Complexity in Corn Fields

Carlos Messina [*]
DuPont Agriculture and Nutrition

Arturo Chavoya [†]
Ecole Doctorale en Informatique et Télécommunications
Universite de Toulouse

August 2006

1 Introduction

Ecological intensification of cropping systems is fundamental to achieve food security under a scenario of rapid population growth and an increasingly unpredictable and changing climate. Agricultural researchers face the challenge to design large throughput, yet sustainable, agricultural systems. Current strategies seek to close the the gap between potential and actual yields by increasing the density of plant stands and the availability of resources [7]; however, this gap between rapidly closing. Under this scenario there is need to develop new approaches that accelerate plant breeders success in developing high yielding varieties. Seminal research by Cooper *et al.* [11] and Hammer *et al.* [14, 15] provide the foundations for a paradigm shift in genetic improvement of crops with prospects to accelerate the genetic gains in yield. Central to this approach is the quantification of gene-to-phenotype relations by means of mathematical models of crop growth and development, a suit of statistical methods, and an extension of Kaufmans' N:K model [11, 14, 15, 9, 10].

Current models simulate crop growth and development for plant canopies based on biophysical principles. In this sense, all plants are assumed identical, to have average behavior, and competition for resources is implicit and simulated through functional relations [21, 20, 17]. The mathematical representation of the biological processes used in these models proved adequate for several applications [18, 1, 25]. However, recent research in reproductive biology of corn [24, 39] and complex systems [16] suggest that this traditional approach may be limited to predict crop responses to resource capture and utilization in response to trait variation. Hübler showed emergent complex behavior in corn

---

[*] charlie.Messina@pioneer.com
[†] achavoya@hotmail.com

fields due to intraspecific competition for resources [16]. This thought-provoking hypothesis is based on principles of physics and dynamical systems. However, this study is based on weak biological principles and the predicted behavior in corn fields as proposed by Hübler [16] is not immediate. Plants have evolved a suit of mechanisms to deal with intra and inter-specific competition. Among those best known is a family of photoreceptors that can increase stem elongation and change leaf expansion and orientation upon detection of neighbor plants [3, 4, 36]. Furthermore, plant breeders had increased the tolerance to intraspecific competition and stress tolerance making the plants stands uniform [13].

Although phenotypes predicted by Hübler are unlikely, his results strongly suggest the need to develop alternative modeling approaches that can simulate emergent behavior, intraspecific plant variability and competition for resources on a population basis. To this end, we focused our work on developing and evaluating a toy-model for corn using a framework based on cellular automata. The biological basis of the model are simple yet realistic. This case study is about complex behavior appearing in yield determination processes such as barrenness and yields in response to levels of intraspecific competition.

2 Model Development

2.1 Agent-Based Corn Field Model

The cellular automata framework is a convenient methodology for modeling systems in which spatial structure and interaction among components can play a critical role in the system behavior. Traditionally, these models represent space as a set of discrete and homogeneous cells arranged in a grid, which behavior change as a function of its current state and the state of the neighbors. Models of this type were developed for a number of applications in many disciplines. But only recently this approach has been used to model systems in plant sciences [12, 19, 44, 23]. Previous work has either focused on studying ecosystem functioning and the emergence of spatial structure using simple dynamic models for each plant species [19], or in developing models for whole plants in the absence of plant competition [12, 44] and roots systems [23]. The model developed in this study implements a more complex physiology at whole plant level than in previous studies [12, 44] yet incorporates simple interactions among neighbors. Hübler have shown that adequate simulation of historical events is critical for understanding and predicting emergent patterns [16].

NetLogo is a programmable modeling environment based on StarLogo that can be used to simulate natural and social phenomena [43]. It works by giving instructions to independent agents all operating concurrently. It is well suited to study emergent properties in complex systems that result from the interaction of simple but often numerous entities. The version used in this work was NetLogo 3.1, which provides an interface that allows visualizing a virtual 3D environment.

An agent-based model of the corn field was devised in which agents com-

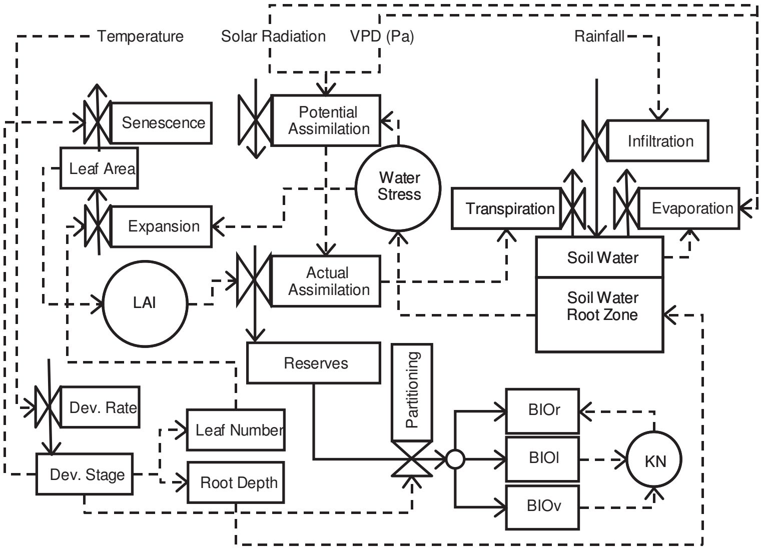

Figure 1: Agent-based model for a crop canopy: representation of the agent behavior

