Figure 12: A tree model with branches competing for access to light, shown without the leaves

Figure 13: A climbing plant growing on the tree from the previous figure

is above a threshold N_{min}. If these conditions are not satisfied, production p_{11} removes (sheds) the branch from the tree using the cut symbol %.

Simulations. The competition for light between tree branches is manifested by two phenomena: reduced branching or dormancy of apices in unfavorable local light conditions, and shedding of branches which do not receive enough light to contribute to the whole tree. Both phenomena limit the extent of branching, thus controlling the density of the crown. This property of the model is supported by the simulation results shown in Figure 11. If the growth was unlimited (production p_6 was always chosen over p_7 and p_8), the number of terminal branch segments would double every year. Due to the competition for light, however, the number of terminal segments observed in an actual simulation increases more slowly. For related statistics using a different tree architecture see [52].

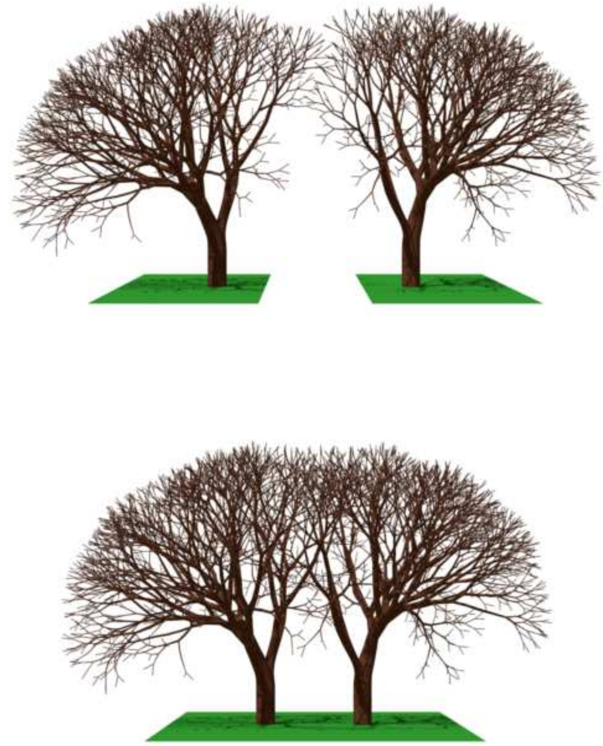

Figure 14: A model of deciduous trees competing for light. The trees are shown in the position of growth (top) and moved apart (bottom) to reveal the adaptation of crown geometry to the presence of the neighbor tree.

A tree image synthesized using an extension of the presented model is shown in Figure 12. The key additional feature is a gradual reduction of the branching angle of a young branch whose sister branch has been shed. As the result, the remaining branch assumes the role of the leading shoot, following the general growth direction of its supporting segment. Branch segments are represented as texture-mapped generalized cylinders, smoothly connected at the branching points (*cf.* [6]). The bark texture was created using a paint program.

As an illustration of the flexibility of the modeling framework presented in this paper, Figure 13 shows the effect of seeding a hypothetical climbing plant near the same tree. The plant follows the surface of the tree trunk and branches, and avoids excessively dense

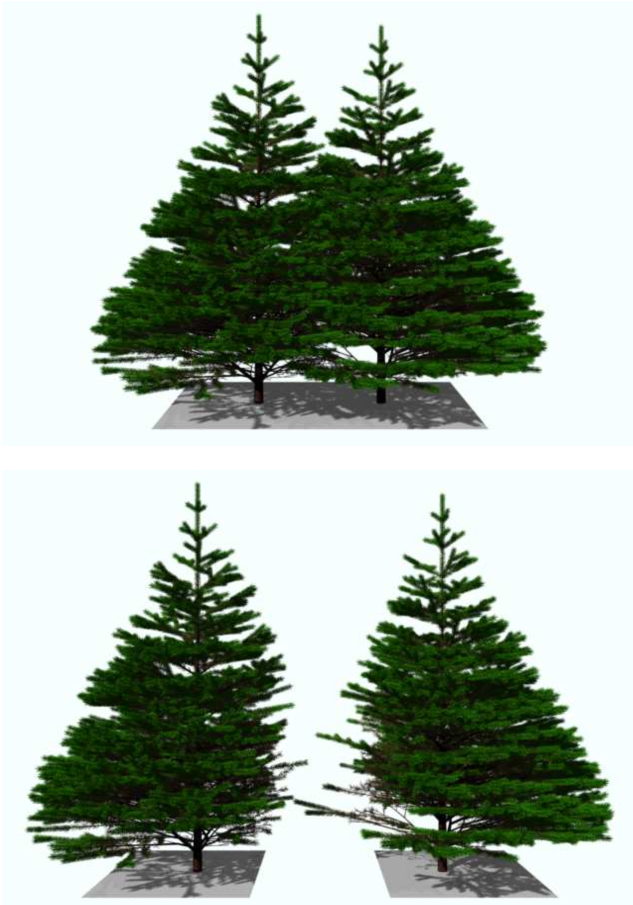

Figure 15: A model of coniferous trees competing for light. The trees are shown in the position of growth (top) and moved apart (bottom).

