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Plants that differ in height investment can coexist if they are distributing non-uniformly within an area

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ABSTRACT

In nature, there is a large variability in the intrinsic height of plants living within an area. The question arises whether these height differences affect the plants' ability to coexist and thus is an adaptive trait.

Using a biologically mechanistic model, we explored the possibilities for coexistence of plant types that differ in their pattern of allocation between stem (i.e. height growth) and other organs. We simulated the competition for light between growing individual plants. The study was game theoretical in the sense that each individual plant at any time affected the light availability for all plants in a locality, making conditions variable throughout the growing season and between seasons when the composition of competing plants changed.

It was found that plant types that differed in their allocation to height growth could coexist over the course of years when these plants distributed their seeds non-uniformly in space, creating local differences in plant density. At each different density, one type with a specific investment in height performed better (i.e. achieved a greater seed production) than the rest of the types, thus preventing the exclusion of that type over the years. The resulting model community was self-assembling; local densities and competitive pressures originated as traits from the model plants themselves and were not the result of imposed external factors acting upon the model community.

This mechanistic modelling approach shows that a condition as simple as a non-uniform distribution of seeds can generate the conditions for plants of various height growth strategies to live together over multiple generations. This study suggests that differences in plant height can be an emerging property of dispersing populations.

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1. Introduction

In nature, there is a large variability in the intrinsic height of plant types living together within an area. An interesting question is whether these height differences do indeed affect the plants' ability to coexist over long periods of time.

For these kinds of large-scale questions on coexistence, a modelling approach can provide quantitative relationships between plant traits, plant–plant interactions and perfor-

mance (growth and reproduction) whereas experimental approaches may suffer from practical problems, such as uncontrolled variability and lengthy experiments.

In dense vegetation stands plants strongly influence each other as they compete for the available resources. Therefore, a model of species coexistence must consider that the relationship between a trait value and performance of a plant is strongly determined by the trait values of neighbours. In such cases, a game theoretical approach is an appropriate way to

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evaluate the fitness of individuals (Riechert and Hammerstein, 1983). This is especially true when analysing the fitness value of a trait, such as plant height (Givnish, 1982; Westoby et al., 2002), because a tall stature is advantageous only when it enables plants to capture light that would otherwise be available to neighbours (Iwasa et al., 1984; Westoby et al., 2002).

Most of the game theoretical studies on this subject found that eventually only one plant type remained (Falster and Westoby, 2003). This plant type possessed the evolutionary stable strategy (ESS), e.g. no other plant type possessing a different strategy could persevere in the presence of this plant type. Nevertheless Huisman et al. (1999) and Perry et al. (2003) found that two species, a tall and a short one, could coexist when evaluated at the steady state of growth. Only the study of Iwasa et al. (1984) revealed that several plants differing in height could coexist. All three studies have in common that they investigate under what conditions of height and crown depth a short plant can remain under a tall plant after a single episode of growth (Iwasa et al., 1984; Huisman et al., 1999; Perry et al., 2003). However, to remain in the vegetation over a longer timescale, plants have to persevere over the course of several generations rather than over a single competition event. Thus, remains the question whether plants can coexist indefinitely over several generations.

Furthermore, for the study of Iwasa et al. (1984), its static nature can be put to question (Falster and Westoby, 2003). Namely, plant height at any point in time incurs costs from former investments in stem tissue and maintenance costs (Westoby et al., 2002). Also, investments in the stem result in a reduced investment in resource harvesting plant organs, such as leaf area and roots (Givnish, 1982; Stutzel et al., 1988; van Hinsberg and van Tienderen, 1997; Anten and Hirose, 1999). In short, one has to take into account the investments and trade-offs within a plant to evaluate whether it can attain a certain size. Additionally, as species allocate their biomass and grow the available light in the vegetation changes. This change affects not only the total light availability but also the distribution of light over the different layers of the vegetation. The adequacy of allocation patterns to height or leaf area may vary from moment to moment under this vertical and temporal variation of the light climate. Consequently, although a plant would be the better competitor once possessing a certain size, in reality the plant may have been out competed at an earlier stage. For this reason, using *a priori* competition parameters (Huisman et al., 1999; Perry et al., 2003) will not suffice. Instead, the explicit lifetime pattern of allocation to light harvesting organs is an important feature of overall plant competitive ability.

To include these essential lifetime costs and benefits of plants that differ in height, we use a biologically mechanistic plant growth model. The light interception, photosynthesis and allocation of resources to different parts of the plant are explicitly modelled. These allocation patterns determine the growth of plant parts. The interaction between plants, growth of the population and interaction between populations follow directly from the assumptions on allocation level and resulting light interception. In contrast to studies on height and coexistence so far (Iwasa et al., 1984; Huisman et al., 1999; Perry et al., 2003), we do not strictly separate crowns of competing plants. In many types of vegetation it is clear that

there is some measure of mutual interference between plants of different height, because of crown overlap (Yokozawa and Hara, 1992; Geritz, 1995; Hirose and Werger, 1995).