pete against each other for resources. The field itself is implemented as a 99 × 99 grid lattice, where each NetLogo unit corresponds to 5 cm. Each grid position is defined by its Cartesian coordinates with the origin at the center of the lattice and each time unit represents a day. Corn plants are implemented as independent agents all running the same growth algorithm. Starting with corn plants sowed in grooves at specific distances, the growth algorithm was applied allowing the plants to grow until all plants attained maturity. For ease of visualization, plants are shown in a 1:10 scale. In the current implementation, agents compete for light, by means of the Leaf Area Index (LAI). The variable LAI is calculated as the sum of leaf areas per plant (L) in one square meter. This implementation allows interactions among agents which are not restricted to immediate neighbors. The competitive ability function *f(L)* for each plant is defined as the ratio between L and LAI. Each agent respond to the environment and to other agents following a well known physiological relationships that govern plant growth and development. The intensity of competition is controlled by variations in availability of resources light and water, and by the spatial arrangement of the agents, which are allowed to vary between rows and within rows.

2.2 Agent Ecophysiological Model

A mechanistic model was used to simulate corn growth, development and yield for each agent [27, 26]. The model describes the carbon and water balance of a corn crop from emergence to maturity as a function of maximum temperature

(*TM*), minimum temperature (*Tm*), solar radiation (*S*), vapor pressure deficit and precipitation (Fig.1). Plant development in corn is mainly driven by temperature and it is described as a function of thermal units (*TU*). Daily thermal units were calculated as, $TU = 0.5 \times (\min(TM, 34) + Tm) - 8$. Leaf appearance is calculated as a function of *TU* and a phyllochron λ characteristic of the genotype ($\lambda = 0.00225$),

$$\frac{dN}{dt} = 2.5 \times \exp(\lambda TU)\lambda$$

$$N(0) = 2.5$$

The model simulates the phenological events 1) anthesis, assumed synchronous with the expansion of the last leaf (N_0), 2) the onset of rapid kernel growth, which usually starts around 100 *TU* after anthesis, and 3) maturity. Time to maturity depends on the time to anthesis and the characteristics of the genotype. Time to maturity is determined when 800 *TU* are accumulated after anthesis. Although there is genetic variation in N_0 for simplicity we assumed a constant value N_0=20.

Plant growth (*W*) is simulated as a function of *S*, that drives photosynthesis, *LAI*, the competitive ability of the plant *f(L)*, and the fraction of soil water available to the plant relative to potential store of water(θ),

$$\frac{dW}{dt} = \beta \times S \times 1 - \exp(-\kappa LAI) \times f(\theta) \times f(L)$$

$$f(\theta) = \frac{1}{1 + 9.0 \times \exp(-15.3 \times \theta)}$$

The parameter β is the efficiently of conversion of solar radiation into biomass including respiration losses and cost of synthesis of plant tissues.; large number of studies suggest an average value of 1.6 MJ m^{-2} [22]. The parameter κ describes the penetration of light through the canopy and accounts for genotypic variations in plant architecture and leaf anatomy. Although κ can vary with row spacing the current version of the model uses a constant value to 0.6 [27]. Daily water availability to the plant is simulated using a water balance as described by Muchow and Sinclair [26]. Potential soil store of water is calculated on a daily basis as a function of the depth of water extraction times the volumetric fraction of available soil water (0.13 $\mathrm{cm}^3\mathrm{cm}^3$). Daily progression of the water extraction front depends on root growth(ρ), which was assumed constant for a given plant. Plant leaf area expansion is simulated as minimum between the maximum leaf area, determined by the intrinsic characteristics of the genotype and the relative soil water content,

$$L = \sum_n A_0 \times f(N) \times g(\theta)$$

$$g(\theta) = \frac{1}{1 + 270 \times \exp(-32.3 \times \theta)}$$

and the biomass available for tissue growth,

$$L = 250 \times W$$

The parameter A_0 is the area of largest leaf and controls the shape of the leaf profile and the potential leaf area. Muchow *et al.* [27] provides a detailed description of *f(N)* and Tardieu [37] review the genetic basis of the effects of water and temperature on leaf expansion. Note that in contrast to the base model develop by Muchow *et al.* and Muchow and Sinclair [27, 26], in this model LAI is an $f(W)$.

Our implementation of the model simulates individual corn plants and expands the model functionality to simulate yield components kernel number and kernel mass. First, barrenness (absence of a corn ear) is simulated as a function of the integral of growth between stages N=12 and anthesis, and a critical threshold W_0 that represents the minimum biomass partitioning to dominant reproductive structures (e.g. tassel). Barrenness is a simply a binary function $x = 0$ for $W \leq W_0$ and $x = 1$ otherwise. This parameter was set to 30g based on empirical observations [6, 41, 40, 39]. Second, kernel numbers are simulated as a function of the integral of growth W between anthesis and the onset of rapid kernel growth as, $y = \max(0, \min(\phi, \alpha W x))$. Parameters ϕ and α are parameters characteristic of the genotype [41, 40, 2]. Third, kernel growth is simulated based on sink-source relationships. Accumulation of mass in reproductive organs can be limited by plant growth (e.g. drought stress, low solar radiation) during grain filling, or it can be limited by the number reproductive sinks determined at flowering (barrenness) or during early postflowering (kernel numbers). Kernel growth rates are relatively constant and kernel weight it determined by early termination of growth [5, 32]. This process is implemented by allowing early termination of grain filling whenever θ fall below 0.1 during the grain filling period.

