Tree and stand architecture and growth described by formal grammars.

II. Sensitive trees and competition.

Modelování stromové a porostní architektury
a růstu pomocí formálních gramatik.
II. Pro stromy senzitivního typu a konkurence.

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Abstract: Growth grammars (extended Lindenmayer systems) provide a standardized formal basis for models of forest trees and tree stands, concentrating on the development of the 3-dimensional structure. "Sensitivity" of such rule systems means that the application of certain rules for growth, branching or mortality is controlled by functions which evaluate the tree or stand structure simulated in the previous step and its environment. Complete grammars are shown for examples where the evaluation concerns orientation in space, density and shadow. We compare two algorithms for reactions of virtual spruce crowns to shadow.

Keywords: virtual tree, competition, growth reactions, Lindenmayer system, growth grammar, sensitivity, simulation, visualization

Abstrakt: Růstové gramatiky (rozšířené Lindenmeyerovy sytémy) dávají standardizovaný formální základ pro modely lesních stromů a porostů, zaměřující se na 3-dimenzionální struktury. "Senzitivnost" pravidelně orientovaných systémů tkví v tom, že aplikace určitých růstových pravidel, např. tvoření větví anebo mortalita, je kontrolována funkcemi, které zhodnocují simulovanou strukturu stromu nebo porostu v předcházejícím kroku a současně jejich okolí. Zde jsou ukázány kompletní gramatiky na příkladech, kde zhodnocení struktury pomocí funkcí zohledňuje její prostorovou orientaci, hustotu a zastínění. Podáváme také srovnání dvou algoritmů vzhledem k reakci virtuálních smrkových korun na stín.

1. Introduction

The development of the Central-European forests during the next decades will be influenced on the one hand by the increasingly fostered "close-to-nature" forms of silviculture, on the other hand by various unplanned anthropogenous impacts (nutrient depositions, groundwater depletion, possible climate change). The classical yield tables, which were developed from long-term measurements and were tailored to conventional treatment practices, loose their reliability under these circumstances (Pretzsch, 1997). Hence, there is a growing need for a causally oriented understanding of the interrelations of forest trees with their environment. The state of theory formation in tree physiology and in silvicultural growth studies manifests itself — like in other scientific areas — in the *models* which describe the relations in precise mathematical terms (and today often find their algorithmic realization in the form of computer simulations). Besides the purely empirical-deductive stand models, which are obviously insufficient for causal insights, there are currently two much-discussed directions of development in plant modelling:

- Process-oriented models which quantify and keep track of the amount and dynamics of the pools of carbon, water, nutrients and energy (e.g. McMurtrie, Wolf, 1983; Bossel, Schäfer, 1989; Bossel, 1996; Pfreundt, Sloboda, 1996),
- Structure-oriented models which reproduce 3-dimensional tree and stand architecture and reflect thus the principal role of structure in forestry (cf. the first part of this paper: Kurth, Sloboda, 1999).

These two approaches were established quite independently from each other. However, to obtain progress in understanding tree growth and its control, it is necessary to consider the relations between structures and processes and hence to unify both approaches. In fact, in the last 10 years, a certain convergence in ecosystemic, botanical and forest modelling can be observed.

In this article, we concentrate on the inclusion of some aspects of environmental impact into architectural models of tree growth, specified by grammars (cf. Kurth, Sloboda, 1999). The modelling of tree-internal processes like carbon allocation within the grammar framework is treated elsewhere (Kurth, Sloboda, 1997; Kurth, 1998).

The first architectural plant models were bare of functional aspects and concentrated on the reproduction of the genetically-determined form, enriched with stochastic variation. Niklas (1986) proposed a dependence of the probability of branching on light interception and water supply of the shoot, but in his simulation model these factors were assessed by purely "internal" traits (branching angles) of the constructed tree.