colonization of any particular area. Thus, the model integrates several environmentally-controlled phenomena: the competition of tree branches for light, the following of surfaces by a climbing plant, and the prevention of crowding as discussed in Section 6. Leaves were modeled using cubic patches (*cf.* [46]).

In the simulations shown in Figure 14 two trees described by the same set of rules (younger specimens of the tree from Figure 12) compete for light from the sky hemisphere. Moving the trees apart after they have grown reveals the adaptation of their crowns to the presence of the neighbor tree. This simulation illustrates both the necessity and the possibility of incorporating the adaptive behavior into tree models used for landscape design purposes.

The same phenomenon applies to coniferous trees, as illustrated in Figure 15. The tree model is similar to the original model by Takenaka [52] and can be viewed as consisting of approximately horizontal tiers (as discussed in Section 5) produced in sequence by the apex of the tree stem. The lower tiers are created first and therefore potentially can spread more widely then the younger tiers higher up (the *phase effect* [46]). This pattern of development is affected by the presence of the neighboring tree: the competition for light prevents the crowns from growing into each other.

The trees in Figure 15 retain branches that do not receive enough light. In contrast, the trees in the stand presented in Figure 16 shed

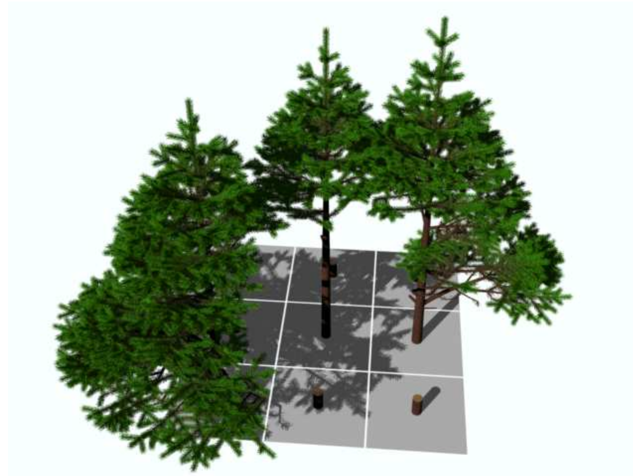

Figure 16: Relationship between tree form and its position in a stand.

branches that do not contribute photosynthates to the entire tree, using the same mechanism as described for the deciduous trees. The resulting simulation reveals essential differences between the shape of the tree crown in the middle of a stand, at the edge, or at the corner. In particular, the tree in the middle retains only the upper part of its crown. In lumber industry, the loss of lower branches is usually a desirable phenomenon, as it reduces knots in the wood and the amount of cleaning that trees require before transport. Simulations may assist in choosing an optimal distance for planting trees, where self-pruning is maximized, yet there is sufficient space between trees too allow for unimpeded growth of trunks in height and diameter.

9 CONCLUSIONS

In this paper, we introduced a framework for the modeling and visualization of plants interacting with their environment. The essential elements of this framework are:

- a system design, in which the plant and the environment are treated as two separate processes, communicating using a standard interface, and
- the language of open L-systems, used to specify plant models that can exchange information with the environment.

We demonstrated the operation of this framework by implementing models that capture collisions between branches, the propagation of clonal plants, the development of roots in soil, and the development of tree crowns competing for light. We found that the proposed framework makes it possible to easily create and modify models spanning a wide range of plant structures and environmental processes. Simulations of the presented phenomena were fast enough to allow interactive experimentation with the models (Table 1).

