

Modeling Leaf Production and Senescence in Chickpea

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ABSTRACT

Quantitative information regarding leaf area development in chickpea (*Cicer arietinum* L.) is scarce. Data from four field experiments with a range of treatments including genotype, sowing date and plant density across 4 location-season combinations were analyzed to quantify main effects of temperature, photoperiod and plant population density on plant leaf area in chickpea. All experiments were conducted under well-watered conditions. Maximum rate of main stem node development was 0.72 nodes d⁻¹. Cardinal temperatures for node appearance were found as 6.0, 22.2 and 31.0 °C for base, optimum and ceiling temperatures, respectively. Plant density had no effect on cardinal temperatures for leaf appearance and phyllochron. Leaf senescence on the main stem started when the main stem had about 12 nodes and proceeded at a rate of 1.67% per each day increase in physiological day (a day with non-limiting temperature and photoperiod). Leaf production per plant versus main stem node number occurred in two phases; phase 1 when plant leaf number increased with a slower and density-independent rate (3 leaves per node), and phase 2 with a higher and density-dependent rate of leaf production (8-15 leaves per node). A close relationship was found between the fraction of senesced leaves per plant and the same fraction on the main stem. The average leaf size per plant increased from 4 cm² when there were 10 nodes on the main stem and stabilized at 10.8 cm² when there were 21 nodes on the main stem. Plant density and sowing date did not affect leaf size. Plant leaf area was also predictable directly from main stem node number. The relationships found in this study can be used in simulation models of chickpea.

Keyword: Leaf area development; Leaf senescence; Node appearance; Temperature; Model.

INTRODUCTION

Crop simulation models that predict plant growth, water use and yield are being used to understand the response of crops to the dynamics of climate-plant-water systems, to evaluate physiological traits for genetic yield improvement and to help make decisions that optimize use of available resources (Boote et al., 1996; Sinclair and Seligman, 1996; Hammer, 1998; Soltani et al., 2000; Soltani et al., 2001).

The ability to predict leaf area development is crucial for crop simulation models. Prediction of leaf area index is required to estimate interception of solar radiation and biomass production. It is also an important determinant of the partitioning of evapotranspiration between evaporation and transpiration.

Leaf area development involves the appearance of new leaves, expansion of newly emerged leaves and the senescence of old leaves (Hofstra et al., 1977; Ranganathan et al., 2001). Temperature can affect plant leaf area via its effects on rate of leaf appearance, on the rate and duration of individual leaf expansion, and on leaf senescence (Craufurd et al., 1997). Temperature and photoperiod can also regulate leaf area via their effects on the duration of leaf production period (Hammer et al., 1993). A range of approaches exist: from those dealing with appearance, expansion and senescence of individual leaves (e.g., Hofstra et al., 1977) to those predicting leaf area at the whole plant or crop level (e.g., Sinclair, 1984). Some others take a middle approach (e.g., Robertson et al., 2002).

There are no reports in the literature analyzing leaf area development in chickpea (*Cicer arietinum* L.) for the purpose of crop modeling except for the results of a 1-year study with only 2 treatments (sowing date) presented by Robertson et al. (2002). Furthermore, the effect of plant density has not been reported. Therefore, the objectives of this research were (1) to develop functional relationships to quantify main effects of temperature, photoperiod and plant population density on plant leaf area in chickpea, and (2) to evaluate the stability of the relationships and their parameters across different environmental conditions and agronomic practices. The present paper is a part of a comprehensive study (Soltani et al., 2004; Soltani et al., 2005; Soltani et al., 2006abc) aimed at improving chickpea modeling capabilities (Soltani et al., 1999; Robertson et al., 2002).

MATERIALS and METHODS

Field Experiments

Four experiments were conducted in the field to gather the data required for this study. Three of the four experiments were carried out at the Gorgan University of Agricultural Sciences Research Farm, Gorgan (36° 85' N, 54° 27' E and 100 m asl), and one experiment was conducted at Gonbad Agricultural Research Station, Gonbad (34° 21' N, 55° 10' E and 37 m asl), both in Iran. The soil was a deep silty loam (fine-silty, mixed, active, thermic, Typic Calcixerolls) at both sites. Some details about the experiments and weather conditions during the experiments are given in Table 1 and 2, respectively.

All the experiments were conducted under well-watered conditions. The plots were irrigated after 60-mm cumulative pan (class A) evaporation and irrigation amount was based on soil moisture depletion. Therefore, there was no effect of flooding or water deficit stresses. In all the experiments weeds were hand-controlled and if necessary appropriate chemicals were applied against *Ascochyta* blight (*Ascochyta rabiei*), fusarium diseases (*Fusarium* spp.), podworm (*Heliothis armiger*), leaf miner (*Liriomyza congesta*) and *Paramacella* spp., so the effect of diseases and pests were minimal. All experiments were over-sown at the correct spacing and thinned to desired density after emergence.

In the first experiment (Exp. 1) four chickpea cultivars (Beauvanij, 90-96c, Hashem and Jam – *kabuli* type) were sown at 11 sowing dates from December 2001 to August 2003 (details in Soltani et al., 2006b). For this study, main stem node number and total number of leaves per plant were measured on two cultivars (90-96c and Hashem) on only two sowing dates of 18 May and 17 June 2002.

The second experiment (Exp. 2) was conducted in Gonbad. The experimental design was single split plot with sowing dates in the main plot and plant densities in the sub plot, replicated four times. Plot size was 1.75 m (7 rows) by 7.0 m, row spacing of 25 cm and different intra-row spacings to achieve population densities of 15, 30, 45 and 60 plants m⁻². Chickpea cultivar was Hashem, a local cultivar.

The third (Exp. 3) and the fourth (Exp. 4) experiments were again conducted in Gorgan with the treatments as in Exp. 2, but the experimental design was a factorial arrangement of treatments based on a randomized complete block with four replicates. In Exp. 3, plot sizes were 6 m long with a row spacing of 25cm and included 20, 12, 10 and 8 rows for plant densities of 15, 30, 45 and 60 plants m⁻², respectively. In Exp. 4, plot sizes were 7 m long with inter-row spacing of 30 cm and included 16, 10, 8 and 7 rows for plant densities of 15, 30, 45 and 60 plants m⁻², respectively.

The chosen sowing dates in the field experiments do not necessarily reflect common practices, but were selected to create different growth environments with a range of temperature, photoperiod and solar radiation. December is the most common sowing date for chickpea in Gorgan and Gonad, but sometimes sowing might occur in late November, January and February.

Measurements

In all experiments, stages of development of emergence, flowering, first pod, beginning of seed growth (first-seed), first-maturity and full-maturity were recorded every 1-2 days (Fehr and Caviness, 1977; Soltani et al., 2006b).

