

Modeling Leaf Production and Senescence in Wheat

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Abstract: A major component in a crop growth model is leaf area development, which has a major influence on photosynthesis and transpiration. The knowledge about the leaf area development of wheat especially in high temperature environments is incomplete. The aim of this study was to quantify leaf production and senescence of 15 spring wheat cultivars. Field experiments were conducted at the research farm of the Islamic Azad University of Ramhormoz Branch, south-western of Iran in 2006-8 using a Randomized Complete Design with four replications. The relationship between main stem leaf numbers (HS) versus degree-days was described using bilinear model. The results indicated that the leaf appearance rate therewith phylochron had no significant across all data. Mean leaf appearance rate ranged from 0.0076 to 0.0083 leaf/°C d. At thirteen of 15 cultivars, The cession time (degree-days) of effective leaf production on main stem had no significant difference and ranged from 1138.0 to 1169.3°C d. Leaf senescence on the main stem started when the main stem had about 5 leaves on main stem and proceeded at a rate of 0.0495 % per each one degree increase in degree-days. Leaf production per plant versus main stem leaf number occurred in two phases: phase 1 when plant leaf number increased with a slower (1.38 leaves per leaf) and phase 2 with a higher (4.97 leaves per leaf). 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 on main stem was increased from 5.65 cm² when there were 6 leaves on the main stem and stabilized at 33.5 cm² when there were 9-10 leaves on the main stem. The parameters related to leaf size had no difference across all data ($p < 0.05$). Plant leaf area was also predictable directly from main stem leaf number. The relationships found in this study can be used in simulation models of wheat.

Key words: Leaf area development % Leaf senescence % Leaf appearance rate % Cultivar % Wheat

INTRODUCTION

Leaf area index (*LAI*) and the radiation extinction coefficient (*k*) determine the proportion of incident radiation intercepted and subsequently potential biomass production. Consequently, modeling of leaf growth has been extensively studied in many crops including cereals [1,2]. Leaf area development involves the appearance of new leaves, expansion of the newly emerged leaves and the senescence of old leaves [3,4,5]. 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 [6]. Temperature and photoperiod can also regulate leaf area via their effects on the duration of leaf production period [5,7].

Methods of predicting leaf area development are varied from those dealing with the individual component processes of leaf growth, viz. leaf appearance, leaf expansion and leaf death [3,8], to the models predicting leaf growth at the whole plant [5,9-11] or whole crop level [12]. Leaf appearance and leaf expansion are among the most environmentally sensitive growth processes [13] and their dependence on temperature has been demonstrated in a range of cereals including wheat and barley [14,15] and legumes including cowpea [8] and soybean [16]. Effects of temperature on leaf appearance rates are usually quantified using some form of thermal time. Air temperature above the canopy has most frequently been used to calculate thermal time (in growing degree-days, °C d).

Leaves senesce because of the natural biological process of ageing, but the effects of water deficit, nutrient deficiency, pest or disease attack, or physical damage can markedly reduce leaf longevity. Low light environments from competitive shading [17] and remobilization of nitrogen from leaves to the developing grain [18] have been closely linked to leaf senescence. Genetic differences in senescence have also been reported among sorghum genotypes [12-19].

Quantitative information regarding leaf area development in wheat especially in environment with high temperature for the purpose of crop modeling are scarce. Furthermore, genotypic variation has not been evaluated. Therefore, the aim of this study was to develop functions and obtain parameters which would allow the prediction of leaf area development in 15 wheat cultivars in warm environments.

MATERIALS AND METHODS

Field Experiments: Two field experiments were conducted at Agricultural Research Station of Islamic Azad University, Ramhormoz branch (latitude 31.16°N, longitude 49.36°E and 151 m asl), south-western of Iran. Planting dates were 1 December in 2006 and 27 November in 2007. The site has a silty clay soil with a mean annual precipitation of 320 mm, mean solar radiation of 19.1 MJ mG² dG¹, mean maximum temperature of 32.7°C and mean minimum temperature of 19.5°C, The climate is warm and dry. Some details about the experiments and weather conditions during the experiments are given in Tables 1 and 2, respectively.