In 1990, Ford et al. (1990; see also Ford and Ford, 1990) included "proper" sensitivity in an integrated model of coniferous branch growth and compared non-sensitive branching rules with rules allowing for an influence of crowding on shoot development. Blaise (1991) reorganized the generic architectural plant model AMAP (cf. Reffye et al., 1995) to include the influence of light availability and branch crowding on shoot growth — an approach which was later combined with a model of carbon allocation and was utilized for simulating competition effects in forest stands (Reffye et al., 1997). An algorithm for modelling mechanical tension or compression effects on growth (formation of reaction wood) was also included there. List (1992) modelled the influence of light and of shoot orientation in space on growth and branching in woody plants (cf. also List et al., 1994; List, Küppers 1998). The conceptual ad-hoc plant model of Takenaka (1994) included light and allocation, that of Chiba et al. (1994a, b) light and hormonal regulation of bud activity. Hauhs et al. (1995) simulated the interception of light (above-ground) and nutrients (below-ground) in an individual-based tree model designed for forest stands, which was part of an ecosystem model. Kellomäki and Strandman (1995) developed a more detailed crown simulation for young Scots pine, including light interception and a model of brightness-intensity of sky segments. Breckling (1996) and Perttunen et al. (1996) devised object-oriented modular plant models with light interception, photosynthesis and carbon allocation. The approach of Breckling (1996) was used by Middelhoff and Breckling (1998) for simulating the growth and competition of root systems and nutrient uptake. Gavrikov and Sekretenko (1996) conducted model experiments concerning competition and grazing with their conceptual light-sensitive tree model; Berezovskaya et al. (1997) included reactions to crowding in their tree crown model. The reliability and efficiency of light interception calculations in virtual plants were considerably improved by Beneš (1996, 1997a, b).

Most of these diverse "sensitive plant models" were developed quite independently, often isolated and in an "ad hoc" manner. Each of the models is normally able to take into account one or — at maximum — two different environmental influences, but not more (exceptions: AMAP and the object-oriented models). Normally, there is no common framework for the treatment of the different influences, and in many cases even the compatibility to nonsensitive, purely empirical models of tree growth and architecture is lacking — a fact which complicates the validation of the sensitive models. The connection to the results of botanists who investigated the reactions of shoot growth to external stimuli (e.g. shade: Kozlowski, 1971; Wilson, Fischer, 1977; Greis, Kellomäki, 1981; Stoll, 1995; Tsel'niker, 1995; Tsel'niker et al., 1996; Kurth, Anzola, 1997; gravity and shoot orientation: Wareing, Nasr, 1958; Longman, Wareing, 1958; Worrall, Little, 1986; contact and mechanical abrasion: Jaffe, 1980; Putz et al., 1984; spectral quality of light: Morgan et al., 1983; Galinski, 1994; Ritchie, 1997) is often missing. We will mention some causes for this lack of interfacing with empirical research in the Discussion section.

The inclusion of reactions to local environmental stimuli into the formalism of L-systems was realized first by Prusinkiewicz and McFadzean (1992), who modelled collision detection of growing shoots by "post-production filters", and — independently — by Kurth (1994, 1996) with "globally sensitive functions" which we will explain below. Prusinkiewicz et al. (1994) used "environmentally sensitive L-systems" with so-called "query modules" in the strings to keep track of position and orientation of simulated shoots, an approach which was used for modelling artificially pruned garden plants; see also Prusinkiewicz et al. (1997). The concept was generalized and put in a concurrent-process framework by Měch and Prusinkiewicz (1996) under the name "open L-systems", utilized for simulating growth reactions to crowding, light and "concentration fields", e.g. of diffusing water in the soil, affecting root development. Kurth and Sloboda (1997) used sensitive L-systems with commands creating and changing local registers for modelling carbon allocation and effects of crown competition on stem shape. Furthermore, the GROGRA software provided a possibility to analyse and compare artificial trees and explicitely measured real trees, thus establishing a bridge to empirical morphological investigations of shade or competition effects on tree architecture and growth (Kurth, Lanwert, 1995;

Kurth, Anzola, 1997).

For the rest of this paper, we assume that the reader is familiar with the extended L-system formalism (nonsensitive, stochastic growth grammars) which was introduced in the first part (Kurth, Sloboda, 1999). We will present sensitive grammars at an abstract level and then demonstrate their performance by some examples — some at a very simplified and one at a more realistic level of architectural detail.

2. Sensitive growth grammars

Sensitivity of grammars means the possibility to let a rule application (or parameters used on the right-hand side of a rule) depend on local environmental influences (as well as on influences from near or far parts of the generated plant structure itself), which are registered at a position in the plant which corresponds to the symbol which is to be transformed by the rule. This symbol can e.g. stand for a bud which has a certain local environment in which conditions like intensity of light or the presence of mechanically-disturbing neighbour shoots can control the fate of this bud and hence the application of a rule encoding growth or mortality.