Measurements regarding leaf production and senescence were the total number of nodes on main stem, the number of nodes on main stem with senesced leaves, the total plant leaf number (green + senesced), the number of primary, secondary and tertiary branches, and plant leaf area. Not all characteristics could be measured in all experiments. The measurements taken in each experiment and the frequency of the measurements are presented in Table 1. In Exp. 1 and 2, the measurements were conducted on 10 tagged plants, but in other experiments the measurements were done on 10 plants separated from bigger samples including 20-30 plants. Mean of the 10 plants measured was considered as an observation.

A leaf was counted when its leaflets were unfolded and a green leaf was considered a leaf with >50% green area. The number of fallen leaves was counted based on visible leaf scars. Leaf area was measured using an electronic planimeter (delta T devices).

In all experiments, daily maximum and minimum temperatures, sunshine hours and rainfall were measured at a standard weather station located a few meters (Gorgan) to a few hundred meters

(Gonbad) from the experimental units. Solar radiation was calculated from sunshine hours and extraterrestrial radiation. Photoperiod for each day was calculated from latitude and calendar day and included allowance for civil twilight when solar angle $\geq -4^\circ$ (Keisling, 1982; Soltani et al., 2006b).

Analysis

The data were analyzed based on functional and allometric relationships between environmental variables (mainly temperature and photoperiod) and plant leaf area determinants. The appropriate relationships were captured from published work (Sinclair, 1984; Hammer et al., 1993; Robertson et al., 2002) when available or were developed when necessary. When there was no appropriate relationship, it was found by (1) examining scatter plots between the two considered variables, (2) fitting of promising equations to the data, and (3) selecting the most appropriate equation based on its simplicity and statistics such as coefficient of determination (R^2) and root mean square of deviations (RMSD). When possible, one equation was fitted to all data or a part of data rather than just a given treatment.

Physiological day per calendar day (PD_t) was calculated as (Soltani et al., 2006b):

$$PD_t = f(T) f(PP) \quad (1)$$

where $f(T)$ is the temperature function and $f(PP)$ the photoperiod function. The $f(T)$ and $f(PP)$ were computed using dent-like and quadratic functions, respectively, as indicated by Soltani et al. (2006b). From sowing to emergence and from flowering to maturity, the value of $f(PP)$ was fixed at 1, indicating no effect of photoperiod for these stages (Soltani et al., 2006b). Cumulative values of PD_t were used in present study. For example, starting at Stage 1, physiological days are accumulated until a threshold is reached. At this time, Stage 2 is predicted to occur. The threshold value is the physiological day requirement of Stage 1 to 2, that is, the minimum number of days from Stage 1 to 2 under optimal conditions for development.

Thermal day was also calculated from Eq. (1) by fixing $f(PP)$ at 1 for all phenological stages. Thermal day is a normalized form of thermal time.

RESULTS and DISCUSSION

Node Appearance and Senescence on Main Stem

The changes of main stem node number versus time, cumulative thermal day and physiological day were describable using a non-linear, segmented regression model. The segmented model consists of two intersecting lines, a sloping line for the linear increase in node number and a horizontal line, which determines maximum node number on the main stem (Fig. 1):

$$\begin{aligned} y &= a + bx & \text{if } x < x_o & \\ y &= a + b x_o & \text{if } x \geq x_o & \end{aligned} \quad (2)$$

where y is the main stem node number, x the time, thermal day or physiological day after sowing, a the intercept with the vertical axis ($x = 0$), b the rate of linear increase in node number (node d^{-1}), x_o the time of cessation of the linear increase in node number and $a + bx_o$ represents maximum node number on main stem. Eq. (2) was used to obtain estimates of the time of cessation of effective node production on main stem (TLG) and the maximum number of nodes on main stem. Using physiological day resulted in more stable estimates of x_o (data not shown). The sudden cessation of node production is a simplified but a satisfactory approximation of the data (Fig. 1). In some cases, a few nodes were produced after TLG, but in many cases no node was produced after the time. The calendar time from emergence to TLG was found and considered as an effective period of node production (ENPP). The linear increase in main stem node number versus thermal time has been reported in chickpea (Robertson et al., 2002), fababean (Dennett et al., 1979; Turpin et al., 2002), soybean (Sinclair, 1984) and pigeonpea (Ranganathan et al., 2001). However, Stutzel and Aufhammer (1991) reported that in fababean a quadratic equation best described this increase.

Estimates of TLG were stable for each experiment (Table 3). They averaged 39.8 physiological days for Exp. 1, 37.5 for Exp. 2, 36.4 for Exp. 3 and 38.0 for Exp. 4. Average across all experiments TLG was 38.0 physiological days, which was mid way between flowering and first-pod stages (Soltani et al., 2006b). Node production after TLG mainly depends on the carbon and nitrogen balance within the plant and the availability of extra assimilates for leaf production on the main stem. At each sowing date, the difference between cultivars in Exp. 1 and between plant densities in other experiments for ENPP was not considerable, but the difference was considerable between sowing dates (Table 3). Similarly, difference between cultivars in Exp. 1 and between plant densities in other experiments for maximum node number was not considerable. There was a significant correlation coefficient ($r = 0.44$; $P = 0.05$) between ENPP and maximum node number. The small difference between plant densities at each sowing date for TLG, ENPP and maximum node number is due to accelerated phenological development with increase in plant density.

For each treatment of Exp. 1 to 4, the rate of node appearance on main stem (d^{-1}) was calculated by dividing maximum node number by ENPP. Then, cardinal temperatures for leaf appearance were obtained by fitting the below model to data of node appearance rate versus mean temperature during ENPP (Fig. 2):

$$\begin{aligned}
 y &= 0 & \text{if } T \leq T_b \text{ or } T \geq T_c & & (3) \\
 y &= (T - T_b)/(T_o - T_b) R_{max} & \text{if } T_b < T \leq T_o & \\
 y &= (T_c - T)/(T_c - T_o) R_{max} & \text{if } T_o < T < T_c &
 \end{aligned}$$

where y is node appearance rate, T the temperature, T_b the base temperature, T_o the optimum temperature, T_c the ceiling temperature and R_{max} the maximum rate of node appearance at optimum temperature. A total of 94% of variation in node appearance rate was explained by Eq. (3). The

estimated cardinal temperatures were 6.0, 22.2 and 31.0 °C for base, optimum and ceiling temperatures, respectively. According to Eq. (3) and its parameter estimates, phyllochron (thermal time period between emergence of successive leaves) in chickpea cv. Hashem is 23.8 °Cd. This value has been reported as 42 °Cd for cowpea (Craufurd et al., 1997), 55.6 °Cd for soybean (Sinclair, 1984), 71.4 °Cd for vigna (Pengelly et al., 1999), 56 °C d for peanut (Leong and Ong, 1983), 100 °Cd for mungbean (Robertson et al., 2002), 31.5 °Cd for pigeonpea (Ranganathan et al., 2001) and 54 °Cd for fababean (Turpin et al., 2002). For chickpea the phyllochron number of 46 °Cd has been reported by Robertson et al. (2002), which is significantly higher than the value found here. This difference is a result of higher base temperature in the current study (6 vs. 0°C). However, the data of Robertson et al. (2002) indicate an R_{max} value of 0.65 node d⁻¹ which is comparable with 0.73 node d⁻¹ found here.

