

Salinity Affects the Timing of Phasic Development in Spring Wheat

C. M. Grieve,* L. E. Francois, and E. V. Maas

ABSTRACT

Understanding effects of environmental factors on crop phenological development is useful for predicting crop growth stages and scheduling management practices. We evaluated the effect of salinity on the rate of leaf appearance and the duration of critical stages of growth in wheat (*Triticum aestivum* L.) in terms of both thermal unit (TU; °C day) and phyllochron intervals. Two hard red spring wheat cultivars, Yecora Rojo and Anza, were grown two cropping years in greenhouse sand cultures and outdoor field lysimeters. In each case, two saline treatments were compared with a nonsaline control. The sand cultures were irrigated with complete nutrient solutions to which NaCl and CaCl₂ were added. The electrical conductivities, κ_w , were 2.0, 14.3, and 18.1 dS m⁻¹ in 1989 and 1.7, 12.2, and 15.1 dS m⁻¹ in 1990. The κ_w for the field lysimeters were 0.9, 10.7, and 17.2 dS m⁻¹ in 1989 and 0.8, 11.4, and 17.1 dS m⁻¹ in 1990. Leaf appearance rate was determined by regressing the number of mainstem leaves against cumulative TU. In all treatments, the cultivars differed in both rate and duration of leaf appearance. The phyllochron increased with salinity. Leaves emerged more slowly in the greenhouse than in the field. Durations of the vegetative stages (°C day) from sowing to the initiation of the flag leaf and its subsequent appearance were relatively insensitive to salinity inasmuch as increases in leaf plastochron (TU between the initiation of successive leaves on a culm) and leaf phyllochron were balanced by decreases in leaf number. However, for both cultivars, salinity significantly reduced the thermal time between sowing and the reproductive phenological stages.

CROP GROWTH MODELS have become important tools for understanding and improving crop management. Several successful models of wheat canopy development are based on the timing of certain morphological events, specifically, the rate of appearance of successive leaves on the main culm (McMaster et al., 1991, 1992a,b; Rickman and Klepper, 1991). The usefulness of simulation models can be extended by evaluation and incorpora-

tion of the effects of environmental factors, such as salinity, on leaf development.

Numerous investigators have addressed the influence of environmental variables on leaf development in wheat. The final number of mainstem leaves is determined early in the life cycle of the crop and depends on the rate and duration of leaf initiation. For a given genotype, total mainstem leaf number can vary with sowing date (Kirby et al., 1985), light intensity (Simmons, 1987), water deficit (Oosterhuis and Cartwright, 1983), temperature (Amores-Vergara and Cartwright, 1984), plant population (Kirby and Appleyard, 1984), soil fertility (Longnecker et al., 1993), and salinity (Maas and Grieve, 1990).

Leaf appearance on the main culm of wheat is a highly significant, linear function of TU expressed as °C day. Regression of leaf number, expressed in terms of Haun growth scale units (Haun, 1973), on TU gives leaf appearance rate. The reciprocal of this rate, the phyllochron, is the TU between appearance of successive leaves on a culm. This procedure for estimating the phyllochron is commonly, but not universally, used. Alternative methods of calculating the phyllochron often give different values even when the same data set is analyzed. Kirby (1988) found that the phyllochron value based on estimates of emerged leaves only (i.e., with the ligule emerged) was substantially shorter (82°C d) than the value obtained when both emerged and emerging leaves were considered (101°C d). McMaster et al. (1992b) determined the phyllochron by dividing the TU from seedling emergence by the Haun growth stage of 30-d-old plants. The phyllochron may also be calculated from the mean TU between growth stages of successive leaves as measured by the time when the youngest expanding blade

USDA-ARS, U.S. Salinity Lab., 4500 Glenwood Drive, Riverside, CA 92501. Received 21 Dec. 1993. *Corresponding author.

can be seen emerging from the enclosing penultimate leaf (Krenzer et al., 1991).