Fifteen wheat cultivars (Atrak, Bayat, Chamran, Chenab, Dez, Ieniya, Kavir, Marvdasht, Shiraz, Shoa-Mald, Star, vie-Nak, Yavaroos and Zagros) were

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

	Experiment 1	Experiment 2
Location	Ramhormoz	Ramhormoz
Growing season	2006-2007	2007-2008
Previous culture	Corn	Rape seed
Soil	Silty clay	Silty clay
Initial condition	Electrical conductivity of 3.5 dS/m; pH of 7.5; organic carbon of 1.10%; total nitrogen of 0.56%; available P (Olsen method) of 8.5 mg/kg; available K (NH ₄ AcO method) of 229 mg/kg	Electrical conductivity of 3.3 dS/m; pH of 7.7; organic carbon of 1.3%; total nitrogen of 0.55%; available P (Olsen method) of 8 mg/kg; available K (NH ₄ AcO method) of 240 mg/kg
Fertilization	40 kg N haG ¹ , 80 kg P ₂ O ₅ haG ¹ and 50Kg K ₂ O haG ¹	Similar to Exp. 1
Treatments	Cultivars (Atr., Bay., Cha., Che., Dez., Ine., Kav., Mar., S78., Shi., Sho., Sta., Vir., Yav. and Zag)	Similar to Exp. 1
Measurements	Phenology, MSGLN, MSSLN, TGLN, TPLN; TPSSLN; TILN;LS; PLA; HS	Similar to Exp. 1

MSGLN, the main stem green leaf number; MSSLN, the number of senesced leaf on main stem; TPLN, the total plant leaf number; TPSSLN, the total number of senesced leaves per plant; TGLN, the total number of green leaves per plant; TILN, the number of Tiller on plant;LS, leaf size; PLA, the plant leaf area; HS, Haun scale units.

Table 2: Monthly means of solar radiation (SRAD, MJ/m²/d), maximum temperature (TMAX,°C), minimum temperature (TMIN,°C) and monthly total rainfall (RAIN, mm) during the two field experiments

	November	December	January	February	March	April	May
Experiment 1							
SRAD	-	9.93	11.11	14.96	15.79	18.53	25.68
TMAX	-	15.68	15.87	20.96	24.03	31.53	41.35
TMIN	-	7.42	6.94	11.18	13.03	19.8	26.13
RAIN	-	117.1	43.4	14.7	21.4	34.9	0
Experiment 2							
SRAD	13.33	10.11	9.29	14.75	18.67	21.17	26.2
TMAX	17.97	19.45	14.35	20.79	31.58	35.5	40.68
TMIN	8.27	9.94	7	9.03	16.13	20.77	25.89
RAIN	23.5	57.4	44.7	6	0	2.1	0

sown in a randomized complete block design with four replications. Individual plots consisted of six rows, 6 m long and spaced 25 cm apart. All cultivars were sown by a seed drill at a population density of 400 seed m². Fertilizer was applied at the time of planting at a rate of 40 kg N ha⁻¹, 80 kg P₂O₅ ha⁻¹ and 50 Kg K₂O ha⁻¹. The rate of N top-dressing was 100 Kg ha⁻¹ that distributed at tillering and stem-elongation stages. Tapic (1 L ha⁻¹) and 2,4-D (2.5 L ha⁻¹) were used as herbicide for monocotyledon and dicotyledonous weeds control, respectively. Insects were controlled by the appropriate chemicals. 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.

Measurements: In both experiments, stages of development of emergence, tillering, stem-elongation, flag leaf appearance, awn appearance, spike appearance, flowering, physiological maturity and harvest maturity were recorded every 2-3 days [20]. Measurements regarding leaf production and senescence were the total number of leaf (green + senesced) on the main stem, the total plant leaf number (green + senesced), the number of tillers, leaf size and plant leaf area. The leaf stage of main stem was determined as Haun scale [21]. Haun stage (HS) was recorded every 4-7 days. A fully expanded leaf was counted when its ligules were unfolded.