The base temperature of 6 °C is significantly different from a base temperature of 0 °C for leaf appearance reported for chickpea (Siddique and Sedgley, 1986), base temperature of 4.5 °C for emergence (Soltani et al., 2006a) and base temperature of 0 °C for development rate (Soltani et al., 2006b) reported for the same cultivar. The optimum temperature of 22 °C falls within the optimum temperature range of 20-29 °C for emergence (Soltani et al., 2006a) and 21-32 °C for development rate (Soltani et al., 2006b). The ceiling temperature of 31 °C is significantly lower than ceiling temperature of 40 °C verified for emergence rate and development rate towards flowering (Soltani et al., 2006ab).

No significant effect of plant density on cardinal temperatures and phyllochron, and similarity of the cultivars with respect to node production on main stem found in the present study (Table 3, Fig. 2), is in agreement with previous studies in fababean (Stutzel and Aufhammer, 1991; Turpin et al., 2002) and pigeonpea (Ranganathan et al., 2001).

The availability of assimilates can affect node appearance and leaf production (Stutzel and Aufhammer, 1991). The decline in node appearance rate with temperature increase over 22 °C might be due to limitation of assimilates for leaf growth.

Based on the results presented here, node production on the main stem can be simulated as influenced by temperature, photoperiod and assimilate availability. Photoperiod and temperature determine the time available for node production (TLG and ENPP) and the rate of node production during this period is determined by temperature. Further studies are needed to reveal the genotypic differences for cardinal temperatures of leaf appearance and R_{max} .

Examination of the fraction of senesced nodes on main stem (ratio of senesced to total nodes) versus thermal day and physiological day in Exp. 2, 3 and 4 indicated that the fraction follows the below model (Fig. 3):

$$\begin{array}{ll}
 y = 0 & \text{if } x \leq x_o \\
 y = b(x - x_o) & \text{if } x > x_o
 \end{array} \tag{4}$$

where y is the fraction of senesced node on main stem, x the thermal day or physiological day, x_o the time when senescence starts on main stem ($^{\circ}\text{Cd}$ or physiological day) and b the rate of increase in the fraction per unit increase in thermal day or physiological day. While there were some differences between sowing dates and densities with respect to b and x_o , these differences were not significant based on 99% confidence intervals of the parameters in each experiment (Table 4). Using physiological day compared to thermal day resulted in higher R^2 , but the differences were not great. Leaf senescence on the main stem started after 15 physiological days (equivalent to 36 thermal days, 756 $^{\circ}\text{Cd}$ and about 12 nodes on the main stem) and proceeded by 1.67% per each day increase in physiological day. Roberson et al. (2002) in their chickpea model (APSIM-chickpea) assumed that leaf senescence on main stem occurs as a linear function of thermal time after flowering and each node senesces after accumulation of 47 $^{\circ}\text{Cd}$.

Leaf Production and Senescence Per Plant

Leaf production and senescence per plant has been related to leaf production and senescence on the main stem (Leong and Ong, 1983; Hammer et al., 1993; Ranganathan et al., 2001; Robertson et al., 2002). Evaluation of data from Exp. 1 and 2 showed that leaf production per plant follows a 2-phase segmented model, which separates leaf production per plant into distinct phases; phase 1 when plant leaf number increases at a slower rate and phase 2 with a higher rate of leaf production per plant. Mathematically, the model may be expressed as (Fig. 4a):

$$\begin{aligned} y &= b_1 x & \text{if } x \leq x_o & \\ y &= b_1 x_o + b_2(x - x_o) & \text{if } x > x_o & \end{aligned} \quad (5)$$

where y is the total (green and senesced) number of leaves per plant, x the number of nodes on main stem, x_o the turning point between the two phases of leaf production, b_1 the rate of increase in plant leaf number in phase 1, and b_2 the same as b_1 for phase 2 of leaf production.

Parameter estimates of Eq. (5) for Exp. 2 are presented in Table 5. Leaf production rate in phase 1 was 3 leaves per node across plant densities. Plant density did not affect rate of leaf production in phase 1 probably because the plants are small and competition is still minimal. In phase 2, rate of leaf production ranged between 8 and 15 leaves per node (Table 5). This rate decreased linearly with increase in plant density up to 41 plants m^{-2} and then stabilized (Fig. 4b).

In Exp. 1, Eq. (5) also adequately described changes of plant leaf number versus main stem node number (data not shown). There was no significant difference between cultivars in each sowing date and estimates of x_o , b_1 and b_2 were 15.1, 2.12 and 7.82 for sowing on 8 May 2002 and 14.7, 1.62 and 2.24 for sowing on 17 June 2002. There was no significant difference between sowing dates in Exp. 1 and between Exp. 1 and 2 for x_o , b_1 and b_2 based on their 99% confidence intervals, except for b_2 at sowing date of 17 June 2002. The significantly lower value of b_2 for this sowing date was likely due to high temperatures (Table 2) and shortage of assimilates for leaf growth.

The increased rate of leaf production in phase 2 was related to the appearance of primary and secondary branches (Fig. 5). The branching pattern was similar for the 3 sowing dates and 4 sowing densities in Exp. 2; production of primary branches began after appearance of 2 nodes on the main stem and stopped when 3 primary branches had emerged. Then, after the appearance of 13-16 nodes on main stem, a second phase of branching started with a faster rate of appearance of primary and secondary branches. The number of secondary branches was approximately twice of the number of primary branches. Density had a major effect on branching; probably via assimilate availability, although the difference between plant densities of 45 and 60 was not significant. The number of tertiary branches was negligible.

In chickpea, a similar pattern of plant leaf production versus main stem node number has been reported by Robertson et al. (2002), but they assumed that in phase 1 plant leaf number was equal to main stem node number (3 here). They reported a leaf production rate of 13.4 leaves per node for phase 2 of leaf production at a plant density of 28 plants m^{-2} , which is comparable to the rate (11.0) found here for density of 30 plants m^{-2} (Table 5).

The fraction of senesced leaves per plant (ratio of senesced to total leaves) versus the same fraction on main stem in Exp. 2 also followed Eq. (5) (Fig. 6). The fraction of senesced leaves per plant increased 0.57% per each percent increase in fraction of senesced leaves on main stem until the fraction was less than or equal to 0.67 on main stem (equivalent to 55 physiological days, mid-way between beginning of seed growth (45) and R7 (67); Soltani et al., 2006b). After this, each percent increase in the fraction of senesced leaves on main stem resulted in a 1.88% increase in the fraction of senesced leaves per plant. There was no significant difference between sowing dates and densities (Fig. 6). In APSIM-chickpea, the rate of leaf senescence per plant is related to the number of senesced leaves on main stem (Robertson et al., 2002); senescence of each leaf on main stem results in senescence of 2% of plant leaves, obtained by calibration of the model against the observed post-flowering decline in leaf area. In pigeonpea, a close relationship has been reported between the fraction of senesced leaves per plant and the number of senesced leaves on main stem (Ranganathan et al., 2001).