Firstly, we analysed the ESS in height investment over several generations of reproducing plants, competing for light at fixed density. Secondly, we studied the influence of density on the ESS. Finally, we studied the influence of a non-uniform distribution of seeds. The ultimate objective was to determine whether, with the assumptions of (initially) overlapping crowns and including the dynamics of plant growth, plant types that possess different height allocation strategies can coexist over more than one generation.

2. The model

2.1. Shape of the model plant

We assume that all plants in the model are annuals. Plants grow within a confined ground surface, referred to as a patch. Only plants that share such a patch compete. All plants start growing simultaneously, possessing an initial leaf area, root mass, and height (Table 1). Each plant has a specified smooth distribution of infinitesimally small leaf elements over its height. The leaf area distribution in leaf area per unit height $\lambda(h)$ per patch basal area is (Caton et al., 1999):

$$\lambda(h) = p_0 \frac{L_t}{h_{pt}} \left(\frac{h}{h_{pt}}\right)^{p_1} \left(1 - \frac{h}{h_{pt}}\right)^{p_2} \quad (1)$$

in which h_{pt} is the height of the plant at time t , L_t the total leaf area of the plant at time t , h the height at which the leaf density is calculated and p_0, p_1, p_2 are shape parameters. Here, the shape parameter p_0 is given in terms of p_1 and p_2 by the integral:

$$p_0 = \frac{1}{\int_0^1 dx x^{p_1} (1-x)^{p_2}} \quad \text{with } x = \frac{h}{h_{pt}} \quad (2)$$

For our simulations, we assume plants have a fixed leaf area distribution, i.e. p_1 and p_2 do not change during growth.

The relation between height h_{pt} and stem volume S_t at time t is given by a standard allometric equation (Stearns, 1992). In this equation, α and β are constants.

$$S_t = \alpha h_{pt}^\beta \quad (3)$$

A root system is present in the model plant; however, it is assumed to only act as a carbon sink. The root mass is a function of the leaf area (Brouwer, 1983):

$$R_t = \sigma \times L_t \quad (4)$$

where σ is a constant.

2.2. The light climate within the vegetation

We assume a light climate in the vegetation patch in which the photons flow vertically downward. At each height h the interception of light by the plants is modelled by Beer's law

Table 1 – Parameters settings of the model

Parameter	Unit	Value	Source
L (initial)	m ²	0.00165	4
H (initial)	m	0.01	4
c _s	g C/m ³	0.000045	1, 4
c _l	g C/m ²	15	2, 4
c _r	g C/g mass	0.45	4
g _f	g C/seed	0.2	1
σ	g C root/m ² leaf	7.5	2, 4
γ	g C/g C NPP	0.5	1
α, β	–	0.018, 1.4	1
P ₀ , P ₁ , P ₂	–	30, 2, 2	1
P _{ml}	μmol CO ₂ /m ² /s	16	3
cos α	leaf inclination	0.5	2, 3
a	–	1	1
Φ	μmol CO ₂ /μmol photons	0.05	3
θ	–	0.7	2, 3, 6
r _s , r _l , r _r	g C/g C	0.213	2, 6
r _{ms} , r _{ml} , r _{mr}	g C/g C plant/day	0.0235	2, 5
c _{rl} , c _{rr}	g C/g C	0.6	1
I _h	ppfd/m ² /s	1700	1
Day length	s/day	25,200	1
From CO ₂ to C	g C/μmol CO ₂	1.2e ⁻⁵	–

Some parameters have been taken as an approximate average of data within (several) literature sources. Sources: (1) Calibrated parameters (this study); (2) Goudriaan and van Laar (1994); (3) Anten and Hirose (2003); (4) Poorter (1991); (5) Caton et al. (1999); (6) Lieth and Reynolds (1988). See Section 2 for a description of the symbols and how they are applied in the model. See Table 3 for results of a sensitivity analysis on several (calibrated) parameters.

(Monsi and Saeki, 1953). The horizontal light intensity $i_h(h)$ is given for each height h in the patch:

$$i_h(h) = i_h(h_v) \exp \left[- \int_h^{h_v} \sum_{j=1}^n dh \lambda_j(h) \cos \alpha a \right] \quad (5)$$

where $i_h(h_v)$ is the horizontal light intensity above the vegetation, h_v the height of the vegetation, $\cos \alpha$ the leaf inclination and a is the absorption coefficient of leaves. For simplicity, we take these parameters equal for all plant types. The rate of photon absorption for the leaf elements at height h is calculated from the light climate at height h , the leaf inclination and absorption coefficient of a plant. It is given by

$$i_{al}(h) = i_h(h) \cos \alpha a \quad (6)$$

2.3. Leaf and plant photosynthetic rates

The relationship between leaf photosynthetic rate ($P_{gl}(h)$) and absorbed light ($i_{al}(h)$) is calculated with a non-rectangular hyperbola. This relationship accurately reproduces the curve of photosynthetic capacity in actual plants (Marchall and Biscoe, 1980):

$$P_{gl}(h) = P_{ml} \frac{(1+x) - \sqrt{(1+x)^2 - 4\theta x}}{2\theta} \quad \text{with} \quad x = \frac{\Phi i_{al}(h)}{P_{ml}} \quad (7)$$

Here P_{ml} is the photosynthetic capacity of the leaves, Φ the quantum yield per unit absorbed light, θ a curvature factor and

$i_{al}(h)$ is the rate of photon absorption of the leaves at height h . For reasons of simplicity, we assume that capacity P_{ml} , quantum yield Φ and curvature θ do not vary with height in the canopy or in time.

