SHARP: Shade-avoidance Response in Plants
An Evolutionary Simulation Software Package

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Abstract: Educational simulators take learning to the next level by bringing students' understanding of a subject closer to their personal experience. In this paper, software to simulate the evolution of shade-avoidance responses in plants is developed. Models and equations to imitate the response are described. An example simulated scenario is illustrated and discussed. This simulation demonstrates typical shade-avoidance response in plants; the competition for sunlight between plants grown in high density conditions channelizes more resources towards longer stems. Additionally, the simulations show how increased competition over plants grown in low density conditions lowers the variability in the overall shapes of the individual plants.

1 INTRODUCTION

The increasing of computing power and its decreasing cost has extended the development of simulation-based educational and training tools to various fields other than their traditional areas of use, *i.e.* aviation (Kincaid and Westerlund, 2009). Various types of educational simulation tools depend on the specific fields and their objectives. For instance, simulation games for teaching Political Science (e.g., The Redistricting Game (USC Annenburg Foundation, 2010)) aims to provide understanding on the mechanics of the real world political systems; the typology of medical simulation tools proposed in (Alinier, 2007) aims to develop students' cognitive, psychomotor and interpersonal skills, and to enhance their experiences with the ultimate goal of saving lives and ensuring patients' well-being; and another visualization tool (Kethireddy and Suthaharan, 2004) helps students to understand the difficult concepts of computer networks.

In the fields of biology, (Tinker and Mather, 1993)'s interactive genetic simulation software can be an educational tool for undergraduate students to learn genetics, selection, the process of meiosis, and phenotypes. The authors in (Martin and Skavaril, 1984), (Fita et. al., 2010) developed a computer simulation program to teach students the concepts in plant breeding, including genetic drift, the steps involved in various breeding methods and the development of different lines. The authors in (Martin and Skavaril, 1984), (Fita et. al., 2010) pointed out that plant breeding simulations allow students to experience the whole plant breeding process as an "actual" plant breeder and at the same time gained their interest in this field.

Inspired by their works (Tinker and Mather, 1993), (Martin and Skavaril, 1984), (Fita et. al., 2010), a simple educational simulation program to simulate the evolution of shade-avoidance responses in plants is proposed. The program will demonstrate the major shade-avoidance traits as they change over multiple generations. An evolutionary algorithm (Deb, 2001), (Engelbrecht, 2007) is used to imitate the biological processes of the plants. The immediate intended users are science teachers in a summer training institute.

2 SHADE AVOIDANCE RESPONSES IN PLANTS

Plants have the ability to survive in various environmental conditions. At high population densities plants compete with their neighbors for limited resources such as water, nutrients, and

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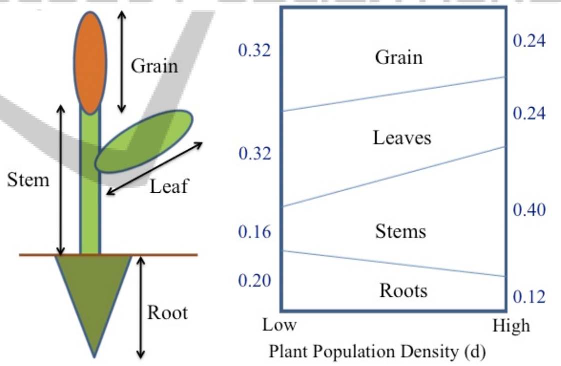
STEP 0: Initialize user-defined parameters (e.g., $t=0$ and $g=0$), . (See Section IV, Table 1)
STEP 1: Plant the shoots (assumed after seed germination) in equal plant space. Display graphic.
STEP 2: At t = t+1:
STEP 3: Calculate plants' growth rates and update plants' parts length. (See Section III.A)
STEP 4: Calculate plants' elevated leaf angles and leaf color index. (See Section III.B)
STEP 5: Check if any plants have lodged. (See Section III.C)
STEP 6: Display graphic with latest plants updates.
STEP 7: If $t \le t_{max}$, go to STEP 2. Otherwise, go to STEP 8.
STEP 8: If $g \le g_{max}$, go to STEP 9. Otherwise, terminate the simulation.
STEP 9: Calculate plants' fitness. (See Section III.D)
STEP 10: Based on calculated fitness, select parents for reproduction. (See Section III.E)
STEP 11: Apply crossover to selected parents with crossover probability to generate offsprings. (See Section III.F)
STEP 12: Apply mutation to offsprings with mutation probability. (See Section III.G)
STEP 13: Set $g=g+1$ and $t=0$. Go to STEP 1.