Leaf Size

In this study, leaf size was not measured on the main stem and branches separately. Therefore, average leaf size was calculated by dividing green leaf area of the plant by the number of green leaves present as these two variables were measured in Exp. 3. The average leaf size increased from 4 cm^2 when there were 10 nodes on main stem and stabilized at 10.8 cm^2 when there was 21 nodes on main stem (Fig. 7). Plant density did not affect leaf size. This pattern of change in leaf size contradicts the pattern reported by Robertson et al. (2002) for chickpea, where leaf size declined after reaching its maximum on 15th main stem node. However, leaf size of 4 cm^2 for 10th main stem node and maximum leaf size of 11 cm^2 in both studies are similar. It has been reported that there is little genetic variation

for leaf size in pigeonpea (Ranganathan et al., 2001). Leaf size in soybean and cowpea has been found to stabilize at about the 5th to 10th node (Hofstra et al., 1977; Littleton et al., 1979; Sinclair, 1984).

Plant Leaf Area

Potential plant leaf area can be predicted from the product of leaf appearance and senescence and the maximum size of leaves based on equations and parameter estimates shown in previous sections. However, some researchers have used allometric relationships between plastochron index (main stem node number) and total number of green leaves and plant leaf area to predict plant leaf area (Hesketh et al., 1973; Sivakumar, 1978; Sinclair, 1984; Hammer et al., 1993; Pengelly et al., 1999).

In Exp. 3, the total number of green leaves and plant leaf area were measured simultaneously. There was a simple, linear relationship between plant leaf area and the number of green leaves with an R² value of 0.91 (Fig. 8). The slope of the linear regression model was 10.5 cm² per leaf, indicating a total average leaf size. Sivakumar (1978) and Ogbuehi and Brandle (1981) reported a linear relationship for soybeans between the count of number of leaflets per plant and the plant leaf area.

Hammer et al. (1993) used a simple, power function to predict plant leaf area from plant leaf number in grain sorghum. The form of the function is:

$$y = x^b \quad (6)$$

where y is the plant leaf area, x the plant leaf number (here, main stem node number) and b the coefficient of the equation. This function gave successful prediction of plant leaf area as a function of plastochron index in vigna (*Vigna trilobata* L.) (Pengelly et al., 1999).

The results of fitting the Eq. (6) to plant leaf area data versus main stem node number for each plant density treatment are presented in Fig. 9 (Exp. 4) and Table 6 (combined data of Exp. 3 and 4). When fitting the function, plant leaf area and main stem data up to 38 physiological days, when main stem node number approached its maximum (Table 3) were used. Plant leaf area ranged between 0 to 3000 cm² per plant. The function gave reasonable fits with R² values of 0.77 to 0.94. The coefficient of the function also indicated highly significant relationship with plant density (Fig. 9b). The effect of plant density on estimation of plant leaf area from main stem node number has not been reported before.

Therefore, plant leaf area in chickpea under well-watered conditions can be predicted using function (6) and its coefficient calculated from plant density. Based on this function plant leaf area can be predicted up to cessation of effective node production on main stem. For the senescence phase other approaches should be used. Sinclair (1986) and Sinclair et al. (2003) simulated plant leaf area in senescence phase based on nitrogen remobilisation from leaves.

CONCLUSIONS

Overall, the results of our study indicated that temperature and photoperiod modulate time available for leaf growth. However, the rate of node appearance on the main stem is controlled by temperature alone. Cardinal temperatures for node appearance were 6.0 °C for base, 22.2 °C for optimum and 31.0 °C for ceiling temperatures. Plant density had no significant effect on node appearance rate, cardinal temperatures for leaf appearance or phyllochron. Leaf production and senescence per plant were closely related to leaf production and senescence on the main stem. The average leaf size stabilized at 10.8 cm² when there were 21 nodes on the main stem. Plant density and sowing date had no effect on leaf size. Potential plant leaf area can be predicted from the product of leaf appearance and senescence and the maximum size of leaves, or directly from the number of nodes on main stem. The relationships presented in this study describe leaf production and senescence under well-watered conditions. They reflect the effects of carbon and nitrogen availability and remobilization under these conditions. They do not account for the effects of shortage of carbon, nitrogen or water on leaf development. Other relationships are required to predict these effects.

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REFERENCES

- Boote, K.J., Jones, J.W., Pickering, N.B., 1996. Potential uses and limitations of crop models. *Agron. J.* 88, 704-716.
- Craufurd, P.Q., Subedi, M., Summerfield, R.J., 1997. Leaf appearance in cowpea: effects of temperature and photoperiod. *Crop Sci.* 37, 167-171.
- Dennett, M.D., Elston, J., Milford, J.R., 1979. The effect of temperature on the growth of individual leaves of *Vicia faba* L. in the field. *Ann. Bot.* 43, 197-208.
- Fehr, W.R., Caviness, C.E., 1977. Stages of soybean development. Iowa State Univ. Coop Ext. Serv. Spec. Rep. 80.
- Hammer, G.L., 1998. Crop modeling: Current status and opportunities to advance. *Acta Hort* 456, 27-36.
- Hammer, G.L., Carberry, P.S., Muchow, R.C., 1993. Modeling genotype and environmental control of leaf area dynamics in grain sorghum. I. Whole plant level. *Field Crops Res.* 33, 293-310.