For this purpose, *context sensitivity* of L-systems like in Prusinkiewicz and Lindenmayer (1990) does not suffice because the signals having impact on the development of a plant do not necessarily come from the immediate context (in the sense of the string encoding) of the plant organ under consideration. Thus, *global sensitivity* (Kurth, 1994) is required. The key feature of globally sensitive growth grammars in the GROGRA system is that functional parameters (i.e. variables declared as "function") which depend on the last generated geometrical structure are allowed in the generative rules. Hence, in the scheme depicted in Fig. 4 of Kurth and Sloboda (1999) we have to add an influence from the geometrical structure S_k (representing a plant or a whole stand) on the creation of the string σ_{k+1} in the next time step (and thereby on S_{k+1}), which is indicated by the broken arrows in Fig. 1.

Technically, GROGRA enables sensitivity by saving the internal addresses of the elementary units of the last created structure in the order of the associated turtle commands and thereby establishing a link between the string to which the generative rules are applied and the last structure. The unit in the last structure to which a symbol is associated is always the unit which was created by the last preceding F command. The sensitive functions itself are allowed to acquire informations from the whole structure as well as from the actual elementary unit. They are implemented in the programming language C, compiled along with the GROGRA software (forming a separated program module called LMETHOD.C), and their behaviour depends on the special purpose, as will be illustrated by the examples. In the present version of GROGRA, the different sensitive functions which are available are simply identified by numbers; it is planned to realize a more flexible management of user-defined functions in a future version of the software. The reference to one of the predefined, available sensitive functions (see Kurth, 1994, 1997 for a complete list) is established via its identification number n in the declaration line

$$\backslash\mathsf{var}\ \ \mathit{function\_name}\ \ \mathsf{function}\ \ n\ \ a,$$

where a is the *arity* (number of arguments) of the function. The head of the corresponding procedural function specification (in C syntax) looks as follows:

float function$n$ (struct unit $*s$, float arg1, $\ldots$, float arg$a$)
{ $\ldots$/* *function body with calculations* */
}

where $*s$ is the address where the data of the elementary unit s under consideration are located in the memory, and arg1, ... are the arguments which can additionally be specified in the grammar when the function is called. The above declaration of *function_name* given, this function call has the form

$$\mathit{function\_name}(\mathsf{ex1}, \ldots, \mathsf{ex}a)$$

where ex1, ... are arithmetical expressions. The elementary unit corresponding to the left-hand side of the rule is taken for s.

Principally, all kinds of information from the (local or global) context of a plant part can be used to exert control in the model on the development of that plant part. We will discuss the grammar implementation of such sensitivity and the resulting behaviour of the model for three types of information which were identified by botanists (see citations in the Introduction above) as important for the morphological development of trees and tree parts: orientation in space, density of plant organs in space, and availability of light. The first three examples presented in the following are not meant to describe "realistic" plant models (in the sense of yielding numerical values on the same scale and directly comparable to field data), but only to demonstrate some fundamental possibilities in a heavily oversimplified manner.

3. Examples

3.1. Sensing orientation

Table 1 shows the grammar specification of a plant growing in a strictly *epitonic* manner, i.e. buds are only allowed to grow out into lateral shoots if they happen to have an orientation which is nearly vertical and if they are situated on the top side of the supporting shoot (cf. Kurth, 1996). Figure 2 shows the developmental steps 7, 11, 17 and 20 of the resulting output produced by the software GROGRA when fed with this sensitive growth grammar. The start word is "t(0)" here.

The growth of the main axis is governed by the rule in line 7. The terminal bud, symbolized by t, produces in each time step a growth unit (gu), surrounded by a ring of 8 lateral sleeping buds (bd) in basal position, and a new terminal bud t$(n+1)$. The parameter of t counts the age of the meristem. If this age reaches the value 10, the rule is no longer applicable due to the condition $(n < 10)$, and the axis stops growing. By RH(u) a random rotation around the growth direction is enforced (cf. the declaration of u in line 3), such that the lateral buds are not always directed into exactly the same directions after each time step.

```
 1  \var i index,
 2  \var e uniform -5 5,
 3  \var u uniform 0 360,
 4  \var f function 7 0,
 5  \set V 0.7,
 6  \axiom t(0) 1–20,
 7  (n < 10) t(n) # RH(u) gu(1,10-n) &(8) < [ @0.2 RH(i*45) RL80 bd(0) ] >
                         RU(e)  RV  L*0.9  t(n+1),   /* terminal growth  */
 8  (n > 2 && f < 40)  bd(n)  #  L  t(1),   /* outburst of sleeping bud  */
 9                      bd(n)  #  bd(n+1),  /* further sleeping of bud   */
10  (n < k)  gu(n, k)  #  gu(n+1, k),   /* ageing of growth unit    */
11  bd(n)  ##  L*0.05  Pl4  F,          /* display of sleeping bud  */
12  (n < 7)    gu(n, k)  ##  Dl(n)  F,  /*  display of growth unit  */
13  (n >= 7)  gu(n, k)  ##  Dl(7)  F
```

