth outcome due to the relatively small size of the elementary plot simulated. To implement the linear mixed-effect models outlined above the lmer function from the lme4 package of the R statistical software (R Development Core Team, 2007) was used.

Stand-level performance was assessed in terms of total accumulated biomass. Data were analysed by classical one-way ANOVA.

Sub-population characteristics in the experiment exploring the interaction between fertility level and plasticity were analysed with ANOVA at year 300. Population dynamics evolution was analysed graphically.

## RESULTS

#### *Plasticity × relative frequency*

A 25 % increase (or decrease) in the Flexi parameter value conferred a moderate (+3 % or -7 %, respectively) albeit highly significant change in accumulated above-ground biomass per tree in mixed stands (Table 1, Fig. 4). Tree average performance was improved by increased crown plasticity in all stand compositions. The effect of stand composition on tree average performance was moderate but statistically significant (Table 1). A plot of least squares mean(s) (Fig. 5) showed that all strategies were affected by stand composition in a similar way. For example, all strategies tended to perform better in the stands dominated by the least flexible strategy than in the stands dominated by the most flexible one. In marked contrast, stand composition did not affect stand productivity, as evidenced by the virtually indistinguishable evolution of total biomass with time for the various compositions (Fig. 5).

Stand composition did not affect the *relative* competitiveness of the strategies in the mixture. Stand composition

TABLE 1. Effect of overall stand composition (either balanced or dominated by one of the three plasticity levels) and plasticity ( $\pm 25\%$  of Flexi reference value) on the performance of trees growing in mixture ( $r^2 = 0.15$ , without random effect), based on 240 simulated stands of 30 years

Source	d.f.	Sum of squares	Mean square	F-ratio	P
Flexi (plasticity level)	2	16.7123	8.3561	64.47	0.000
Stand composition	3	1.4038	0.4679	3.61	0.013
Composition $\times$ Flexi	6	0.2075	0.0346	0.27	0.95
Residual	707*		0.12962		

\* One degree of freedom lost by using simulation identifier as random effect.

seemed to determine a global level of competitiveness of the stand that affected all strategies indiscriminately.

*Plasticity  $\times$  density*

Both stand density and degree of plasticity had a significant effect on individual tree growth performance (Table 2). The plasticity effect was an order of magnitude less than the density effect, as can be seen from a plot of least squares mean(s) (Fig. 6). Increased flexibility conferred a competitive advantage to the light-demanding species whatever the overall density. Stand density and crown plasticity did not show any significant interaction (Table 2, Fig. 6). Crown plasticity did not appear to be more advantageous in denser plots, in contrast to what might have been expected. It may be that lateral flexibility played a significant role under less dense conditions, while the vertical flexibility conferred the competitive advantage in denser stands.

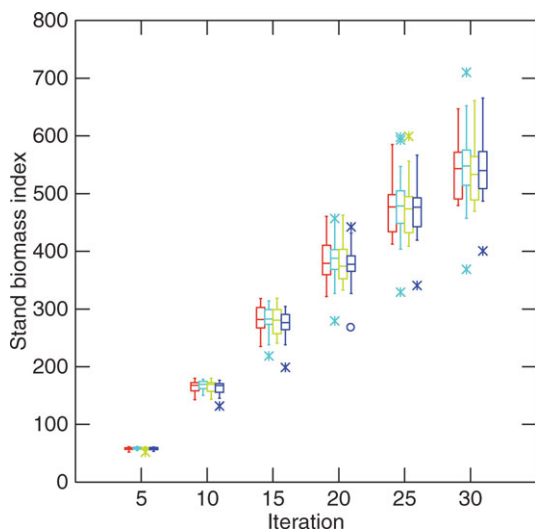


FIG. 4. Boxplot of above-ground biomass accumulation for various stand compositions (at each time step from left to right: balanced stand composition, stand dominated by most plastic type, stand dominated by intermediate type, stand dominated by least plastic type). The length of each box shows the midrange of observations, i.e. the range within which the central 50% of the values fall.