Temperature has a significant effect on leaf appearance rate, although plant response may be moderated by the change in photoperiod (Baker et al., 1980). Cao and Moss (1989) reported that the phyllochron of winter wheat varied from 56°C d leaf⁻¹ at 7.5°C to 116°C d leaf⁻¹ at 25°C. Leaf appearance is relatively unresponsive to nutritional deficiencies unless they become severe. Longnecker et al. (1993) reported that severe N deficiency increased the phyllochron of spring wheat grown in sand cultures. Other investigators (Bauer et al., 1984; Frank and Bauer, 1982) found that, under field conditions, N status had no effect on the timing of leaf emergence. Reports on the effects of water deficit on leaf appearance of spring wheats are inconsistent. Bauer et al. (1984) found that, under field conditions, the phyllochron was insensitive to changes in the soil water regime. However, water stress, imposed under growth chamber conditions, slowed leaf appearance of several winter wheat cultivars, and the phyllochron increased from 87°C d leaf⁻¹ under well-watered conditions to 102°C d leaf⁻¹ in response to mild water deficit (Krenzer et al., 1991). Based on their finding that the phyllochron of water-stressed, nonirrigated wheat was significantly less than that of irrigated plants, Baker et al. (1986) speculated that higher canopy temperatures may have resulted in a faster rate of TU accumulation by the meristems of the nonirrigated plants. Leaf appearance rate also decreased in response to salinity. Compared with that of the control plants, the phyllochrons for a spring wheat and a durum cultivar salt stressed at -0.65 MPa increased 12 and 9%, respectively (Maas and Grieve, 1990).

The objectives of the current study were to investigate the phasic patterns of two hard red spring wheat cultivars, Yecora Rojo and Anza, grown in the greenhouse and in field lysimeters and to quantify the effect of salt stress on the duration of discrete developmental periods.

MATERIALS AND METHODS

Greenhouse! Experiments

The semidwarf hard red spring wheat cultivars, Yecora Rojo and Anza, were grown in sand tanks in a greenhouse at the U.S. Salinity Laboratory at Riverside, CA. Description of the tanks, nutrient solution composition, maintenance of the sand cultures, and irrigation scheduling are given in Grieve et al. (1993). Two salinity treatments were imposed by adding NaCl and CaCl₂ (2:1 molar ratio to simulate saline soil conditions) to the nutrient solutions. The base nutrient solution served as the nonsaline control treatment. In 1989, the electrical conductivities of the irrigation waters were 2.0, 14.3, and 18.1 dS m⁻¹ to give osmotic potentials of -0.05, -0.65, and -0.85 MPa, respectively. In 1990, the electrical conductivities of the irrigation waters were 1.7, 12.2, and 15.1 dS m⁻¹ with osmotic potentials of -0.05, -0.55, and -0.70 MPa, respectively, and are hereafter designated as C, M, and H salinity treatments. Salination began at seedling emergence, 3 d after planting. The osmotic potentials of the saline treatments were decreased to target levels by incremental additions of the salts for 3 consecutive d to avoid osmotic shock to the seedlings. The experimental design consisted of three salinity

treatments replicated three times in a randomized complete-block, split-plot design, with salinity level as the main plots and cultivar as the subplots.

During the 1989 experiment, daytime air temperatures ranged from 21 to 36°C (mean = 30°C) and nighttime temperatures, from 14 to 30°C (mean = 20°C). Relative humidity ranged from 40 to 99%, with a mean of 60% during the day and 81% during the night. In 1990, daytime air temperatures ranged from 23 to 36°C (mean = 28°C); nighttime from 6 to 19°C (mean = 15°C). Relative humidity ranged from 42 to 96%, with a mean of 59% during the day and 81% during the night.

Field Lysimeter Experiments

Description of the lysimeters and the cultural practices followed in the field plots are given in Grieve et al. (1993).

Seeds of both cultivars were sown in the center 5.8-m² area of the lysimeters on 11 January in both 1989 and 1990. Eight rows of each cultivar were planted per lysimeter each year. Rows were spaced 0.15 m apart, with the seeds placed 4 cm apart within the rows to give a sowing density of 167 seeds m⁻². Sowing depth was ≈ 1.5 cm.