Table 1: The sensitive growth grammar epiton.ssy.
(See the Appendix of part I of this article for a short overview of the functionality of all used symbols and keywords of the grammar.)

The construction "&(8) < ... >" stands for a repetition command which iterates the part enclosed in $<\ldots>$, i.e. the lateral bud, 8 times. In each iteration the variable i, declared as "index" in line 1, is automatically augmented by 1, which leads to a symmetrical distribution by the command RH$(i * 45)$ of the lateral buds in the directions $0°$, $45°$, $90°$, ..., $315°$. The branching angle of each lateral bud (and of each branch eventually produced by it) is fixed to $80°$ by the command RL80. The further rotation command RU(e) in this rule, making use of the random variable e declared in line 2 to vary in the small interval $[-5°, 5°]$, enables small deviations of the growth direction of the axis from the initial vertical direction. Without these deviations, the axis would never hang down, and the lateral buds would never come into the vertical orientation necessary for their outburst.

The geotropic tendency itself ("hanging down") is caused by the operator RV. Its strength is specified by the \set statement in line 5, but it naturally depends also on the deviation from the vertical which the axis has already obtained: the stronger this deviation, the stronger the effect of RV.

Furthermore, the length of the produced growth units is steadily diminished by the factor 0.9 (command L*0.9).

The key function introducing sensitivity into this grammar is declared in line 4. The identifying number 7 of this function refers to a routine implemented in GROGRA which calculates the angular deviation of the element associated with the actual symbol (here bd) from the vertical. The function f has no numerical argument ("0" in the declaration). If its return value exceeds $40°$, the application of the rule in line 8 is forbidden by the condition "$f < 40$". (The further condition, "$n > 2$", tells us that a certain phase of resting — at least 2 time steps — must have been passed before a bud can evolve.) If Rule 8 is applied, a terminal bud (t(1)) is the result, which is capable of producing a shoot according to Rule 7 again, with the initial shootlength put to the default start value by the "L" command without arguments. Botanically, this lateral branch is nothing else than a simple case of reiteration.

If Rule 8 is not applicable, the next rule (line 9) will be applied, which has just the effect to increase the age of the sleeping bud. A similar ageing of already created growth units is executed in the first parameter of gu in line 10. This age parameter n controls the thickness of the growth unit in the interpretative rule in line 12 ($\mathsf{D}\ell(n)$). However, the application of Rule 10 depends also on the second parameter of gu, k, which is decremented along an axis by Rule 7. If n exceeds this threshold k, the growth unit stops its growth in diameter. This prevents distal parts of axes which already have stopped to grow in length from becoming unnaturally thick. A further limit for diameter growth is given by the condition $n < 7$ of Rule 12, together with Rule 13, fixing a final thickness of 7 length units.

As can be seen from Fig. 2, only a small number of lateral buds (displayed as very short lines specified in line 11) comes into a position which enables the application of the sensitive rule 8, i.e. the creation of a reiterated axis. However, after some further time steps there emerge again reiterations in an epitonic manner from the few new axes, so that a complex of reiterations begins to develop (see right part of Fig. 2). This can often be found in shrubs.

3.2. Sensing density

In an ordinary, non-sensitive L-system, there is no mechanism foreseen to prevent shoots to grow arbitrarily close to each other, or even to grow "into" each other. To exclude such physically unnatural behaviour, some sensitive function is necessary which detects other shoots (or other kinds of obstacles) in the neighbourhood of a plant organ. In GROGRA, the function with identification number 2 fulfills this task. It can be used with a numerical argument which specifies a maximal length of elementary units which are to be considered as "irrelevant" during the search for neighbouring shoots — e.g. to exclude the buds themselves or their components from having influence on their outburst. The return value of the function is the distance to the nearest other elementary unit (having a length greater than the specified argument). The unit under consideration and its mother unit are excluded from the possible set of nearest neighbours in this search. (To be precise, it is the distance to the nearest unit *end* or unit *basis* which is returned in the present GROGRA version, but a "true" distance to the cylindrical unit could be calculated equally well.)