- Hesketh, J.D., Myhre, D.L., Willey, C.R., 1973. Temperature control of time intervals between vegetative and reproductive events in soybeans. *Crop Sci.* 13, 250-254.
- Hofstra, G., Hesketh, J.D., Myhre, D.L., 1977. A plastochron model for soybean leaf and stem growth. *Can. J. Plant Sci.*, 57, 167-175.
- Keisling, T.C., 1982. Calculation of the length of day. *Agron. J.* 74, 758-759.
- Leong, S.K., Ong, C.K., 1983. The influence of temperature and soil water deficit on development and morphology of groundnut. *J. Exp. Bot.* 34, 1551-1561.
- Littleton, E.J., Dennett, M.D., Elston, J., Monteith, J.L., 1979. The growth and development of cowpeas (*Vigna unguiculata*) under tropical field conditions. *J. Agric. Sci. (Cam.)* 93, 291-307.
- Ogbuehi, S.N., Brandle, J.R., 1981. Limitations in the use of leaf dry weight and leaf number for predicting leaf area of soybeans. *Crop Sci.* 21, 344-346.
- Pengelly, B.C., Muchow, R.C., Blamey, F.P.C., 1999. Predicting leaf area development in response to temperature in three tropical annual forage legumes. *Aust. J. Agric. Res.* 50, 253-259.
- Ranganathan, R., Chauhan, Y.S., Flower, D.J., Robertson, M.J., Sanetra, C., Silim, S.N., 2001. Predicting growth and development of pigeonpea: leaf area development. *Field crops Res.* 69, 163-172.
- Robertson, M.J., Carberry, P.S., Huth, N.I., Turpin, J.E., Probert, M.E., Poulton, P.L., Bell, M., Wright, G.C., Yeates, S.J., Brinsmead, R.B., 2002. Simulation of growth and development of diverse legume species in APSIM. *Aust. J. Agric. Res.* 53, 429-446.
- Siddique, K.M.H., Sedgley, R.H., 1986. Chickpea (*Cicer arietinum* L.), a potential grain legume for south-western Australia: Seasonal growth and yield. *Aust. J. Agric. Res.* 37, 245-261.
- Sinclair, T.R., 1984. Leaf area development in field-grown soybeans. *Agron. J.* 76, 141-146.
- Sinclair, T.R., 1986. Water and nitrogen limitations in soybean grain production: I. Model development. *Field Crops Res.* 15, 125-141.
- Sinclair, T.R., Farias, J.R., Neumaier, N., Nepomuceno, A.L., 2003. Modeling nitrogen accumulation and use by soybean. *Field Crops Res.* 81, 149-158.
- Sinclair T.R., Seligman, N.G., 1996. Crop modelling: from infancy to maturity. *Agron. J.* 88, 698-704.
- Sivakumar, M.V.K., 1978. Prediction of leaf area index in soybean. *Ann. Bot.* 42, 251-253.
- Soltani, A., Ghassemi-Golezani, K., Rahimzadeh-Khooie, F., Moghaddam, M., 1999. A simple model for chickpea growth and yield. *Field Crops Res.* 62, 213-224.
- Soltani, A., Khooie, F.R., Ghassemi-Golezani, K., Moghaddam, M., 2000. Thresholds for the leaf expansion and transpiration response to soil water deficit in chickpea: Experimentation and simulation. *Field Crops Res.* 68: 205-210.
- Soltani, A., Khooie, F.R., Ghassemi-Golezani, K., Moghaddam, M., 2001. A simulation study of chickpea crop response to limited irrigation in a semiarid environment. *Agric. Water Manag.* 49: 225-237.

- Soltani, A., Torabi, B., Zeinali, E., Sarparast, R., 2004. Response of chickpea to photoperiod as a qualitative long-day plant. *Asian J. Plant Sci.* 3, 705-708.
- Soltani A., Robertson, M.J., Torabi, B., Yousefi-Daz, M., Sarparast, R., 2006a. Modeling seedling emergence in chickpea as influenced by temperature and sowing depth. *Agric. For. Meteorol.* (Accepted)
- Soltani A., Hammer, G.L., Torabi, B., Robertson, M.J., Zeinali, E., 2006b. Modeling chickpea growth and development: phenological development. *Field Crops Res.* (Submitted)
- Soltani A., Robertson, M.J., Manschadi, A.M., 2006d. Modeling chickpea growth and development: nitrogen accumulation and use. *Field Crops Res.* (Submitted)
- Soltani, A., Torabi, B., Zarei, H., 2005. Modeling crop yield using a modified harvest index-based approach: Application in chickpea. *Field Crops Res.* 91, 273-285.
- Stutzel, H., Aufhammer, W., 1991. Canopy development of a determinate and an indeterminate cultivar of *Vicia faba* L. under contrasting plant distributions and densities. *Ann. Appl. Biol.* 118, 185-199.
- Turpin, J.E., Robertson, M.J., Hillcoat, N.S., Herridge, D.F., 2002. Fababean (*Vicia faba*) in Australia's northern grains belt: canopy development, biomass, and nitrogen accumulation and partitioning. *Aust. J. Agric. Res.* 53, 227-237.

Table 1. Summary of cultural practices and measurements in field experiments.

	Exp. 1	Exp. 2	Exp. 3	Exp. 4
Location	Gorgan	Gonbad	Gorgan	Gorgan
Growing season	2001-2002	2002-2003	2002-2003	2003-2004
Previous culture	Lettuce	Wheat	Fallow	Canola
Soil	Silty loam	Silty loam	Silty loam	Silty loam
Initial conditions	Electrical conductivity of 0.80 dS m ⁻¹ ; pH of 7.6; organic carbon of 1.18%; total nitrogen of 0.15%; available P (Olsen method) of 5.1 mg kg ⁻¹ ; available K (NH ₄ AcO method) of 402 mg kg ⁻¹	Electrical conductivity of 0.73 dS m ⁻¹ ; pH of 8.1; organic carbon of 1.20%; total nitrogen of 0.12%; available P of 9.5 mg kg ⁻¹ ; available K of 640 mg kg ⁻¹	Electrical conductivity of 0.80 dS m ⁻¹ ; pH of 7.7; organic carbon of 1.31%; total nitrogen of 0.13%; available P of 4.0 mg kg ⁻¹ ; available K of 380 mg kg ⁻¹	Electrical conductivity of 0.51 dS m ⁻¹ ; pH of 7.9; organic carbon of 1.22%; total nitrogen of 0.14%; available P of 5.1 mg kg ⁻¹ ; available K of 380 mg kg ⁻¹
Fertilization (at sowing)	150 kg ha ⁻¹ triple super phosphate and 20 kg ha ⁻¹ urea	150 kg ha ⁻¹ ammonium phosphate	150 kg ha ⁻¹ triple super phosphate and 50 kg ha ⁻¹ urea	150 kg ha ⁻¹ triple super phosphate and 20 kg ha ⁻¹ urea
Treatments	2 sowing dates (18 May 02 and 17 June 02) × 2 cultivars (90-90c and Hashem)	3 sowing dates (7 Dec. 02, 23 Jan. 03 and 6 Mar. 03) × 4 plant densities (15, 30, 45 and 60)	3 sowing dates (5 Jan. 03, 6 Mar. 03 and 28 Apr. 03) × 4 plant densities (15, 30, 45 and 60)	3 sowing dates (6 Dec. 03, 20 Jan. 04 and 21 Mar. 04) × 4 plant densities (15, 30, 45 and 60)
Measurements ^a	Phenology, MSNN, TPLN	Phenology, MSNN, MSSNN, TPLN, TPSLN, BN	Phenology, MSNN, MSSNN, TGLN, PLA	Phenology, MSNN, MSSNN, PLA
Frequency of measurements	Until first-pod or first-seed; every 10 days	Whole season; every 7 to 10 days	Whole season; every 5 to 20 days	Whole season; every 5 to 10 days

^a MSNN, the main stem node number; MSSNN, the number of nodes on main stem with senesced leaf; TPLN, the total plant leaf number; TPSLN, the total number of senesced leaves per plant; TGLN, the total number of green leaves per plant; BN, the number of primary, secondary and tertiary branches; PLA, the plant leaf area.