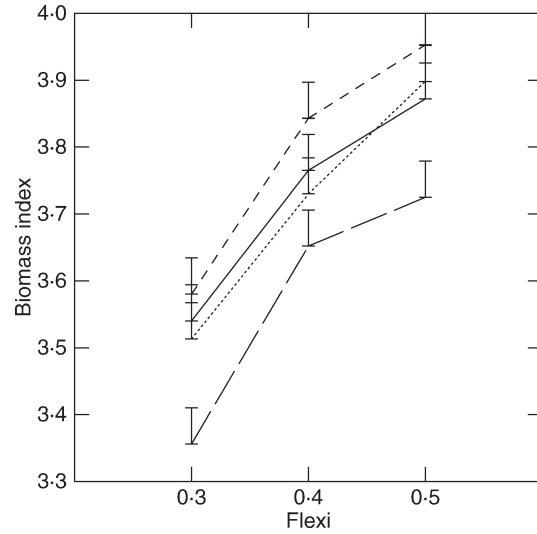


FIG. 5. Least square mean(s) estimates of average individual tree performance after 30 years of growth (Biomass index) per level of plasticity (value of Flexi) by stand composition (dashed line: stand dominated by least plastic type, continuous line: balanced composition, dotted line: stand dominated by intermediate type, broken line: stand dominated by most plastic type).

Overall growth was strongly affected by density as expected. In the absence of self-thinning (disabled for those simulations) standing biomass of the densest stands remained ahead of the others after 30 years of growth (Fig. 7).

*Plasticity  $\times$  growth rate*

Both Flexi and growth rate effects were highly significant (Table 3). The change in performance associated with varying Flexi by  $\pm 25\%$  was approx.  $\pm 4\%$  after 30 years whereas the increase in performance due to an increased growth rate of 10% was approx. 20%.

A statistically significant interaction between plasticity and growth rate was detected. This interaction resulted from a lower beneficial effect of plasticity in fast growing trees, contrary to our prediction (Fig. 8).

TABLE 2. Effect of stand density (300, 600 or 900 trees  $ha^{-1}$ ) and crown plasticity ( $\pm 25\%$  of Flexi reference value) on the performance of trees growing in mixture ( $r^2 = 0.90$ , without random effect), based on 90 simulated stands of 30 years; random seed used as random effect

Source	d.f.	Sum of squares	Mean square	F-ratio	P
Flexi (plasticity level)	2	4.9502	2.4751	84.77	0.000
Stand density	2	26.4333	13.2167	452.67	0.000
Density $\times$ Flexi	4	0.0851	0.0213	0.73	0.57
Residual	260*		0.029197		

\* One degree of freedom lost by using simulation identifier as random effect.

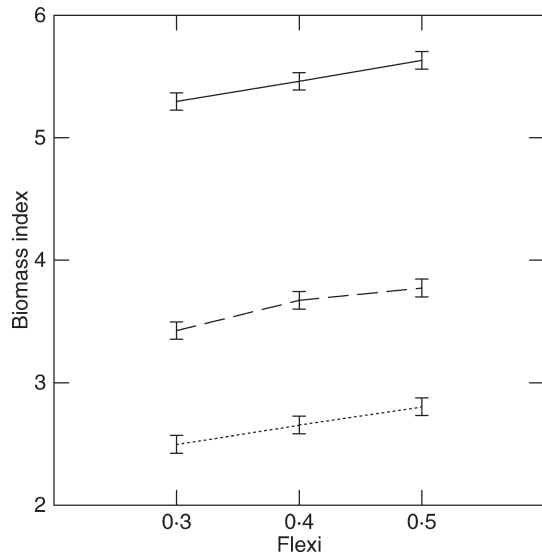


FIG. 6. Least square mean(s) estimates of average individual tree performance after 30 years of growth (Biomass index) per level of plasticity (value of Flexi) grouped by stand density (continuous line: 300 trees ha<sup>-1</sup>; broken line: 600 trees ha<sup>-1</sup>; dotted line: 900 trees ha<sup>-1</sup>). Error bars show  $\pm$  s.e.m.