In both years, the experimental design was identical to that given for the greenhouse study. To facilitate germination each year, 25 mm of low-salinity water (0.9 dS m⁻¹) was applied to each lysimeter after sowing. When the coleoptiles had just emerged through the soil surface, differential salination was initiated by applying irrigation water containing equal weights of NaCl and CaCl₂. This represents a NaCl/CaCl₂ molar ratio of 1.9:1, similar to the solution composition used for the greenhouse study. The average irrigation water salinities (κ_s) were 0.9, 11.3, and 17.5 dS m⁻¹ in 1989 and 0.8, 12.2, and 17.7 dS m⁻¹ in 1990 to give the C, M, and H salinity treatments, respectively.

A neutron probe and tensiometers were used to monitor soil matric potential and to guide irrigation frequency. Soil water contents were measured before and after most irrigations at depths of 25, 45, 75, and 105 cm and at two locations within each lysimeter. Soil water salinity was determined at these same depths by extracting soil solutions with porous ceramic suction tubes and measuring their electrical conductivity.

Time- and depth-averaged salinities imposed on the cultivars from sowing in the field lysimeters to the end of various phenological growth stages are presented for 1989 and 1990 in Table 1. The following example illustrates the method for estimating the salinity stress encountered by the plants from sowing to the end of shoot primordium initiation. In 1990 Treatment M, terminal spikelet formation in Yecora Rojo occurred about 6 15 °C d (5 1 calendar d) after sowing. Rooting depth, based on neutron probe measurements of soil water extraction at this time, was ≈ 45 cm. The average salinity in the 0- to 45-cm profile had ranged from 14.9 dS m⁻¹ at sowing to 17.7 dS m⁻¹ on Calendar Day 50 with a mean of 16.3 dS m⁻¹. The 1990 soil salinity values (Table 1) were higher than in 1989 because the soil profiles were still salinized from the previous year.

Standard meteorological measurements were made with a Class I agrometeorological station adjacent to each experimental location. Soil-sand temperatures were measured at a depth of about 1 cm; air temperatures were measured about 2 m above the soil surface. Hourly temperatures were measured and integrated during the 24-h period; daily mean temperatures were summed to give cumulative thermal time ("C d). A base temperature of 0°C was used. At each location, PPFD was

Table 1. Time- and depth-averaged soil salinities from sowing to various phenological stages of Yecora Rojo and Anza spring wheat grown during two seasons in field lysimeters.

Stage	1989			1990		
	Control	Medium salt	High salt	Control	Medium salt	High salt
	dS m ⁻¹					
	Yecora Rojo					
Flag leaf initiation	2.6	5.1	5.4	4.4	15.8	23.0
Terminal spikelet formation	2.4	7.0	7.0	4.2	16.3	23.5
Flag leaf appearance	2.4	8.0	8.6	4.0	16.7	24.0
Booting	2.4	8.6	9.5	3.9	17.0	24.2
Heading, first awns visible	2.4	8.9	9.8	3.8	17.1	24.3
Anthesis	2.4		11.4	3.4	17.6	24.1
Maximum culm length	2.3	10.0	11.2	3.6	17.8	24.7
Maturity	2.2	14.2	16.7	2.9	19.4	26.3
	Anza					
Flag leaf initiation	2.5	6.0	5.7	4.4	15.9	23.1
Terminal spikelet formation	2.4	7.7	7.8	4.0	16.6	23.7
Flag leaf appearance	2.4	9.8	9.7	3.9	17.1	24.3
Booting	2.3	10.2	10.2	3.7	17.3	24.4
Heading, first awns visible	2.3	9.7	10.9	3.5	17.5	24.6
Anthesis	2.3	10.8	12.5	3.5	18.0	25.1
Maximum culm length	2.3	10.8	11.6	3.5	17.9	24.9
Maturity	2.2	15.0	17.6	2.8	19.8	26.5

measured 2 m above the soil surface with a LI-190SB quantum sensor¹ (LI-COR, Inc., Lincoln, NE).