3 Simulation Experiments

A series of simulations experiments were conducted to study the system behavior, to develop and intuition for the system performance under various degrees of stress and to test specific hypothesis. Simulation results could provide insights on strategies to increase genetic gains in corn and to need for the need of new modeling approaches for simulating corn growth and development.

3.1 General settings

Ensembles varying between 5 and 20 simulations were run for each experiment. The number of realizations were set depending on the stability of the results. All simulations started at emergence on day of year (DOY) 135 and emergence date was allowed to vary ± 5 d. Model inputs *TM*, *Tm*, *S* were generated using two out-of-phase sin functions that describe the annual cycle in temperature in solar radiation. Water input to the system was set at constant intervals (10 d) and the amount was varied to simulate low (50 mm) and high (25 mm) levels of abiotic stresses. Random variation was allowed in water inputs by adding a random amount sampled from a uniform distribution in the interval [-5,5]. Daily variations in *TM*, *Tm*, *S* were allowed for each agent to capture random variations within fields using the following equations,

$$\bar{T}(t) = 10 \times \ \sin(360 \times \frac{(240 + t)}{365}) + 12 + \epsilon$$

$$S(t) = 10 \times \ \sin(360 \times \frac{(270 + t)}{365}) + 15 + \epsilon$$

$$TM(t) = \bar{T}(t) + 7 + \epsilon$$

$$Tm(t) = \bar{T}(t) - 7 + \epsilon$$

To estimate $\bar{T}(t)$ and $S(t)$, ϵ was sampled from a uniform distribution in the interval [-2,2], otherwise ϵ was sampled from a uniform distribution in the interval [-1,1].

3.2 System response to throughput

In complex systems the key control parameter is the throughput [16]. One can vary the system throughput by increasing the flow through the system or by maintaining the flow constant (e.g. a liquid flowing through a pipe) and modifying one component of the system (e.g. pipe diameter). In this study we choose the later approach and we varied the spatial arrangement of plants in the field so that throughput increase with increasing plant stand density. In agricultural systems there is more capacity to modify the system and its management than the environment controlling the throughput. We generated a range of plant densities between 3.2 and 20 pl m^{-2} by varying intergroove spacing between 50 and 70 cm and interplant spacing between 5 and 40 cm every 5 cm in a factorial arrangement. Simulations were conducted under high and low abiotic stress conditions as describe above.

3.3 Sensitivity analysis

Previous research showed that faster root growth ρ increase resource capture and yields under drought stress conditions [34]. The same study suggested that reductions in A_0 did not increase seed mass under drought. This study neither considered intraspecific competition nor the effects of drought stress on yield components. These results could hold valid, even under intraspecific competition, if the increased resource capture decrease the system throughput. However, if either ρ or A_0 affect historical events and biomass distribution among plants the validity of these previous results is doubtful. The area of the largest leaf determine the profile and total plant leaf area. Therefore, increasing A_0 can increase the intensity and the onset of interplant plant competition for light, and historical events such as the patterns of water use. Increasing ρ can increase resource capture but also can modify the pattern of water use. Both A_0 and ρ can generate symmetry breaking in biomass, barrenness and yield.

Sensitivity analysis on model parameters A_0 and ρ were conducted for three plant densities. These were generated by varying setting interplant distance at 15, 25 and 50 cm for a fixed intergroove distance of 60cm. All simulations were conducted under high abiotic stress or drought conditions for A_0 550, 750, and 950, and ρ 23.5, 33.5, and 43.5.

3.4 System response to random microenvironment variation

Recent advances in reproductive biology of corn showed that plant-to-plant variability, and the establishment of hierarchies among plants is a major determinant of kernel set, and the cause of yield reduction in crops grown at high plant populations [24]. It is being suggested that plant hierarchies is established as early as N=7. Plant mass for these plant types tend to follow a normal distribution [39]. A fundamental question follows about the role of a) microenvironment variability and b) intraspecific competition for resources as a disturbance and a mechanism capable of generating emergent patterns of barrenness and changes in biomass distributions with increases in plant population. Alternative hypothesis appeal to sophisticated biological control mechanisms for early detection of neighboring plants to explain emergent patterns [4, 36].

Sensitivity analysis were conducted under under high abiotic stress, intergroove spacing of 60cm, and interplant spacing of 10, 15, 30 and 45 cm. One set of simulations used constant input signals in TM, Tm, S, and irrigation by setting $\epsilon = 0$. A second set of simulations allowed ϵ to vary in the interval [-6, 6] and [-2, 2] for S and $\bar{T}$ respectively. Allowing large variations in S was intended to simulate any of the various sources of variation that can affect photosynthesis, and the dynamics of competition for resources, regardless of the realism of variations *per se* in S.