*Below-ground  $\times$  above-ground competition*

Increased fertility reduced below-ground competition and, consequently, increased competitive advantage of more plastic types (Fig. 9). Increased fertility also translated into higher total biomass, lower number of stems and higher turnover rates (Table 4). Absolute values of mortality rates should not be considered as realistic: they are at least twice lower than those reported in Indonesian agroforest (G. Vincent, unpubl. res.) or tree mortality rates in tropical forests (see, for example, Madelaine *et al.*, 2007). This is not surprising as no calibration of the mortality function

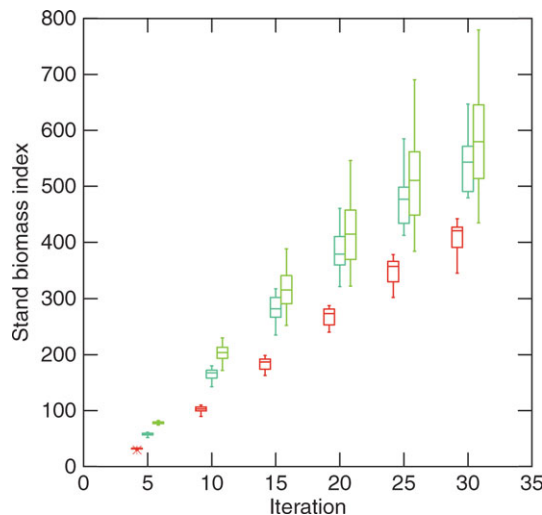


FIG. 7. Boxplot of above-ground biomass accumulation for various stand densities (at each time step from left to right: 300, 600 and 900 trees ha<sup>-1</sup>). The length of each box shows the midrange of observations, i.e. the range within which the central 50% of the values fall.

TABLE 3. Effect of growth rate (either unchanged or increased by 10%) and crown plasticity ( $\pm 25\%$  of Flexi reference value) on the performance of trees growing in mixture ( $r^2 = 0.43$ , without random effect), based on 60 simulated stands of 30 years; random seed of simulation used as random effect.

Source	d.f.	Sum of squares	Mean square	F-ratio	P
Flexi (plasticity level)	2	5.192	2.596	59.87	0.000
Growth rate	1	48.517	48.517	1119.01	0.000
Growth rate $\times$ Flexi	2	0.633	0.316	7.29	0.000
Residual	260*		0.029197		

\* One degree of freedom lost by using simulation identifier as random effect.

was attempted prior to simulation. The changes in structure and dynamics, however, do mirror those predicted for monospecific stands from an analytical growth model incorporating explicit below-ground and above-ground competition (Clark, 1990).

DISCUSSION AND CONCLUSIONS

The computer simulation experiments presented here explored the impact of enhanced or reduced plasticity of crown development on tree growth performance in a variety of contexts. Sensitivity analysis of crown plasticity was restricted to varying the Flexi parameter (controlling maximum deformation). Qualitatively similar results have been found for the Sensi parameter (controlling precocity of response, data not shown) and both parameters are likely to be correlated in nature.

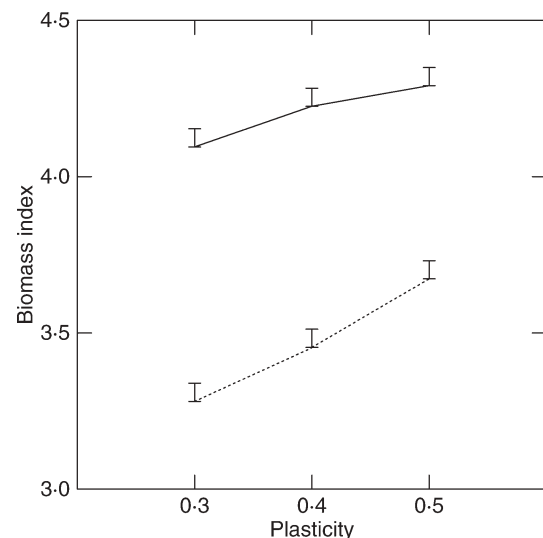


FIG. 8. Least square mean(s) estimates of average individual tree performance after 30 years of growth (Biomass index) per level of plasticity (value of Flexi) by growth rate (default: dashed line; enhanced: continuous line). Vertical bars represent s.e.m.