For each plant, the total photosynthetic rate is given by the integral over the plant's height of the leaf photosynthetic rate times the leaf area:

$$P_g = \int_0^{h_p} dh P_{gl}(h) \lambda(h) \quad (8)$$

2.4. Carbon balance and the allocation program

From gross photosynthetic production, the plant firstly allocates carbon to account for maintenance costs:

$$P_n = P_g - R_m \quad \text{with} \quad R_m = r_{ml} c_l L + r_{ms} c_s S + r_{mr} c_r R \quad (9)$$

R_m is the maintenance rate and is based on the weights of the plant parts. The parameters r_{mb} , r_{ms} , r_{mr} are the maintenance respiration rates in gram carbon per unit carbon mass per unit time. The conversion factor c_l is in gram carbon per meter square leaf, c_s is in gram carbon per volume stem, c_r is in gram carbon per gram roots.

All further investments in structural mass are made of resulting net photosynthetic production P_n , following the rules of a carbon balance. The carbon balance we use in the model is according to the following set of rules: (1) The consumption of carbon should be, at any time, equal to the carbon gain from photosynthesis P_n . (2) Height growth rate dh_p/dt is always non-negative. (3) Leaf area rate dL/dt can be either positive or negative. (4) If the carbon balance at any moment is negative, because the plant consumes more carbon than it acquires from gross photosynthetic production (so, $P_n < 0$), leaf area is shed and carbon from this leaf area (and from the associated roots) is used to account for the shortage. If the carbon balance is positive, extra leaf area is produced. (5) If the plant has no more leaf area, it is considered dead.

The carbon balance is applicable for any specific allocation program the plant may follow. For the carbon balance we write:

$$P_n = [\dots] \frac{dL}{dt} + \left[(c_s + r_s) \frac{dS}{dh_p} + (c_l + r_l) \int_0^{h_p} dh \text{POS} \left(\frac{d\lambda}{dh_p} \right) - c_{rl} \int_0^{h_p} dh \text{NEG} \left(\frac{d\lambda}{dh_p} \right) \right] \frac{dh_p}{dt} \quad (10)$$

For a negative ($dL/dt < 0$) or a positive ($dL/dt > 0$) rate of leaf production, the leaf production rate in Eq. (10) is written, respectively:

$$[-(c_{rl} + \sigma c_{rr})] \frac{dL}{dt} \quad \text{or} \quad [(c_l + r_l) + \sigma(c_r + r_r)] \frac{dL}{dt} \quad (11)$$

In Eqs. (10) and (11) c_l , c_r , c_s are the carbon imbedded in leaves, roots and stem, respectively. Parameters r_l , r_r , r_s are the growth respiration with leaf growth, root growth and stem growth. If a plant grows in height dh_p this requires costs for the casting

and production of leaves at certain positions along the stem. The variables POS ($d\lambda/dh_p$) and NEG ($d\lambda/dh_p$), respectively, depict the leaf area that is produced at the upper side of the crown and the leaf area that is cast away at the lower side with a growth in height. This does not change the total amount of leaf area, but maintains the crown shape as dictated by the parameters p_1 and p_2 in Eq. (1). Parameters c_{rl} and c_{rr} depict the carbon that can be retrieved if leaves and roots, respectively, are cast away.

Part of the net photosynthetic production is stored for the production of seed. For reasons of simplicity, we use a constant partial storage γ (Table 1) of carbon from P_n (see Eq. (9)) for the production of seed mass. We assume that the stored carbon for seed production is a measure of fitness. This fitness now is closely related with lifetime P_n (see Eq. (9)) and biomass increment. In the last part of Section 4, we discuss the effects of this assumption. The carbon storage for seeds, which is equal to the subsequent seed mass production of the plant, is given by:

$$\frac{dF_m}{dt} = f(P_n) = \gamma P_n \tag{12}$$

Here F_m is the seed mass that is stored, γ the portion of net photosynthetic production that is invested in seed mass. If P_n is negative or zero, the allocation rate to seed mass is zero.

The actual height growth dh_p/dt is calculated from the relation between stem volume and height, net photosynthesis P_n and the allocation of carbon to height growth a_s . That is, using

$$\frac{dS}{dt} = f(P_n) = \frac{a_s(1-\gamma)P_n}{c_s} \quad \text{and} \quad \frac{dh_p}{dt} = \frac{f(P_n)}{dS/dh_p}$$

the height growth can be written as:

$$\frac{dh_p}{dt} = \frac{(a_s(1-\gamma)P_n)/c_s}{\alpha\beta(h_p)^{\beta-1}} \tag{13}$$

The denominator of the equation is the allometric height-volume relation, derived from Eq. (3). As generally investments in the stem result in a reduced investment in organs, such as leaf area and roots (Givnish, 1982; Stutzel et al., 1988; Anten and Hirose, 1999), leaves and roots receive whatever of the carbon flow of P_n is left after the allocation to stem. In practice, for each plant in the model, in case of a shortage of light (e.g. P_n is negative: less carbon is fixed than what is needed for maintenance respiration) the plant will not invest in height or seed storage (both are a fraction of P_n) and it will drop part of its leaf area and associated roots. In doing so, the plant corrects the carbon balance with the carbon that can be retracted from the shed leaf area and associated roots. Simultaneously, it is relieving the maintenance requirement making a further growth possible, provided that the carbon balance is positive in the future.

