# Modelling the population dependence of canopy development and biomass partitioning of field peas (Pisum sativum L.) 

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#### Abstract

In developing a pea crop model, the green area of the leaf canopy was calculated as the sum of the leaf area of all the nodes on all the stems of an average plant, multiplied by the plant population. The effects of plant population were defined in terms of its effects on stem branching, leaf area expansion per node on each stem and biomass partitioning. Decreases of the average number of stems per plant and the harvest index with increasing population were modeled using arctangent functions by specifying their average and maximum values, their sensitivity coefficient to population change and the most sensitive population. Simulations of canopy development, biomass accumulation and biomass partitioning to seed with the model produced results that closely matched measurements from a field experiment with peas grown at populations of 50,100 and 150 plants per $\mathrm{m}^{2}$.


## Key words

pea model, plant population, main stems, branching stems, leaf area per node, arctangent function

## Introduction

Accurate simulation of canopy development and biomass partitioning is vital in models for predicting crop growth and yield. Both features depend on plant population in field pea crops. This paper reports our methods in modelling the response of canopy development and biomass partitioning to plant population of field peas grown under ample water and nutrient conditions. This is a part of project aiming to develop a crop-soil interaction model for simulating pea growth and yield in variable environmental conditions.

## Methods

The model was developed using information from field peas that were grown in an experiment with three replicates of three plant populations ( 50,100 and 150 plants per $\mathrm{m}^{2}$ ). The cultivar 'Primo' was sown on 23 December 1997 in a deep (>1.6 m), free-draining silt loam soil (Udic Ustochrept, USDA Soil Taxonomy) at Lincoln, New Zealand. The crop was managed intensively, with enough fertilizer and irrigation to minimise the risk of nutrient and water deficits and best management practices for peas to achieve good weed, pest and disease control.

The crops were sampled regularly during growth. Measurements on each occasion included the number of nodes on the main stem, number of branches and number of nodes on each branch, leaf area per node, and above-ground biomass and its partitioning into leaf, stem, pod and seed components. Radiation interception was measured regularly with a ceptometer. The node of first flower and times of leaf senescence from lower nodes were also observed.

## Model description

The model Peasius was developed to simulate the growth and development of a pea crop from sowing until maturity using a similar approach to the companion Sirius wheat model (Jamieson et al., 1998). It calculates the potential growth and development of a pea crop without any resource limitations as a baseline, and the potential is reduced to actual by simulating the effects of resource deficits. The model has a daily time step consisting of four processes carried out sequentially:
(1) Weather/soil update. Solar radiation, rainfall, and maximum and minimum and temperatures are updated. Soil is not reported here because it is assumed there is no water limitation.
(2) Canopy development. A pea plant may have zero to several branch stems in addition to the main stem. Each stem produces a series of nodes, and each node develops leaf area. The leaf area index (LAI) at a given time is the sum of the leaf area of all the nodes on all the stems of an average plant, multiplied by plant population.
(3) Phenological development. The crop emerges when the accumulation of thermal time (TT) from sowing reaches a fixed value (EMG, ?C days) above a base of 4.5?C (Wilson and Robson, 1996). Thereafter nodes appear at a constant rate in thermal time ( $\mathrm{R}_{\text {node }}$, node per ?C days) on the main and branch stems until the final node number (FNN) is attained. Therefore, the number of nodes at any time after emergence is $\mathrm{N}_{\text {node }}=\mathrm{TT} ? \mathrm{R}_{\text {node }}$. The node of first flower (NFF) is reached during this period of node production. The crop reaches physiological maturity (LAG, ?C days) after the appearance of the final node.
(4) Biomass accumulation and partitioning. The biomass is calculated as the product of the daily intercepted total solar radiation and radiation use efficiency (RUE): $\Delta$ biomass = RUE ? Radiation ? (1-e ${ }^{0.45^{*} \text { LAl }}$ ), where the value of RUE is $1.1 \mathrm{~g} / \mathrm{MJ}$ (Jamieson et al., 1984; Wilson et al., 1985) and 0.45 is an extinction coefficient. The biomass is partitioned to stems, leaves and pods (husk and seeds), as described below.