Figure 1: Pseudocode of the SHARP evolutionary simulation software package.

especially sunlight (Casal, 2012), (Franklin and Whitelam, 2005), (Sasidharan et. al., 2010), (Keuskamp and Pierik, 2010), (De Wit et. al. 2012). In competing for sunlight, plants utilize photosensitive molecules in their leaves to sense red (R) and far-red (FR) wavelengths; the R:FR ratio is an indicator of nearby neighboring plants (De Wit et. al., 2012). A low R:FR ratio indicates shading by other plants and induces shade-avoidance response to secure more sunlight (*i.e.* light interception). The phenotypic traits that constitute the shade-avoidance response include stem elongation, petiole elongation, reduction of chlorophyll concentration, and leaf hyponasty (*i.e.* increase in leaf elevation angle) (Casal, 2012), (Franklin and Whitelam, 2005), (Sasidharan et. al., 2010), (Keuskamp and Pierik, 2010), (De Wit et. al., 2012). Plants under long-term shading exhibit traits that are related to shade-avoidance syndrome (SAS). These include reduced branching and acceleration of flowering (albeit with fewer seeds) to ensure reproduction (Sasidharan et. al., 2010). Thus, in agriculture, plants undergoing shade-avoidance syndrome will results in a lowered crop yield.

3 THE FRAMEWORK OF THE SIMULATION PROGRAM

The proposed simulation tool assumes there are no water and nutrient limitations; the simulated shade-avoidance phenotypic traits are stem elongation, leaf elevation angle, reduction of chlorophyll concentration, reduced root size and shorter leaf length (Casal, 2012), (Franklin and Whitelam, 2005). The pseudocode of the simulated program is presented in Figure 1. Parameters and variables will be elaborated in the next Section.



(a) (b)

Figure 2: (a) Specification of a plant with arrows represents the length of a specific plant part. (b) Shade-avoidance response graph with x-axis represents the plant population density.

3.1 Plant Growth Model

For visualization, every plant has one root mass, a stem, two leaves, and a grain mass. As depicted in Fig 2(a), the lengths of these plant parts (*i.e. Grain*, *Stem*, *Root*, and *Leaf*) are approximated via Euler integration. At current generation denoted as g and current day denoted as t, the plant parts' lengths for plants $i = 1, \ldots, N$ are updated via (1a) to (1d):

$$Grain_i(g, t + \Delta t) = Grain_i(g, t) + \Delta t \frac{d}{dt} Grain_i(g, t) \tag{1a}$$

$$Stem_i(g, t + \Delta t) = Stem_i(g, t) + \Delta t \frac{d}{dt} Stem_i(g, t) \quad (1b)$$

$$Root_i(g, t + \Delta t) = Root_i(g, t) + \Delta t \frac{d}{dt} Root_i(g, t) \quad (1c)$$

$$Leaf_i(g, t + \Delta t) = Leaf_i(g, t) + \Delta t \frac{d}{dt} Leaf_i(g, t) \quad (1d)$$

