A Canopy Architectural Model to Study the Competitive Ability of Chickpea with Sowthistle

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INTRODUCTION

It is now widely accepted that the best approach to manage weeds is through the development and implementation of integrated weed management (IWM) systems (Swanton and Murphy, 1996). Choosing an appropriate individual crop plant architecture, integrated with an appropriate crop planting density is an important component of IWM to suppress weed growth (Lemerle et al., 2001). Evaluation of these effects is particularly important in view of the growing interest in reducing the reliance on chemical weed management (Blackshaw et al., 2006). A higher crop competitive ability is desirable as it decreases weed seed production, which in turn reduces weed infestation size in subsequent years (Jordan, 1993).

Plant architecture is the size, number and spatial arrangement of plant organs upon the plant body. It determines the interaction of a plant with its environment and neighbouring plants (Aphalo and Ballare, 1995). A recent advance in the study of biological systems, such as plant architecture and crop–weed competition, is the use of computers to model and simulate such systems. In the last two decades different models have been developed to simulate crop–weed competition (Bastaans et al., 1997; Olesen et al., 2004) but none of them have taken into account the actual architecture of the individual crop plant and its effects on weed performance. Having a virtual plant model will help one to see the results of competition over time and combine different cultivars or different planting rules to analyse the competitive ability of that crop plant in silico (i.e. by running a computer simulation). A variety of modelling approaches can be used to implement a virtual model of plant development (Prusinkiewicz, 1998). The ability to express branching patterns and to describe relatively complex architectural structures based on rewriting rules makes the L-systems formalism (Lindenmayer, 1968) an appropriate candidate for modelling plant architectural development (Prusinkiewicz and Lindenmayer, 1996). In order to capture environmental influences, a virtual plant model can be interfaced with an environment program (Mech, 1997). The environment program takes the current structure of the plant as input, then processes it to determine certain environmental conditions (such as degree of shade or light availability), which are returned to the plant model and influence future development. Surface-based light models (Chelle et al., 1998) are one type of these environment models.

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models that can compute light distribution over the 3-D canopy architecture of the virtual plants by taking the geometry of each organ into account. The present research study is the first attempt to use these 3-D virtual modelling techniques to help select crop cultivars that are more competitive with weeds or to select crop planting geometries that are also more conducive to weed-growth suppression.

Chickpea (Cicer arietinum), as one of the important grain legumes and sowthistle (Sonchus oleraceus), as one of the common weeds found in this crop (Holm et al., 1988), were chosen for the study. A virtual plant model called the chickpea–light environment–sowthistle (CLES) was developed to study competitive ability of different chickpea cultivars with sowthistle. In this model, simulated development of sowthistle plants in response to the light environment under the chickpea plants serves as an indicator of the weed-suppression ability of chickpea cultivars. The model is also validated and its potential power in non-chemical IWM is discussed. This version of the CLES relies on the idea of size-asymmetric competition to simulate the effect of chickpea plants on sowthistle plants. Size-asymmetric competition (Schwinning and Weiner, 1998) suggests that increased crop density and spatial uniformity can have large effects on weed growth when the crop has a significant initial number/size advantage over the weed and also when enough water and nutrients are provided for plant growth and development. Here competition for light is important enough to dominate the crop–weed interaction. However, when below-ground competition is structuring the crop–weed interaction, a size-symmetric competition (Schwinning and Weiner, 1998) would be expected, which in turn reduces the potential for suppressing weeds by crops (Weiner et al., 2001). This second criterion has not yet been incorporated into the CLES model.

MATERIALS AND METHODS

Botany of chickpea and sowthistle

Chickpea (Cicer arietinum L.) is a legume with distichous (one leaf per node) phyllotaxy and its first two nodes have only scale leaves. The main stem is indeterminate and there is a delay in the outgrowth of the axillary buds (Singh, 1997). Leaves in most of the cultivars are pinnate (fern) with the number of leaflets differing by position on the main stem.

Annual sowthistle (Sonchus oleraceus L.) is a broad-leaf weed from the Asteraceae. It is a rosette plant that first produces all its leaves and then produces a terminal flowering bud. Sowthistle has two different forms of leaves; rosette leaves grow in crowded circles from a common centre or crown, close to the ground, while cauline leaves grow on the upper part of the stem. The length of the stem internodes associated with cauline leaves increases dramatically after the appearance of the first flowering buds (bolting). All nodes on the main stem have an axillary bud that have the potential to grow out and form a branch (Holm et al., 1988).

