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Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings

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TIIVISTELMÄ: MÄNNIKÖN SIEMENPUIDEN VAIKUTUS PINTAKASVILLISUUDEN JA TAIMIEN MÄÄRÄÄN

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The study uses the methodology of ecological field theory to model the effect of Scots pine seed trees on the density of tree seedlings and other plants in the field layer. The seed trees had a clear effect on the expected value of the amount and distribution of the ground vegetation. The vicinity of seed trees had an adverse effect on the growth of grasses, herbs and seedlings, while mosses were most abundant near the trees. Models based on the ecological field approach were derived to describe the effect of seed trees on the ground vegetation.

Tutkimuksessa sovelletaan ekologista kenttäteoriaa taimien ja muun kenttäkerroksen kasvillisuuden tiheyden ennustamiseen männyn siemenpuualalla. Siemenpuut vaikuttivat selvästi kenttäkerroksen kasvillisuuden määrään, siten että siemenpuiden läheisyys vähensi heinien, ruohojen ja taimien määrää. Sammalia oli eniten siemenpuiden lähellä. Siemenpuiden vaikutusta aluskasvillisuuteen kuvattiin yhtälöillä, joiden selittävä muuttuja laskettiin ekologisen kenttäteorian perusteella.

Keywords: natural regeneration, regeneration models, ecological fields, resource consumption, competitive interference, spatial variation.
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1. Introduction

Competition in a tree stand, as in any plant community, is in essence a spatial process where the trees are adversely affected by the presence of close neighbors. This is because the area from which a tree extracts resources (light, water, nutrients) overlaps with those of other trees (Harper 1985). From the forester's point of view a relevant question is: what is the mechanism of competition and how does it affect the growth and survival of trees and other vegetation interfering with trees? Therefore, description and prediction of the competitive interaction between neighboring individuals constitute a major problem also in silvicultural growth studies.

In particular, a methodologically difficult problem has been the description of the competition between plants of very different sizes. In forestry, this problem is most relevant in natural regeneration where the effect of shelter trees on the growth and survival of tree seedlings should be known when developing efficient regeneration methods. There are empirical studies on the effect of root competition on the growth of the field layer (e.g. Björkman and Lundeberg 1971) and efforts have been made to model the light regime in a shelter stand (Satterlund 1983). However, no widely applicable methodology has been proposed until recently for the modelling of the competitive influence of large trees in the field layer (cf. McMurtrie and Wolf 1983).

The ecological field theory (Wu et al. 1985, Sharpe et al. 1985, Walker et al. 1986) provides a new methodology for modelling the spatial interaction between plants of different sizes (Pukkala 1986, 1989). This study applies the methodology of ecological fields to predict the effect of Scots pine seed trees on growth potential in the field layer. The growth potential is used to estimate the density of tree seedlings and other plants in the field layer.

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2. Material and methods

21. The concept of ecological fields

In their approach to describe the spatial competitive interactions among plants, Wu et al. (1985) defined the competitive interference as the influence of a plant upon its neighbors' environment through resource competition or less direct interaction. The interference potential at a point was defined as the combined effect of all factors contributing to the interaction intensity. Thus, the interference potential is also the interference that a newly germinated plant must overcome to establish itself and subsequently grow within the influence of all neighboring plants.

The growth and survival of a plant on a given site at a given point depend on the combined effect of a multitude of factors, the most important of which are temperature and the availability of light, water and nutrients. In a tree stand, light, water and nutrients are characterized by a heterogenous spatial distribution. If the site is homogeneous, this heterogeneity is partly due to the consumption of growth resources by trees and other vegetation (Figs. 1a-c). Thus, the strength of the interference potential is a result of the combined consumption of the resource pool by neighboring plants at a given point (Fig. 1d).

In general, the effect of a tree on the resource level is strongest near the stem and diminishes with increasing distance from the tree. The influences of different tree parts on the resource level around the tree are described as 1) roots, 2) crown and 3) stem spatial influences (Wu et al. 1985).

The resource uptake by roots decreases the water and nutrient levels around the tree. Nitrogen fixation by root bacteria may also increase the nutrient content of the soil.

The crown intercepts both light and water and consequently decreases these resources as well as soil temperature, but at the same time litter fall and nutrient leaching from the crown increase nutrients near the tree. Shading can also reduce evaporation beneath crowns.