Table 2 shows a grammar in which this function is applied to prevent two 2-dimensional tree crowns from growing into each other. The start word is "$*$" here. The two trees are initiated (with a 1-step time delay between them) in line 6. The sensitive rule is to be found in line 10. It is only applied — enabling an elongation of the branch initiated by b by one further growth unit — if the distance $f(50)$ to the nearest unit longer than 50 length units is larger than $mdist$, i.e. if a ball with radius $mdist$ around the shoot tip under consideration is free of "large" shoots. The value of $mdist$ is demanded from the user (line 3) and held in a *global register* (declared in line 2) during the simulation.

The register variable, once declared, could be referred to by "*mdist*" in every arithmetical expression and in every rule.

A further condition appears in line 10, involving the variable z declared in line 4 as having the type "zcoordinate". This demonstrates another kind of sensitivity which will only be briefly mentioned here: z returns the height (z coordinate) of the actual shoot tip in a global Cartesian system. The condition "$z > 90$" prevents the hanging branches from growing into the soil.

```
1   \var f function 2 1,
2   \var mdist register 1,
3   \ask l1 minimal distance?,
4   \var z zcoordinate,
5   \set V 0.2,
6   * # P2 D1 [ L120 a0 tbd(8) ] RU90 f450 RU-90 [ L100 a1 tbd(8) ]
            RU-90 f1250 RU180 P6 F1950,
7   a1 # a0,
8   a0 # i(1.8,0) F [ RU40 L70 b(0) tbd(8) ] [ RU-40 L70 b(0) tbd(8) ] a0,
9   i(s,t) # i(s,t+1),
10  (f(50) > mdist && z > 90) b(t) # i(0.8,0) RV RH(90+t*180) F
                                      [ RU30 tbd(6) ] RH180 b(t+1),
11  i(s,t) ## Dl(1+s*t),
12  tbd(x) ## P6 D0.5 L(x) RU-90 f*0.5 RU180 F RU-104.5 F*2 RU-151 F*2
```

Table 2: The sensitive growth grammar densi2d.ssy

The structure generated from the density-dependent grammar densi2d after 15 time steps is shown in Figure 3. The specified minimal distance was 60 here. One has to note that the growth units are not completely prevented from close contact to each other because the distance check is made *before* they grow.

3.3. Sensing overshadowing

The perhaps most important type of sensitivity is the dependence of shoot growth upon light. Our first approach to this problem will make use of a strongly simplifying concept, the notion of the *shadow-relevant cone*. It means that for the estimation of the light conditions of a certain shoot, a cone is considered with its axis of symmetry having vertical direction, with a fixed opening angle and with its apex exactly in the shoot tip under consideration. All other shoots or obstacles lying inside or intersecting this cone are considered to have potential influence on the amount of light which is received by the considered shoot, others have not (Figure 4).

Former investigations have yielded some evidence that there is a good relation between the leaf area located in a shadow-relevant cone and the potential photosynthetic productivity at its apex (Pfreundt, Sloboda, 1996), hence the notion of shadow-relevant cone seems to have some justification.

```
1  \const nmax 5,
2  \const ang 40,
3  \var f1 function 1 1,
4  \var f3 function 3 0,
5  \var le1 uniform 80 120,
6  \var le2 uniform 60 80,
7  \var su uniform 0.7 0.9,
8  \set V -0.2,
9  * #  P2 D1 [ f0.001 a(-4) tbd ] RU90 f500 RU-90
          [ f0.001 a(0) tbd ] RU-90 f1000 RU90
          [ f0.001 a(-8) tbd ] RU-90 f750 RU180 P6 F2500,
10 (k < 0)                          a(k) # a(k+1),
11 (f1(30)>ang && k >= 0) a(k) # P2 L(le1) seg(1.8, 0, k)
        [ @(su) RU70 D1 b tbd ] [ @(su) RU-70 D1 b tbd ] f0.001 a(k+1),
12 (f1(30)>ang)         b # P2 seg(0.8,0,-1) L(le2) RV RH90 f0.001 b,
13 (f3 >= 5)            seg(s,t,u) # seg(s,t+1,u),
14 (f3 < 5 && u < 0) seg(s,t,u) # %,
15 (f3 < 5 && u = 0) seg(s,t,u) # P15 D(1+s*t) F*0.5 RU100 F*0.5,
16 (t < nmax)   seg(s,t,u) ## N(100-(100/nmax)*t) Dl(1+s*t) F,
17 (t>= nmax)  seg(s,t,u) ## P15 N(0) Dl(1+s*t) F,
18 tbd ## [ P6 D0.7 L5 RU-90 f*0.5 RU180 F RU-104.5 F*2 RU-151 F*2 ]
```