4 Results and Discussion

4.1 Dynamics and response surface of seed mass to spatial arrangements and environment

The agent based model simulated biomass accumulation dynamics that compared well with those shown by Muchow *et al.* [27](Fig.2). The model simulated an initial phase during which biomass accumulation was limited by leaf area development and light interception, a second phase of rapid vegetative growth until flowering time, and a final phase of linear reproductive growth. The model, however, simulated yield higher than those reported by Muchow *et al.* [27]. This difference is not surprising and it is due to the model parameterization of phenology and the environmental conditions set in our simulations. Muchow *et al.* [27] simulated yields under tropical environments. In contrast

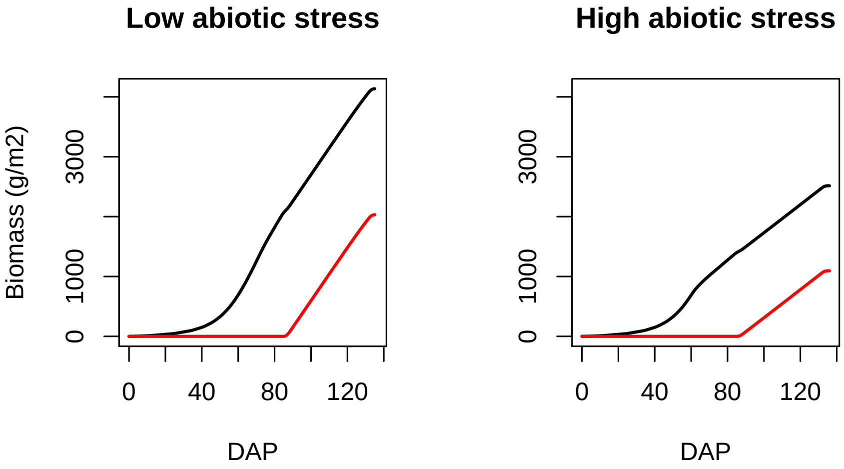

Figure 2: Dynamics of biomass accumulation under low and high abiotic stress environments. Simulations run for intergroove spacing of 60 cm and interplant spacing of 20 cm.

we simulated yields under temperate conditions that led to longer duration of the growing season (120 d vs. 136 d). Simulated yields are within the range of observed values for modern hybrids of $N_0 = 20$ typically grown in the corn belt [13]. The harvest index, the fraction of total mass allocated to reproductive tissues was ≈ 0.5, which is consistent with empirical data [13, 27]. Plant development is slightly longer than expected but within reasonable values. Simulations under high abiotic stress imposed by a reduction in water inputs to the system decreased yield approximately by 50 percent (Fig. 2).

Figure 3 shows the simulated seed mass for a factorial combination of interplant and interrow spacings under two contrasting environments. In this experiment throughput increase with decreasing interplant and intergroove distance. Landscapes for both environment scenarios show a nonlinear response of seed mass with increasing throughput. This nonlinear response of corn to plant population is commonly observed in empirical studies [13, 33, 45] but it is not adequately simulated by crop models that operates on canopy basis [30]. Furthermore, the agent-based model simulated changes in optimal plant between environments as suggested by Westgate *et al.* [42]. Seed mass increase with increasing throughput is due to the increase in interception of solar radiation under low to nil intraspecific competition. After the onset of intraspecific competition, further increases in throughput cause symmetry breaking in plant biomass, increase in barrenness, and yield reduction.

The seed mass response surfaces shows multiple optima that vary in number and location in the landscape with the level of abiotic stress (Fig. 3). The

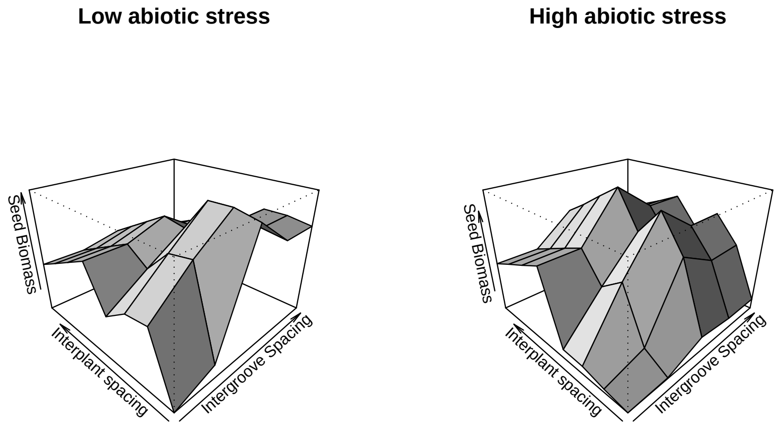

Figure 3: Seed mass response surface to variations in intergroove and interplant spacing under low and high environmental stress conditions

existence of multiple optima is an unexpected result considering empirical evidence [13, 33]. We cannot offer a good hypothesis to explain this behavior of the model and we shall not discard artifacts due to numerical integration. Yet this pattern is is highly repeatable for various combinations of model parameters (data not shown) and environments (Fig.3). Multiple local optima in the seed mass response to plant density was observed but the magnitude of the differences is not significantly different [42]. Due to the trends in agricultural systems to increase plant population and the effects of plant breeding in modifying how hybrids respond to plant density, these patterns deserved further study.

4.2 Effect of plant architecture on seed mass production

A simulation factorial experiment of plant population and three levels of A_0 was conducted to test the hypothesis that increasing A_0 increases the intensity and the onset of interplant plant competition for light, affects patterns of water use and generates significant genotype (levels of A_0) by management (throughput) interactions. Figure 4 shows a nonlinear response of seed mass to increase in plant population for all levels of A_0. This response is consistent with our previous simulations (Fig.2). Significant main effects ($P \leq 0.0001$) of plant population and A_0 were detected, however, interactions were not significant.

These results suggest that within the range of plant population values and environmental conditions explored in this study, light interception limited seed mass production more than it did the availability of water. Increases in A_0 increased light interception and total mass production for all plant densities (Fig. 5). The average effect of A_0 on seed mass at 11 pl m^{-2} was 50 g m^{-2}, which is a marginal increase relative to the expected yield loss. Assuming a harvest index of 0.5 [13, 39] simulated yields estimated from total biomass at high plant populations are in the interval [1100, 1200] g m^{-2} while the actual simulated yields were in the interval [700, 870] g m^{-2}. This results are consistent with previous simulation studies [34].