Stem flow, which is partly affected by the crown size, increases the availability of water and nutrients near the stem base.

The effect of the whole plant on the particular growth resource is obtained by combining the effects of roots, crown and stem. These spatial influences are described with ecological fields, i.e. interference surfaces showing the relative three-dimensional effect of a plant on the resource level (Fig. 1). The strength of the interference field is 0, when there is no spatial interference, and 1 when interference is so high that growth cannot occur. Finally, the availability of water, light and nutrients is combined in a definite manner into a continuous surface of the interference potential (Wu et al. 1985, Walker et al. 1986).

22. Material

The field data were collected from a Scots pine stand in a state of natural regeneration located in North Karelia (63°40'N, 31°5'E), Finland, on a rather poor site (Fig. 2). About 50 seed trees per hectare were left in the area in the seed tree cut three years prior to the measurements. The height of the seed trees varied from 20 to 28 m and their diameters from 28 to 37 cm. The area was disc plowed one year after the regeneration cut. Plowing removed the humus layer from 0.5-m-wide parallel strips 2 to 3 m apart.

A sample plot of 140 m by 140 m was demarcated in the area. All the seed trees were measured by coordinates, diameter and height. The ground vegetation was measured in the central part of the plot, over an area of 100 m by 100 m, leaving a 20 m border zone. In this central part, a total of 441 pairs of small sample plots were measured at 5 m intervals in x- and ydirection. The first plot of the pair was a 1 m by 1 m plot which was placed in the nearest possible location outside the trace of the disc plow. In these plots the amounts of the following components of the ground vegetation were estimated:

- Seedlings
- Dwarf shrubs
- Grasses and herbs
- Mosses

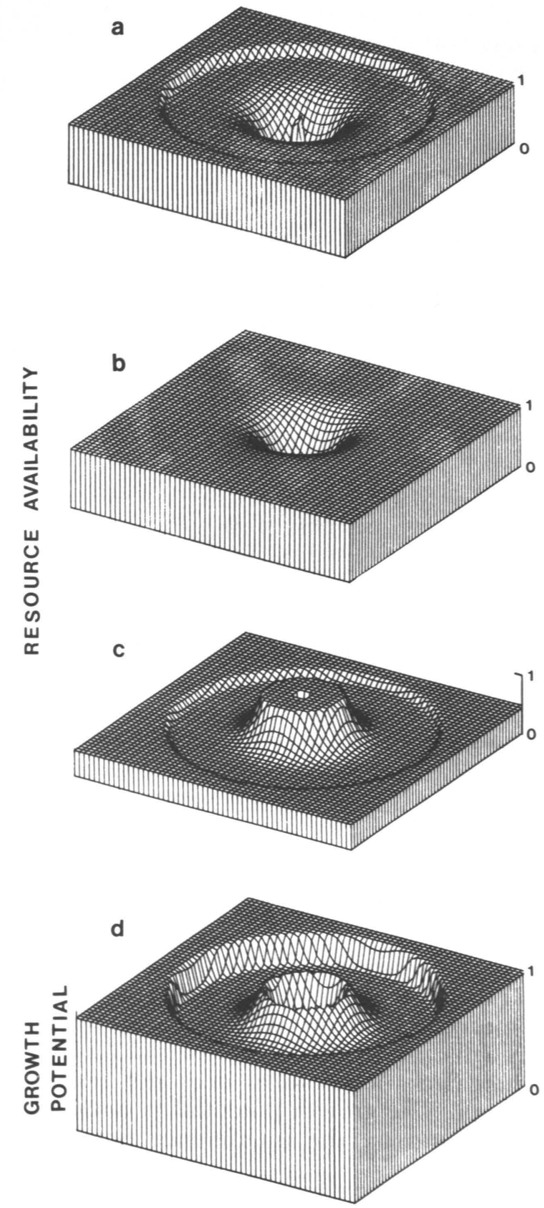

Fig. 1. Schematic illustration of the effect of a tree on the availability of water (a), diffuse radiation (b), nutrients (c) and the growth possibilities of seedlings (d). Surfaces (a)...(c) describe the resource availability (1-interference potential) after the effect of a tree locating in the center of the area has been taken into account. Surface (d) is combined from surfaces (a)...(c).

