CHAPTER 21

A GRAMMAR-BASED MODEL OF BARLEY INCLUDING VIRTUAL BREEDING, GENETIC CONTROL AND A HORMONAL METABOLIC NETWORK

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Abstract. The incorporation of some genetic and physiological processes in a developmental model of *Hordeum vulgare* L. (barley) is presented. The model exhibits different hierarchical scales and has been conceived as a Relational Growth Grammar (RGG). RGG is a new formalism that has been developed as an extension of L-Systems and implemented using a new modelling language, eXtended Lsystems (XL). Models written in XL can be executed using the interactive, Java-based modelling platform GroIMP, which has been developed for this purpose.

The barley model proper is a set of morphogenetic rules. These are combined with a set of rules representing a metabolic network simulating some key steps of the biosynthesis of gibberellic acid (GA_1). The transport of GA_1 and GA_{19} (a metabolic precursor of GA_1) along the developing simulated structure has also been foreseen. In the model, the local concentrations of GA_1 in a module induce the elongation of internodes. In an extension of this base model, called "BarleyBreeder", individual virtual specimens are chosen interactively from a population, followed by the simulation of reproduction. Both genotype and phenotype of the population are visualized. So far, the model is restricted to a few Mendelian genes, one of which (the dwarfing gene *Zeocrithon*) is directly interacting with the biosynthesis of GA_1.

INTRODUCTION

Within the frame of research on plant structure ontogenesis, Lindenmayer systems have proven their suitability to capture essential aspects of growth and architecture. On the other hand, L-systems have still some disadvantages with respect to transparency and simplicity when complex, multilevel processes, including functional aspects, environmental influences and/or genetic control, have to be

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captured in a single model. The reasons for the shortcomings of L-Systems are explained and discussed at length in Kniemeyer et al. (this volume).

Cereal-crop FSPMs have recently come into the focus of crop plant research and agronomy, as one of their ultimate promises lies in the delivery of improved yield predictions, both in the context of cereal breeding and agricultural production. A good example for the potential effect of plant architecture on yield are the semi-dwarf short-strawed cereal varieties bred in the past 40 years that through the trait of short upright stems induced a lower incidence of layering (associated with fungal diseases) and, thus, improved yields. Architectural models have been devised for several cereal crops, such as maize (Fournier and Andrieu 1998), wheat (Fournier et al. 2003; Evers et al. 2005), rice (Watanabe et al. 2005), sorghum millet (Kaitaniemi et al. 2000) and barley (Buck-Sorlin 2002; Buck-Sorlin et al. 2005). In contrast to the other models, which are mainly ecophysiological and concerned with the faithful geometrical description of architectural development under controlled environmental conditions, the barley model was based on morphological observations and biometric measurements carried out on different barley genotypes and developmental mutants, thereby providing both an estimate of genetically determined phenotypic plasticity and a library of the potential growth and development of general phenotypes mapped to defined Mendelian (major) genes and Quantitative Trait Loci (QTL). Meanwhile the barley model has been upgraded to an ecophysiological model, too, exhibiting a response to temperature and day length.

In the following, we will briefly sketch the different ad-hoc approaches to the formal description of a genotype and genetic processes (crossing-over, mutation) and compare them with our implementation as a Relational Growth Grammar (RGG, Kniemeyer et al. this volume). We will then present two examples of barley models, an ecophysiological individual model and a population model called *BarleyBreeder*. The two models share several common modules, all specified as RGG: a set of morphogenetic rules and a regulatory network describing the biosynthesis and internal transport of bioactive gibberellic acid, its two precursors and its decay product. The *BarleyBreeder* model also has rules that specify genetic processes operating on a genotype attached to a virtual barley individual. Finally the potential application of the two models in plant physiology and breeding will be discussed briefly. More details concerning the models are found in Buck-Sorlin et al. (2005).