In the above equations, the time increment Δt is equal to 1 day. The derivative terms above that represent the growth rate (changes of length each unit time) of each given plant part, are as follows:

$$\frac{d}{dt} Grain_i(g, t) = k_G L_I (1 + \varepsilon_{G,i}) A_G \quad (2a)$$

$$\frac{d}{dt} Stem_i(g, t) = k_S L_I (1 + \varepsilon_{S,i}) A_S \quad (2b)$$

$$\frac{d}{dt} Root_i(g, t) = k_R L_I (1 + \varepsilon_{R,i}) A_R \quad (2c)$$

$$\frac{d}{dt} Leaf_i(g, t) = k_L L_I (1 + \varepsilon_{L,i}) A_L \quad (2d)$$

Subject to:

$$1 + \varepsilon_{G,i}, 1 + \varepsilon_{S,i}, 1 + \varepsilon_{R,i}, 1 + \varepsilon_{L,i} > 0 \quad (2e)$$

The equations in (2) model the growth rate of each plant part as proportional to the light interception per day per leaf, a proxy for rate of photosynthesis, and to a factor (*i.e.* $(1 + \varepsilon)$) defining the fraction of each new increment of photosynthate that is allocated to each tissue type.

The variables A's (*i.e.* A_G, A_S, A_R, and A_L) in (2) are the allocation factors of photosynthate (*i.e.* the product of photosynthesis). They are determined by the user-defined plant population density parameter, d value that is represented by the x-axis of the shade-avoidance response graph in Fig.2b. As shown in Fig. 2b, the range of the d values is low to high densities. If d is a high value (crowded conditions), the graph depicts the shade-avoidance traits of stem elongation, reduced root size and lowered seed production relative to plants grown in uncrowded conditions. The range of d is set as [0.001,1] for this framework. The equations to calculate the A values are derived from the graph and are presented in (3a) to (3d) below:

$$A_G = 0.32(1 - d) + 0.24d \quad (3a)$$
$$A_S = 0.16(1 - d) + 0.40d \quad (3b)$$
$$A_R = 0.20(1 - d) + 0.12d \quad (3c)$$
$$A_S = 0.32(1 - d) + 0.24d \quad (3d)$$

The variable, L_I in (2) is the light intercepted by the leaf in one day, representing a proxy for rate of photosynthesis. It is equal to the angle θ (see Fig. 3) multiplied by the plant leaf's area. The angle θ is defined from the plant's leaf node to the maximum heights of its nearest neighboring plants, and the maximum degree is 180° or π (in radians). The rationale is that the plant's leaf can only receive sunlight when the sun is above the horizon and the amount received in a day will be proportional to the time it is not shaded; that is, the time during which the sun is within the subtended angle. In this program, the assumption is that the leaves have unit area and receive θ (in radians) of sunlight, *i.e.* $L_I = \theta$. The four ε's (*i.e.* ε_G, ε_S, ε_R and ε_L) values (or the four "loci") in (2) represent the genetic makeup of a plant, meaning each plant has four genes. Every plant has different set of ε values that mimic the genetic variation between plants. Lastly, the fixed parameters, k's (*i.e.* k_G, k_S, k_R, and k_L) in (2) are plant part growth rated adjustment factors set by experts to improve simulation realism.

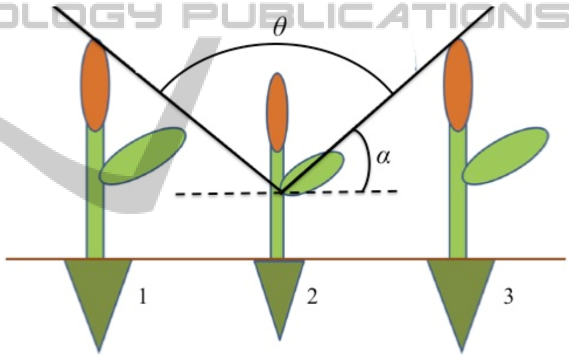


Figure 3: An illustration of plant 2 (i.e. $i=2$) and its nearest neighboring plants, plant 1 and plant 3. The angle θ represents the amount of sunlight exposed by plant 2 and angle α is the leaf elevation angle.