We assume that the amount of net photosynthetic production invested in the stem is type-specific. We therefore distinguish ten plant types that invest different fixed fractions (a_s) of P_n in the stem, ranging from 2 to 47% (top part of Table 2). Simulations revealed that investing more than 47% of P_n in the stem leaves so little carbon for investing in leaf area that the plant cannot intercept enough light for growth. Such a plant will achieve a lower stature than a plant with a smaller investment in height. We do not consider such plants.

To summarize, three state variables determine the state of the plant. They are total leaf area L (with associated roots), total height h_p and stored carbon for seed mass F_m . The relative allocation (this is a part of P_n) to stem and stored carbon for seed mass is an imposed control; it determines the strategy of the plant, which we will investigate in this paper. In contrast, the allocation rate to the leaf area and roots can be determined from the carbon balance as written in Eq. (10).

Table 2 – Carbon investment strategy per plant type and carbon storage for seed (i.e. pay-off) of the different plant types in pair-wise competition

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
% NPP in stem	2	7	12	17	22	27	32	37	42	47
	Opponent types									
	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
Type 1	1.67	0.70	0.78	0.92	1.09	1.29	1.52	1.78	2.08	2.41
Type 2	3.52	1.72	0.92	1.02	1.22	1.53	2.13	3.52	3.52	3.52
Type 3	3.49	3.49	1.72	1.23	1.62	3.49	3.49	3.49	3.49	3.49
Type 4	3.45	3.45	3.45	1.70	3.45	3.45	3.45	3.45	3.45	3.45
Type 5	3.40	3.40	3.40	1.00	1.68	3.40	3.40	3.40	3.40	3.40
Type 6	3.34	3.34	0.66	0.68	0.84	1.65	3.34	3.34	3.34	3.34
Type 7	3.26	3.26	0.45	0.48	0.58	0.77	1.61	3.26	3.26	3.26
Type 8	3.17	0.38	0.33	0.36	0.42	0.52	0.72	1.57	3.17	3.17
Type 9	3.06	0.27	0.25	0.27	0.31	0.37	0.47	0.67	1.52	3.06
Type 10	2.90	0.20	0.20	0.21	0.23	0.27	0.33	0.43	0.61	1.44

The top part of the table shows the percentage of net photosynthetic production (NPP) that the different types invest in stem (i.e. height growth). The rows of the bottom part of the table show the produced seed mass (gram per plant) at the end of growth of these types, in pair wise competition at a density of 200 plants per meter square.

3. Simulations

3.1. The ESS height investment

We start with simulating competition between pairs of plants of the different types (see top part of Table 2). This means that two plants, sharing the same patch, have to compete for the available light. The simulations run until all competing plants have reached the point at which the cost of maintenance of plant mass equals the income from gross photosynthetic production and no growth can occur any longer. Plants die at the end of each simulation period. We refer to this period as one ‘simulation year’. At the end of a simulation year, we evaluate the amount of stored carbon for seed that a plant has accumulated, as a measure of fitness. The fitness of a plant in a particular combination of types is the ‘pay-off’ for the plant in that combination (Riechert and Hammerstein, 1983).

With the pay-offs of competing pairs as a basis, we evaluate the performance in the presence of the other types. We use game theoretical principles. In this approach, the success of a plant does not only depend on its competitive vigour in combination with every other plant type, but also on the frequency at which every type is present. The frequencies of the types determine the chance that a given pair competes. The total pay-off for a plant type is calculated as:

$$P_i = f_i \sum (p_{ij} f_j) \quad (14)$$

Here P is the total payoff for type i . It is the summed total of pay-offs (p_{ij}) for that type i competing with the other types; opponents j . The frequency of a type is f .

Every year, all plants start growing anew. The frequency of a plant type in the next generation is calculated from the contribution of its total pay-off within a simulation year, relative to the total combined pay-off of all competing plant types within that year:

$$f_{i,t+1} = \frac{P_{i,t}}{\sum P_{j,t}} \quad (15)$$

With each repeated calculation, the frequencies of plant types in the community will change. If there is no change in the frequencies of all participating plant types, equilibrium is reached. In that situation different plant types coexist, each one with its own frequency, or there is no coexistence and only one plant type perseveres. We calculate the development in frequency for pair-wise competing plants and we use different random initial frequencies. We present the ESS height investment and average extinction time for types that are not the ESS.