FORMAL DESCRIPTION OF GENETIC PROCESSES

Genetic information is stored in the genome, i.e. the entirety of the DNA sequence, which is a linear array of nucleotide bases (usually occurring as a double molecule of paired bases). Of these nucleotide bases, some stretches are genes, others are putatively linked to various functions (induction of DNA transcription, etc.) or have (so far) not been assigned any meaning (so called ‘junk’ or repetitive DNA). The genotype of an organism is the class to which that organism belongs as determined by the description of the actual physical material made up of DNA (genome) that was passed to the organism by its parents at the organism’s conception (Lewontin 2004). Correspondingly, the phenotype is another classification for the organism,

this time determined by the description of the physical characteristics of the organism, for example size and shape of its organs, its metabolic activities, etc. (Lewontin 2004). Partial genotypes and phenotypes represent practical restrictions to the entireties of genotype and phenotype: they are (usually rather small) subsets of all the genes and observable/measurable traits. In most higher organisms, the genetic information is redundant, i.e. there are usually two equal copies of each gene locus (in diploid organisms), distributed over two homologous chromosomes. However, due to mutations and genetic recombinations (see below), the actual DNA sequence of the two gene copies may change with time so that one ends up with two or more different alleles (i.e. correspondences) at the same gene locus. This is the case for almost all known genes.

An obvious and ad-hoc way of genotype formalization for use in a model has been proposed by Buck-Sorlin and Bachmann (2000): here, each allele is declared separately as a variable, where the name of the variable is derived from the locus name plus an index 1 or 2 to identify the copy number (or chromosome), and its value is an integer (0, 1, 2, …, *n*) that arbitrarily indicates the allele. Using this simple method, a number of basic genetic processes can already be modelled, such as dominance (of an allele over another allele of the same locus), additivity (adding up of allelic effects), epistasis (dominance of an allele over another allele of a different, usually downstream, locus). We will just give one example, that for dominance, written in C-preprocessor code (here, each #-statement is separated by a tab stop, in the original code it is a new line; for further details see Buck-Sorlin and Bachmann 2000):

```
#define G1 1      #define G2 0   #define G G1 + G2      #if G >= 1
#define P 40      #else          #define P 20           #endif
```

Here, `G1` and `G2` are the two alleles – dominant (1) and recessive (0) – of gene `G`. By summing up the allelic values in `G`, one obtains a simple means to check the four different possible allelic combinations: 0,0 (recessive phenotype) and 0,1; 1,0; 1,1 (dominant phenotype). A very similar approach has been used by de Visser et al. (2003) for their modelling of flower mutants of Arabidopsis.

The declarations stated above assume segregational independency of all declared genes (Mendel's law of independent assortment), which is, of course, only given if two genes are found on two different chromosomes. To introduce segregational bias, it is necessary to specify a genuine genotype. Consider the following rule specification that initiates, using the RGG formalism, a population using a 'founder' organism:

```
Axiom ==> Population Genome [Chromo[0 0 0 0 0] Chromo[0 1 2 1 1]];
```

Here a new `Population` is initiated with a (partial) `Genome` consisting of two homologous chromosomes `Chromo`, initiating linear arrays of the alleles of five genes. The recombinatorial distances have not been specified but this can be done separately using a function fed with the left positional index (0..*n*–1) of any successive gene pair (0,1; 1,2; ..., *n*–1,*n*), as shown at the example of the BarleyBreeder genotype (see Buck-Sorlin et al. 2005 and Section "*Reproduction, Genetics and Breeding*" for further details).

SIMPLE INCORPORATION OF GENETIC PROCESSES INTO MORPHOGENETIC RULES

With our relational approach, we can easily represent the situation that is characteristic for somatic cells in eukaryotes: The genome (which is a concrete token of the more abstract genotype, Lewontin 2004), is present in every part of the organism (cell, tissue, organ, etc., depending on the level of detail of the model). We just let a specific relation, let us say "`x -contains-> g`", depict the presence and accessibility of the genome string `g` in organ `x`. An RGG rule describing one developmental step at the macroscopic level, e.g., the formation of an internode from an apical meristem, can then have the following form (the parentheses (*…*) denote a context in the graph that must be present in order for the rule to be applied):

```
Meristem(t)  (*  -contains-> g : Genome *)
    ==> F(internodesize(t)/a + b*g[2], ...) ... Meristem(t + Δt).
```

Here, `F` symbolizes a new internode object (which is similar to the use of `F` in L-systems); its size depends on meristem age `t` (mediated by a function "internodesize") and on the current allele at locus 2 of genome `g`. Thus the genes, which are accessible via edges of the graph, affect the morphological features of the growing plant directly in this version of the model.