A leaf was considered senesced when half or more of its area had yellowed. Lamina length (LL) and the maximum lamina width (LW) was registered and used to calculate the area of a leaf (LA) as in Montgomery [22]:

$$LA = 0.75 \times LL \times LW \quad (1)$$

Where 0.75. Leaf area per plant was estimated as the sum of the area of all green leaves.

Experiments 1 and 2, 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. In both experiments, daily maximum and minimum temperatures, sunshine hours and rainfall were measured at a standard weather station near the experimental sites. Solar radiation was calculated from sunshine hours and extraterrestrial radiation.

Analysis: The data were analyzed based on functional and allometric relationships between environmental variables (mainly temperature) and plant leaf area

determinants. The appropriate relationships were captured from published work when available or were developed when necessary [5]. 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 based on statistics obtained from combined fit and separate fits.

Daily thermal units (Growing degree-days, *GDD*) were calculated from daily maximum (*T*_{MAX}) and minimum (*T*_{MIN}) air temperatures as follows [23]:

$$GDD = [(T_{MAX} + T_{MIN}) / 2] - T_{base} \text{ if } T_{MAX} > 30 \text{ then } T_{MAX} = 30^{\circ}\text{C} \\ GDD < T_{base} \text{ then set equal to } T_{base} \quad (2)$$

*T*_{base} was considered as 0°C [24-25]. The SAS statistical package [26] was used for data analysis.

RESULTS AND DISCUSSION

Leaf Appearance and Senescence on the Main Stem:

The changes of main stem leaf number versus growing degrees days (*GDD*, °C d) was describable using a non-linear, segmented regression model. The segmented model consists of two intersecting lines, a sloping line for the linear increase in leaf number and a horizontal line, which determines maximum leaf number on the main stem (Fig. 1):

$$Y = a + bx \quad \text{if } x < x_0 \quad (3) \\ Y = a + bx_0 \quad \text{if } x \geq x_0$$

Where *y* is the leaf stage of main stem; *x*, the growing degree-days after sowing; *a*, the intercept with the vertical axis (*x* = 0), *b* the rate of linear increase in leaf number (leaf appearance rate, leaf/°C d); *x*₀, the time of cessation of the linear increase in leaf number and *a* + *b**x*₀, represents the maximum leaf number on main stem. Eq. (3) was used to obtain estimates of the leaf appearance rate (*b*), the time of cessation of effective leaf production on main stem (*x*₀) and the maximum number of leaves on main stem. A plot of the regression of *HS* against degree-days is indicated in Fig. 1.

The differences in leaf appearance rate among cultivars was not significant (with *p* < 0.05 and *R*² all greater than 0.99). On average, rate of leaf appearance across all cultivars and years was constant and ranged

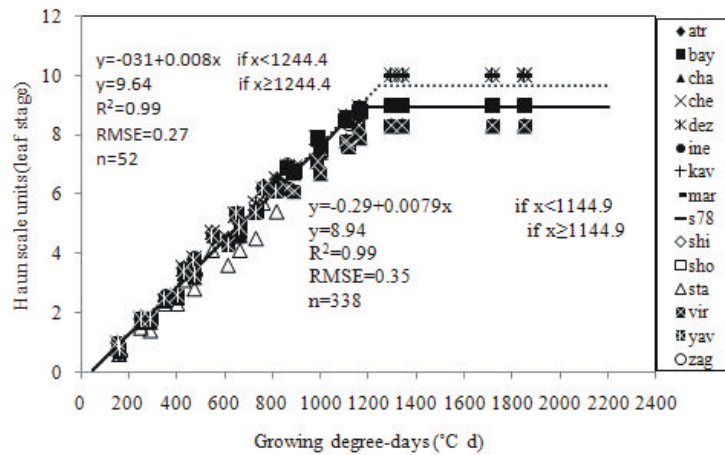


Fig. 1: Fit of a segmented non-linear regression model to data of main stem leaf number vs. degree-days after sowing. (broken line is related to shiraz (Shi) and star (sta) cultivars and solid line indicates response of other cultivars). Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons.