There are many research topics that may be addressed using the simulation and visualization capabilities of the proposed framework. They include, for instance:

- Fundamental analysis of the role of different forms of information flow in plant morphogenesis (in particular, the relationship

Fig.	Number of		Derivation		Time[a]	
	branch segments	leaf clusters	steps	yrs	sim.	render.
5	138	140	5	5	1 s	1 s
7	786	229	182	NA	50 s	2 s
9	4194	34[b]	186	NA	67 s	3 s
10	37228	448[b]	301	NA	15 min	70 s
12	22462	19195	744	24	22 min	13 s[c]
15	13502	3448	194	15	4 min	8 s[d]

[a] Simulation and rendering using OpenGL on a 200MHz/64MB Indigo^2 Extreme
[b] active apices
[c] without generalized cylinders and texture mapping
[d] branching structure without needles

Table 1: Numbers of primitives and simulation/rendering times for generating and visualizing selected models

between endogenous and exogenous flow). This is a continuation of the research pioneered by Bell [4] and Honda *et al.* [7, 33].

- Development of a comprehensive plant model describing the cycling of nutrients from the soil through the roots and branches to the leaves, then back to the soil in the form of substances released by fallen leaves.
- Development of models of specific plants for research, crop and forest management, and for landscape design purposes. The models may include environmental phenomena not discussed in this paper, such as the global distribution of radiative energy in the tree crowns, which affects the amount of light reaching the leaves and the local temperature of plant organs.

The presented framework itself is also open to further research. To begin, the precise functional specification of the environment, implied by the design of the modeling framework, is suitable for a formal analysis of algorithms that capture various environmental processes. This analysis may highlight tradeoffs between time, memory, and communication complexity, and lead to programs matching the needs of the model to available system resources in an optimal manner.

A deeper understanding of the spectrum of processes taking place in the environment may lead to the design of a mini-language for environment specification. Analogous to the language of L-systems for plant specification, this mini-language would simplify the modeling of various environments, relieving the modeler from the burden of low-level programming in a general-purpose language. Fleischer and Barr's work on the specification of environments supporting collisions and reaction-diffusion processes [20] is an inspiring step in this direction.

Complexity issues are not limited to the environment, but also arise in plant models. They become particularly relevant as the scope of modeling increases from individual plants to groups of plants and, eventually, entire plant communities. This raises the problem of selecting the proper level of abstraction for designing plant models, including careful selection of physiological processes incorporated into the model and the spatial resolution of the resulting structures.

The complexity of the modeling task can be also addressed at the level of system design, by assigning various components of the model (individual plants and aspects of the environment) to different components of a distributed computing system. The communication structure should then be redesigned to accommodate information transfers between numerous processes within the system.

In summary, we believe that the proposed modeling methodology and its extensions will prove useful in many applications of plant modeling, from research in plant development and ecology to landscape design and realistic image synthesis.

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REFERENCES

[1] AGRAWAL, P. The cell programming language. *Artificial Life 2*, 1 (1995), 37–77.

[2] ARVO, J., AND KIRK, D. Modeling plants with environment-sensitive automata. In *Proceedings of Ausgraph'88* (1988), pp. 27 – 33.

[3] BELL, A. *Plant form: An illustrated guide to flowering plants.* Oxford University Press, Oxford, 1991.

[4] BELL, A. D. The simulation of branching patterns in modular organisms. *Philos. Trans. Royal Society London, Ser. B 313* (1986), 143–169.

[5] BELL, A. D., ROBERTS, D., AND SMITH, A. Branching patterns: the simulation of plant architecture. *Journal of Theoretical Biology 81* (1979), 351–375.

[6] BLOOMENTHAL, J. Modeling the Mighty Maple. Proceedings of SIGGRAPH '85 (San Francisco, California, July 22-26, 1985), in *Computer Graphics*, 19, 3 (July 1985), pages 305–311, ACM SIGGRAPH, New York, 1985.

[7] BORCHERT, R., AND HONDA, H. Control of development in the bifurcating branch system of *Tabebuia rosea*: A computer simulation. *Botanical Gazette 145*, 2 (1984), 184–195.

[8] BORCHERT, R., AND SLADE, N. Bifurcation ratios and the adaptive geometry of trees. *Botanical Gazette 142*, 3 (1981), 394–401.

[9] CHEN, S. G., CEULEMANS, R., AND IMPENS, I. A fractal based *Populus* canopy structure model for the calculation of light interception. *Forest Ecology and Management* (1993).

[10] CHIBA, N., OHKAWA, S., MURAOKA, K., AND MIURA, M. Visual simulation of botanical trees based on virtual heliotropism and dormancy break. *The Journal of Visualization and Computer Animation 5* (1994), 3–15.