METABOLIC REGULATION OF MORPHOLOGICAL TRAITS

The RGG formalism can also account for the fact that gene effects are usually mediated by metabolites (transcription factors, hormones), the latter representable by graph nodes, too, their concentrations being numerical attributes. The access to these nodes within morphological rules is obtained by edges as in the previous example. In addition, the concentration nodes themselves may be subjected to the application of RGG rules: Their dynamics is given by regulatory networks, which perfectly fit into the RGG framework of graphs and graph transformation rules. One possibility is to represent the network itself as a graph, using specific "activator", "inhibitor", etc. edges between concentration nodes. The dynamics is then specified by a few quite general rules that describe the behaviour of activators, inhibitors, etc. according to, e.g., the equations of Michaelis-Menten (Bisswanger 2000). Transcriptional networks are completely based on activation and inhibition, and K_M-values can describe the affinity of the transcription factor to the DNA-binding site. As an output mRNA expression levels of the target genes can be included. A reimplementation in RGG of Kim's (2001) ABC-model of floral morphogenesis based on such a network can be found in Kniemeyer et al. (2004). Another possibility is to specify one reaction rule for every single reaction in the network. Whatever possibility is chosen, the effect is a simulation of the network in discrete time steps, and the resulting metabolite levels in turn can control morphogenesis within one and the same RGG model. Traditional L-systems lack this feature due to the plain string nature of their data and dynamics.

The GA metabolism presently used in our model is a very simplified version of the current state of knowledge of the biosynthetic pathway (cf. Sachs 1965; Graebe

1987; Hedden and Kamiya 1997) and, thus, our model is to be understood as a prototype. In particular, the function simulating the transport of the GA molecules is rudimentary and only considers fixed transport rates from one macroscopic organ to the next (internode → internode, leaf → internode). Aspects of receptor-based active transport (Ueguchi-Tanaka et al. 2005) in the signal transduction cascade have so far not been considered; however, an extended version of the model is in preparation. A detailed description of the metabolism submodel can be found in Buck-Sorlin et al. (2005): briefly, the simplified version consists of the three metabolites GA_1 (bioactive), GA_{19} and GA_{20} (metabolic precursors), GA_{19} being produced in the apical meristem and in the leaf bases. The pathway involves the enzymatically catalysed transformation of GA_{19} via GA_{20} to GA_1, with GA_1 competing with GA_{19} for the binding site on GA_{19} oxidase (competitive inhibition). It goes without saying that such a simplified model with parameters from the literature and databases does not replace a biosynthesis network properly parameterized for barley.

To implement this metabolism in RGG/XL, we have written a rule for each reaction in the network, e.g., to specify the production of GA_{20} (in competition with GA_1):

```
Organ [s:GA19] [p:GA20] [f:GA1] ::>
       competitiveInhibition(s, p, f, Vmax, KM, KI);
```

which translates like this: for every matching instance of the left-hand side of the rule operator `::>` , namely every set of concentration values `s`, `p`, `f` (substrate, product, inhibitor) of metabolites of type GA_{19}, GA_{20}, GA_1, respectively, within the same organ, execute the right-hand side, namely perform the numerics of a competitive inhibition, parameterized by V_{max}, K_M, K_I. This is an example of a so-called execution rule, which does not change any structure but simply modifies parameters of existing elements. Here, concentrations are updated by invoking the method `competitiveInhibition`. This function (described in Buck-Sorlin et al. 2005) can thus be reused in other RGG models using regulatory networks. Two further, similar execution rules provide the conversion of GA_{19} to GA_{20} as well as GA_1 catabolism, using simple Michaelis-Menten reactions.

We have also considered the transport of metabolites. This is done using a single parameter-updating rule. In each time step, a fixed amount of a substance is transported from each organ to its predecessor, which is the next organ below. The transport rate is equal to the concentration, multiplied by a constant C. This rather ad-hoc transport mechanism will be replaced by a more realistic diffusion-based mechanism in the future.