Table 2. Monthly means of solar radiation (SRAD, MJ m⁻² d⁻¹), maximum temperature (TMAX, °C), minimum temperature (TMIN, °C) and monthly total rainfall (RAIN, mm) during the four field experiments. Locations and years of the experiments are indicated in Table 1.

	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
<i>Exp. 1</i>									
SRAD	–	–	–	–	–	18.8	23.3	24.2	17.0
TMAX	–	–	–	–	–	25.0	31.6	34.7	32.8
TMIN	–	–	–	–	–	14.4	19.7	23.9	29.3
RAIN	–	–	–	–	–	23.5	38.1	4.5	44.6
<i>Exp. 2</i>									
SRAD	8.4	8.6	6.2	11.7	13.0	23.3	22.8	18.8	–
TMAX	11.6	13.8	12.9	13.6	18.8	27.0	31.9	33.9	–
TMIN	1.8	3.7	4.6	5.6	9.1	12.6	17.6	23.2	–
RAIN	54.6	28.3	56.5	90.1	71.7	39.4	8.5	5.4	–
<i>Exp. 3</i>									
SRAD	–	8.2	8.3	11.0	12.2	23.1	20.9	16.1	22.1
TMAX	–	13.8	13.1	12.8	18.8	26.2	29.1	31.0	33.9
TMIN	–	3.4	4.5	5.6	9.4	13.3	18.4	23.1	22.8
RAIN	–	11.8	2.2	110.9	56.2	50.9	53.8	6.2	30.0
<i>Exp. 4</i>									
SRAD	7.4	8.9	11.4	12.8	17.5	19.2	21.7	21.9	–
TMAX	15.1	15.3	16.8	18.3	20.8	26.9	31.6	30.4	–
TMIN	6.7	4.9	5.2	7.9	9.2	15.5	20.6	21.3	–
RAIN	56.4	51.4	10.7	101.8	52.6	30.4	14.5	73.8	–

Table 3. Time of cessation of node production on main stem (TLG, physiological day), duration of effective node production (ENPP, day), and maximum node number on main stem (MXN) for the field experiments.

<i>Exp. 1</i>				<i>Exp. 2</i>			
Treatment	TLG	ENPP	MXN	Treatment	TLG	ENPP	MXN
8 May 02				7 Dec. 02			
90-96c	42.6	51	21.7	15	37.8	135	31.9
Hashem	39.5	47	21.0	30	35.1	133	30.0
17 Jun. 02				45	34.7	132	30.3
90-96c	36.1	45	19.8	60	34.5	132	30.1
Hashem	41.0	52	20.4	23 Jan. 03			
				15	39.2	110	28.1
				30	38.3	109	27.7
				45	38.0	109	27.1
				60	38.3	109	27.1
				6 Mar. 03			
				15	40.0	74	28.0
				30	38.5	73	26.4
				45	38.2	73	27.4
				60	37.0	71	25.5
<i>Exp. 3</i>				<i>Exp. 4</i>			
5 Jan. 03				6 Dec. 03			
15	35.6	116	34.5	15	36.8	128	38.4
30	34.6	115	33.1	30	36.4	127	37.5
45	35.1	115	33.0	45	36.8	128	36.7
60	33.8	114	31.6	60	35.8	126	36.2
6 Mar. 03				20 Jan. 04			
15	38.2	71	33.3	15	39.6	104	35.8
30	39.0	72	32.1	30	39.3	104	35.9
45	35.2	68	30.8	45	38.7	100	34.1
60	35.7	68	30.4	60	37.8	101	35.1
28 Apr. 03				21 Mar. 04			
15	38.9	48	36.1	15	39.4	63	33.9
30	36.9	46	33.2	30	38.8	59	30.8
45	36.3	45	31.8	45	38.2	60	30.7
60	37.1	46	31.6	60	37.9	58	29.8

Table 4. Parameter estimates for the non-linear segmented model (Eq. 4) describing changes of fraction of senesced leaf number on main stem versus thermal or physiological days after sowing.

Experiment	R ²	<i>b</i>	<i>x_o</i>
Thermal day			
Exp. 2	0.90	0.0149 ± 0.0064	36.0 ± 1.59
Exp. 3	0.75	0.0128 ± 0.0040	35.0 ± 1.33
Exp. 4	0.68	0.0115 ± 0.0049	36.8 ± 1.62
Physiological day			
Exp. 2	0.96	0.0191 ± 0.0043	14.8 ± 0.59
Exp. 3	0.93	0.0142 ± 0.0040	14.6 ± 1.23
Exp. 4	0.93	0.0168 ± 0.0058	15.0 ± 0.95

Table 5. Parameter estimates for the non-linear segmented model (Eq. 5) describing changes of total leaf number per plant and number of nodes on main stem for different plant densities of Exp. 2. *b**₂ represents the value of *b*₂ after fixing *b*₁ at 2.98 and *x*_o at 14.4.

Plant density	R ²	<i>b</i> ₁	<i>x</i> _o	<i>b</i> ₂	<i>b</i> * ₂
15	0.99	3.1 ± 0.399	14.1 ± 0.73	14.7 ± 0.50	15.1 ± 0.22
30	0.99	2.9 ± 0.390	12.8 ± 1.02	10.1 ± 0.43	11.0 ± 0.21
45	0.99	2.9 ± 0.223	15.0 ± 1.16	7.8 ± 0.40	7.5 ± 0.15
60	0.98	3.0 ± 0.319	15.6 ± 1.32	8.9 ± 0.58	8.3 ± 0.22

Table 6. Parameter estimates for the power function (Eq. 6) describing changes of plant leaf area versus the number of nodes on main stem for different plant densities of Exp. 3 and 4.

Plant density	R ²	B
15	0.91	2.227 ± 0.0176
30	0.90	2.164 ± 0.0186
45	0.94	2.072 ± 0.0134
60	0.77	2.039 ± 0.0281

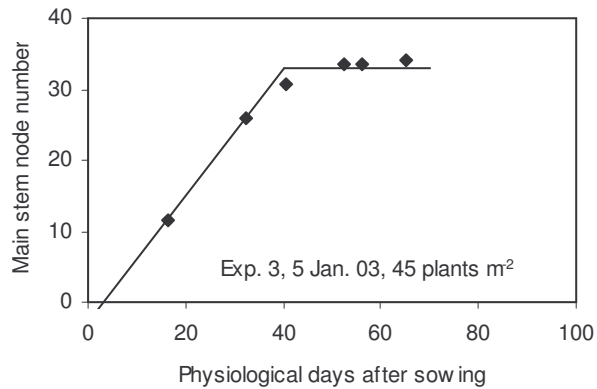


Fig. 1. Example fit of a segmented non-linear regression model to data of main stem node number versus physiological days after sowing.

