

Modeling Leaf Production and Senescence in Chickpea (*Cicer arietinum* L.): Leaf Lifetime

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ABSTRACT

Quantitative information regarding leaf lifetime in chickpea (*Cicer arietinum* L.) is scarce. Data from a field experiment with a range of planting date and density were analyzed to estimate leaf lifetime and its variation in chickpea. The experiment was conducted under well-watered conditions. An average leaf lifetime of 23.5 physiological days was estimated. A physiological day is a calendar day with no limitation of photoperiod and temperature for plant development. Planting date and density did not affect leaf lifetime. The results of this study can be used in simulation models of chickpea.

Keyword: Leaf; Leaf lifetime; Photoperiod; Temperature; Model.

INTRODUCTION

Chickpea (*Cicer arietinum* L.) is one of the major pulse crops in the world with a total annual global production of 7.5 M tones from 10.3 M ha (FAO, 2003). It is cultivated on a large scale in arid and semiarid environments, and has considerable importance as food, feed and fodder.

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). 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). The concept of leaf lifetime has been used in some crop simulation models to quantify leaf senescence after the accumulation of a specified thermal time (e.g. Rickman et al., 1996).

There are no reports in the literature regarding estimates of leaf lifetime in chickpea for the purpose of crop modeling. Therefore, the objective of this research was to estimate this across different environmental conditions and agronomic practices.

MATERIALS and METHODS

The experiment was conducted at Gonbad Agricultural Research Station, Gonbad (34° 21' N, 55° 10' E and 37 m asl) in Iran. The soil was a deep silty loam (fine-silty, mixed, active, thermic,

Typic Calcixerolls). Some details about the experiment and weather conditions are given in Table 1 and 2, respectively. The experiments was conducted under well-watered conditions. 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 chosen sowing dates 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 Gonad, but sometimes sowing might occur in late November, January and February.

Stages of development of emergence (50% of plants with some parts at soil surface), flowering (50% of plants with at least one flower at any node, R1), first pod (50% of plants with a 0.5 cm pod at one of the 4 upper nodes with unfolded leaf, R3), beginning of seed growth (50% of plants with peas beginning to develop, R5), first-maturity (50% of plants with at least one pod yellowed, R7) and full-maturity (50% of plants with 95% pods yellowed, R8) were recorded every 2 days (Fehr and Caviness, 1977).

Table 1. Summary of cultural practices and measurements in the field experiment.

Location	Gonbad
Growing season	2002-2003
Previous culture	Wheat
Soil	Silty loam
Initial conditions	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
Fertilization (at sowing)	(at 150 kg ha ⁻¹ ammonium phosphate
Treatments	3 sowing dates (7 Dec. 02, 23 Jan. 03 and 6 Mar. 03) × 4 plant densities (15, 30, 45 and 60)
Measurements ^a	Phenology, MSNN, MSSNN, TPLN, TPSLN
Frequency of measurements	Whole season; every 7 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.

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 and the total plant leaf number (green + senesced). The frequency of the measurements are presented in Table 1. The measurements were conducted on 10 tagged 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.

Daily maximum and minimum temperatures, sunshine hours and rainfall were measured at a standard weather station located a few hundred meters 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., 2005a).

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

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

where $f(T)$ is the temperature function and $f(PP)$ the photoperiod function. Physiological day is similar to thermal time corrected for the effect of photoperiod. The $f(T)$ was obtained as:

$$\begin{aligned} f(T) &= (T - T_b) / (T_{o1} - T_b) & \text{if } T_b < T < T_{o1} \\ f(T) &= (T_c - T) / (T_c - T_{o2}) & \text{if } T_{o2} < T < T_c \\ f(T) &= 1 & \text{if } T_{o1} < T < T_{o2} \\ f(T) &= 0 & \text{if } T \leq T_b \text{ or } T \geq T_c \end{aligned} \quad (2)$$

where T is temperature, T_b the base temperature, T_o the optimum temperature, T_{o1} the lower optimum temperature, T_{o2} the upper optimum temperature, and T_c the ceiling temperature (Soltani et al., 2006a). The $f(PP)$ was computed as:

$$\begin{aligned} f(PP) &= 1 & \text{if } PP \geq P_c \\ f(PP) &= 1 - PS \times (P_c - PP)^2 & \text{if } PP < P_c \end{aligned} \quad (3)$$

where PP is photoperiod (h d^{-1}), P_c the critical photoperiod below which development rate decreases due to short photoperiod, and PS the photoperiod sensitivity coefficient. 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., 2006a). The values of T_b , T_{o1} , T_{o2} and T_c were 4.5, 20, 29 and 40 °C for sowing to emergence (Soltani et al., 2006b) and 0, 21, 32 and 40 °C for other stages (Soltani et al., 2006a). The value of P_c was 21 h and the value of PS was 0.00845 for Hashem (Soltani et al., 2006a). Cumulative values of PD_t were used in present study. Thermal day was also calculated from Eq. (1) to (3) by fixing $f(PP)$ at 1 for all phenological stages. Thermal day is a normalized form of thermal time.

RESULTS and DISCUSSION

Summary of weather conditions during the experiment is indicated in Table 2. To obtain an estimate of average leaf lifetime, a logistic regression model was used to describe changes of total and senesced plant leaf number versus thermal day and physiological day (Fig. 1):

$$y = y_{max} / [1 + \exp(-a(x - b))] \quad (4)$$

where y is the total or senesced plant leaf number, x the thermal day or physiological day after sowing, a the steepness of increase in leaf number and b thermal day or physiological day when total or senesced leaf number reached to 50% of their maximums. When fitting Eq. (4) to data of senesced leaf number, the value of y_{max} was fixed to that found for total plant leaf number. The difference between b for senesced leaf number (b_2) and total leaf number (b_1) gives an estimate of average leaf lifetime ($b_2 - b_1$).