The seedling count included only seedlings younger than 3 years, i.e. seedlings germinated after the regeneration cut. The dwarf shrubs and the 'grasses and herbs' component were estimated by coverage (0...1) and average height, mosses by coverage only.

The second plot of the pair was a 0.5 m by 1 m plot in the trace of the disc plow. Its location was as near as possible to the location defined by the systematic grid of plots. In this plot, only the number of seedlings younger than three years was counted. For both plot types the exact coordinates (in dm) of the center of the plot were recorded and used in the computations.

For statistical analyses the amounts of different components of the ground vegetation were expressed in the following units:

Component	Unit
Seedlings	Seedlings/m²
Dwarf shrubs	Coverage (0..1) x average height (cm)
Grasses and herbs	Coverage (0..1) x (50 + average height in cm)
Mosses	Coverage (%)

23. Calculation of growth potential

In this study the concept "growth potential" refers to the relative amount of growth resources. Value 0 is a level at which growth cannot occur any more and 1 a level where lack of resources does not restrict growth. The growth potential is obtained by subtracting the interference potential from the original resource pool (without any consumption).

It was assumed that one function is enough to describe the effect of a tree on the growth potential at a particular point. The function, which was found by trial and error, is as follows:

$$\emptyset_i(s) = \emptyset_i(O)\exp(-b_i s^2) \quad (1)$$

where $\emptyset_i(s)$ = effect of tree i on growth potential at distance s (meters) from the tree,
s = distance from the tree to the calculation point,
$\emptyset_i(O)$ = effect of tree i at the point of tree location,
b_i = parameter.

Parameters $\emptyset(O)$ and b depended on tree size as follows:

$$\emptyset(O) = d/35 \quad (2)$$

$$b = 1/(0.4\,h) \quad (3)$$

where d is the breast height diameter (cm) and h is the height (m) of the tree.

The effect of all trees on the growth resources at point (x,y) was obtained as a product of the relative amounts left by individual trees:

$$R_i(x,y) = (1-\emptyset_i)R_{i-1}(x,y),\ i=1,\ldots,N \quad (4)$$

where R_N is the relative amount of resources at point (x,y) after the effect of all trees (N) is calculated. The growth potential without any trees, i.e. R_O, was taken as 1 at every point.

3. Results

The seed trees affected very clearly the abundance of grasses and herbs in their vicinity (Figs. 2 and 3); at the distance of 8 meters from the nearest tree there were four or five times as many grasses and herbs as in the immediate vicinity of a seed tree. The amounts of the other types of the ground vegetation were not as closely connected with the location of seed trees, but it seems that the amount of seedlings between the plow traces increases and the moss cover decreases as distance from the nearest seed tree increases (Fig. 3).

Since there was very much plot-to-plot

Fig. 2. The studied regeneration area. Around each seed tree there is a zone almost empty of grasses and herbs.