[11] CHIBA, N., OHSHIDA, K., MURAOKA, K., MIURA, M., AND SAITO, N. A growth model having the abilities of growth-regulations for simulating visual nature of botanical trees. *Computers and Graphics 18*, 4 (1994), 469–479.

[12] CLAUSNITZER, V., AND HOPMANS, J. Simultaneous modeling of transient three-dimensional root growth and soil water flow. *Plant and Soil 164* (1994), 299–314.

[13] COHEN, D. Computer simulation of biological pattern generation processes. *Nature 216* (October 1967), 246–248.

[14] COHEN, M., AND WALLACE, J. *Radiosity and realistic image synthesis*. Academic Press Professional, Boston, 1993. With a chapter by P. Hanrahan and a foreword by D. Greenberg.

[15] DE REFFYE, P., HOULLIER, F., BLAISE, F., BARTHELEMY, D., DAUZAT, J., AND AUCLAIR, D. A model simulating above- and below-ground tree architecture with agroforestry applications. *Agroforestry Systems 30* (1995), 175–197.

[16] DIGGLE, A. J. ROOTMAP - a model in three-dimensional coordinates of the structure and growth of fibrous root systems. *Plant and Soil 105* (1988), 169–178.

[17] DONG, M. *Foraging through morphological response in clonal herbs*. PhD thesis, Univeristy of Utrecht, October 1994.

[18] FISHER, J. B. How predictive are computer simulations of tree architecture. *International Journal of Plant Sciences 153 (Suppl.)* (1992), 137–146.

[19] FISHER, J. B., AND HONDA, H. Computer simulation of branching pattern and geometry in *Terminalia* (Combretaceae), a tropical tree. *Botanical Gazette 138*, 4 (1977), 377–384.

[20] FLEISCHER, K. W., AND BARR, A. H. A simulation testbed for the study of multicellular development: The multiple mechanisms of morphogenesis. In *Artificial Life III*, C. G. Langton, Ed. Addison-Wesley, Redwood City, 1994, pp. 389–416.

[21] FORD, E. D., AVERY, A., AND FORD, R. Simulation of branch growth in the *Pinaceae*: Interactions of morphology, phenology, foliage productivity, and the requirement for structural support, on the export of carbon. *Journal of Theoretical Biology 146* (1990), 15–36.

[22] FORD, H. Investigating the ecological and evolutionary significance of plant growth form using stochastic simulation. *Annals of Botany 59* (1987), 487–494.

[23] FRIJTERS, D., AND LINDENMAYER, A. A model for the growth and flowering of *Aster novae-angliae* on the basis of table (1,0)L-systems. In *L Systems*, G. Rozenberg and A. Salomaa, Eds., Lecture Notes in Computer Science 15. Springer-Verlag, Berlin, 1974, pp. 24–52.

[24] GARDNER, W. R. Dynamic aspects of water availability to plants. *Soil Science 89*, 2 (1960), 63–73.

[25] GREENE, N. Voxel space automata: Modeling with stochastic growth processes in voxel space. Proceedings of SIGGRAPH '89 (Boston, Mass., July 31–August 4, 1989), in *Computer Graphics* 23, 4 (August 1989), pages 175–184, ACM SIGGRAPH, New York, 1989.

[26] GREENE, N. Detailing tree skeletons with voxel automata. SIGGRAPH '91 Course Notes on Photorealistic Volume Modeling and Rendering Techniques, 1991.

[27] GUZY, M. R. A morphological-mechanistic plant model formalized in an object-oriented parametric L-system. Manuscript, USDA-ARS Salinity Laboratory, Riverside, 1995.

[28] HANAN, J. Virtual plants — Integrating architectural and physiological plant models. In *Proceedings of ModSim 95* (Perth, 1995), P. Binning, H. Bridgman, and B. Williams, Eds., vol. 1, The Modelling and Simulation Society of Australia, pp. 44–50.

[29] HANAN, J. S. *Parametric L-systems and their application to the modelling and visualization of plants*. PhD thesis, University of Regina, June 1992.

[30] HART, J. W. *Plant tropisms and other growth movements*. Unwin Hyman, London, 1990.

[31] HERMAN, G. T., AND ROZENBERG, G. *Developmental systems and languages.* North-Holland, Amsterdam, 1975.

[32] HONDA, H. Description of the form of trees by the parameters of the tree-like body: Effects of the branching angle and the branch length on the shape of the tree-like body. *Journal of Theoretical Biology 31* (1971), 331–338.

[33] HONDA, H., TOMLINSON, P. B., AND FISHER, J. B. Computer simulation of branch interaction and regulation by unequal flow rates in botanical trees. *American Journal of Botany 68* (1981), 569–585.