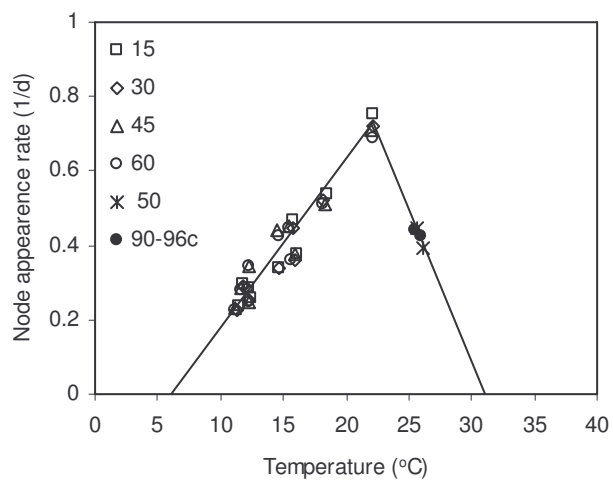


Fig. 2. Rate of node appearance on main stem as a function of temperature across the four field experiments. Numbers indicate plant densities. Filled circles belong to cv. 90-96c at plant density of 50 plants m⁻², other points belong to cv. Hashem at plant densities indicated in the figure.

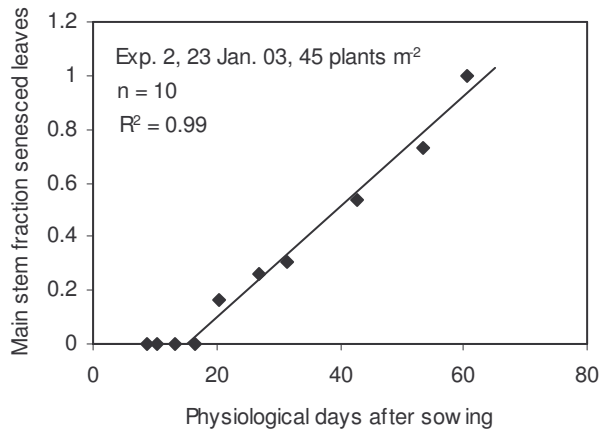


Fig. 3. Example fit of a segmented non-linear regression model to data of fraction of senesced leaf number on main stem versus physiological days after sowing.

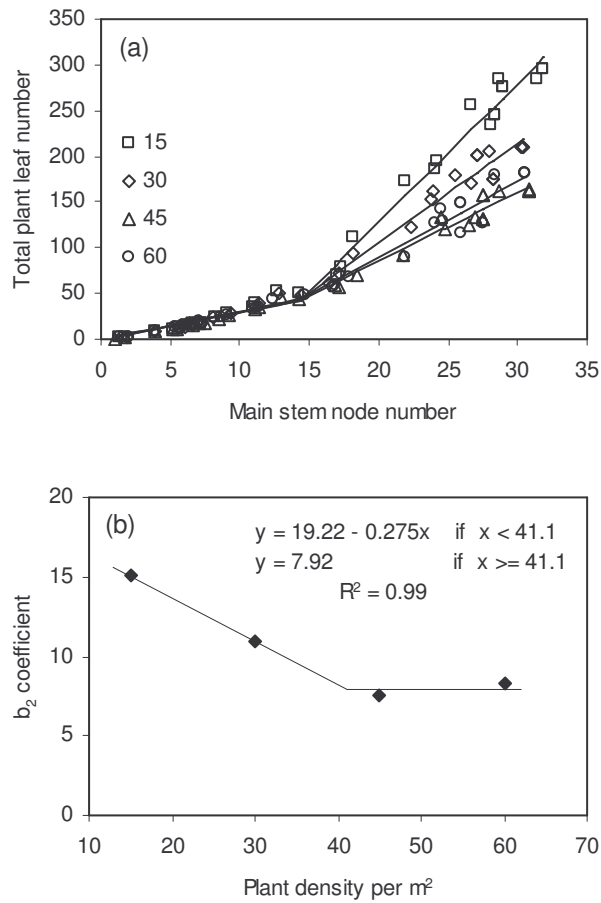


Fig. 4. (a) Changes of total leaf number per plant as a function of node number on main stem for different plant densities (numbers within figure). (b) Dependency of the rate of increase in plant leaf number during the second phase (b_2 coefficient-see Eq. 5) to plant density in Exp. 2.