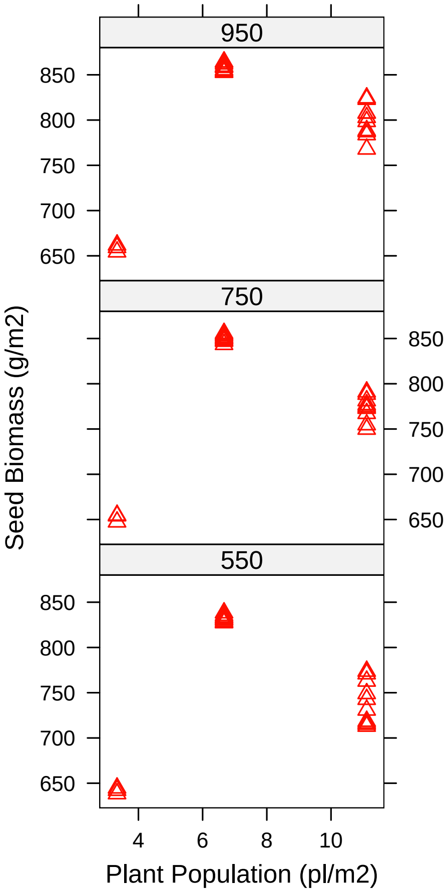

Figure 4: Effects on total leaf area and leaf area distribution A_0, and plant population on seed mass

Seed mass variability increased for all levels of A_0 when plant population increased from 7 to 11 pl m^{-2}. This behavior is associated with variations in

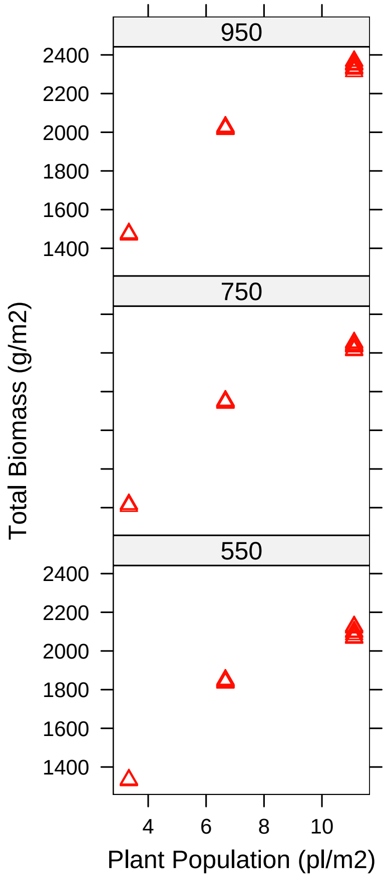

Figure 5: Effects of total leaf area and leaf area distribution A_0, and plant population on total biomass

the fraction of barren plants as a main mechanism of controlling yield under this throughput level (data not shown). Previous research suggested increasing plant populations to increase rapid canopy closure, therefore yields [42]. Our simulation results suggest that this strategy could lead to system instabilities that could vary between environments (Fig. 4).

4.3 Effect of Root growth and plant population on seed mass production

Root elongation and architecture could have major control on water uptake, crop growth and their dynamics. Both the increase in water uptake and the timing of resulting θ values with critical phenological events determine the resulting effect

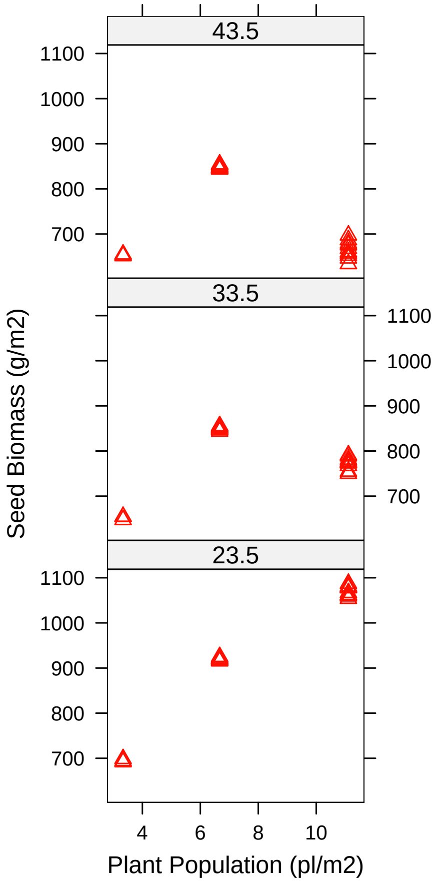

Figure 6: Seed mass response to plant population and root elongation rate characteristics ρ

of root traits on yields. Since the seventies researchers sought to define phenotypic characteristics of root systems that could increase reproductive ability under drought stress [34, 28, 38]. In this study we conducted a sensitivity analysis in which we varied the parameter ρ to allow rapid root growth and access soil water stored in deep layers. The prediction of the underlying hypothesis is that yield increase with increasing ρ.