Model development and parameterization

The virtual models of chickpea and sowthistle plants were developed using the L-systems formalism (Prusinkiewicz and Lindenmayer, 1996). The basic components of the virtual plant models are represented by these modules: apical meristem of the main stem, A; internodes, I; leaves, L; and axillary buds, B. The topology of the plants is captured by the order of the modules in the string (Prusinkiewicz and Lindenmayer, 1996). As an example, the basic apex (apical meristem) production rule used in the plant model is:

$$A \rightarrow I[L][B]A$$

where apex (A) gives rise (→) to an internode (I), a leaf (L), an axillary bud (B) and an ongoing apex (A). Square brackets are used for specifying branches. In order to quantify the properties of the plant components, numerical parameters (Hanan, 1992) are associated with the modules. The numerical parameters are real values expressed using arithmetic expressions, predefined functions and condition statements. Each module has two parameters; node number and age (represented as growing degree-days, °Cd). To capture plant development, the L-systems formalism uses rewriting rules that are applied in parallel and simultaneously replace all previous modules in a given string. For details of the language syntax see the cpfg user’s manual in conjunction with the L-studio package from http://algorithmicbotany.org/. A visual example of the growth and development of a chickpea plant (Fig. 1) is shown using the L-studio software version 4.0 (Prusinkiewicz et al., 2000).

In order to calculate the distribution of light under the chickpea canopy, plant models were interfaced with a model of light environment using the formalism of open L-systems (Mech and Prusinkiewicz, 1998). The calculation of light distribution is based on the quasi-Monte Carlo (QMC) method (Lemieux et al., 2004). Paths of photons are traced through the scene, reflected, absorbed and transmitted by the polygons representing the leaflets of chickpea (Fig. 2). Three L-systems were combined to simulate the ability of virtual chickpea plants to intercept light. The main L-system was for switching between chickpea development and the light modelling processes, the chickpea L-system was for plant development, and the light model L-system was for controlling the communication between the chickpea plant and the light computation program QMC. A communication module (Mech, 1997)

![Fig. 1. Side view of a virtual chickpea plant 15 and 60 d after germination, with the in silico thermal time set to 20 °C per day.](https://academic.oup.com/aob/article-abstract/101/9/1311/132757)
was used to send and receive environmental information. The light model processed the received information and returned the new values to the communication module parameters carrying the output from the light model to the virtual sensors. The direction of the light source in the model was set to the x, y and z co-ordinates of 0.5, −0.86, and 0.0, which are the noon co-ordinates of the sun during the autumn (the time of the year when the experiments were conducted) in Brisbane, Queensland, Australia.

It is possible to simulate the light direction for a whole day but this has not yet been built into the current version of the CLES model. The hemispherical reflectance and transmittance of the chickpea leaflets were set to 0.089 and 0.037, respectively, according to previously published data on this topic (Gaumann and Allen, 1973).

In order to simulate the growth of sowthistle plants over time, the amount of light that a sowthistle plant receives had to be calculated on a daily basis. Therefore the main L-system that controls the communication of the light model with the plant models (sub-L-systems 1 and 2) was created. Sub-L-system 1 was the chickpea plant model with its leaflets interfaced with the light model. Sub-L-system 2 was the sowthistle plant model with a virtual sensor. When the virtual sensor (rectangular polygon, Fig. 2) was under full light it sent 100% light availability to the virtual sowthistle. The amount of light availability (%) would decrease if there was a canopy of chickpea (to decrease the light availability to 70 and 50%) and in full sun light (as a control). The phyllochron (Rickman and Klepper, 1995) and bolting time of sowthistle increased when the light availability decreased. In contrast, the number of branches, number of capitula and, consequently, seeds in sowthistle were significantly decreased under reduced light availability.

**CLES model parameterization**

The final CLES model was then parameterized based on data sets collected for various chickpea cultivars. To do this, an experiment was conducted using three replicates of four chickpea cultivars (‘Macarena’, ‘Bumper’, ‘Jimbour’ and ‘90071-1001’). Five chickpea seeds were planted at a depth of 3–4 cm in soil contained in plastic pots (16 cm diameter and 24 cm depth) and arranged adjacent to each other on a glasshouse bench. The soil used was a light-textured loam with a neutral pH. After emergence, only one seedling was kept in each pot and the remainder were removed. The soil was watered to field capacity and was fertilized every other week with 20 mL liquid fertilizer (2-5 g L⁻¹ water soluble NPK, 15:18:12). Plants were monitored every other day using a plant mapping approach (Hanau and Room, 1997) to record their leaf production, number of branches and the appearance of the first flower. At the end of the experiment, 20 leaves from each cultivar were randomly sampled and their leaflet dimensions measured using a ruler.