3.2. The influence of the number and density of individuals on the ESS

In the competition between plants, there might be indirect competition effects, i.e. the performance of two competing types may be different if a third type is present. We investigate this by letting three plants per patch compete. We proportionally increase the size of the patch such that the plant density about the same as in the former calculations with

competing pairs. For a total of 400 patches, a trio is picked randomly from the collection of types (top part of Table 2) to fill one patch. In every patch, plants grow and store carbon for seed. It is assumed that every individual seed has the same weight g_f (Table 1). The amount of seed that a type has produced in a year in all patches combined serves as the seed pool for that type in the next simulation year. From the types’ seed pools again trios are randomly picked to fill the separate patches. We repeat this procedure for 30 simulation years, until the frequencies of the types are at equilibrium. We perform several runs with different initial randomly picked individuals of types. We show the ESS height investment for three plants per patch and the average extinction time for types that are not the ESS.

We also investigate the influence of density on the frequency development of types. For this purpose, we again assume pair-wise competing plants. We decrease the surface area of the patch, thus increasing the density of individuals per unit area (this gives the same results as increasing the number of individuals). We show the ESS height investment and the average extinction time for the types that are not the ESS.

3.3. A non-uniform distribution of seeds

In the final simulation, we introduce a non-uniform distribution of the seeds produced by the plant types. The environment consists of 400 patches, each of 0.01 m². We initialize by distributing 80 plants from every type randomly between patches of the environment. The plants do not necessarily compete pair-wise or trio-wise, such as was the case in the former two simulations. The performance of plants (growth and seed production) will depend on the density and type of neighbours within the patch. For every plant it is calculated how many seeds it can produce from its stored carbohydrates, assuming an equal mass g_f per seed (Table 1). Every simulation year the seeds of the previous year are randomly distributed in the environment. We simulate the development of the different types in the environment for 30 simulation years, and show the ESS height investment. We repeat this calculation several times with different random placement of the initial plants.

4. Results

4.1. The ESS height investment for competing pairs

Listed in Table 2 are the pay-offs (i.e. stored carbon for seed) of competing pairs of height investment types. For pay-off matrices it always holds that, if there is a pay-off that is a minimum in its row and a maximum in its column, this is the ESS (Nelson, 2003). In our case, this means that a plant type with a height investment that outperforms types with any other height investment than its own has automatically the ESS. From Table 2 we can derive that plant Type 4 has the ESS.

The mechanistic approach that we follow allows for an evaluation on why this type perseveres, and not others. Fig. 1 shows examples of the height and leaf area development of pair-wise competing types. With a small investment in height

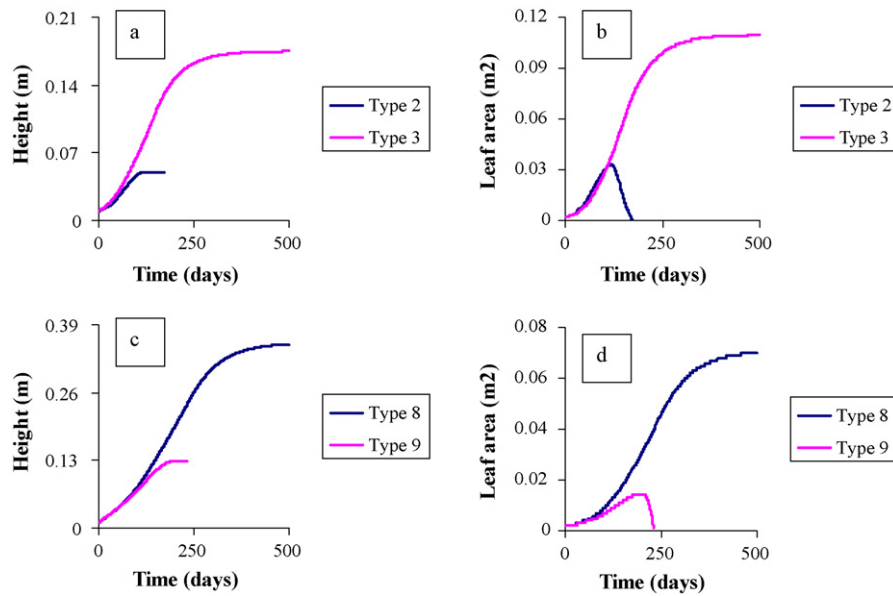


Fig. 1 – Development of height and leaf area of pair-wise competing plant types within a simulation year. For a description of types, see top part of Table 2.

(Type 2, Fig. 1a and b), the height growth of plants is slow, making them prone to shading by competitors with slightly higher investment in height (Type 3, Fig. 1a and b). However, with an extremely high investment in height (Type 9, Fig. 1c and d), plants invest little in leaf area and intercept low amounts of light, leading to a slow overall growth. Consequently, competitors with a slightly lower investment in height (Type 8, Fig. 1c and d) easily shade this type. Evidently, a plant type that invests a sufficient amount of carbon in both leaf area and height wins competition and has the highest pay-off.

At each simulation year, plant types with a pay-off that is higher than the average of all types in the model vegetation increase in frequency, whereas the others decrease. Listed in part ‘A’ of Fig. 2 are the exact extinction times of pair-wise competing types. It shows that the perseverance of types increases with a height investment closer to that of the ESS, Type 4. Apparently, there is a hierarchy in the perseverance of types, decreasing from the ESS type to types with lower investments in height or leaf area.