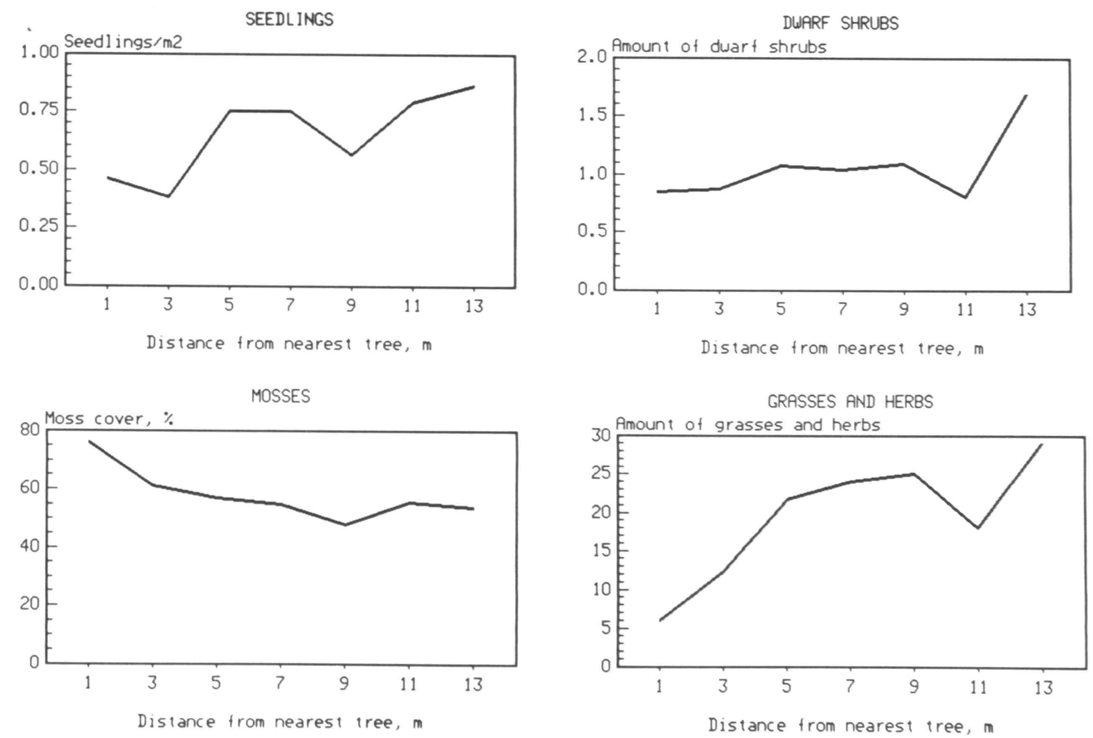

Fig. 3. Dependence of the amount of ground vegetation on the vicinity of a seed tree. Each point shows the average amount of vegetation of the plots in a 2-m-wide distance class.

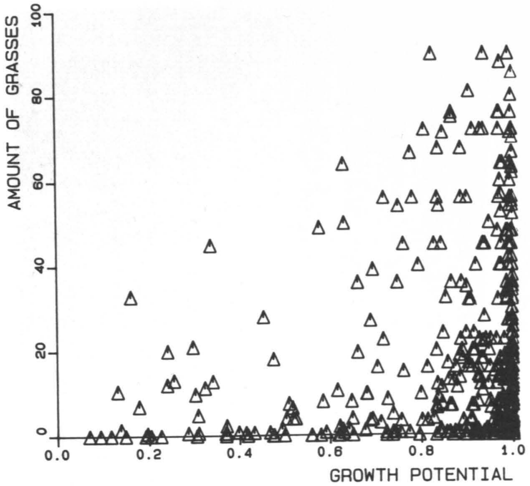

Fig. 4. Correlation of the amount of grasses and herbs with the estimated growth potential.

Table 1. Correlation coefficients between the amount of ground vegetation in a 1 m² sample plot and the estimated growth potential or the distance to the nearest seed tree.

Type of ground vegetation	Correlation of the amount of ground vegetation with	
	Growth potential	Distance to nearest seed tree
Seedlings	0.098	0.065
Dwarf shrubs	0.075	0.075
Grasses and herbs	0.230	0.183
Mosses	-0.189	-0.154

variation in the ground vegetation that was independent of the seed trees, the correlations of the amount of vegetation with the estimated growth potential and the distance from the nearest tree remained very low (Table 1, Fig. 4).

The amount of the ground vegetation correlated better with the estimated growth potential than with the distance from the nearest seed tree. This was because the growth potential takes into account the variation in tree size, the combined effects of several trees and the non-linear relationship between the effect of a seed tree and its distance.

The number of seedlings in the plow trace did not correlate with the growth potential nor with the distance from the nearest seed tree. Thus it seems that in the traces of the disk plow the conditions for the germination of seeds and survival of seedlings are independent of the seed trees. Later, when the seedlings in the plow traces grow older, the competitive interference of seed trees will probably have a much stronger effect on the growth rate and survival of the seedlings (Lehto 1956).