Table 3: Parameters of the model fitted to Haun scale units (leaf stage on main stem) vs. Growing degree-days (see Eq. 4) for different cultivars. (data were polled in the 2006-2008 experiments).

Cultivars	A±SE	B± SE (leaves/°C d)	X0± SE (°C ^d)	Maximum main stem leaf number	Phyllochron (°C ^d)	n	RMSE	R ²
Atr	-0.32±0.07	0.0081±0.00010	1138.0±11.2	8.9	123.5	104	0.27	0.99
Bay	-0.40±0.06	0.0082±0.00009	1141.4±10.4	9	122	104	0.26	0.99
Cha	-0.35±0.07	0.0081±0.00010	1145.7±11.8	8.9	123.5	104	0.29	0.99
Che	-0.25±0.06	0.0079±0.00008	1167.5±12.6	9	126.6	104	0.25	0.99
Dez	-0.38±0.06	0.0081±0.00009	1145.1±10.3	8.9	123.5	104	0.25	0.99
Ine	-0.42±0.07	0.0081±0.00009	1150.5±10.9	8.9	123.5	104	0.26	0.99
Kav	-0.44±0.08	0.0077±0.00011	1154.2±14.4	8.4	129.9	104	0.31	0.99
Mar	-0.31±0.06	0.0079±0.00008	1169.3±13.5	8.9	126.6	104	0.26	0.99
S78	-0.26±0.07	0.0080±0.00009	1138.9±10.8	8.9	125	104	0.26	0.99
Shi	-0.29±0.06	0.0080±0.00098	1237.7±13.4	9.6	125	104	0.26	0.99
Sho	-0.31±0.07	0.0080±0.00011	1148.5±12.3	8.9	125	104	0.3	0.99
Sta	-0.32±0.07	0.0080±0.00009	1241.2±14.2	9.6	125	104	0.27	0.99
Vir	-0.35±0.07	0.00801±0.00009	1140.6±10.8	8.9	123.5	104	0.26	0.99
Yav	-0.43±0.07	0.0077±0.00010	1147.1±12.8	8.4	129.9	104	0.28	0.99
Zag	-0.30±0.07	0.0080±0.00010	1141.6±11.6	8.8	125	104	0.28	0.99

between 0.0077 to 0.0082 (Table 3) and this is in agreement with the findings of Kirby and Perry [27] who indicated that a rate of leaf appearance is constant among wheat different cultivars. The reciprocal of leaf appearance rate is the thermal time intervals between appearance of successive leaves and is called the phyllochron interval [28,29]. Phyllochron values ranged between 122 to 130 across all cultivars and years. Previously reported degree-days required for the appearance of successive leaves for wheat were 77°C d [15], 80°C d [29], 101°C d [30]. Phyllochrons obtained in the present study for spring wheat cultivars were higher than those reported in temperate regions, possibly due to high temperatures

greater than 30°C that occurred during the growing season. This agrees with the findings of Cao and Moss [31] who indicated that plants of winter wheat grown at high temperature had longer phyllochron than grown in low temperature.

In 13 out of 15 cultivars, the mean cessation time (degree-days) of effective leaf production were similar and ranged from 1138 to 1169 degree-days. In growing season of 2006-7 the cessation time of effective leaf production were 4% lower compared to growing season of 2007-8. This was due to higher air temperatures in 2007-8 sowing (Table 2). Only Shi. and Sta. cultivars showed longer time to cessation of effective leaf production compared to