4.2. The influence of the number of individuals and density on the ESS

Part ‘B’ of Fig. 2 shows the extinction times of types with three competing plants per patch (e.g. competition is not pair-wise). The average extinction order and times with three plants per patch remain the same as with pair-wise competing plants (compare part ‘A’ and part ‘B’ in Fig. 2). We can therefore assume that indirect interactive effects do not influence the competitive rank of types in our model plants.

Parts ‘A’, ‘C’, ‘D’, ‘E’ and ‘F’ in Fig. 2 show the extinction times of the plant types at increased densities. Competition is again pair-wise. Fig. 2 clearly shows that, with increasing density, the ESS for height investment is higher.

4.3. A non-uniform distribution of seeds

Fig. 3 shows that, when plants of all types are distributed randomly over the patches in the area, there are some transient dynamics initially. As the area starts with a (on average) low density of plants, types with low investment in height are dominant. When the average density increases, types that invest more in height become more abundant. At a very high density of con-specific plants, none of the plants have enough carbon for even a single seed. This automatically regulates the average density of plants in the patches. In contrast to the simulations with constant (always pair-wise or trio-wise) density per patch, the stabilization of overall density

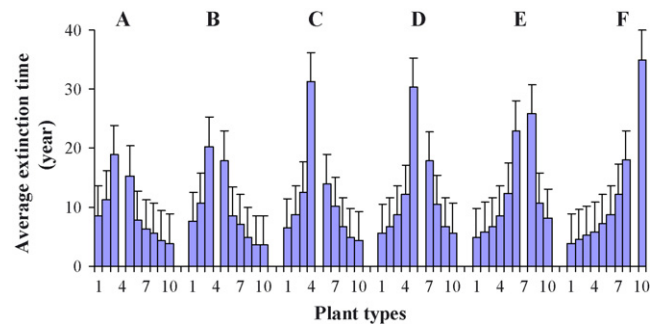


Fig. 2 – The average number of years to extinction of the types at different fixed densities, based on random initializations (n = 10). Empty bars within the range of types depict the type with ESS height investment. (A) 200 plants/m²; (B) 208 plants/m²; (C) 408 plants/m²; (D) 800 plants/m²; (E) 1250 plants/m²; (F) 2222 plants/m². Plants under (B) compete with three plants per patch; all others compete pair-wise. For a description of types, see top part of Table 2.

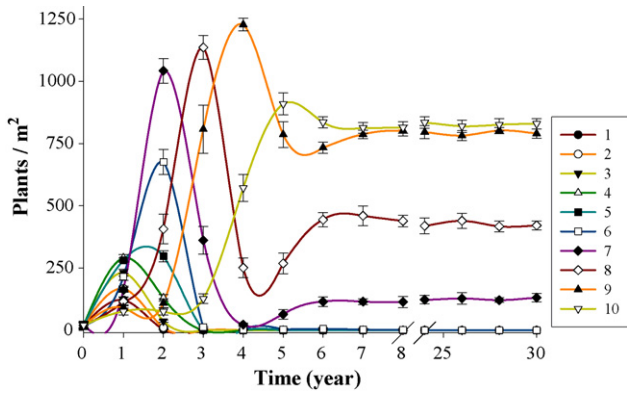


Fig. 3 – Average density of individuals of different height investment types in an area of 20 by 20 patches, each of 0.01 m². Initial plants (80 per type) were placed randomly in the area (n = 10). The distribution of seeds in the area between years is random. Between year 7 and year 24 the average density remains in equilibrium (not shown). For a description of types, see top part of Table 2.

of plants does not imply that plants with lower or higher height investment go extinct. Four types with rather high investment in height can persevere. The cause lies in the persistently different densities per patch in the area (Fig. 4). From the simulations on the effect of density on the ESS height investment, it was clear that with every different density there is a different ESS height investment. Several types with different investment in height can find patches in which they can perform better than all other types.

The height distribution at the end of the simulation of the total community does not show a normal distribution. Most plants are of a low stature, but there are several ‘layers’ of plants above the short plants at approximately 0.17, 0.21, 0.23, 0.34, and 0.36 m (Fig. 5).

4.4. The effect of parameter settings and assumptions

It is important to realize that the coexistence of plants is a robust result of the mechanisms in the model, and not a

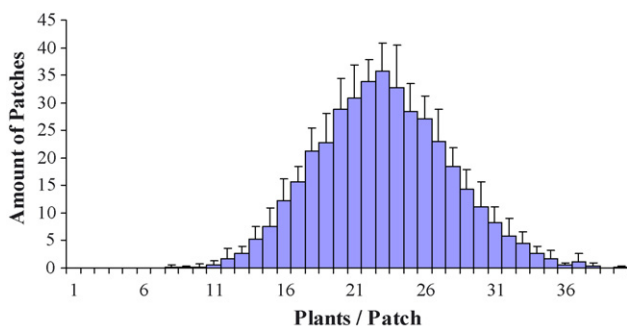


Fig. 4 – Average density distribution of plants per patch (0.01 m²) at equilibrium in an area of 20 by 20 patches. Seeds are dispersed randomly every year. For the number of individuals from each type in the area, see the densities at equilibrium in Fig. 3. For a description of types, see top part of Table 2.