Figure 6 show the variation of seed mass with plant population and ρ under drought stress. Seed mass response to plant population was dependent upon root growth; significant interactions ($P \leq 0.0001$) were detected between plant population and ρ. At high plant population seed mass increased with decreasing ρ. These differences were both significant and of large magnitude ($\Delta Y \approx$4000 g m^{-2}). Regardless of the magnitude of the differences we should emphasize

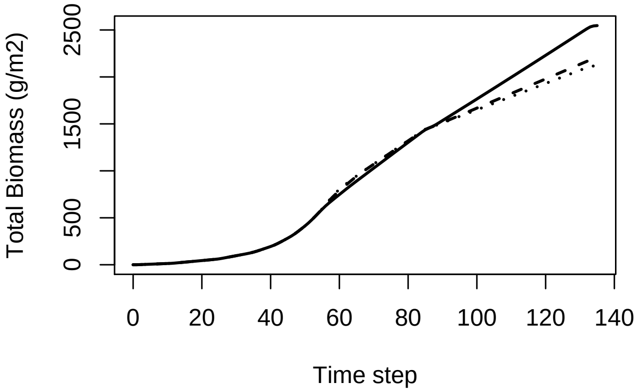

Figure 7: Dynamics of total mass for genotypes of contrasting root elongation rates ρ. Solid line $\rho = 23.5$, dashed line $\rho = 33.5$ and dotted line $\rho = 43.5$ mm d^{-1}. Simulated conducted for high plant population (Fig. 6)

that our results are unexpected, counterintuitive, and controversial. Previous studies [34] and the current conceptual model for root ideotype for drought tolerant corn suggest a plant with large ρ [38, 34].

Variations in ρ did not affect the dynamics of biomass accumulation during the vegetative period at the canopy level (on area basis) (Fig.7). Changes in biomass dynamics were noticeable only in postflowering. This suggest that ρ affects either the determination of kernel numbers or barrenness, which is determined by biomass accumulation in preflowering and early postflowering. On an area basis there were no differences in total water use as it is evident from the almost identical biomass values up to begin grain filling (Fig. 7. time step 90). Figure 8 shows that barrenness increase with increasing values of ρ. Spatial patterns of barrenness shifted from random to increasingly organized clustered patterns. For these patterns to emerge it is necessary for ρ to affect the dynamics of biomass accumulation of individual plants, thus affecting the distribution of total biomass among plant types.

Figure 9 shows frequency distributions of vegetative, preflowering ($12 \leq N \leq N_0$) and seed mass for simulations conducted at high density (Fig.6) and three levels of ρ. During the vegetative period ($N \leq 11$) the frequencies of large plants ($W \geq 71$ g pl^{-1}) increased with increasing ρ. This subpopulation of plants had increased water use early in development. The pattern reversed during preflowering. During this period the highest frequency of plants with low biomass accumulation corresponded to those with highest ρ and highest biomass accumulation during early stages. Early consumption of water limited

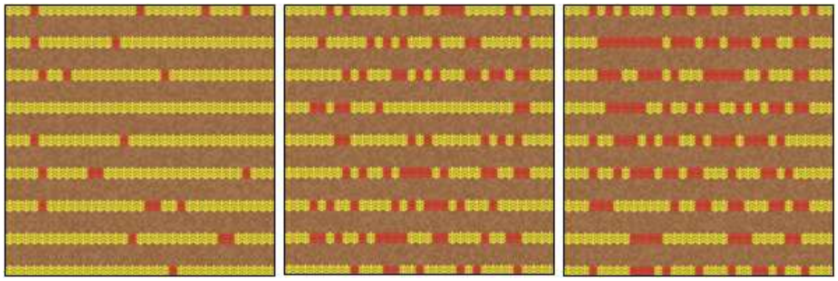

Figure 8: Spatial patterns of barrenness for genotypes of contrasting root characteristics. Panels from left to right correspond to simulations run for ρ parameter 23.5, 33.5 and 43.5 mm d^{-1}.

the biomass accumulation during a critical period causing an increase in the frequency in barrenness and plants producing low seed mass.

The relevance of an optimal partitioning of water use between vegetative and reproductive periods to maximize yields it is well known [29]. Our simulation results suggest that patterns of water use within the vegetative period could also be relevant to increase yields, in particular under high plant populations. Reduced water use and transpiration due to reduced root hydraulic conductance has been shown to increase wheat yields under drought stress [31, 28]. Although we modified a parameter in the model that controls root elongation rates, the biologically relevant effect of ρ was to delay water use toward the critical period for yield determination in corn. The same effect could be attained by increasing the root hydraulic conductance as proposed by Passioura [31, 28]. Reduced transpiration due to stomata closure in response to ABA root signals [8] is another mechanism that would allow shifting water consumption to critical stages. Recently, Sinclair *et al.* [35] showed benefits of this trait in sorghum grown in low yielding environments.

Increasing root elongation, in our virtual environment ρ, through breeding can increase resource capture but also can modify the pattern of water use and biomass accumulation. In this study, ρ played a major role as a determinant of historical events (biomass accumulation during preflowering) which caused symmetry breaking in preflowering biomass, barrenness and yields. There is no guarantee that this specific result regarding the set of values for ρ, not even the sign of the association between ρ and seed mass, could be generalized to all drought stress environments. Instead, this results supports the concept proposed by Hammer *et al.* [14, 15] of investigating interactions between environment types and plant traits that could confer drought tolerance. Our results suggest the need to conduct these studies using agent-based modeling as shown by the contrasting results obtained with respect of those found by Sinclair and Muchow [34]. The mechanisms generating symmetry breaking are of general value, without which biomass allocation among plants and final seed yield could not be adequately predicted.