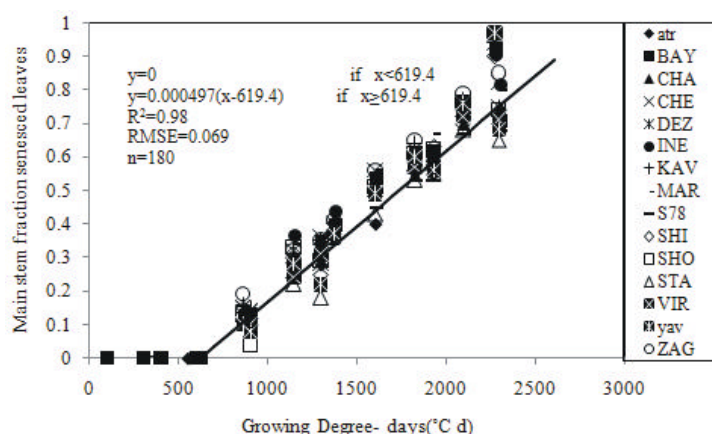


Fig. 2: Fit of a segmented non-linear regression model to data of fraction of senesced leaf number on main stem vs. degree-days after sowing. Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons.

other cultivars. The cessation time of effective leaf production on main stem determines the final leaf number on main stem and flowering time [32]. One leaf difference in prediction of leaf appearance can have considerable impact on prediction of phenological stages as well as leaf area expansion [33].

The linear increase in main stem leaf number versus degree-days has been reported in wheat [31,32,33], barley [31], chickpea [5,34], faba bean [35], soybean [10] and pigeon pea [4]. However, Baker *et al.* [24] found a discontinuity in the HS vs. degree-days at about the time of double ridge formation in the developing spike (800 degree-days after sowing).

Examination of the fraction of senesced leaves on main stem (ratio of senesced to total leaves) versus degree-days in Exp. 1 and 2 indicated that the fraction follows the below model (Fig. 2):

$$y=0 \quad \text{if } x \leq x_0 \quad (4)$$

$$y=b(x-x_0) \quad \text{if } x > x_0$$

Where y is the fraction of senesced leaf on main stem, x the degree-days, x_0 the time when senescence starts on main stem ($^{\circ}\text{C d}$) and b the rate of increase in the fraction per unit increase in degree-days. While there were some differences between years and cultivars with respect to x_0 , these differences were not significant based on 99% confidence intervals of the parameters in each experiment (data not shown). Leaf senescence on the main stem was initiated at around 614 degree-days from sowing (about leaf stage of 5 on main stem) (Fig. 2). Leaf senescence rate (b coefficient) was not different across all cultivars and years. However, in 2007-8 season, leaf senescence rate

was 16% lower but the difference between years was not significant ($p < 0.05$). Leaf senescence rate was 0.0495% per each degree day. The following equation was fitted to all the data:

$$y=0 \quad \text{if } x \leq 613.5 \quad (5)$$

$$y=0.0495(x-613.5) \quad \text{if } x > 613.5$$

Other study, Ishagh *et al.* [36] in spring wheat cultivars reported that cultivars started to lose their leaves at leaf stages between 4 and 6.2 and that this stage was affected by sowing date. Borrás *et al.* [37] reported that in maize the senescence started around 400-450 $^{\circ}\text{C d}$ from sowing; they indicated that highly contrasting plant populations, row spacing and irradiance values did not modify the early ontogenic stage (ca. V6-V9) at which senescence of the lowermost leaves started. Robertson *et al.* [34] 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 $^{\circ}\text{C d}$. Also, Soltani *et al.* [5] found that leaf senescence on the main stem of chickpea plants started after 756 $^{\circ}\text{C d}$.

Leaf Production and Senescence per Plant: Leaf production and senescence per plant has been related to leaf production and senescence on the main stem [4,5,7,34]. 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. 3):

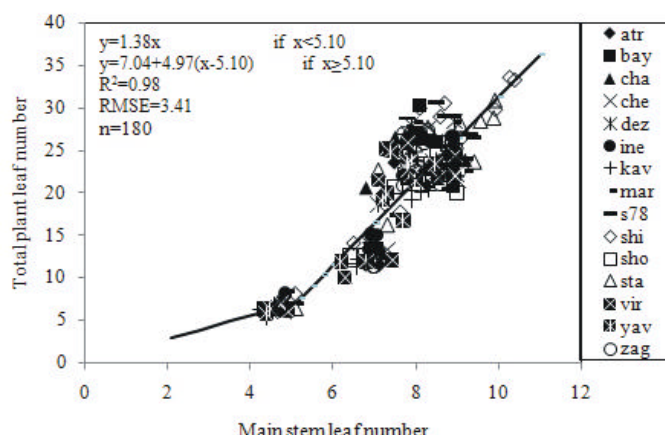


Fig. 3: Changes of total leaf number per plant as a function of leaf number on main stem. Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons

$$y = b_1 x \quad \text{if } x \leq x_0 \quad (6)$$

$$y = b_1 x_0 + b_2 (x - x_0) \quad \text{if } x > x_0$$

Where y is the total (green and senesced) number of leaves per plant, x the number of leaves on main stem, x_0 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. There were no differences for the leaf production rates in phases 1 and 2 and turning point (x_0) between two phases across all cultivars and years. (Fig. 3). The mean leaf production rate in phase 1 was 1.28 leaves per leaf. In phase 2, the mean rate of leaf production was 6.7 leaves per leaf number increase of main stem. The turning point between two phases was 5.5 in Exp. 1.

In Exp. 2, Eq. (6) also adequately described changes of plant leaf number versus main stem leaf number. There was no significant difference between cultivars and estimates of x_0 , b_1 and b_2 were 5.6, 1.48 and 6.3, respectively. Also, there was no significant difference between cultivars in experiment 1 and 2 for x_0 , b_1 and b_2 based on their 99% confidence intervals (Fig. 3).

The increased rate of leaf production in phase 2 was related to the appearance of tillers. In Chickpea, Soltani *et al.* [5] reported that genotype and sowing dates had no effect on b_1 , b_2 and x_0 . They stated that the reason of increase in leaf production rate in phase 2 was due to branching in plant. Because of the non-significant differences between cultivars and years, the following equation was fitted to all the data:

$$y = 1.38x \quad \text{if } x \leq 5.10 \quad (7)$$

$$y = 7.04 + 4.97(x - 5.10) \quad \text{if } x > 5.10$$

Based on Eq. (7), in phase 1 of leaf production 1.38 leaves was added per each leaf number increase on the main stem. But, after 5.10 leaves on the main stem and the beginning of tillering 5 leaves were added to the plant per each leaf increase on main stem.

The fraction of senesced leaves per plant (ratio of senesced to total leaves) versus the same fraction on main stem in both Experiments also followed Eq. (6) (Fig. 4). In Exp.1, the fraction of senesced leaves per plant increased 0.76% per each percent increase in fraction of senesced leaves on main stem until the fraction was less than or equal to 0.28 on main stem (equivalent to 1296 degree-days, near flag leaf emergence). After this, each percent increase in the fraction of senesced leaves on main stem resulted in a 1.20% increase in the fraction of senesced leaves per plant. The values of b_1 , b_2 and x_0 were 0.68, 1.16 and .30 in Exp.2. There was no significant difference between cultivars in experiment 1 and 2 for x_0 , b_1 and b_2 based on their 99% confidence intervals (Fig. 4). Because of the non-significant differences between cultivars and years, the following equation was fitted to all the data:

$$y = 0.71x \quad \text{if } x \leq 0.28 \quad (8)$$

$$y = 0.20 + 1.16(x - 0.28) \quad \text{if } x > 0.28$$

In summer crops, such as sunflower, maize and sorghum, senescence starts before all leaf area is fully developed (i.e. previous flowering) and progresses at an increased rate during the grain filling period [38-39]. To modeling of leaf senescence, Borrás *et al.* [37] fitted a bilinear model to their data. They proposed that this model can give information on: (i) changes in senescence rate along the cycle and (ii) the ontogenic stage when this change takes place.