3.2 Leaf Specifications

The above SHARP model focuses on variable growth rates of plant parts reared in a high-density environment. The larger stem allocation factor at high density (Fig. 2b) leads to increasing plant height under shading. Other traits such as elevated leaf angle and reduced chlorophyll concentration are two of the responses that aim to "elevate leaves towards unfiltered daylight and provide an essential survival strategy in rapidly growing population" (Franklin and Whitelam, 2005).

This model incorporates the elevated leaf angle calculate via the following equation:

$$leafangle_i(g,t) = \frac{1}{2}leafangle_i(g,t-1) + \frac{1}{2}\left(0.8333\alpha + \frac{5\pi}{180}\right) \quad (4)$$

Equation (4) has two roles. First, it maps the angle α in radians (See Fig.3) to the biological elevated leaf angle, which ranges from 5 degree to 80 degree (Sasidharan et. al., 2010), (Keuskamp and Pierik, 2010), (De Wit et. al., 2012), (Hammer et. al., 2009). These are rough estimates garnered from several articles not necessarily representative of any single species. However, the range serves the purpose of demonstrating how plants respond to shade in crowded environments. The second role is to adjust the elevated leaf angle by taking the average of the leaf angle calculated from the previous day (*i.e. t-1*) and the current day (*i.e. t*) to avoid any unrealistically sudden changes of elevated leaf angle that will be displayed on the graphic.

The changes in chlorophyll concentrations are depicted in different levels of green color. The darker green color represents leaf with high chlorophyll content; while the lighter green color represents the opposite. In this program, we use a color index to represent different levels of green listed in a look-up table. Currently, the look-up table has seven green shades. From darkest to lightest, they are: Dark Green, Forest Green, Dark Sea Green, Medium Sea Green, Lime Green, Lawn Green, and Green Yellow. These articles (10, Keuskamp and Pierik, 2010) , (Smith and Whitelam, 1997) stated the reduction in chlorophyll production due to lack of light is commonly observed in leaf development during shade-avoidance. To model this trait, we borrow the idea of mapping the leaf angle α in radians to the leaf color index in Equation(4); the model is formulated as the following:

$$leafcolorIndex_i(g,t+1) = Round\left(\frac{1}{2}leafcolorIndex_i(g,t-1) + \frac{1}{2}(3.9197\alpha + 1)\right) \quad (5)$$

3.3 Plant Lodging

In nature, there are multiple sources of plant mortality. In this program, the only source is plant lodging – the plant falls over if it becomes top-heavy relative to its root mass. The threshold probability of lodging (P_{Lodge}) in one-day period is calculated by the following equations:

$$P_{Lodge,i}(g,t) = k_{Lodge}\left(1 - \frac{Root_i(g,t)}{S}\right) \quad (6a)$$

where,

$$S = Grain_i(g,t) + Stem_i(g,t) + Root_i(g,t) + Leaf_i(g,t) \quad (6b)$$

In the above equation, k_{Lodge} is a fixed parameter that is set to a large enough value to insure that the effects of lodging are clear to learners. Plant *i*'s chances to survive the next day will be decided when a uniform random number, *r* is greater or equal to P_{Lodge} (*i.e.* $r \geq P_{Lodge}$). Smaller k_{Lodge} value will lower the P_{Lodge}, thus allowing the plants to survive longer period of days.

3.4 Plant Fitness

Generation times were set to t_{max}=120 days. At day 120, the surviving plants' ability to produce the amount of seeds after pollination is the metric for plants' fitness. In this model, the length of each grain plant part is an indicator of fitness. The fitness calculation for surviving plants $i = 1, \ldots, N_{Survive}$ is given in (7) below:

$$fitness_i(g,t=120) = \frac{Grain_i(g,t=120)}{\sum_{j=1}^{N_{survive}} Grain_j(g,t=120)} \quad (7)$$

3.5 Selection Scheme

This program implemented roulette-wheel selection (Deb, 2001) in which the probability of reproducing is proportional to fitness. This method has two advantages: 1) Plants with high fitness are likely to be selected but there is also some chance that they won't be selected; and 2) Due to its randomness, plants with low fitness may be selected giving a chance to preserve certain genes that are associated with better traits.