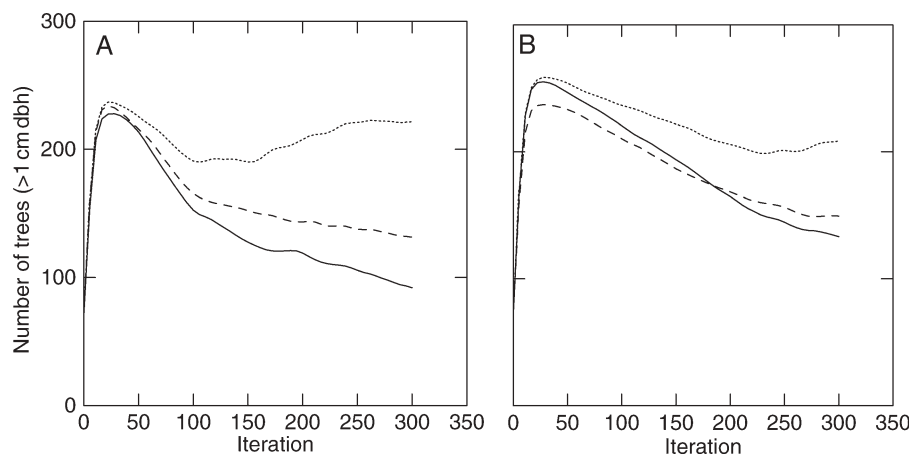


FIG. 9. Evolution of tree number per sub-population type (dotted line: most plastic; dashed line: intermediate; continuous line: least plastic crown) over 300 years. Average of five simulations per level of fertility: (A) increased fertility, (B) standard fertility. Initial composition of  $50 \times 50$ -m stand is balanced. Smoothing algorithm: Distance-Weighted Least Squares (Systat v. 11.0).

As hypothesized, it was found that the degree of crown plasticity had an impact both at individual tree level (compare Figs 2 and 3) and population level (H1) but no impact was found at stand level. Altering the relative proportion of more or less plastic strategies did not change the above-ground accumulation rate to any measurable extent not even at early stages. Of course simulation of a more strongly contrasted growth strategy may have induced such a stand-level effect. The point remains that compensation mechanisms occurred at stand level that offset the observed impact of plasticity at population level, partially contradicting hypothesis (H1). The simulations which explored a limited range of plasticity with a modest impact on growth, only partially supported (H2) stating that competitiveness of a particular strategy is context-dependent (and notably frequency-dependent). The competitive edge of any particular strategy (i.e. its performance relative to the average performance) is expected to decrease when it becomes more frequent simply because by increasing in relative frequency it is contributing to increasing the average performance, a purely arithmetical reason which would hold in the absence of any interaction. Additionally, absolute performance of any given strategy is expected to be affected by the overall competitiveness on the environment, which modifies resource

availability to individual trees. This overall competitiveness was manipulated via changes in stand composition and stand density. For composition modification, the most flexible type performed better under the least competitive stand (dominated by the least productive types). However, the decrease in individual tree performance observed with increasing competition was not limited to any particular strategy (Fig. 5). The lack of change in relative competitiveness of the various strategies (also found when planting density was varied; Fig. 6 and Table 2) can be related to the fact that the strategies being confronted were very similar: they differed only in respect to their crown plasticity and even so to a moderate extent. A mixture of more contrasted strategies may reveal complementarity in resource partitioning such as that observed for light and space between tall, light-demanding types and short, shade specialist types. In such a context, change in relative frequency of the various types in mixture would probably affect their relative competitiveness.

Negative interaction between growth rate and crown plasticity was found with the present range of plasticity and growth rate explored (Fig. 8) contradicting (H3), which conjectured positive interaction. Instead, fast growing types gained little additional competitive advantage from being more plastic. More simulations are needed to see how systematic this response may be. But with hindsight the observed pattern certainly makes sense and this result also calls for a re-examination of hypothesis (H3). It may be that high morphological responsiveness to heterogeneity in light distribution is more directly beneficial to plants with high organ turnover rate (and fast return on investment) rather than plants with high growth rate *per se*.

Increased plasticity conferred a significant absolute advantage in all cases examined even though the below-ground competition tended to mitigate this advantage (Fig. 9). As hypothesized in (H4), changing the below-ground competition intensity affected the relative competitiveness of the different types. Lower competition for below-ground resources *increased* the competitive edge of more plastic trees and was accompanied by changes in

TABLE 4. Stand-level parameters per fertility level (five stands of mixed composition were simulated per fertility level for 300 years)

	Site fertility level		P value (one-way ANOVA F-test)
	Standard	Improved	
Final number of stems (>0.01 m dbh) per stand	491	444.4	0.012
Final total standing biomass index	233.1	404.5	0.001
Mean annual mortality rate (%)	0.36	0.61	0.018

structure and dynamics consistent with theoretical expectations (Table 4).