**CLES model simulation**

The simulated inter- and intra-row spacings between virtual chickpea plants were 20 and 12 cm, respectively. Five rows of virtual chickpea plants were simulated with a virtual sowthistle plant growing in the middle of the 2nd and 3rd rows. The exact position of the sowthistle plant in the simulation could be anywhere between the two rows of virtual chickpea plants, but it should be the same in all the simulations for the sake of comparison. The L-studio software version 4.0 (Prusinkiewicz et al., 2000) was used to interpret and visualize the CLES model.

**CLES model validation**

The above-mentioned chickpea cultivars growing with a sowthistle were used for model validation. The experiment
was designed with four replicates. Seeds of all chickpea cultivars were sown 3–4 cm below the soil surface and seeds of sowthistle were planted onto the surface of the soil. The soil was a light-textured loam with a neutral pH. Sufficient amount of water was supplied to moisten the soil to field capacity and plants were fertilized as described above. The size of the pots used to grow the sowthistle and chickpea plants was 20 cm in diameter and 24 cm in depth. The crop density created was about 40 m\(^{-2}\) with 20 cm inter-row spacing. Two chickpea plants were grown in each pot (12 cm apart) and a 5-d-old sowthistle seedling was placed in the middle of the rows of the chickpea seedlings in a separate pot. In addition, four sowthistle plants (in separate pots) were grown in full light and used as a control treatment with their growth responses being compared to those seen in the treatments (i.e. for features such as bolting time, area of rosette leaves, final height and number of capitula produced). The bolting time of sowthistle plants was recorded and their heights were measured every 10 d using a ruler. The leaf area was measured over time using a sonic digitizer and a ruler. The total number of all capitula on sowthistle plants was counted when all capitula on sowthistle plants was counted when the treatment (i.e. for features such as bolting time, area of rosette leaves, final height and number of capitula produced). The bolting time of sowthistle plants was recorded and their heights were measured every 10 d using a ruler. The leaf area was measured over time using a sonic digitizer and a ruler. The total number of all capitula on sowthistle plants was counted when the plant producing more branches and capitula in the earlier stages was decreased by 58 % (Fig. 5). 'Jimbour' is a cultivar with a long delay in the production of branches and with a long phyllochron (Table 3). 'Macarena' (Table 3, Fig. 3C) was a unifoliate cultivar with a short phyllochron, a short delay in branching and large leaf size that increased the bolting time of sowthistle plants growing under cultivar 'Jimbour' (Fig. 3A) was increased by 5 % (Fig. 4) and the growth index of sowthistle plants was decreased by 58 % (Fig. 5). ‘Jimbour’ is a cultivar with a long delay in the production of branches and with a long phyllochron (Table 3).

Whilst the cultivar ‘Bumper’ (Fig. 3 B) has a long phyllochron as well (Table 3), it has the shortest delay in the production of branches (Table 3). ‘Bumper’ increased the bolting time of sowthistle plants to 720 GDD (Fig. 4). The SGI for this treatment was 65 % lower than that of full light (Fig. 5). ‘Macarena’ (Table 3, Fig. 3C) was a unifoliate cultivar with a short phyllochron, a short delay in branching and large leaf size that increased the bolting time of sowthistle plants to 740 GDD (Fig. 4) and decreased the SGI by as much as 68 % (Fig. 5). In addition, this cultivar had a negative effect on the leaf area produced by sowthistle, as had ‘Bumper’ after 70 d of growth (Table 4). This negative effect on sowthistle was more obvious in the earlier stages in ‘Macarena’ than in ‘Bumper’.

Cultivar ‘99071-1001’ (Table 3) had the shortest phyllochron observed and was the most competitive cultivar (Fig. 3D). The bolting time of sowthistle plants was increased by 15 % and its SGI decreased by 76 % in the presence of this cultivar (Figs 4 and 5). Figure 3E visualizes two growth stages of sowthistle plants under full light, with the plant producing more branches and capitula in comparison with those plants grown under a chickpea
canopy. It can be seen that the bolting time of sowthistle plants (Fig. 4) is the earliest, the SGI (Fig. 5) the highest, and its leaf area (Table 4) also the highest in plants grown under full light. The results of this in silico experiment show that the cultivar ‘99071-1001’ is the most competitive among those examined. The simulated results fell within the spread of the experimental data and the virtual model gave good estimates of the bolting time, the SGI and the leaf area of sowthistle plants growing under different cultivar canopies (Figs 4 and 5, Table 4).