Ultimately GA_1 influences internode elongation. This is again modelled with a single rule:

```
i:Internode [s:GA1]  ::>  i.length :+= L * s.concentration * ΔT;
```

Here, the length of each internode `i` bearing a GA_1 node `s` is increased by an amount proportional to the metabolite concentration of `s`. (In our model, `Internode` is a subclass of `Organ`.) It is part of a set of morphological rules based on earlier work (Buck-Sorlin 2002). We thus create structure using a traditional L-system style,

while the parameters of simulated structures are then modified by the effects of a metabolic network within the frame of the internode elongation rule shown above.

The distribution of final internode lengths in barley is quite characteristic: whereas lower internodes hardly elongate at all, final internode lengths rapidly increase with higher rank, with the peduncle (uppermost internode) usually being longest. This length distribution is probably directly caused by local concentrations of GA_1: by running the GA biosynthesis network and additionally implementing two simplified modes of transport (basipetal for GA_{19}, acropetal for GA_1), we succeeded in qualitatively reproducing the distribution. Figure 1 shows the output of two model runs: in the wild type, before the onset of internode elongation, GA_{19} is produced and, thus, locally accumulating, whereas GA_1 is not yet available in high concentrations (Figure 1 a,c). At a late stage of internode elongation, concentrations of both GA_{19} and GA_1 are highest in the peduncle and rapidly declining towards the shoot base. Contrary to this, in the dwarf mutant Zeocrithon (Figure 1b,d; see also the next section), no or little GA_{19} is being produced and, thus, no appreciable concentration gradient is building up, thus leading to stunted internodes.

REPRODUCTION, GENETICS AND BREEDING

The 'virtual breeding' mechanism that is used in the actual *BarleyBreeder* model, is based on Dawkins' (1986) and our own (Kniemeyer et al. 2003) implementation of 'biomorphs'. The rules of the original XL-biomorph model were adapted to barley (Buck-Sorlin et al. 2005). Further details about the rules specifying morphology, biometry and phenology can be found in Buck-Sorlin and Bachmann (2000) and Buck-Sorlin (2002). Each of the two copies of the virtual genome used in the model currently consists of eight Mendelian genes determining various morphological traits (Buck-Sorlin et al. 2005).

Normally, a gene's action takes place at the level of a single rule (Buck-Sorlin and Bachmann 2000). A typical declaration is thus, e.g., `int Lks2 = g[0][1] + g[1][1];` or `int awnlength = (Lks2 >= 1) ? 140 : 70;`. Here the variable representing the gene *Lks2* is declared and immediately initiated with the sum of the corresponding allele values in the two integer arrays representing the two chromosomes (`g[0]` and `g[1]`, the possible single allele values being 0 (recessive) and 1 (dominant)). Using this sum, the dominant (long awns) and recessive (short awns) case are distinguished (see "Formal description of genetic processes"). Similar constructs have been used for the ear genes *vrs1*, *Kap* (a dominant mutant epistatically interacting with *Lks2*), *Blp* and *glo-b* as well as for *cul2* (control of tillering). The dwarfing gene, *Zeo*, however, is a pleiotropic gene, and it imposes a direct effect on the biosynthesis of gibberellic acid, viz., by inhibiting the production of GA_{19}. This inhibition effect is modelled thus:

```
c:Meristem [ga:GA19] –contains-> g:Genome ::>
     ga.concentration :+= ga19Prod(time, g[0][3] + g[1][3]) * ΔT;
```

GA_{19} production in meristems depends on the genome, more specifically on the *Zeo* gene, the position of which is at index 3 in the genome array (first index is 0), and on time. `ga19Prod` is a parameterized function defined in the model: it reduces the production of GA_{19} if a single copy of the mutant, dominant *Zeo* allele is present in the genome. *Zeo* thus directly affects the regulatory network by its determining the local values of GA_{19} in meristems (and young leaves, which is modelled analogously, see also Figure 1 b,d).