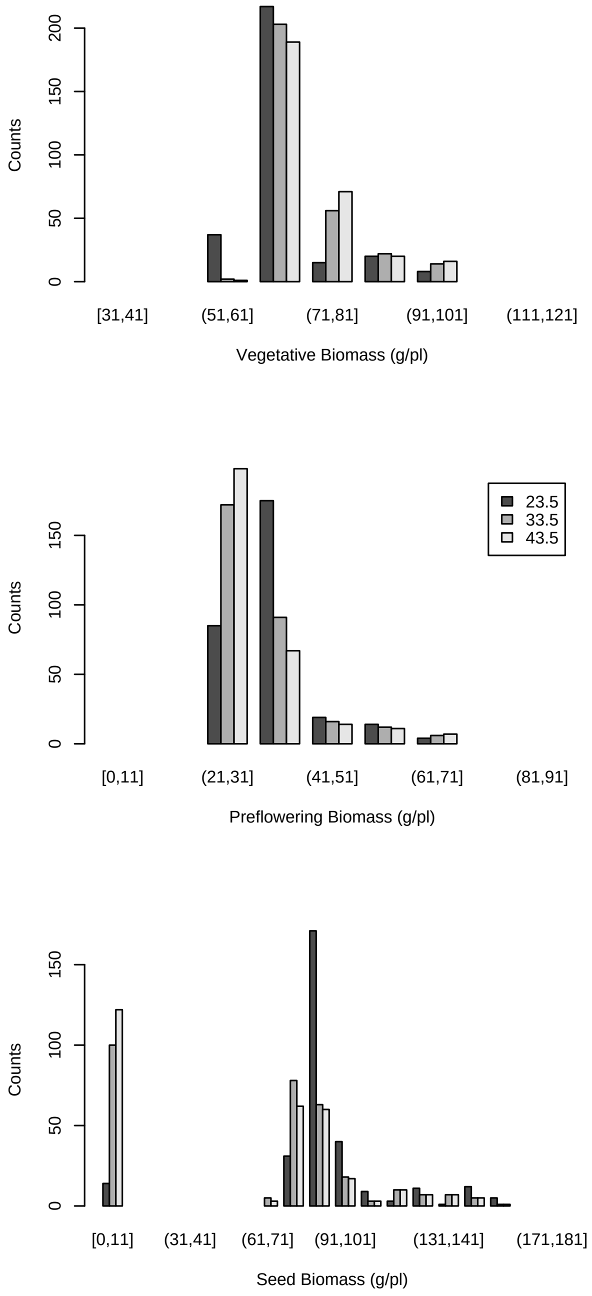

Figure 9: Frequency distribution of vegetative, preflowering and seed mass for genotypes of contrasting root characteristics ρ

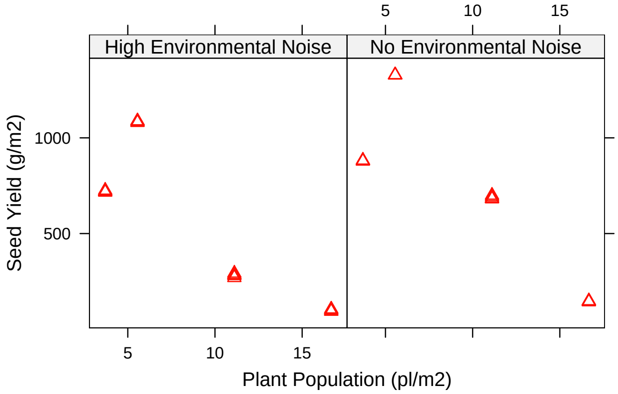

Figure 10: Yield response to plant stand density and environment variability

4.4 Environmental noise and corn productivity

A simulation experiment was conducted to study the role of microenvironment variability and intraspecific competition as mechanisms capable of producing emergent behavior commonly observed in corn canopies. Both in the presence or absence of environmental noise the agent-based model generated typical responses of seed mass to increasing plant population (Fig.10, Fig. 4, Fig. 6) [13, 33]. The mechanism underlying these responses were identical as those presented in previous simulation experiments (Fig.8, Fig.9). The proportion of barren plants increased with increasing system throughput. The results showed that intraspecific competition for light alone is sufficient to generate multimodal distributions, and emergent patterns of barrenness. However, the frequency distributions of simulated total mass and seed mass tended to a set of discrete classes rather than to a continuous variation as shown in empirical studies [24, 39]. The addition of environmental noise increased biomass variability and approximated the simulated distributions closer to the observed normal distributions of shoot mass. Average yields decreased for all plant populations as the frequency of barren plants increased with the addition of environmental noise. Yield reductions were highest at 11 pl m^2. At higher throughput the system collapsed.

Although the agent-based model simulated bimodal distributions of shoot mass and barrenness, it was not capable to simulate a realistic frequency of plants of low mass. The distributions of simulated seed and total mass were consistently skewed toward high mass end. Additional mechanisms that allows plants to adjust their behavior in response to neighbors, for example to change biomass allocation to root and shoots, or to vary specific leaf areas [36, 4] may be required to enhance the model and approximate the solutions closer to observed mass distributions.