Despite the fact that no specific cost of plasticity has been included in the model, some negative feedback loops did tend to reduce the advantage of crown flexibility. The main two such negative loops were reduced crown expansion rates (smaller crowns and subsequent lower growth potential as a result of vertical stretching; as previously discussed) and reduced below-ground competitiveness.

As mentioned in the Introduction, some specific costs are undoubtedly associated with crown deformation in nature. Those could, in principle, be included in the model either in the form of reduced growth efficiency (notably related to the expected reduced LUE) or in terms of increased mortality (notably as a result of increased susceptibility to wind throw of higher, more asymmetric trees) (Young and Perkoča, 1994). A function of susceptibility to wind throw depending on crown asymmetry, crown mass and tree height could be considered (e.g. Olesen, 2001). However, tree morphological responses to mechanical stress associated with crown deformation (such as trunk tapering, buttresses, asymmetric stem thickening, root growth or stem bending; Fourcaud *et al.*, 2003; Ancelin *et al.*, 2004) may all affect this susceptibility as well as the overall net growth efficiency of deformation. So calibration of this type of susceptibility function is certainly a delicate task.

Neglecting the negative feedback that may occur in terms of LUE (see Introduction) may have contributed to overestimating the benefits of crown plasticity at individual tree level and hence affected the *in silico* experimental results presented. However, the negative effects associated with crown deformation are likely to be of significant amplitude only when deformation is large (in terms of either vertical stretching or lateral crown asymmetry), which was not the case in the simulations conducted. So it is reasonable to assume that neglecting such negative feedback probably had only a minor impact on the output of the numerical experiment presented.

Simulation scenarios were not completely realistic even where they incorporated demographic processes, notably in that they considered mixtures of a reduced set of species of similar ecology immune to invasion by other species. From an ecological standpoint, a more relevant analysis of the impact of crown shape plasticity on tree performance may, however, be attempted using the same or similar model. Simulations should then feature truly multi-species stands (i.e. combination of different successional status and adult size) and systematically incorporate the demographic processes.

Clearly not all tree species in nature show the same degree of crown plasticity. For example, Gilbert *et al.* (2001) have shown that early-successional species tend to be more etiolated when shaded or exposed to low R:FR than late-successional shade-tolerant species. Muth and Bazzaz (2002) also noted that the magnitude and precision of canopy displacement at forest edges are generally greater for earlier successional trees and hardwoods than for later successional trees and conifers, suggesting that (1) global

plasticity may be higher in early-successional species and (2) conifers are globally less plastic. The latter point may be related to their fairly rigid morphogenetic development (and notably the maintenance of a dominant main stem for most conifer species almost until death of the tree). The present study examined how the growth performance of a fast-growing, light-demanding species was affected by changes in crown plasticity and found that high plasticity appeared to confer an absolute advantage. Of course such conclusions are conditional on the assumptions made in the model and on the growth characteristics of the species that was simulated (Kuppers, 1989). In shade-tolerant species, for example, crown deformation under a suboptimal light regime may actually entail crown horizontal flattening rather than vertical stretching, through altering growth rates between leader shoot and main branches or bending of the leader shoot (Henry and Aarssen, 2001). Growing fast towards light is not necessarily the best strategy and may not be sustainable due, for example, to excessively high maintenance costs whereas a more conservative strategy may provide better survival chances, notably in the face of rapidly fluctuating levels or extremely low levels of resources: non-morphologically plastic crowns may be favoured in shade-specialist species. Physiological adaptation to unpredictable heterogeneous incoming light in the form of reduced induction time and better use of sunflecks is apparently a common strategy of slow-growing understorey specialists (Pearcy, 1990). Lower responsiveness of more shade-tolerant species [as repeatedly pointed out by Givnish (2002, and references therein)] is essentially adaptive as it 'reduces the energy overhead associated with stem construction for a plant that can maintain positive photosynthesis in shade'.

Computer simulations of tree stands using realistic growth rules and realistic crown deformation pattern and degree of flexibility were conducted. Simulation experiments showed that crown shape plasticity could provide a significant competitive advantage over less plastic trees through enhanced LCE. Hence, simulation results support the statement that the crown shape plasticity observed in many tree species is of adaptive value and more generally point at the importance of morphogenetic plasticity as a determinant of performance in trees.

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