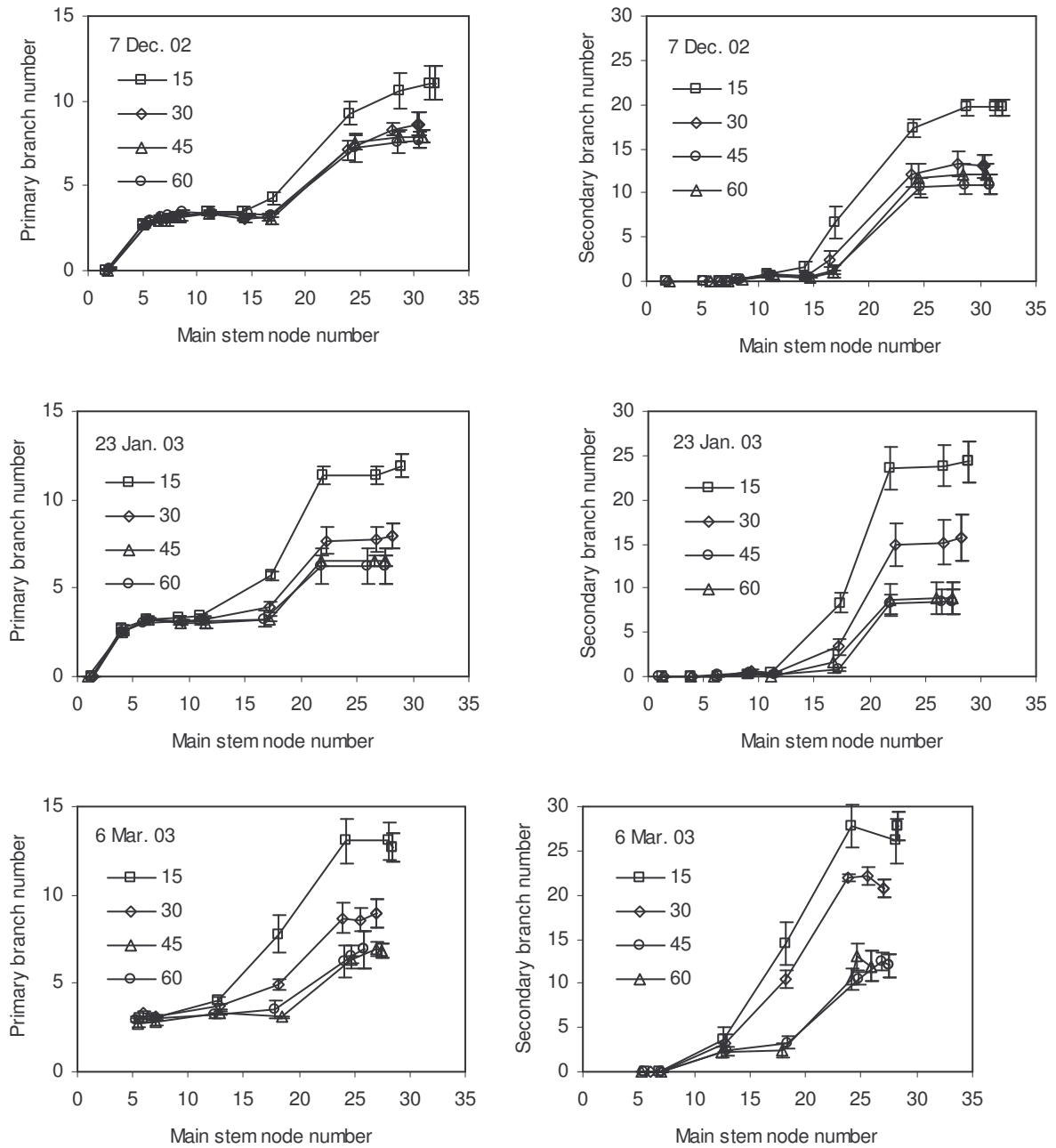


Fig. 5. Production of primary and secondary branches in relation to node number on main stem in Exp. 2. Numbers within figures indicate plant densities. Vertical bars indicate standard errors.

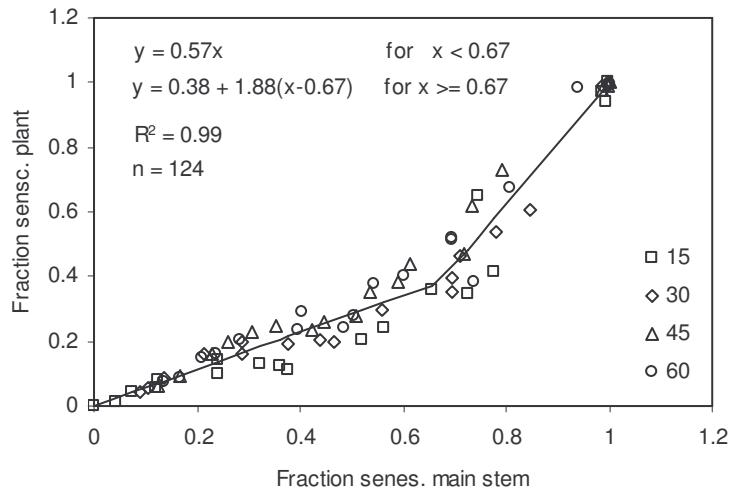


Fig. 6. Fraction of senesced leaf number per plant versus the fraction on main stem in Exp. 2. Numbers indicate plant densities.

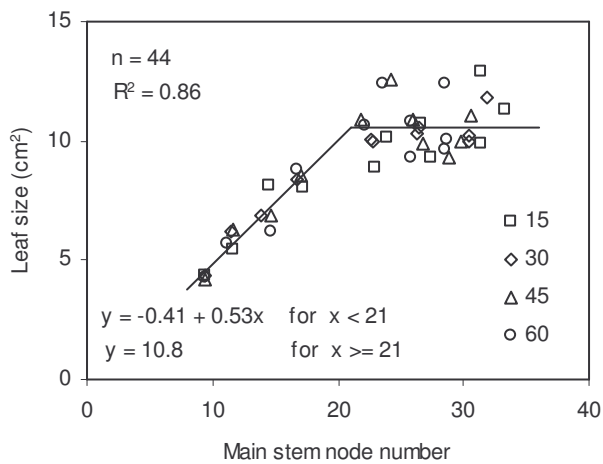


Fig. 7. Average leaf size as a function of main stem node number in Exp. 3. Numbers indicate plant densities.

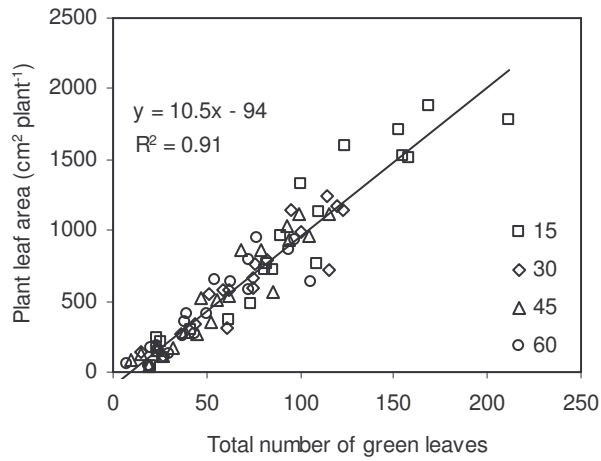


Fig. 8. Plant leaf area as a function of the number of green leaves per plant in Exp. 3. Numbers indicate plant densities.

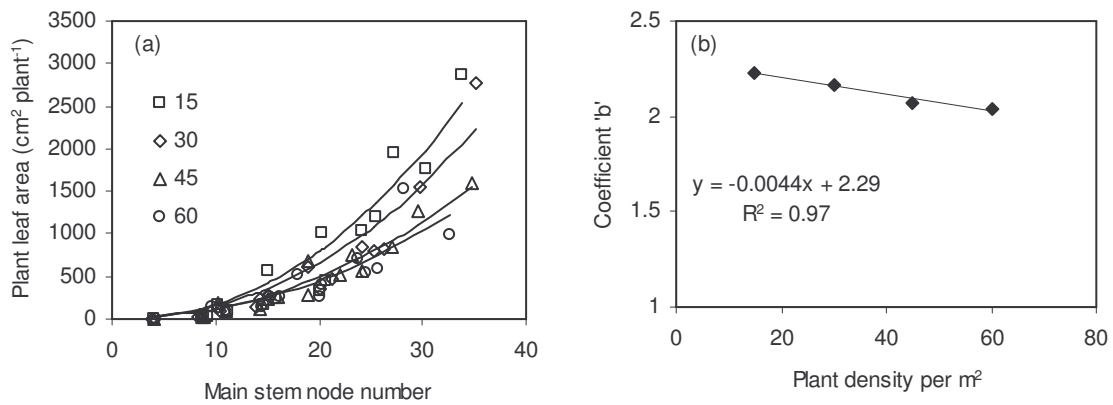


Fig. 9. (a) Plant leaf area as a function of main stem node number described by a power function as $y = x^b$ in Exp. 4. Numbers indicate plant densities. (b) Dependency of the coefficient of the power function on plant density.