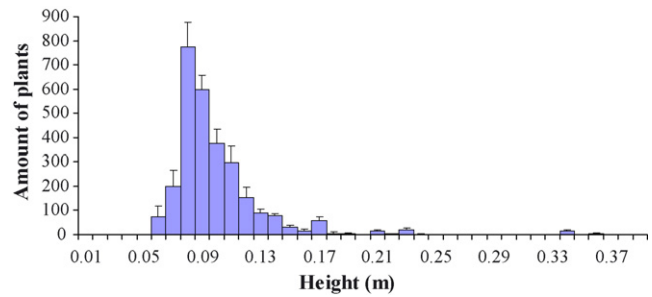


Fig. 5 – Height distribution of plants at equilibrium (dead plants not included) in an area of 20 by 20 patches (0.01 m² per patch). For the number of individuals (dead and alive) from each type in the area, see the densities at equilibrium in Fig. 3. For a description of types, see top part of Table 2.

consequence of any specific parameter settings. Table 3 shows the effects of changing the values of parameters. Generally, when parameters were thus set that it resulted in less carbon being available for investment in leaf area, this was at the disadvantage of plants with a high investment in height. These plants are limited already in their light interception because they possess a small leaf area. Additionally, when less carbon was available for seed production, average density was lowered, meaning that the average height that plants need to win competition decreases. This shifted the possibilities for coexistence towards the types that invested less in height. The shift was achieved in various ways: by shortening the simulation (growing season) time so not all plants reached steady state, lowering the retrievable carbon from dying roots and leaves (c_r), lowering the light intensity above the canopy (l_h), and lowering the amount of carbon allocated to seed production versus vegetative growth (γ). Similar effects were obtained when heightening the ratio between root mass and leaf area (σ) so more carbon is allocated to roots, heightening the maintenance constants (r_m) and heightening the growth respiration (r).

The other way around, changing parameters so plants had more carbon available was beneficial for plants with higher investment in height. This was because more could be invested in seed, leaf area and consequently height. This, however, is less clear because we do not consider plants with a higher investment in height than type 10 (47% of NPP). In Table 3, we show the changes in parameters that benefit the types with a small investment in height. The table shows that, in all performed simulations, plants that differ in investment in height can still coexist and this result is not a consequence of specific parameter settings.

In the model, we assume plants constantly store part of their NPP for the production of seed. We do this mainly because it is an insightful way of monitoring plant growth as it results from available NPP and the type-specific allocation pattern of competing plants at any time during the growing season (see Fig. 1). However, real annual plants exhibit a relatively abrupt shift from initial investment in vegetative growth to investment in reproduction (e.g. Cohen, 1976; Iwasa, 2000). Intuitively, we can foresee the consequences of such a shift. If, in our model, we assume that the switch is simultaneous for competing plants, the individual that has

Table 3 – Results of a sensitivity analysis, showing the effect of a 50% change in parameter value

	+/-	4	5	6	7	8	9	10
Original parameters		-	-	-	131	421	790	829
Simulation time	-50%	-	-	92	498	858	123	5
$c_{r(l,r)}$	-50%	-	-	157	650	1266	-	-
I_h	-50%	-	-	218	355	571	35	-
γ	-50%	-	253	394	131	-	-	-
σ	+50%	-	-	-	375	500	875	50
$r_{m(s,l,r)}$	+50%	-	331	536	404	-	-	-
$r_{(s,l,r)}$	+50%	-	-	-	361	612	1105	-

Results of the simulations with original parameter values are depicted in Fig. 3. Shown in this table are the abundances (plants/m²) at equilibrium. For an explanation of symbols, see Section 2. For original values of parameters, see Table 1.

the highest NPP at the time of the switch will also have the highest seed mass at the end of the growing season because vegetative growth ceases and plants can no longer improve on their competitive position. To investigate how exactly the timing of this switch would affect our results, we model the plants in such a way that they first invest all carbon from NPP in vegetative growth and then shift instantly to invest all carbon from NPP in the production of seed. For now, within each simulation, the timing of the switch is kept the same for all types of plants.

This modification does not qualitatively change results; rather it gives some interesting new insights. Because plants that invest much in height have less to invest in leaves, they have a slow growth and reach their maximum NPP late in the growing period. Therefore, if the shift is late, this benefits the types possessing a high investment in height. If the shift is earlier, this benefits the plants with little investment in growth. Height growth and the onset of seed production thus are correlated traits: a plant that invests much in height growth should start seed investment late in its life, and plants that invest more in their leaf area should start seed production earlier. Consequently, if all the plant types shift early, at 200 simulation days, plant Types 7, 6 and 5 coexist (results not shown). If all the plant types shift to the production of seed slightly later, at 250 simulation days, plant Types 10, 9, 8, and 7 coexist (results not shown). An early shift also allows for a long period of seed production, increasing the density in the following year. This phenomenon counteracts the shift towards plants that invest little in height, because a large stature is beneficial at high densities. At a shift of 100 days therefore Types 9 and 10, which have a large investment in height, coexist (results not shown).