## Canopy development

The responses of canopy development are defined in terms of the effects of plant population on stem branching and leaf area expansion per node.
(1) Branching. The maximum stem number of a pea plant is a cultivar trait, and the average attainable stem number $\left(S_{p}\right)$ at a specific plant population $(P)$ is calculated as:

$$
\begin{equation*}
S_{p}=\left(S_{\max }+1\right) / 2-\left\{\left(S_{\max }-1\right) / \pi ? \text { Arctangent }\left[\left(\alpha ?\left(P-P_{m}\right) / P_{m}\right)\right]\right. \tag{1}
\end{equation*}
$$

where $S_{\max }$ is the asymptote of the average stem number of the cultivar at a low population (i.e. no interplant competition), $\mathrm{P}_{\mathrm{m}}$ is the population at which the stem number is the most sensitive to population change (inflection point of the curve in Figure 1), and $\alpha$ is the sensitivity coefficient ( $\alpha=0$ means independent of population). If $S_{p}$ is bigger than one for a cultivar at a specified population, the second stem will appear after a stem delay number (SDN) node on the main stem, and the third stem starts growing at one node after that, and so on. So the stem number $\left(S_{n}\right)$ of a pea plant at a given time is calculated as $S_{n}=N_{\text {node }}-S D N+1$. The nodes on branching stems also develop at the rate of $R_{\text {node }}$.


Figure 1. Response of average stem number per plant to population. For the example cultivar, the most sensitive population ( $\mathrm{P}_{\mathrm{m}}$ ) is 80 plants $/ \mathrm{m}^{2}$, a typical agronomic population, the attainable stem number ( $\mathrm{S}_{\max }$ ) is 2.2 and the sensitivity coefficient $(\alpha)$ is 2.5 . 'Measured' indicates the average stem numbers in the experimental crops.
(2) Leaf area. The leaf area per node at a given time is calculated as the result of the leaf area expansion at the node (LAPN) and leaf lost by senescence from the node (LSPN).

LAPN is the accumulation of daily leaf growth ( $\triangle$ LAPN ) which is determined by the potential leaf area per node (PLAPN), leaf area growth rate ( $R_{\text {leaf }}$, found as $0.6 ? R_{\text {node }}$ per ?C days), the daily thermal time $\Delta T T_{d}$, as well as a population factor $\left(F_{p}\right)$ :

$$
\begin{equation*}
\Delta L A P N=R_{\text {leaf }} ? \Delta T T_{d} ? P L A P N ? F_{p} \tag{2}
\end{equation*}
$$

where PLAPN is a cultivar trait, determined by a maximum and an average leaf area (MLA and ALA) and the position of the node on the stem $\left(\mathrm{N}_{\mathrm{pos}}\right)$ using a quadratic function:

$$
\begin{gather*}
\mathrm{PLAPN}=\mathrm{MLA}+12(\mathrm{ALA}-\mathrm{MLA})\left[\left(\mathrm{N}_{\mathrm{pos}}-\mathrm{FNN} / 2\right) / \mathrm{FNN}\right]^{2} \text {, and }  \tag{3}\\
\mathrm{F}_{\mathrm{p}}=1+\mathrm{k} ?\left(\left(\mathrm{P}_{\mathrm{m}}-\mathrm{P}\right) / \mathrm{P}_{\mathrm{m}}\right) \tag{4}
\end{gather*}
$$

where $P_{m}$ is the average population ( 80 plants $/ \mathrm{m}^{2}$ ) and $k$ is the dependent factor ( $0 \sim 1$ ).
LSPN depends on the age of leaf on a node ( $\mathrm{TT}_{\text {leaf, }}$ ?C days) and crop physiological stage. Leaf at a node starts to senescence at a rate of $R_{\text {sene }}\left(\mathrm{cm}^{2} /\right.$ ?C days) after its age reaches its life span (TTS) or when the crop is physiologically mature. In addition, the leaf senescence is deemed accelerated by 1.5 times after crop reaches physiological maturity.

$$
\begin{equation*}
\mathrm{LSPN}=\left(\mathrm{TT}_{\text {leaf }}-\mathrm{TTS}\right) ? \mathrm{R}_{\text {sene }} \quad \text { (when } \mathrm{TT}_{\text {leaf }}>\mathrm{TTS}, \text { or after PM) } \tag{5}
\end{equation*}
$$

(3) LAI. The LAI at a given time is the sum of the leaf area of all the nodes on all the stems of an average plant, multiplied by plant population:

$$
\begin{equation*}
\text { LAI }=\sum_{\text {Mnnaie }}(L A P N-L S P N) \times \text { Population } \tag{6}
\end{equation*}
$$