Table 3: The sensitive growth grammar light2d.ssy

In the first, 2-dimensional example (Table 3), this concept is further simplified to the degree that the cone has to be completely free from other shoots to allow the bud to develop into a new shoot. This is performed with the help of the sensitive function $f1$, declared in line 3 and applied in the condition in lines 11 and 12, which returns the maximal opening angle of a vertically-oriented cone (or sector) free of elementary units. The argument of $f1$ specifies, like in the previous example, a length threshold for shoots to be considered not relevant. The opening angle is defined to be 40° in line 2.

Another sensitive function, $f3$, comes into action in lines 13, 14 and 15. It measures the surface of leaves supported by a branch. The call of this function could be replaced by a more explicit construction, using the sum operator of the GROGRA syntax (Kurth 1997), but we used $f3$ as a shortcut to keep things simple here. — The ageing and loss of leaves (lines 1, 16 and 17), together with the appearance of a *cut operator* (%) in line 14 when the leaf surface on a branch falls under a threshold of 5, causes a self-pruning of overshadowed branches. Furthermore, if a whole tree has lost its leaves, it will fall down, an event which is caused by a transformation of its basic stem segment in line 15.

The growth of 3 trees with different ages is encoded by this grammar (line 9). Branch growth is orthotropic here, which is enabled by the negative value of v (line 8). As there is some randomness in the lengths of growth units and in the positions of branching nodes (lines 5–7), the outcome of the simulation is not deterministic. Figure 5 shows a simulation run where the middle tree dies from overshadowing, but in other runs the middle tree can survive.

The three-dimensional version of the "shadow-relevant cone" function, in the following denoted by f_c, takes the opening angle of the cone as an argument. It returns the sum of the foliage surfaces located in the cone (making no difference between the foliage of the tree under consideration and that of neighbouring trees). The foliage surface is a numerical attribute which can be specified for each elementary unit in the growth rules (by the N command, see Kurth and Sloboda, 1999; Kurth, Früh, 1998).

An objection to this type of calculation could be that in Central-European latitudes the sun does never stand in the zenith, and that light emerging from parts of the sky outside the "shadow-relevant cone" can play an important role. As an alternative to function f_c that takes this objection into account, we implemented another sensitive function f_h, which returns an estimation of the "shadowed part" of the celestial hemisphere seen from the shoot under consideration. This is achieved with the help of a discretization of the hemispere into 46 parts, exhibiting resemblance to the shell of a turtle (Fig. 6).

The function f_h projects each elementary unit to the celestial hemisphere and calculates the number n of regions (i.e. a number between 0 and 46) which are touched by some elementary unit. The return value of f_h is $n/46$, i.e. a value between 0 and 1 indicating the degree of "sky closure". Elementary units with and without leaves are treated alike; foliage surfaces do not enter the calculation.

Both sensitive functions, the shadow-relevant cone function f_c and the hemisphere-coverage function f_h, were experimentally inserted into a non-sensitive growth grammar which was shown to reproduce the morphology of young spruce crowns in a quantitatively rather realistic manner (Kurth, Früh, 1998). The grammar, which consists of 33 rules, was shortly introduced in the first part of this article (Kurth, Sloboda, 1999) and is documented in full detail by Kurth and Früh (1998).

To keep the changements in the grammar limited, we assumed that the local sensitivity to light is only reflected by the *mortality* of meristems. In the original (nonsensitive) grammar, a dependence of the death probability of an apical meristem upon the length ℓ of the subtending growth unit was assumed:

$$p_\dagger(\ell) = \min(1;\ 1.06 - 0.0105\ell) \tag{1}$$

(see Kurth, Früh (1998) for the empirical justification of this relation) — a term which was used as the probability expression for a rule with left-hand side $\mathsf{bud}(\ell, \ldots)$ encoding the end of meristematic activity. Now we introduce a second rule, which is deterministic but has in its condition the sensitive function f_x ($x = c$ or h):