The timing of this switch is an extra variable that influences fitness of plants. In a next paper (in preparation), we investigate competition between plants with different switches to reproduction.

Plants in a real field situation do usually not spread their seeds perfectly random. The actual distribution of seed originating from a mother plant can be approximated by a Gaussian curve (see Pronk, 2004). When plants spread their seeds according to such a distribution, the density distribution does change slightly. This results in a shift in abundances of types. As an example: If plants disperse seed on average 3 cm, many plants end up clumped, resulting in a sharply peaked density distribution and plant Types 7–10 coexist at densities of 53, 247, 1042 and 525 plants per meter square (results not

shown). If plants disperse seed on average 10 cm, plants are more evenly distributed and plant Types 7–10 coexist at densities of 151, 515, 862 and 645 plants per meter square (results not shown).

5. Discussion

With a biologically mechanistic model we investigated the possibilities for plant types to coexist over several generations when they were competing for light and each plant type possessed a different investment in height growth.

Whereas some authors found stable coexistence of plants that differed in height at a fixed density for a single competition event (Iwasa et al., 1984; Huisman et al., 1999; Perry et al., 2003), this possibility did not occur in our simulation study where competition between plants was calculated over several generations.

Partly, this was due to the fact that we incorporated the frequency development of plant types over several generations. Plants that had a persistently low relative fitness decreased in the course of generations, to finally go extinct. For another part this was due to the incorporation of overlapping crowns and lifetime investments of carbon in the simulation of our competition events. We showed that a larger height (assumed implicitly from an increased investment in height) does not always imply that the plant becomes competitively stronger, as is assumed in many studies that do not consider the dynamics of plant growth (e.g. Iwasa et al., 1984; Weiner and Thomas, 1992; Gaudet and Keddy, 1995; Huisman et al., 1999). In our study, plants that invested much of their carbon in height were out competed at a very early stage by plants with lower investment in height. An intermediate investment of carbon in height (resulting in a larger asymmetric competitive advantage) and leaves (resulting in more light interception, hence larger growth rate) to such an extent that both shading by other plant types was prevented and growth rate was sufficient, was the single evolutionary stable strategy (ESS).

In contrast to our findings at fixed densities, several plant types with different investment in height could coexist when we introduced non-uniformly distributing seeds over an assemblage of patches. This coexistence was a result of two well-documented characteristics of vegetation stands. Firstly, at increasing density, a type with higher height investment was the ESS. There is strong empirical evidence for this. Plants

with greater height investment achieve greater fitness in crowded stands while the reverse holds for stands of low density (e.g. Dudley and Schmitt, 1996; Schwinning and Weiner, 1998). Secondly, it has been found that when plants disperse between patches, there is a consistent stochastic difference in plant density per patch (Geritz, 1995). Because of these two phenomena, different types in our model found 'windows of opportunity' to perform well. This prevented the exclusion of these types from the area. This is a specific example of coexistence on a single resource by means of a transitive dominance (Aarssen, 1992), i.e. a different type is dominant at every different circumstance. In our case, we showed that plants can create their own variability in circumstances in a principally homogeneous area, by dispersing irregularly and making use of resulting differences in density with differences in the investment in height growth. It is important to realise that these differences in local conditions proved to be refugia for specific types was not superimposed but emergent, as we also made no *a priori* assumptions on the performance of types with different investments in height. The performance was emergent as a trait of carbon allocation pattern of plants to stem or leaves and their consequent light interception in relation to neighbouring plants.

Aside from single plant performance, system level specifications also match between the model and natural situations. A height distribution similar to that of plants in our assemblage of patches can also be found in natural canopies (Mitchley, 1988; Liira and Zobel, 2000). However, in our model each canopy layer consisted of a mixture of plants with different height investment, whereas in natural canopies each layer contains species of comparable growth shapes (Mitchley, 1988). The layers in our model developed because some of the plant types were of low stature at some densities, as a result of suppression, and tall at other densities. On the other hand, distributions of the individuals over size classes, such as we found them have been observed repeatedly for dense stands of single-species (e.g. Nagashima et al., 1995; Anten and Werger, 1996; Anten and Hirose, 1998).

The question thus remains to what extent our results – coexistence of plant types with different height growth strategies being the result of the density dependence of the ESS height growth and the spatially stochastic distribution of seeds – apply to real-life natural communities. After all, species in natural vegetations differ in many more traits than only in height investment. Apparently, the mechanisms that underlie the development of suppressed and superior plants as found in our study resemble more those of a mono-specific stand than those of a natural vegetation consisting of many species. Nevertheless, it is interesting to consider that differences in the height investment trait, if able to evolve, could establish and persevere under such simple conditions as a non-uniform distribution of individuals of a single population, an example of sympatric evolution. It will depend on the density distribution, how many and which types can eventually coexist. The stable coexistence of plants with inherently different height investment could be a starting point for further diversification of plant traits within a population.

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