3.6 Crossover Operator

The real-valued blend crossover operator (BLX-*α*) (Deb, 2001); (Engelbrecht, 2007); (Eshelman and Schaffer, 1993) is implemented to simulate cross-pollination. Firstly, two surviving plants are selected as parents 1 and 2. Next, the crossover operator ((8) and (9)) is applied to the parental loci *j* with crossover probability (*pc*) and to generate a plant offspring's (or seed's) loci *j* that contains both the parents' genetic materials. If the crossover probability isn't met, the offspring's (or seed's) loci *j* is copied directly from one of the parents' loci *j*.

$$\varepsilon_i^o = (1-\gamma)\varepsilon_i^1(g,t=120) + \gamma\varepsilon_i^2(g,t=120) \quad (8)$$

$$\gamma = (1 + 2\alpha) rand(0,1) - \alpha \qquad (9)$$

Here, α, an user-defined parameter is an exploration coefficient and $\alpha \geq 0$. The *rand*(0,1) represents the uniformly distributed random number generator with the range of 0 and 1. The ε_j^o, ε_j^1 and ε_j^2 values represent the offsping's, parent 1's, and parent 2's loci *j* respectively. The *pc* parameter is set to 0.5, meaning there is a 50% chance for recombination to happen. There are total of four loci for each offspring. Self-pollination (or "selfing" occurs if the plant offspring has the exact same four ε values as its parent plant.

3.7 Mutation Operator

After plant offspring are produced, a mutation operation is applied to locus *j* of each new individual with mutation probability (*pm*). A Gaussian distribution mutation operator (Deb, 2001) is utilized for this step.

$$\varepsilon_j^o = \varepsilon_j^o + N(0, \sigma^2) \qquad (10)$$

Here, ε_j^o represent the offspring's loci *j*, $N(0,\sigma^2)$ denotes a zero-mean Gaussian probability distribution with variance, σ^2. The parameter σ is set to 0.005 and *pm* set to 0.01 (*i.e.* 1% chance for a mutation event to happen).

4 SIMULATIONS

This section illustrates the visualization and output generated by the simulation program. Table 1 contains parameters that require user-defined settings. The k values and lodge weighting are not shown as they are not accessible to users.

Table 1: SHARP parameter settings.

Parameter Name	Value	
	High Density	**Low Density**
Maximum generation (g_{max})	25	25
Maximum number of days (t_{max})	120	120
Ground length (meter)	8	48
d parameter (Figs. 2(b))	0.9	0.1
Number of plants	16	16
Crossover probability (*pc*)	0.5	0.5
alpha parameter (α)	0.0	0.0
Mutation probability (*pm*)	0.01	0.01

Fig.s 4 and 5 are the examples of simulated plants graphics. Both consist of two panels: panel (a) illustrates a high population density environment; panel (b) is low population density. The plants are aligned uniformly (*i.e.* equal initial distances between neighboring plants). Current generation and days after planting information are displayed on the top left of panel (b). Although 16 plants are simulated in both conditions, panel (b) only illustrates five plants to demonstrate plants in non-crowded environment versus those living in crowded environment. At 120 days in every generation, two tables report the highest and lowest fitness values, along with their corresponding ε values (*i.e.* genes). See Fig. 5 for an example. Only roots are shown to designate plants that have lodged. Students can observe the effects of crowding on the plants' behavior to compete for sunlight during their growth period and how this behavior changes as the number of generation increases. They can compare the resulting plant traits in the two different environments (e.g. plant height, elevated leaf angle, chlorophyll content and root mass in every generation).