**Sensitivity analysis**

When the virtual chickpea in the CLES model was manipulated for different canopy traits it was found that the plants with the shortest phyllochron, the greatest branch number or the greatest leaflet number per leaf could suppress the growth and development of sowthistle plants (shown here as reductions in sowthistle height) more than chickpea plants with longer stem internodes (Fig. 6). It can be seen that by doubling the length of internodes in virtual chickpea (Table 2), the height of sowthistle was suppressed by 16% (Fig. 6). In addition, when the length of internodes was shortened (Table 2) the suppressive ability of chickpea decreased the height of sowthistle by only 2.5%.

**DISCUSSION**

In order to simulate the effect of different chickpea cultivars on the growth and development of sowthistle plants...
over time, the architectural models of chickpea and sowthistle plants were combined with a light-environment program. The final CLES model integrates a large amount of experimental data (i.e. size of individual organs) measured at frequent time intervals to present the results as images that aid rapid interpretation. One of the advantages of this type of model is that it uses directly measurable morphological traits that can be easily scored and hence used by plant breeders.

The CLES model was used to simulate the effects of different above-ground canopy architectures of chickpea cultivars on the growth and development of sowthistle plants. Sowthistle plant bolting time and growth index (which combines the effect of light on stem elongation and flower production) were used for identifying the most competitive chickpea cultivar among the four studied. Both the in silico simulated and empirical data sets suggested that the most important competitive traits in the chickpea plant are having a short phyllochron, a short delay in branching and a large leaflet size (Table 3 and Figs 3–5). Cultivars with longer internodes also would be more competitive (as reviewed by Lemerle et al., 2001). However, the sensitivity analysis test suggested that other changes (such as leaf size and phyllochron of chickpea) had more effect on sowthistle (Table 2 and Fig. 6). The performance of sowthistle plants was most affected by cultivar ‘99071-1001’ (Fig 3D), a cultivar with a short phyllochron and a short delay in its ability to branch (Table 3). This is also well supported by the results of the sensitivity analysis (Fig. 6). When the phyllochron of the virtual chickpea plant was decreased from 43 to 22 GDD the height of the virtual sowthistle plant was suppressed nine-fold. This reaffirms the significance of early canopy closure in chickepa crops to attain better sowthistle control. The second ranked cultivar for competitive ability in both simulated and observed experiments was ‘Macarena’ (Fig. 3C and Table 4). ‘Bumper’ (Fig. 3B), the third most competitive cultivar (Figs 4 and 5, Table 4), was a plant with a long phyllochron that was compensated for by having a short delay in its ability to produce branches; this was also the shortest cultivar in stature. Having the longest delay in its ability to produce branches, ‘Jimbour’ (Fig. 3A) was the least-competitive cultivar (Figs 4 and 5, Table 4). Thus, it could be seen that the competitive ability of a crop cultivar cannot be described by a single trait and the CLES model may be an invaluable computer tool in helping to find more competitive cultivars from those that are already present. Recently, a study on the weed-suppressing ability of several chickpea cultivars (Paolini et al., 2006) also showed that cultivars with a rapid early growth and an erect canopy architecture were those that were the most competitive. These conclusions were consistent with those of recently published reports on other crops (Williams et al., 2006). It is anticipated that the CLES model could be used as a tool to aid with the direction of plant breeding programs designed to develop more competitive chickpea crops. The model takes into account direct morphological traits and one can see the results immediately. It is worth noting that breeders are unlikely to select a new cultivar solely on its competitive ability, but the CLES will help them notice what the effect of changing a specific architectural characteristic will be on its weed-suppressing capacity.

### Table 4. Observed (mean ± s.e.) and simulated area (cm² plant⁻¹) of rosette leaves of sowthistle plants growing with different chickpea cultivars