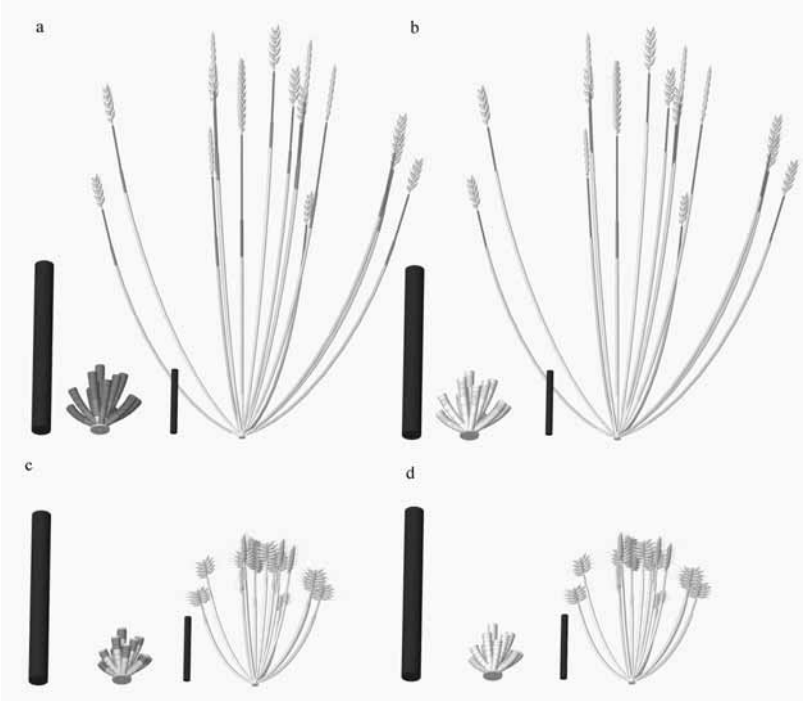

Figure 1. *Two stages (50, 100 steps) of internode elongation as a function of local GA_1 concentrations, in wild type (a, b) and Zeocrithon dwarf (c, d) plants. Concentrations of GA_{19} (a, c) and GA_1 (b, d) are represented as a colour gradient, from low (light grey) to high (dark grey) concentrations. Scale bar = 10 cm. Leaves have been omitted in simulation*

The model is invoked using the modelling platform GroIMP (Kniemeyer et al. this volume; see also http://www.grogra.de). A small population of different virtual barleys is drawn on the output screen, representing the visible phenotypes of different diploid genomes. Initial variability is due to a ‘mutate’ rule, which modifies the original genome specified in another RGG rule. User interaction

consists in the selection of one or two phenotypes by clicking on a box below a virtual barley individual (the box representing the genome, containing the current allelic settings of the seven genes). The next generation of virtual barleys is then simulated and a mutation of the allelic values of the genomes according to a given mutation probability in all cases. Some developmental mutants created with this model are shown in Figure 2.

DISCUSSION

The model presented here is able to produce realistically-looking 3-dimensional above-ground plant architectures, including those of some well-known barley mutants. However, it is not parameterized with measured values of hormone reaction kinetics (as these data are difficult to measure and are mostly unavailable for barley), and further factors influencing morphogenesis are still completely missing. Thus, in the current state of work our model has to be regarded as a prototype demonstrating the integrative potential of the Relational Growth Grammar formalism with its capability to describe metabolic, genetic and morphological structures in one and the same framework. In order to be considered a complete crop model exhibiting predictive properties it would need considerable enlargement, especially regarding ecophysiological aspects. We are currently working on the integration of the leaf-based photosynthesis model LEAFC3 (Nikolov et al. 1995; Müller et al. 2005) into our barley model.

We have incorporated in our model the action of the hormone GA on internode elongation to test the capacity of RGG/XL to represent network topologies. Other recent papers have dealt with the modelling of the effect of auxin on various morphogenetic processes (e.g. Rolland-Lagan et al. 2003; using L-systems; see also Niklas 2003). We are fully aware that our model is a crude simplification and that for a physiologically reflected view on the process of stem formation, one would have to consider all relevant hormones (auxins, GAs, cytokinins, abscisic acid, ethylene) in one model. Apart from the very difficult validation of such a big model, relatively little is known about the downstream targets of bioactive GA_1 and its effect on stem elongation (Peter Hedden, pers. comm.). The signal transduction pathway for bioactive GA has been reviewed recently by Fleet and Sun (2005): according to these authors, GA-signalling works as a de-repressible system that is moderated by DELLA-domain proteins, which are transcriptional regulators that repress GA responses. The extension of the current barley model to implement GA signal transduction will be the next logical step for us.