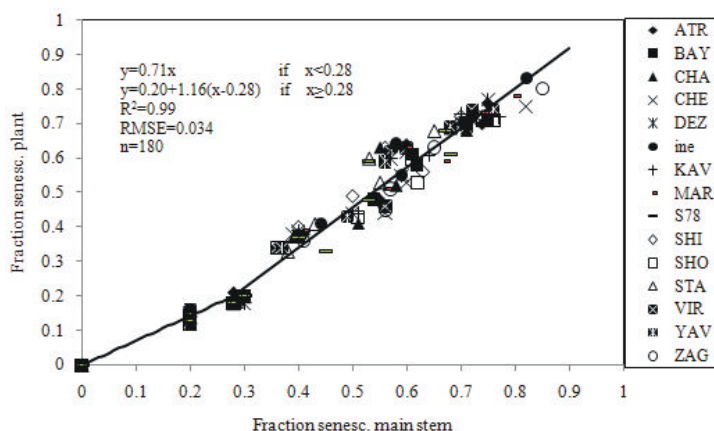


Fig. 4: Fraction of senesced leaf number per plant vs. the fraction on main stem. Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons

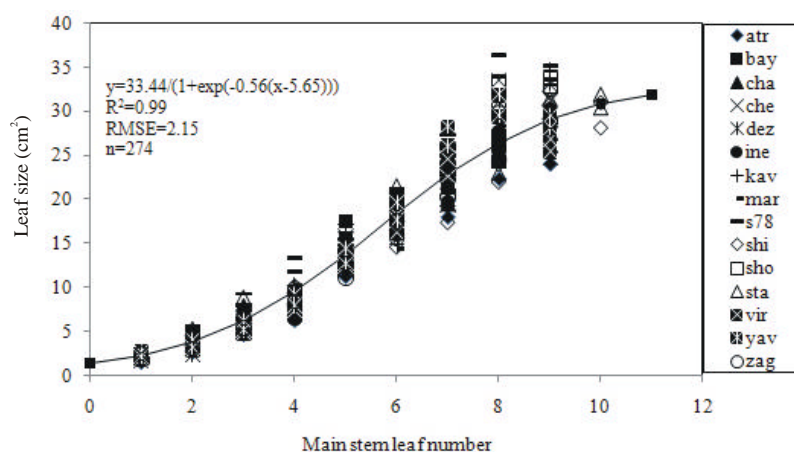


Fig. 5: Leaf size as a function of main stem leaf number. Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons

Leaf Size: Area of individual leaves is usually calculated from leaf length (LL) and the leaf width (at the widest point; LW) as Eq.1. The relationship between leaf size and number of leaves on main stem is shown in Fig. 5. A logistic equation was used to describe the relationship between leaf size and leaf number on main stem:

$$Y = \frac{maxa}{1 + \exp(-a(x-b))} \quad (9)$$

Where y is individual leaf area, $maxa$ is the maximum leaf area, x is the leaf number on main stem and a and b are equation coefficients. As leaf number on main stem increased, the area of the leaf also increased (Fig. 5). There were no significant difference among cultivars and years for estimates of $maxa$, a and b . Therefore, the following equation was fitted to all the data:

$$Y = \frac{33.44}{1 + \exp(-0.56(x-5.65))} \quad (10)$$

Based on Eq.10, mean leaf size started to increase from 5.7 cm^2 when there was 6 leaves on main stem and stabilized at 33.4 cm^2 when there was 8 to 10 leaves on main stem (Fig. 5). No studies have investigated such as patterns in wheat while, other researchers reported similar functions in chickpea, soybean and navy bean [3,5,8,10,34]. It has been reported that there is little genetic variation for leaf size in pigeon pea [4]. Leaf size in chickpea, soybean and cowpea has been found to stabilize at about the 5th to 10th node [3,5,8,10].

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 plant leaf area and main stem leaf number (HS) and total number of green leaves in plants

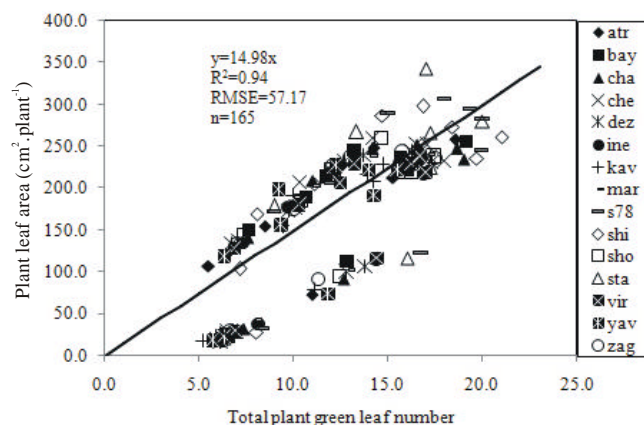


Fig. 6: Plant leaf area as a function of the number of green leaves per plant. Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons

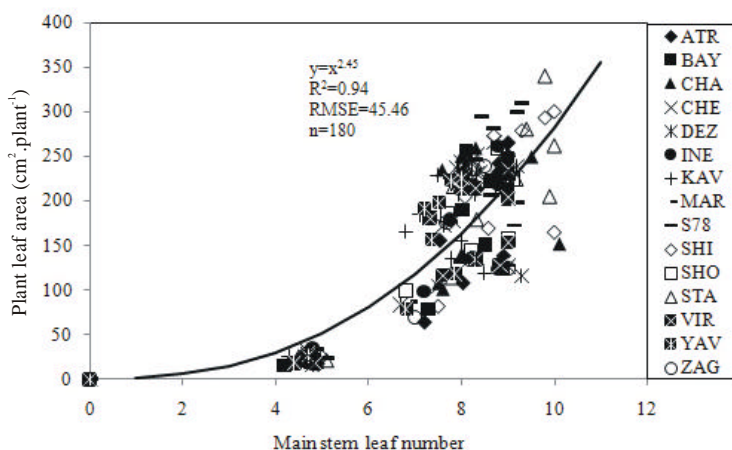


Fig. 7: Plant leaf area as a function of main stem leaf number described by a power function as $y=x^b$. Data correspond to the experiments carried out in 2006-7 and 2007-8 seasons.

[5,9,10,16,40]. In our study, the total number of green leaves and plant leaf area were measured simultaneously in all cultivars. There was a simple, linear relationship between plant leaf area and the number of green leaves with an R^2 value greater than 0.92 (Fig. 6). There was no significant difference in the slope of the linear regression model (b) among cultivars in both experiments. Therefore, a general model was found as follows:

$$y=14.98x \tag{11}$$

It means that per each leaf increase on plant, 15 cm^2 is added to plant leaf area, indicating average leaf size. Soltani *et al.* [5] reported a linear relationship for chickpea between the total plant node number and the plant leaf area.

Hammer *et al.* [7] and Soltani *et al.* [5] used a simple, power function to predict plant leaf area from plant leaf

number in grain sorghum and chickpea. The form of the function is:

$$y=x^b \tag{12}$$

Where y is the plant leaf area; x , the plant leaf number (here, main stem leaf 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.) [40] and chickpea [5]. The results of fitting the Eq. (12) to plant leaf area data versus main stem leaf number for cultivars are presented in Fig. 7. Plant leaf area ranged between 0 and 350 cm^2 per plant. The function gave reasonable fits with R^2 values of 0.79-0.98. The coefficient of the function also did not indicate significant relationship among cultivars in both experiments. Hence, based on all data, a generalized equation as was found:

$$y=x^{2.45} \quad (13)$$

Therefore, plant leaf area in wheat under well-watered conditions can be predicted using function (13). Based on this function plant leaf area can be predicted up to cessation of effective leaf production on main stem. For the senescence phase other approaches should be used. Sinclair [10] and Yoshida *et al.* [41] simulated plant leaf area in senescence phase based on nitrogen remobilization from leaves.

CONCLUSIONS

Mean leaf appearance rate ranged from 0.0076 to 0.0083 leaf/°C d. Leaf senescence on the main stem started when the main stem had about 5 leaves on main stem and proceeded at a rate of 0.0495 % per each one degree increase in degree-days. Leaf production and senescence per plant were closely related to leaf production and senescence on the main stem. The average leaf size stabilized at 33.5 cm² when there were 9-10 leaves on the main stem. Plant density and leaf size had no significant difference among cultivars (p<0.05). 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 leaves 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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