Plant Measurements

In each sand tank or lysimeter plot, 10 plants of each cultivar were randomly selected. Mainstem leaves were identified as they emerged and tagged with colored wire rings. Leaf development was measured weekly according to the Haun growth scale (Haun, 1973). Final mainstem leaf number was determined at the time of full flag leaf extension. Dates of booting (ZCK scale 45; Zadoks et al., 1974), heading (awns visible, ZCK

¹ Reference to specific products is made for identification purposes and does not imply endorsement by the United States Government.

Table 2. Effect of salinity on mean leaf number and phyllochron intervals of Yecora Rojo and Anza spring wheat grown in greenhouse sand cultures and in field lysimeters during two growing seasons.

Treatment	Lysimeter		Greenhouse	
	Mainstem leaves	Phyllochron	Mainstem leaves	Phyllochron
	No.	°C d	No.	°C d
	Yecora Rojo (1989)			
Control	8.7 at	91 a	8.6 a	115 a
Medium salt	8.1 b	94b	7.8 b	116 a
High salt	8.1 b	93 b	7.0 c	126 b
	Yecora Rojo (1990)			
Control	8.2 a	93 a	8.3 a	118 a
Medium salt	8.1 b	97 ab	7.5 b	123 b
High salt	8.0 b	101 b	7.1 b	126c
	Anza (1989)			
Control	11.0 a	78 a	10.1 a	103 a
Medium salt	10.1 b	82 b	9.7 a	106b
High salt	10.1 b	81 b	9.0 b	113 c
	Anza (1990)			
Control	11.0 a	81 a	10.0 a	106a
Medium salt	9.9 b	84b	9.3 ab	112 b
High salt	9.9 b	91 c	8.9 b	115 c

‡ Within columns for a given cultivar and year, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's Studentized Range Test.

49), and anthesis (ZCK 65) were recorded for each selected plant. Estimates for the timing of primordium initiation were obtained from destructive measurements of plants grown in the 1990 experiment (Grieve et al., 1993). At the time of terminal spikelet formation and at biweekly intervals for 2 mo, three to six plants per treatment, other than those selected for leaf development, were dissected and mainstem culm lengths above the soil surface were recorded. The beginning of culm elongation coincided with formation of the terminal spikelet and was roughly equivalent to the ear at 1 cm stage shown in Kirby and Appleyard (1987). Plants were rated as mature when the spike was devoid of green color and the kernels could no longer be dented by thumb nail (ZCK scale 92).

Tukey's Studentized Range test was used to differentiate between the observed developmental parameters across the three salinity levels. Durations of leaf and spikelet primordia initiation were determined with a three-piece linear spline model (Grieve et al., 1993). The time of maximum culm elongation was estimated by fitting a two-piece model using SAS procedure NLIN (Method DUD) (SAS, 1985).

RESULTS

Mainstem Leaf Number

In both seasons, number of mainstem leaves of both cultivars grown in field lysimeters decreased significantly in response to the medium level of salinity (Table 2). However, further increase in salt stress had no additional effect. In the 1989 greenhouse experiment, leaf number of Yecora Rojo decreased consistently and significantly as salinity increased, whereas reduction in numbers of Anza leaves was significant only in the high salt treatment. The response observed in the 1990 greenhouse experiment was similar to that obtained from the field in that mainstem leaf number was reduced by medium salinity and was not further affected as salt stress increased. Under nonsaline conditions, the number of leaves produced by Yecora Rojo main stems was significantly lower in 1990 than in 1989 ($\alpha = 0.05$) in both experimental locations. This variation may reflect a

difference in seed source from one year to the next. The mainstem leaf number of Anza control plants was unaffected by cropping year.

Phyllochron Interval

Regression of Haun values against TU gave a linear relationship for all experiments. With few exceptions, r^2 values were **X.985**. Under nonsaline conditions, the phyllochron of the two cultivars ranged from 78 to 93°C d in the field lysimeters and from 103 to 118°C d in the greenhouse (Table 2). Phyllochron values from the field are in the range of those determined for spring wheats grown in the Northern Great Plains (Bauer et al., 1984).