The model presented here could in the future be used as a ‘breeder’s tool’ using recombination distances of an arbitrary set of marker genes and QTL, thereby allowing ideotype breeding. The model would then ideally compute the ‘breeding path(s)’ to be gone and the number of steps required to achieve this goal, as well as potential difficulties and bottlenecks (i.e. proximity of target genes to undesired genes).

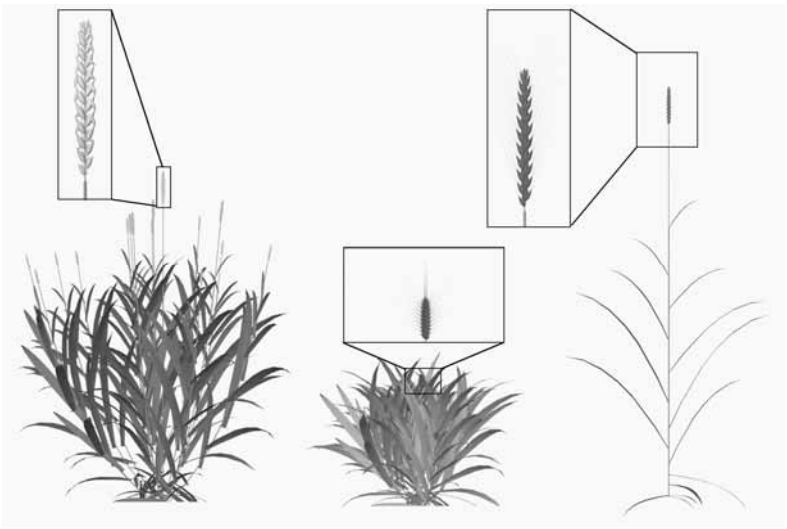

Figure 2. *Rendered view of several developmental mutants produced with the BarleyBreeder model. Left: Hooded, two-rowed. Middle: Zeocrithon dwarf, six-rowed. Right: Uniculm, six-rowed. Middle and right: Black lemma and pericarp (Blp). Left and right: eceriferum-ze (cer-ze, waxless leaves)*

In this chapter, we have tried to show that our new formalism is principally and practically suitable to reconstruct the morphology of a plant by simulating its morphogenesis. This can be done easily using sets of rules, where a set of rules may act at a given hierarchical scale but have effects at a different (higher or lower) scale. Plant morphologists and developmental geneticists alike are interested in achieving a comprehensive view on the body plan of a plant, and RGG/XL could be a potential research tool in this context.

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REFERENCES

Bisswanger, H., 2000. *Enzymkinetik: Theorie und Methoden.* 3rd edn. Wiley-VCH, Weinheim.

Buck-Sorlin, G.H., 2002. L-System model of the vegetative growth of winter barley (*Hordeum vulgare* L.). *In:* Polani, D., Kim, J. and Martinetz, T. eds. *Fifth German workshop on artificial life: abstracting and synthesizing the principles of living systems.* AKA Akademische Verlagsgesellschaft, Berlin, 53-64. [http://taxon.ipk-gatersleben.de/homepage/Bucksorlin-GWAL5.pdf]

Buck-Sorlin, G.H. and Bachmann, K., 2000. Simulating the morphology of barley spike phenotypes using genotype information. *Agronomie*, 20, 691-702.

Buck-Sorlin, G.H., Kniemeyer, O. and Kurth, W., 2005. Barley morphology, genetics and hormonal regulation of internode elongation modelled by a relational growth grammar. *New Phytologist*, 166 (3), 859-867.

Dawkins, R., 1986. *The blind watchmaker*. Longman, London.

De Visser, P.H.B., Marcelis, L.F.M., Van der Heijden, G., et al., 2003. 3D digitization and modeling of flower mutants of *Arabidopsis thaliana*. *In:* Hu, B.G. and Jaeger, M. eds. *2003 International Symposium on plant growth modeling, simulation, visualization and their applications*. Tsinghua University Press, Beijing, 218-226.