The simulated is run 50 times (*i.e.* 50 *in silico* experiments) to gather enough data to plot the distributions of the simulated plant traits in every generation. The distributions are presented in box-plots as shown in Figs. 6-9. In Fig 6(b), plants tend to inherit larger grain size (*i.e.* yield more seed) in the less densely populated area while in the crowded environment (Fig. 6(a)), majority of the plants' trait with smaller grain size (*i.e.* lower yield) is more prevalent, indicating plants will produce offspring to be adaptable to shade-avoidance responses and survive in such environment. There are outliers in both plots. They indicate variability and diversity of plants' trait that may due to mutated genes or other unexpected factors such as neighboring plants lodge and that affected the plants' response to growth. Figs 7(b) illustrates the majority of the plants' stem heights maintain almost consistent lower and upper quartiles (or consistent distribution shapes) starting from the 8th generation. This shows the majority of the plants do not need to compete for sunlight in the less crowded environment. On the other hand, Fig 7(a) shows the variability of distributions in some generations, reflecting some plants were competing in response to shade-avoidance and increase stem height to get access to more sunlight. Fig 8(a) clearly shows smaller plants' root mass in the crowded environment due to every plant compete for limited water resource; while the large root mass is more prevalent for plants growing in the low density

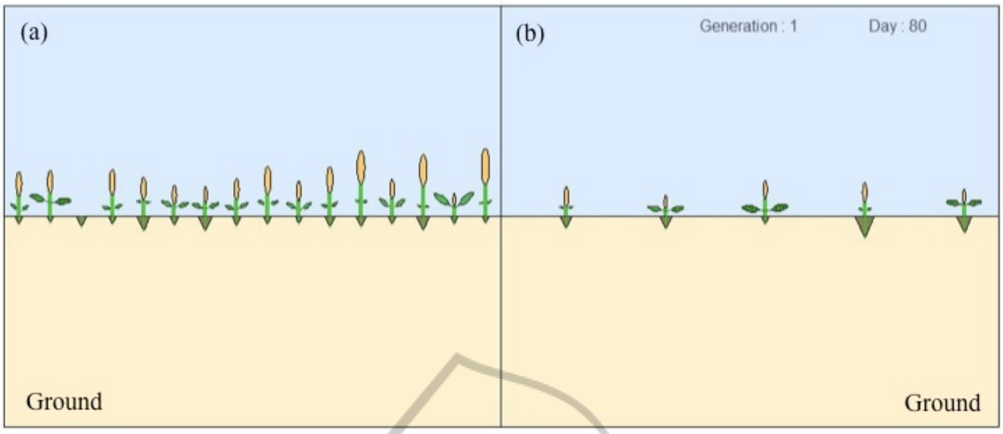


Figure 4: Illustration of the plants status growing in (a) high and (b) low population density at first generation and 80 days after planting.