[34] KAANDORP, J. *Fractal modelling: Growth and form in biology*. Springer-Verlag, Berlin, 1994.

[35] KANAMARU, N., CHIBA, N., TAKAHASHI, K., AND SAITO, N. CG simulation of natural shapes of botanical trees based on heliotropism. *The Transactions of the Institute of Electronics, Information, and Communication Engineers J75-D-II*, 1 (1992), 76–85. In Japanese.

[36] KURTH, W. *Growth grammar interpreter GROGRA 2.4: A software tool for the 3-dimensional interpretation of stochastic, sensitive growth grammars in the context of plant modeling. Introduction and reference manual*. Forschungszentrum Waldökosysteme der Universität Göttingen, Göttingen, 1994.

[37] LIDDELL, C. M., AND HANSEN, D. Visualizing complex biological interactions in the soil ecosystem. *The Journal of Visualization and Computer Animation 4* (1993), 3–12.

[38] LINDENMAYER, A. Mathematical models for cellular interaction in development, Parts I and II. *Journal of Theoretical Biology 18* (1968), 280–315.

[39] LINDENMAYER, A. Developmental systems without cellular interaction, their languages and grammars. *Journal of Theoretical Biology 30* (1971), 455–484.

[40] MACDONALD, N. *Trees and networks in biological models.* J. Wiley & Sons, New York, 1983.

[41] PRESS, W. H., TEUKOLSKY, S. A., VETTERLING, W. T., AND FLANNERY, B. P. *Numerical recipes in C: The art of scientific computing. Second edition*. Cambridge University Press, Cambridge, 1992.

[42] PRUSINKIEWICZ, P. Visual models of morphogenesis. *Artificial Life 1*, 1/2 (1994), 61–74.

[43] PRUSINKIEWICZ, P., HAMMEL, M., HANAN, J., AND MĚCH, R. Visual models of plant development. In *Handbook of formal languages*, G. Rozenberg and A. Salomaa, Eds. Springer-Verlag, Berlin, 1996. To appear.

[44] PRUSINKIEWICZ, P., AND HANAN, J. L-systems: From formalism to programming languages. In *Lindenmayer systems: Impacts on theoretical computer science, computer graphics, and developmental biology*, G. Rozenberg and A. Salomaa, Eds. Springer-Verlag, Berlin, 1992, pp. 193–211.

[45] PRUSINKIEWICZ, P., JAMES, M., AND MĚCH, R. Synthetic topiary. Proceedings of SIGGRAPH '94 (Orlando, Florida, July 24–29, 1994), pages 351–358, ACM SIGGRAPH, New York, 1994.

[46] PRUSINKIEWICZ, P., AND LINDENMAYER, A. *The algorithmic beauty of plants*. Springer-Verlag, New York, 1990. With J. S. Hanan, F. D. Fracchia, D. R. Fowler, M. J. M. de Boer, and L. Mercer.

[47] ROOM, P. M. 'Falling apart' as a lifestyle: the rhizome architecture and population growth of *Salvinia molesta*. *Journal of Ecology 71* (1983), 349–365.

[48] ROOM, P. M., MAILLETTE, L., AND HANAN, J. Module and metamer dynamics and virtual plants. *Advances in Ecological Research 25* (1994), 105–157.

[49] ROZENBERG, G. T0L systems and languages. *Information and Control 23* (1973), 357–381.

[50] SACHS, T., AND NOVOPLANSKY, A. Tree from: Architectural models do not suffice. *Israel Journal of Plant Sciences 43* (1995), 203–212.

[51] SIPPER, M. Studying artificial life using a simple, general cellular model. *Artificial Life 2*, 1 (1995), 1–35.

[52] TAKENAKA, A. A simulation model of tree architecture development based on growth response to local light environment. *Journal of Plant Research 107* (1994), 321–330.

[53] ULAM, S. On some mathematical properties connected with patterns of growth of figures. In *Proceedings of Symposia on Applied Mathematics* (1962), vol. 14, American Mathematical Society, pp. 215–224.

[54] WEBER, J., AND PENN, J. Creation and rendering of realistic trees. Proceedings of SIGGRAPH '95 (Los Angeles, California, August 6–11, 1995), pages 119–128, ACM SIGGRAPH, New York, 1995.

[55] WYVILL, G., MCPHEETERS, C., AND WYVILL, B. Data structure for soft objects. *The Visual Computer 2*, 4 (February 1986), 227–234.