Evers, J.B., Vos, J., Fournier, C., et al., 2005. Towards a generic architectural model of tillering in Gramineae, as exemplified by spring wheat (*Triticum aestivum*). *New Phytologist*, 166 (3), 801-812.

Fleet, C.M. and Sun, T.P., 2005. A DELLAcate balance: the role of gibberellin in plant morphogenesis. *Current Opinion in Plant Biology*, 8 (1), 77-85.

Fournier, C, Andrieu, B., S., Ljutovac, et al., 2003. ADEL-Wheat: a 3D architectural model of wheat development plant growth modeling and applications. *In:* Hu, B.G. and Jaeger, M. eds. *Plant growth modeling and applications: proceedings-PMA03: 2003 international symposium on plant growth modeling, simulation, visualization and their applications, Beijing, China, October 13-16 2003.* Tsinghua University Press, Beijing, 54-66.

Fournier, C. and Andrieu, B., 1998. A 3D architectural and process-based model of maize development. *Annals of Botany*, 81 (2), 233-250.

Graebe, J.E., 1987. Gibberellin biosynthesis and control. *Annual Review of Plant Physiology*, 38, 419-465.

Hedden, P. and Kamiya, Y., 1997. Gibberellin biosynthesis: enzymes, genes and their regulation. *Annual Review of Plant Physiology and Plant Molecular Biology*, 48, 431-460.

Kaitaniemi, P., Hanan, J.S. and Room, P.M., 2000. Virtual sorghum: visualisation of partitioning and morphogenesis. *Computers and Electronics in Agriculture*, 28 (3), 195-205.

Kim, J., 2001. A generic formalism for modelling regulatory networks in morphogenesis. *In: Advances in artificial life: proceedings of the 6th European Conference, ECAL 2001, Prague, Czech Republic, September 10-14, 2001*. Springer, Berlin, 242-251. Lecture Notes in Artificial Intelligence no. 2159.

Kniemeyer, O., Buck-Sorlin, G.H. and Kurth, W., 2003. Representation of genotype and phenotype in a coherent framework based on extended L-Systems. *In: Advances in artificial life: 7th European Conference, ECAL 2003 Dortmund, Germany, September 14-17, 2003: proceedings*. Springer, Berlin, 625-634. Lecture Notes in Artificial Intelligence no. 2801.

Kniemeyer, O., Buck-Sorlin, G.H. and Kurth, W., 2004. A graph grammar approach to Artificial Life. *Artificial Life*, 10 (4), 413-431.

Lewontin, R., 2004. The genotype/phenotype distinction. *In:* Zalta, E.N. ed. *The Stanford encyclopedia of philosophy*. [http://plato.stanford.edu/archives/spr2004/entries/genotype-phenotype]

Müller, J., Wernecke, P. and Diepenbrock, W., 2005. LEAFC3-N: a nitrogen-sensitive extension of the CO_2 and H_2O gas exchange model LEAFC3 parameterised and tested for winter wheat (*Triticum aestivum* L.). *Ecological Modelling*, 183 (2/3), 183-210.

Niklas, K.J., 2003. The *Bio*-Logic and machinery of plant morphogenesis. *American Journal of Botany*, 90 (4), 515-525.

Nikolov, N.T., Massman, W.J. and Schoettle, A.W., 1995. Coupling biochemical and biophysical processes at the leaf level: an equilibrium photosynthesis model for leaves of C 3 plants. *Ecological Modelling*, 80 (2), 205-235.

Rolland-Lagan, A.G., Bangham, J.A. and Coen, E., 2003. Growth dynamics underlying petal shape and asymmetry. *Nature*, 422 (6928), 161-163.

Sachs, R.M., 1965. Stem elongation. *Annual Review of Plant Physiology*, 16, 73-97.

Ueguchi-Tanaka, M., Ashikari, M., Nakajima, M., et al., 2005. GIBBERELLIN INSENSITIVE DWARF1 encodes a soluble receptor for gibberellin. *Nature*, 437, 693-698.

Watanabe, T., Hanan, J.S., Room, P.M., et al., 2005. Rice morphogenesis and plant architecture: measurement, specification and the reconstruction of structural development by 3D architectural modelling. *Annals of Botany*, 95 (7), 1131-1143.