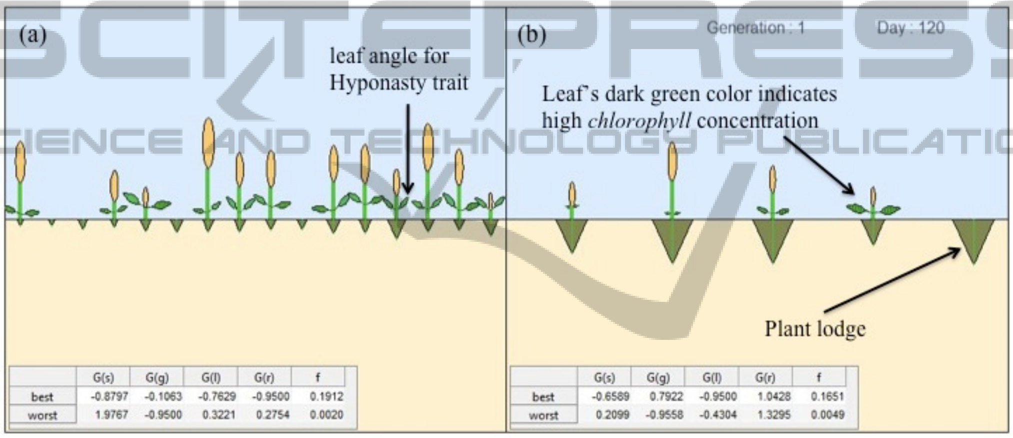
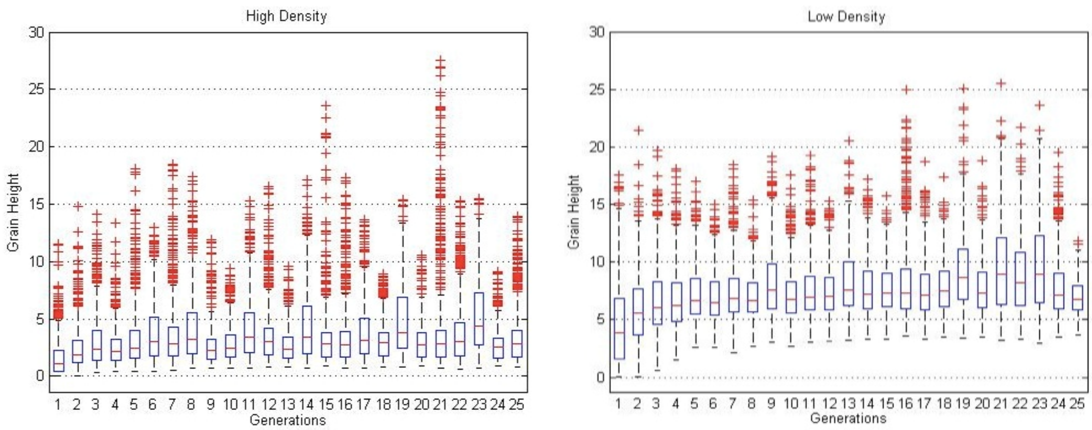


Figure 5: Illustration of the plants status after 120 days of planting at first generation.



a b

Figure 6: Box plots of grain height in two plant growing conditions in the period of 25 generations for 50 test runs.

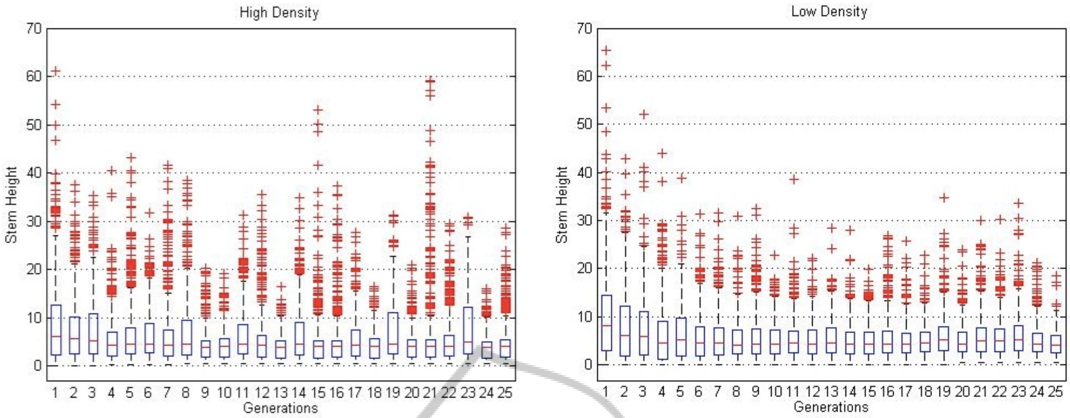


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Figure 7: Box plots of stem height in two plant growing conditions in the period of 25 generations for 50 test runs.