Phyllochrons were greater in the 1990 experiments for both cultivars in both locations (Table 2). Genotypic differences were evident in that Anza phyllochrons were consistently shorter than those obtained for Yecora Rojo grown under the same treatment. Under field conditions in both years when imposed salt stress significantly reduced mainstem leaf production, the rate of appearance was also reduced. Thus, the phyllochrons increased while mainstem leaf number decreased significantly in response to M. Differences between the M and H salt levels were negligible. In the 1989 greenhouse experiment, the increase in the phyllochron of Yecora Rojo was significant only at the highest salinity level. The phyllochrons for Anza in 1989 and for both cultivars in 1990 increased consistently and significantly as salinity increased under greenhouse conditions.

For both cultivars, the TU required for production of a mainstem leaf under nonsaline-control conditions was greater in the greenhouse than in the field. Averaged for both seasons, the phyllochrons for Yecora Rojo were 92°C d in the field and 116°C d in the greenhouse. For Anza, these values were 80 and 104°C d, respectively. Differences in light intensity between the two locations may, at least in part, account for the higher TU requirement for the production of successive leaves in the greenhouse. For example, on 5 Feb. 1990 (22 d after emergence), the average Haun value for Anza control plants grown in the greenhouse was 4.3. At this time, the cumulative PPFd was 282 mol m^{-2} , with an average PPFd of 12.8 mol $m^{-2} d^{-1}$. Anza controls in the field lysimeters averaged 4.3 leaves on 20 Feb. 1990 (29 d after emergence) when the cumulative PPFd was 655 mol m^{-2} with an average of 22.6 mol $m^{-2} d^{-1}$. By the time the eighth leaf of the Anza controls was partially emerged (Haun value 7.4-7.5), the average PPFd was 15.2 and 22.5 mol $m^{-2} d^{-1}$ in the greenhouse and field lysimeters, respectively. The increase in phyllochron under light-limiting conditions is consistent with observations from growth chamber experiments (Rickman et al., 1985). Because of the substantial differences in phyllochron that are attributable to differences in location and because data from field experiments are undoubtedly more useful for crop simulation models than those collected from more controlled environments, the remainder of this report will focus on information obtained from the field lysimeters.

DISCUSSION

Effect of Salinity on the Timing of Phenological Development

One response of cereals growing under different salinity regimes is that those plants that are under the most severe salt stress are the first to mature. The difference in time to maturity between salinized wheat plants and the nonsaline controls was such that the salt-stressed wheat was ready for harvest 1 to 2 wk before its less-saline-stressed counterpart (Francois et al., 1986). The TU from sowing to specific phenological stages is given for the 1990 field lysimeter experiment in Table 3. For example, the total TU from sowing to maturity of Yecora Rojo in the high salinity treatment was 250°C d less than the nonsaline controls. Likewise, the Anza controls matured 274°C d later than Anza-H. The phyllochron concept can also be used to describe differences in phasic development (McMaster et al., 1992a). If, as has been suggested by numerous investigators (see McMaster et al., 1992a for review), wheat maintains a constant phyllochron throughout the life-cycle of the crop, then salinity shortened time to maturity of Yecora Rojo and Anza by 4.2 and 5.8 phyllochrons, respectively.

To enhance the ability of mechanistic crop growth models to simulate salinity effects, data are required that give functional relationships between salinity levels and the duration of important growth stages. During early seedling growth, the major effect of salt stress on the timing of shoot primordia initiation is to reduce the duration of the spikelet initiation phase, whereas the period from sowing to flag leaf initiation is unaffected by salinity (Table 3). Because the highest level of salinity decreased time to terminal spikelet formation, subsequent events, e.g., culm elongation (jointing) and spike growth in salt-stressed Yecora Rojo and Anza mainstems, commenced about 0.8 and 1.6 phyllochrons earlier, respectively, than in the nonsaline controls.

Table 3. Influence of salinity on thermal time from sowing to various phenological stages of Yecora Rojo and Anza spring wheat grown in lysimeters in 1990.