$$(f_x > \mathit{threshold})\ \ \mathsf{bud}(\ell, \ldots\ )\ \ \#\ \ ,$$

with an empty left-hand side. (The only further changement in the grammar compared to that in Kurth and Früh (1998) was the replacement of the empirical rules for secondary growth by a rule which ensures the preservation of cross-section area throughout all branching of order ≥ 1. This became necessary since otherwise some shoots with early-died apex would exhibit an unnatural secondary growth.) We experimented with several thresholds (for f_c and for f_h, in separate grammars), and each time it was necessary to fit the coefficients in relation (1) for the probability expression in the first, stochastic rule (which remained in the grammar!) to ensure that the resulting tree had overall dimensions (total shoot length, foliage and wood biomass) which were reasonably close to reality. The more frequently the sensitive rule (2) caused the death of a bud, the more the probability in (1) had to be reduced, particularly for long growth units. We can speak of a "tradeoff" between deterministic (sensitive) and random (non-sensitive) mortality, which is due to the self-shading of the tree.

The "crucial" test came when the grammar was modified such that two virtual trees were grown at a distance which enforced an early contact between the crowns. In the case of the cone function f_c, the effect of sensitivity on the appearance of the trees was small and hardly apparent (Fig. 7): In contrast to the simplified example light2d above, the tree crowns grow into each other like in the nonsensitive case. (Of course we could enforce a much stronger competition effect by manipulating the threshold in (2), but the price would be an unrealistically "pruned" tree with low biomass — due to self-shading — in the case of the solitary tree!)

However, in the case of the hemispherical-coverage function f_h, a marked effect of crown interaction can be seen (Fig. 8, 9).

5. Discussion and Conclusions

The last examples, showing sensitive growth grammar-based simulations for spruce, can be criticized for several reasons. First of all, the sample spruce trees from which the non-sensitive grammar rules for the "reference tree" were obtained were not really solitary trees, but grown under "weak" competition (Kurth, Früh, 1998; Kurth, Lanwert, 1995). This could have had a certain distortion as a consequence when we fitted the bud mortality of sensitive solitary trees against the non-sensitive tree under the assumption that only tree-internal self-shading and no shading from outside occurred. But more important is our simplification to make only mortality depend on the external factors. Recent empirical investigations gave instead rise to the supposition that it is shootlength which is to a great extent controlled by the amount of available light, whereas the length-mortality relation and other determinants of the branching structure are either influenced by other factors or show no significant sensitivity at all (Kurth, Anzola, 1997). Thus the sensitive grammar for spruce will have to be modified to a great extent; our example can only be seen as a first attempt.

A reason for the uncertainty connected with this type of model (and also for the neglect of botanical results in foregoing attempts of sensitive tree models) is that quantitative data on reactions at shoot level under field conditions are rare and expensive to obtain. In forest research, the monitoring of height, *dbh* and crown height is common, but bud fate or the number of internodes per annual shoot are not data which are routinely taken. And even for botanists, there are still gaps of knowledge concerning the reactions to external factors like e.g. light under field conditions: "It is clear that sun-shade acclimation of the photosynthetic apparatus, and of leaf structure and posture, occurs. But we have very limited information on whether branch production or branching angles may also show acclimation to sun-shade differences, or whether the changes that do occur are simple responses to changing growth rates" (Ford, 1992). "The structural growth of the crown system in terms of ... allocation of growth to the diameter and length of shoots is still poorly known" (Kellomäki, Strandman, 1995). This deficiency in knowledge is even more pronounced when external factors are concerned which are not so easily measurable, like the red : far red ratio of light which seems to have the function of a signal for the presence of non-shading neighbours, detectable by trees of several species (amongst them Douglas fir) and exerting influence on growth, probably mediated by the phytochrome enzymatic system (Ritchie, 1997). Further empirical investigations will certainly be necessary before such interactions can be modelled on a sound basis. This does also apply to the question of possible interferences between several growth-influencing factors (e.g. shadow + crowding). Can their effects on growth, senescence etc., when they were identified in specialized experiments, be simply added together, or do synergistic effects occur? This is not a merely academic question, since it is recognized by botanists that tree shape and function are the results of *multiple-goal optimization* processes during evolution, not just best-fit solutions to a single functional requirement (Farnsworth, Niklas, 1995). That means, the tree has to maintain a high efficiency of light capture, a low water loss, a secure level of mechanical stability, and a high chance to reach the reproductive phase and to disperse fruit — all simultaneously. Hence it is likely that environmental influences affecting the tree with respect to these requirements can have some combined effects. With a tool like GROGRA, it is at least possible to study several factors in the same simulation framework, even in the same grammar. However, for a first analysis it is necessary to investigate the different factors exerting influence on tree morphology one by one. Due to the various possible interactions of effects, and in view of the great heterogeneity of forest stands, it will probably never be possible to predict the architectural development and growth of a tree in a completely deterministic manner — i.e. a rest of unexplained variance will remain, and a stochastic component will therefore be indispensable in virtual tree models, even if multiple-factor sensitivity is included (Tomlinson, 1982).