Even though it is impossible to predict the exact amount and composition of the ground vegetation on a 1 m² subarea on the basis of the size and location of the seed trees, it is reasonable to study the effect of seed trees on the expected value of a certain type of ground vegetation. For this purpose the following models were computed from the study material:

Grasses and herbs

$$GH = 23.83GP \quad (5)$$

$F(2, 434) = 452, \quad s_e = 22.1$

Dwarf shrubs

$$DS = 0.6385 - 0.01893GH + 0.9020GP \quad (6)$$

$F(2, 432) = 30.4, \quad s_e = 1.14$

Seedlings (between disk traces)

$$S = 0.1904 - 0.006978GH + 0.6973GP \quad (7)$$

$F(2, 432) = 6.31, \quad s_e = 1.11$

Mosses

$$M = 79.66 - 0.6638GH - 11.09GP \quad (8)$$

$F(2, 432 = 78.3, \quad s_e = 26.66$

where GH = amount of grasses and herbs (the unit explained above),
GP = growth potential (0...1),
DS = amount of dwarf shrubs (the unit explained above),
S = number of seedlings per square meter,
M = moss cover (%).

The equations can be used for estimating the effect of seed trees on the amount of the ground vegetation. Since there are also other sources of variation in the growth potential than the effect of seed trees, e.g. the variation in soil properties, the estimates are very unreliable for a small subarea. Also the clonal growth habit of many plants in the field layer may increase the residual variation. If the size of the sub-area increases, the residual variation around the estimates of equations (5)...(8) will probably decrease.

Although the seed trees explained only a minor part of the variation in the ground vegetation in small sub-areas, their effect on the expected or average composition and amount of the ground vegetation was notable, as can be seen from Figures 3 and 5 and from equations (5)...(8).

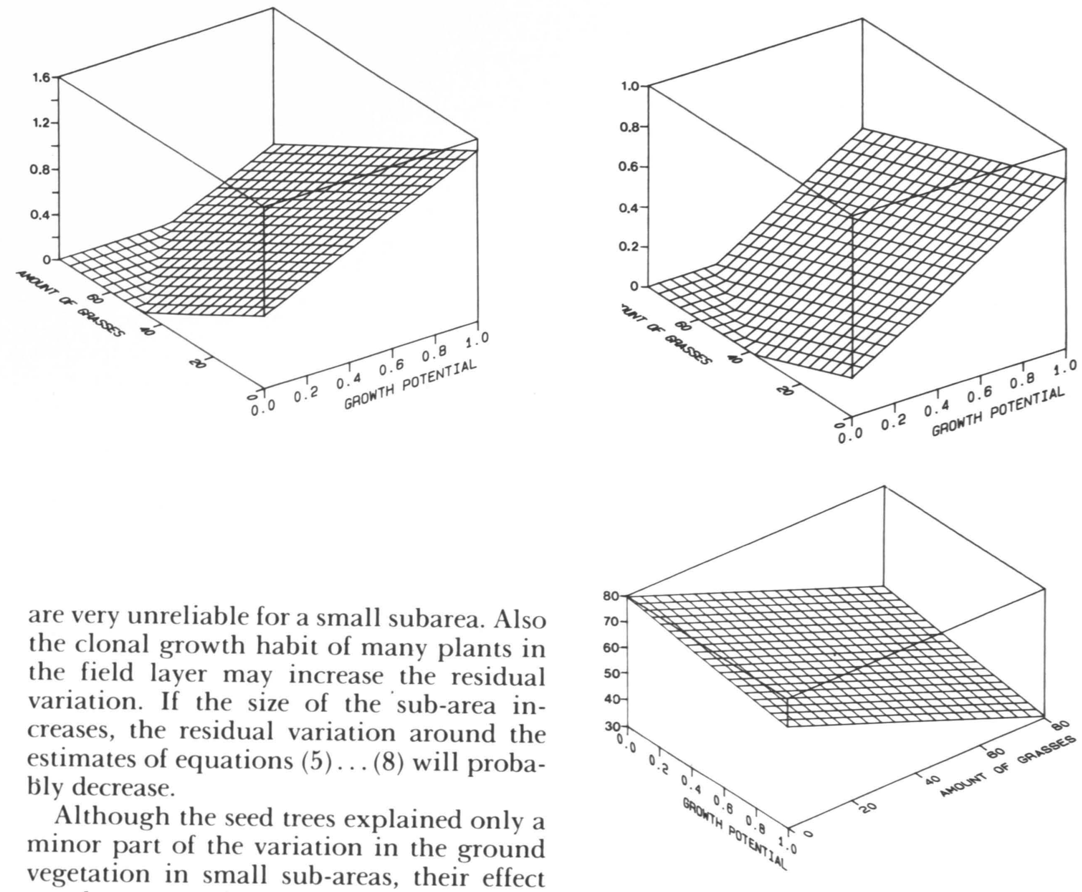

Fig. 5. Expected amount of dwarf shrubs, seedlings and mosses as a function of growth potential and the amount of grasses and herbs. The surfaces are calculated by Equations (6)...(8).