<table>
<thead>
<tr>
<th>Treatment*</th>
<th>Treatment</th>
<th>Days after germination</th>
<th>50</th>
<th>70</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed, ‘Jimbour’</td>
<td></td>
<td>1028 ± 14</td>
<td>1378 ± 7.7</td>
<td></td>
</tr>
<tr>
<td>Simulated, ‘Jimbour’</td>
<td></td>
<td>1053 ± 3</td>
<td>1375 ± 5</td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td></td>
<td>24.50</td>
<td>5.40</td>
<td></td>
</tr>
<tr>
<td>Observed, ‘Bumper’</td>
<td></td>
<td>1025 ± 32</td>
<td>1350 ± 12</td>
<td></td>
</tr>
<tr>
<td>Simulated, ‘Bumper’</td>
<td></td>
<td>1038 ± 1</td>
<td>1354 ± 4</td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td></td>
<td>7.00</td>
<td>5.00</td>
<td></td>
</tr>
<tr>
<td>Observed, ‘Macarena’</td>
<td></td>
<td>883 ± 21</td>
<td>1346 ± 10</td>
<td></td>
</tr>
<tr>
<td>Simulated, ‘Macarena’</td>
<td></td>
<td>975 ± 3</td>
<td>1350 ± 2</td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td></td>
<td>60.20</td>
<td>7.10</td>
<td></td>
</tr>
<tr>
<td>Observed, 99071–1001</td>
<td></td>
<td>811 ± 4.27</td>
<td>1290 ± 10.8</td>
<td></td>
</tr>
<tr>
<td>Simulated, 99071–1001</td>
<td></td>
<td>830 ± 1</td>
<td>1282 ± 2</td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td></td>
<td>20.00</td>
<td>5.70</td>
<td></td>
</tr>
<tr>
<td>Observed, Control (full light)</td>
<td></td>
<td>1245 ± 41.7</td>
<td>1562.5 ± 66.9</td>
<td></td>
</tr>
<tr>
<td>Simulated, Control</td>
<td></td>
<td>1230 ± 2</td>
<td>1400 ± 1</td>
<td></td>
</tr>
<tr>
<td>RMSE</td>
<td></td>
<td>54.00</td>
<td>70.55</td>
<td></td>
</tr>
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</table>

* RMSE: root mean-square error.
The potential power of the CLES model becomes more obvious when we consider using it to simulate the effect of different combinations of cultural practices, such as different relative times of weed emergence, crop seeding rate, crop row spacing and choice of cultivar (as shown above) on the performance of weeds in different environments (examples can be found in Cici, 2007). Crop density can be modelled by incorporating chickpea response to intra-specific density and changing the parameters that control the seeding rate and the row spacings in the model. The choice of cultivars can be modelled by changing model parameters such as the phyllochron, delay of branching, the size of leaflets and the length of internodes (as shown above). Environmental effects (such as those due to temperature) can be modelled by changing the growing degree-days the model uses.

The sensitivity analysis can help to assess how much change in an architectural trait would be significant to improve its competitive ability. However, in real plants a single trait is determined by its physical links with others. This physical linkage of traits does not easily allow for an independent plant breeding changes to be made (Bastiaans et al., 1997). Models are simplified versions of the real world in which all the physical linkages are not well known, so models cannot completely account for certain kinds of side effects. This can be seen in the chickpea cultivars examined here; when the phyllochron was longer, plants had a shorter delay in branching (such as ‘Bumper’), and when they had larger leaflets their numbers were fewer (such as ‘Macarena’).

The present work provides a computer-modelling approach to help improve our understanding of weed suppression by crop canopies through different in silico experiments. Selection of more competitive cultivars will help ensure better weed suppression in an IWM program and ultimately reduce the need for herbicide application. The sensitivity analysis can help to assess how much change in an architectural trait would be significant to improve its competitive ability. However, in real plants a single trait is determined by its physical links with others. This physical linkage of traits does not easily allow for an independent plant breeding changes to be made (Bastiaans et al., 1997). Models are simplified versions of the real world in which all the physical linkages are not well known, so models cannot completely account for certain kinds of side effects. This can be seen in the chickpea cultivars examined here; when the phyllochron was longer, plants had a shorter delay in branching (such as ‘Bumper’), and when they had larger leaflets their numbers were fewer (such as ‘Macarena’).

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The long computation time required to run the simulations is a limiting factor in the present model (depending on the age of plants, each simulation takes about 2.5–4.0 h to produce the visualizations and numerical outputs) but advances in grid computing (Berman et al., 2003) are quite promising, as they allow larger number of simulations to be run in a shorter time. Indeed, by using a grid-computing approach it may be possible to test hundreds of ‘what if’ scenarios in just a few hours. A program such as Nimrod (http://www.csse.monash.edu.au/~davida/nimrod/index.htm; Lee et al., 2006) could be used to distribute the simulations over the grid.

There is no limit to the application of computer models, in conjunction with field experiments, in addressing agricultural and weed science problems. However, developing realistic architectural models of plants is a tedious task since it needs extensive experimental data over time. This present research forms the basis of an architectural plant modelling approach that would enable a weed researcher or breeder to conduct in silico experiments before stepping out into the field (Hanan and Room, 1997). In other words, it can help one make a better experimental design and try different experimental combinations before conducting an actual experiment in the field.

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### LITERATURE CITED