## Biomass partitioning

The daily biomass increment is partitioned into stems, leaves or pods depending on crop phenological stage, and the pod biomass is re-partitioned into seeds and husk. The fraction of biomass partitioned to pods (pods index, Pl ) decreases with increasing plant population $(\mathrm{P})$ following the function:

$$
\begin{equation*}
\mathrm{PI}=\mathrm{PI}_{\mathrm{m}}-\left\{2 ?\left(\mathrm{PI}_{\max }-\mathrm{PI}_{\mathrm{m}}\right) / \pi ? \operatorname{Arctangent[\alpha ?(\mathrm {P}-\mathrm {P}_{\mathrm {m}})/\mathrm {P}_{\mathrm {m}}]\} ,~}\right. \tag{7}
\end{equation*}
$$

where $\mathrm{PI}_{\text {max }}$ is the asymptote of the PI which determines the maximum a cultivar can reach at the lowest population (i.e. no inter-plant competition), $\mathrm{P}_{\mathrm{m}}$ is the population at which Pl is most sensitive to population change (inflection point of the curve in Figure 2), and $\mathrm{PI}_{\mathrm{m}}$ is the PI when population is $\mathrm{P}_{\mathrm{m}}$.


Figure 2. Response of the fraction of biomass partitioned to pods ( P ) to plant population. For the example cultivar, the most sensitive population $\left(\mathrm{P}_{\mathrm{m}}\right)$ is 80 plants $/ \mathrm{m}^{2}$, the maximum asymptote fraction ( $\mathrm{PI}_{\text {max }}$ ) is 0.8 , the mean fraction $\left(\mathrm{PI}_{\mathrm{m}}\right)$ is 0.45 and the sensitivity coefficient ( $\alpha$ ) is 2.0. 'Measured' indicates the fraction measured in the experimental crops.

The partitioning of biomass to pods starts after the appearance of the NFF, but mainly after the FNN. The partitioning rules are defined according to phenological stages as follows:

- From emergence to NFF, 0.6 of new daily biomass is partitioned to stems and the rest goes to leaves.
- From NFF to FNN: the fraction of new daily biomass partitioned to pods increases linearly from 0 to 0.2 ? PI, 0.6 of the rest is partitioned to stems and the remainder goes to leaves.
- From FNN to physiological maturity, PI fraction of the new daily biomass is partitioned to pods as well as a portion of the vegetative biomass during the LAG period after FNN appearance ( $\mathrm{B}_{\mathrm{fn}}$ ). The latter is calculated as ( PI ? $\mathrm{B}_{\mathrm{fn}}-$ Pod $_{\mathrm{f}_{\mathrm{f}}}$ ) ? $\Delta \mathrm{T}_{\mathrm{d}} / \mathrm{LAG}$, where Pod $_{\mathrm{f}_{\mathrm{n}}}$ is the pod biomass at FNN appearance. Then, the ( $\left.1-e^{-0.004 ? \text { TTt }}\right)$ proportion of pod biomass is partitioned into seeds, where $\mathrm{TT}_{\text {fn }}$ is the thermal time after FNN appearance.
Results
Model simulation results closely matched corresponding values from the field experiment at populations of 50, 100 and 150 plants per $\mathrm{m}^{2}$ in terms of canopy development (Figure 3) and biomass accumulation (Figure 4). The simulated biomass was slightly higher than that measured at a population of 150 plants $/ \mathrm{m}^{2}$, but the simulated biomass and seed yields matched well around the typical agronomic population ( 80 plants $/ \mathrm{m}^{2}$ ).


Figure 3. Simulated versus measured leaf area index of the pea crops at three plant populations.


Figure 4. Simulated versus measured (a) biomass and (b) seed yield of the experimental pea crops at three plant populations (Legend is the same as in Figure 3).

## Conclusions

Stem branching and harvest index (though biomass partitioning to pods) both increase as plant population decreases in peas. With these increases predicted using our arctangent functions, simulations of canopy development and biomass and grain accumulation matched well with measurement values from the crops.

Results from the experiments showed that the leaf area per node (LAPN) on main stems increases with decreasing population and that the LAPN on the branches is generally smaller than that on main stems. The proportion of nodes with smaller LAPN also increases together with branch number as population decreases. As these two effects compensated, the average LAPN of a pea plant did not change with population (i.e. $F_{p}=1$ ). The LAI simulation confirmed this result, but the details and mechanism of determining the difference between LAPN on main and branching stems needs to be investigated and simulated, possibly from the point of photosynthate availability and allocation. Also, the model needs to be generalised by comparing predictions with measurements from more crops with different cultivars sown at various populations and sowing times.

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