4. Discussion

In this study the theory of ecological fields (Wu et al. 1985, Walker et al. 1986) was applied to describe the effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. The methodology enables one to describe the competition effects between plants of very different size. Another advantage of the method is that it makes it possible to assess the resource consumption and the competitive interference in a spatial framework (Harper 1985, cf. McMurtrie and Wolf 1983).

In the studied seed tree stand growing on a rather poor site, the seed trees had in their vicinity a clear adverse effect on the amount of grasses and herbs; the same was also true, although less clearly, in the case of seedlings, whereas mosses were more abundant near the trees. The influence of seed trees on the probability of the germination of seeds and the survival of seedlings is probably stronger than indicated by these results since the seed density falls off along with the distance from the parent tree (Kellomäki et al. 1987). Also the probability that a seed is eaten by seed-eating animals is greater in the vicinity of trees where the ground vegetation is scanty (Lehto 1956).

The distribution of different plant groups in the field and ground layer reflects the physiological differences between the plant groups and the consequent resource requirements in these groups. Fast-growing annual grasses and herbs are the strongest competitors in places where resources are abundant. Seedlings are thus adversely affected by both the seed trees and grasses and herbs. Mosses with low resource requirements can thrive in places where the competition by the seed trees is strong, preventing the growth of grasses, herbs and dwarf shrubs.

The existence and origin of a competition zone around older trees growing on nutrient-poor and dry sites has usually been related to root competition (Aaltonen 1920, Kalela 1942, Lehto 1956). The study of Björkman and Lundeberg (1971) gives ample evidence that the root influence, the extraction of the available nitrogen especially, is mainly responsible for the growth reduction in the ground vegetation in the vicinity of Sconts pine trees, since the roots of older trees completely dominate the upper soil layer within an area of 5 . . . 7 m from the stem. Also the interception of precipitation may have an adverse effect on seed germination below the crowns because the moisture content of litter increases rapidly with increasing precipitation (Halvey 1964).

It is unlikely that the shading effect of the seed trees could account for the detected spatial patterns of the ground vegetation, since when the crown base is far from the ground, like in the present experimental stand, the radiation regime at the ground level is rather even (Kuuluvainen and Pukkala 1987, Pukkala et al. 1989). This conclusion is also supported by the fact that the number of seedlings in plow traces was not affected by seed trees.

In general, the removal of the humus layer appears, to a high extent, to surpass the competitive interference caused by the seed trees and other plants in the field layer. Thus, plowing not only increases the number and growth of seedlings but also promotes an even distribution of seedlings in the regeneration area.

In this study the ecological field approach was simplified in such a way that the root, crown and stem influences of a tree on the growth potential were not separated, as proposed by Wu et al. (1985), but were described by a single empirically derived function (see also Pukkala 1988). Thus, the description of the influence of a tree was simplified, which may be one reason for the low proportion of explained variation in the estimated amount of the ground vegetation. Other possible sources of residual variation may have been the errors in the visual estimation of the ground cover and the height of vegetation.

It is also obvious that it is not possible to describe all the influences of a tree with a distance-dependent symmetrical function, since the soil is heterogeneous, the crowns of the trees are not always symmetrical and there may be gaps in the distribution of roots as well (Laitakari 1929). Neither is the shading of direct radiation symmetrically distributed around the tree, even if the tree is symmetrical (Kuuluvainen and Pukkala 1987).

In spite of the low degree of determination of the derived models, the seed trees had a notable effect on the expected composition and amount of the ground vegetation. For the development of the method, more attention should be paid to the separate and accurate description of the effect of a tree on the level of light, water and nutrients, and on the dependence of growth on the amounts of these resources (Pukkala 1989). This presupposes that the empirical field data also includes the measurement of the amounts of different resources, not only their effects as reflected in the vegetation. This would facilitate the incorporation of spatial competitive interactions in physiologically-based growth models (Sharpe et al. 1986, Walker et al. 1986).

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