However, it is hoped that the usage of such sensitive virtual-plant models as they are provided by the software systems AMAP (Reffye et al., 1995), *cpfg* (Prusinkiewicz et al., 1997), GROGRA (Kurth 1994, 1998) and some others (List et al., 1994; Breckling, 1996; Perttunen et al., 1996) will lead to considerably improved predictions of the growth and architectural response of the single tree when it is subject to forestry operations. This simulation technique will also apply to small parts of stands (groups of trees), and it can be extended to whole stands by means of typification and replication as it was indicated in the first part of this article (Kurth, Sloboda, 1999). In agronomy, virtual-plant based techniques are already used in fields like plant breeding, management of pathogens, analysis of remote-sensing data, and in research concerning developmental biology and genetics (Room et al., 1996). Since human perception is especially efficient in detecting patterns in complex information when it is presented in *visual* form, the visual aspect of such models will be of special importance, e.g. for diagnostic purposes, for planning and education in forest management. However, it should be emphasized that a virtual tree model is much more than just a nice, coloured image (Room et al., 1996): it contains a lot of developmental information about the tree and its reactions, and it can include many non-visual aspects, like mechanical resistance of wood, hydraulic conductivity of branches, or patterns of photosynthetic efficiency, if appropriate process-based submodels are linked (cf. e.g. Lanwert et al., 1998).

We conclude that virtual plant models with sensitive components provide an unprecedented tool to combine the knowledge of morphologists, and even the intuitive knowledge and experience of foresters (e.g. concerning reactions of trees to pruning or to changements in stand structure), with exact mathematical algorithms and with process-based approaches from physiology and ecosystem research. The authors hope it has been demonstrated that the mathematical basis of such models is not more difficult to understand than elementary biostatistics or applied calculus.

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Figure captions

Fig. 1: Structure generation by a sensitive, two-phase growth grammar.

Fig. 2: Plant with epitonic growth habit, produced by GROGRA from the sensitive grammar epiton.ssy (see Table 1).

Fig. 3: Two trees with density-dependent shoot growth, produced by GROGRA from the sensitive growth grammar densi2d.ssy (see Table 2) after 15 steps.

Fig. 4: The shadow-relevant cone of a shoot.

Fig. 5: Competition for light in a simple 2D tree stand, consisting of 3 uneven-aged trees, produced by GROGRA from the sensitive growth grammar light2d.ssy (see Table 3). The steps 12, 25 and 31 are shown.

Fig. 6: Subdivision of the celestial hemisphere into 46 regions, each of them being represented by a direction vector towards its midpoint and indexed by an integer from 0 to 45 (taken from Blaise, 1991, according to den Dulk, 1989).

Fig. 7: Simulated spruce trees after 10 steps (each corresponding to a year), viewed from above, generated by GROGRA. A sensitive grammar with the "shadow-relevant cone" function f_c affecting bud mortality was used (threshold of foliage surface in cone $= 0.2\text{m}^2$, cone opening angle $= 30°$). Left: Solitary tree, right: left one of two close neighbours (distance between the stems = 40 cm). The competition effect (asymmetry of crown on the right) is rather weak and hardly visible.

Fig. 8: Simulated spruce trees after 10 steps, viewed from above (generated by GROGRA). A sensitive grammar with the "hemisphere-coverage" function f_h affecting bud mortality was used (threshold of covered sky = 0.7). Left: Solitary tree, right: left one of two close neighbours (distance between the stems = 40 cm).

Fig. 9: The same interacting GROGRA-generated trees as in Fig. 8. Left side: the two neighbouring spruce trees grown with the sensitive growth grammar using f_h, seen from the side; right: the same view, but the right of both trees rendered invisible to show crown asymmetry caused by competition for light.