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 field experiment.

	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
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

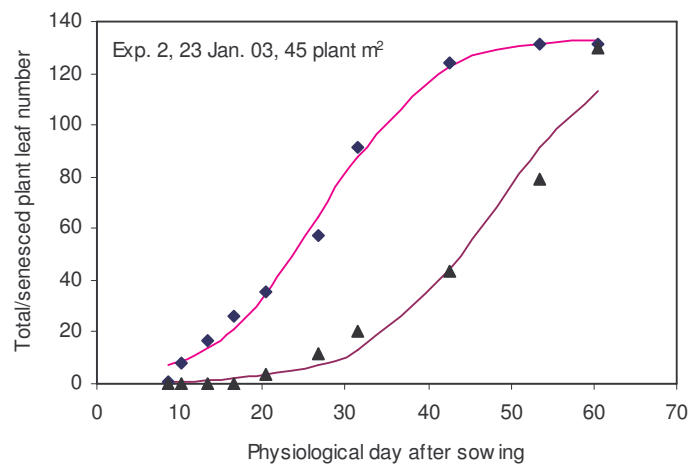


Fig. 1. Example fit of a logistic model to total (◆) and senesced (▲) leaf number per plant to determine average leaf lifetime.

Using physiological day resulted in stable estimates of leaf lifetime across sowing dates (Table 3), while leaf lifetime estimates based on thermal day were dependent on sowing date (data not shown), indicating a possible effect of photoperiod on leaf lifetime, probably due to linkage between phenology and the timing of carbon and nitrogen retranslocation (Prof. G.L. Hammer, personal communications). The logistic model gave a good description of leaf number changes versus physiological day with R² values higher than 0.98 and 0.94 for total and senesced plant leaf number, respectively. Regression of leaf lifetime versus plant density using a simple, linear model did not result in significant slope (data not shown). Average leaf lifetime across sowing dates and densities

was 23.5 physiological days. This means that under optimal temperature and photoperiod a leaf in average lasts for 23.5 days.

Table 3. Parameter estimates for the logistic model (Eq. 4) describing total and senesced plant leaf number versus physiological day after sowing to obtain leaf lifetime (physiological days).

Treatment	Total leaves				Senesced leaves			Lifetime
	R ²	<i>MxLN</i>	<i>a</i> ₁	<i>b</i> ₁	R ²	<i>a</i> ₂	<i>b</i> ₂	
7 Dec. 02								
15	0.99	297 ± 6.5	0.227 ± 0.0208	25.9 ± 0.559	0.98	0.199 ± 0.0253	52.1 ± 0.765	± 26.1
30	0.99	214 ± 5.43	0.205 ± 0.0201	24.4 ± 0.676	0.97	0.127 ± 0.0157	49.4 ± 1.136	± 24.9
45	0.99	166 ± 4.675	0.203 ± 0.0220	23.0 ± 0.746	0.97	0.112 ± 0.0137	47.2 ± 1.355	± 24.2
60	0.99	186 ± 5.211	0.199 ± 0.0211	23.6 ± 0.750	0.97	0.121 ± 0.0139	47.2 ± 1.162	± 23.6
23 Jan. 03								
15	1.00	277 ± 6.388	0.204 ± 0.0207	30.0 ± 0.577	0.95	0.423 ± 0.1313	54.8 ± 0.690	± 25.0
30	1.00	179 ± 4.015	0.177 ± 0.0148	27.8 ± 0.593	0.94	0.148 ± 0.0329	50.6 ± 1.668	± 22.9
45	0.99	134 ± 3.272	0.155 ± 0.0128	27.3 ± 0.692	0.97	0.135 ± 0.019	47.8 ± 1.248	± 20.5
60	0.99	129 ± 3.061	0.156 ± 0.0125	27.2 ± 0.670	0.95	0.132 ± 0.0248	48.8 ± 1.659	± 21.6
6 Mar. 03								
15	1.00	244 ± 2.006	0.198 ± 0.0073	28.6 ± 0.222	1.00	0.126 ± 0.0069	53.4 ± 0.426	± 24.8
30	1.00	199 ± 4.883	0.179 ± 0.0186	28.0 ± 0.694	0.99	0.128 ± 0.012	51.5 ± 0.696	± 23.5
45	0.99	155 ± 5.377	0.152 ± 0.0202	28.4 ± 1.044	0.97	0.121 ± 0.0184	51.0 ± 1.267	± 22.6
60	0.98	146 ± 5.744	0.171 ± 0.028	27.3 ± 1.131	0.96	0.133 ± 0.0265	50.0 ± 1.485	± 22.7

MxLN: Maximum leaf number per plant.

Inverse prediction of Eq. (4) indicated that total plant leaf number reaches 95% of its maximum (y_{max}) when 43 physiological days have elapsed, which is the physiological day when first-pod occurs (Soltani et al., 2006a). This stage can be considered as when effective leaf growth terminates. The termination of leaf growth is important in some simulation models (Sinclair, 1986; Sinclair et al., 2003; Robertson et al., 2002).

Overall, average leaf lifetime was 23.5 physiological days. Plant density and sowing date had no effect on leaf size and lifetime.

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