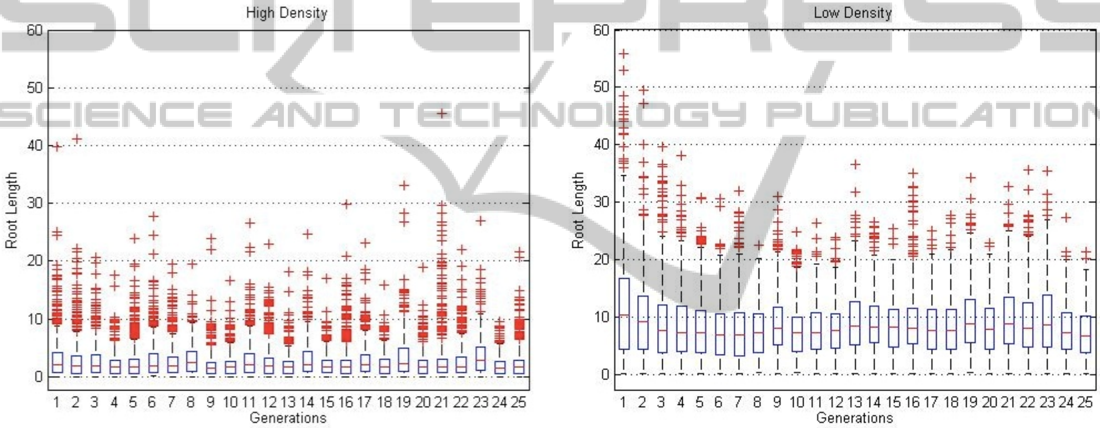

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Figure 8: Box plots of root length in two plant growing conditions in the period of 25 generations for 50 test runs.

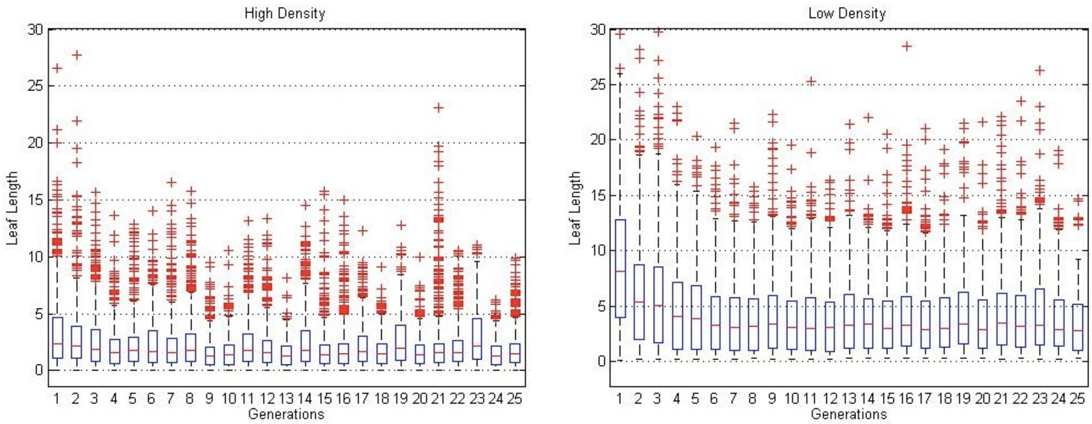

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Figure 9: Box plots of leaf length in two plant growing conditions in the period of 25 generations for 50 test runs.

environment (see Fig. 8(b)). Plants grown in the wide-open space tend to produce larger leaves length with higher variability (in Fig. 9(b)). This isn't the case for plants grow in crowded condition. As illustrated in Fig. 9(a), majority of the plants continue to produce offspring with small leaf length, a trait reflects receiving lesser sunlight.

5 FUTURE WORK

The above modeling framework shows the potential of developing a simulated educational program to educate students about shade-avoidance responses in plants. Several improvements will be implemented to bring the simulated response closer to nature. For example, one improvement is to define the leaf area equation and make light interception proportion to leaf area. Another idea is to transfer this program into graphic user interface (GUI), allowing students play with the parameters to create different experimental scenarios, learn, and observe the simulated results (*i.e.* plants' responses).

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