5 Conclusions

We developed the first ecophysiological agent-based model involving interaction among individual corn plants. Despite the simplifications introduced in the model at this stage of development, the model behavior was remarkably consistent with empirical observations. Agent based modeling proved a useful tool for understanding corn growth and development under competition for limited resources. Our results suggest that intraspecific competition alone can generate emergent patterns in barrenness and explain yield variations in response to plant population. However, other mechanism should be included to simulate more realistic shoot and seed mass distributions. Simulations conducted for three levels of root elongation rates demonstrated the importance of historical events and dynamics in agricultural systems as deteminants symmetry breaking, emergent behavior and the formation of complex patterns. Consistenly accross simulation experiments, maximum levels of production were achieved just before the formation of complex patterns. Further increases in throughput led to a system collapse.

Due to the existence of multiple local optima, the emergence of complex patterns under high plant competition and the yield dependence on multiple traits, our simulation results suggest an important role of simulation in assisting genetic improvement of crops. Future work could focus on a) extending the model to include a spatial water balance model, b) quantify the value of traits using large soils and weather databases, c) integrating the model with a genetic algorithm and QU-GENE to investigate evolutionary processes underlying genetic gains and variation in plant form and function, and d) couple the agent-based model with statistical models underlying genetic variation in model parameters.

6 Acknowledgments

The authors would like the acknowledge to the support provided by the Santa Fe Institute, DuPont and the Universite de Toulouse. [1]

References

[1] R.M. Adams *et al., Nature* **345**, 219 (1990).

[2] F.H. Andrade *et al., Crop Science* **39**, 453 (1999).

[3] C.L. Ballaré *et al., Science* **247**, 329 (1990).

[4] C.L. Ballaré *et al., Proceedings Academy of Science* **91**, 10094 (1994).

[5] L. Borrás *et al., Annals of Botany* **91**, 857 (2003).

[6] L. Borrás *et al., Crop Science* Submitted (2006).

[7] K.G. Cassman, *Proceedings National Academy of Science* **96**, 5952 (1999).

[8] A. Christmann *et al., Plant Physiology* **137**, 209 (2005).

[9] M. Cooper and D. W. Podlich, *Complexity* **7**, 31 (2002).

[10] M. Cooper *et al., In Silico Biology* **2**, 151 (2002).

[11] M. Cooper *et al., Australian Journal of Agricultural Research* **56**, 895 (2005).

[12] P. H. B. de Visser *et al., Acta Horticulturae* **654**, 171 (2004).

[13] D. N. Duvick, *et al., Long-term selection in a commercial hybrid maize breeding program*, in *Long term selection: Crops, animals, and bacteria* J. Janick, Ed. (John Wiley and Sons, New York, 2004), Plant Breeding Reviews, 24, in press.

[14] G. L. Hammer *et al., Australian Journal of Agricultural Research* **56**, 947 (2005).

[15] G. L. Hammer *et al., Science* (submitted).

[16] A. Hübler, *Complexity* **10**, 11 (2005).

[17] G. Hughes, *Nature* **332**, 16 (1988).

[18] M. Hulme *et al., Nature* **397**, 688 (1999).

[19] G. D. Jenerette and J. Wu, *OIKOS* **107**, 273 (2004).

[20] J. W. Jones *et al., European Journal of Agronomy* **18**, 235 (2003).

[21] B. Keating *et al., European Journal of Agronomy* **18**, 267 (2003).

[22] J. Kiniry *et al., Field Crops Research* **20**, 51 (1989).

[23] J. Luck *et al., Annals of Botany* **79**, 375 (1997).

[24] G. A. Maddonni and M. E. Otegui, *Field Crops Research* **85**, 1 (2004).

[25] R. B. Matthews and W. Stephens, *Crop-Soil Simulation Models: Applications in Developing Countries* (CABI Publishing, New York, 2002).

[26] R. C. Muchow and T. R. Sinclair, *Agronomy Journal* **83**, 1052 (1991).

[27] R. C. Muchow *et al., Agronomy Journal* **82**, 338 (1990).

[28] J. B. Passioura, *Australian Journal of Agricultural Research* **23**, 745 (1972).

[29] J. B. Passioura, *Functional Biology* **29**, 537 (2002)

[30] E. L. Piper and A. Weiss, *Agricultural Systems* **33**, 199 (1990).

[31] R. A. Richards and J. B. Passioura, *Australian Journal of Agricultural Research* **40**, 943 (1989).

[32] H. S. Saini and M. E. Westgate, *Advances in Agronomy* **68**, 58 (2000).

[33] L. Sangoi*et al., Field Crops Research* **79**, 39 (2002).

[34] T. R. Sinclair and R. C. Muchow, *Agronomy Journal* **93**, 263 (2001).

[35] T. R. Sinclair*et al., Functional Plant Biology* **32**, 945 (2005).

[36] H. Smith, *Nature* **407**, 585 (2000).

[37] F. Tardieu, *TRENDS in Plant Science* **8**, 9 (2003).

[38] R. Tuberosa and S. Salvi, *TRENDS in Plant Science* **11**, 405 (2006).

[39] C. R. C. Vega and V. O. Sadras, *Annals of Botany* **91**, 795 (2003).

[40] C. R. C. Vega *et al., Crop Science* **41**, 748 (2001).

[41] C. R. C. Vega *et al., Field Crops Research* **72**, 163 (2001).

[42] M. E. Westgate *et al., Field Crops Research* **49**, 249 (1997).

[43] U. Wilensky, *Netlogo* (Center for Connected Learning and Computer Based Modeling, Northwestern University. Evanston, IL,, 1999) (available at http://ccl.northwestern.edu /netlogo/).

[44] Z. Yang and D. J. Midmore, *Ecological Modelling* **181**, 59 (2005).

[45] C. Zinselmeier, Upublished data, 2005.