Stage	Control	Medium salt	High salt
	°C d		
	Yecora Rojo		
Flag leaf initiation	381 a†	381 a	381 a
Terminal spikelet formation	647 a	615 b	588 c
Flag leaf appearance	810 a	785 a	814 a
Booting	956 a	901 b	898 b
Heading, first awns visible	1001 a	943 b	941 b
Anthesis	1202 a	1141 b	1138 b
Maximum culm length	1272 a	1245 b	1110 b
Maturity	2053 a	1909 b	1803 c
	Anza		
Flag leaf initiation	422 a	422 a	422 a
Terminal spikelet formation	789 a	727 b	686 c
Flag leaf appearance	920 a	906 a	917 a
Booting	1108 a	1023 b	984 c
Heading, first awns visible	1202 a	1098 b	1069 c
Anthesis	1412 a	1302 b	1279 c
Maximum culm length	1416 a	1285 b	1204 c
Maturity	2183 a	2053 b	1909 c

† Within rows and cultivars, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's Studentized Range Test.

Salinity had no effect on the observed TU between planting and the emergence of the total complement of mainstem leaves (Flag leaf appearance, Table 3). For all treatments, the time of flag leaf emergence was similar because the salinity-induced decrease in mainstem leaf number was balanced by the increase in the phyllochron. The predicted duration of leaf appearance, the product of the mean number of mainstem leaves and the phyllochron (Table 2), gave a close approximation of the observed values. The durations of both pre-emergence (initiation) and postemergence (appearance) phases of foliar development appear to be relatively insensitive to salt stress and thus made negligible contributions to the salinity-induced acceleration of growth and development that are observed. The response of wheat to stress induced by N deficit follows a similar pattern. Under severe N deficiency, the number of main stem leaves decreased, whereas the phyllochron increased to such a degree that the flag leaves emerged at the same time regardless of N treatment (Longnecker et al., 1993).

The thermal time necessary for full culm extension decreased with salinity (Table 3). In Yecora Rojo, the intervals between the beginning of culm elongation (shortly after the formation of the terminal spikelet) and the time of maximum length were 6.7, 6.5, and 5.2 phyllochrons for C, M, and H salt treatments, respectively. The decrease was significant only at the highest salt treatment. The duration of Anza culm elongation decreased consistently and significantly with increasing salt stress, and these intervals were 7.7, 6.3, and 5.7 phyllochrons for C, M, and H salt levels, respectively.

Phasic development, described in terms of the phyllochron concept, was cultivar dependent (Table 4). The values for the two cultivars grown under nonsaline control conditions were also different from those reported for winter wheat grown under optimum conditions. A review (McMaster et al., 1992a) of published estimates

of phyllochron intervals reveals that booting occurs 2 phyllochrons after flag leaf appearance, 3 phyllochrons after jointing, and 0.5 phyllochrons prior to heading. Anthesis in winter wheat occurred about 0.5 phyllochrons after heading. Differences between these reported values and those observed in our study may reflect genotypic-specific values for the cultivars we studied compared with the generalized values (McMaster et al., 1992a) as well as differences in the methodology used to identify various growth stages.

Timing of phenological development stages as well as the date of physiological maturity of wheat may also be influenced by environmental stresses other than salinity. High plant densities often result in vigorous interplant competition that may lead to decreased time to maturity. Faris and De Pauw (1981) found that ripening of 'Nee-pawa' wheat was delayed about 8 d as seeding rate decreased from 675 to 75 seeds m^{-2} . Under conditions of water or N deficit, the response varied with the level of stress. Mild drought shortened the durations of developmental stages and reduced time to maturity; although under conditions of extreme water deficit, phasic development was slowed, i.e., developmental stages were lengthened (Meyer and Green, 1980; Amir and Sinclair, 1991). McMaster et al. (1992b) reported that the phyllochron estimates for the durations of various growth stages of well-watered wheat were about 20% greater than for wheat grown under dryland conditions. Time to maturity was also reduced by mild to moderate N deficit, although severe N deficiency tended to delay barley (*Hordeum vulgare* L.) development (Halse et al., 1969).

Salt stress decreased the time from sowing to maturity of wheat by reducing the duration of specific growth stages, i.e., spikelet initiation, booting, heading, and anthesis. These results provide data that can be useful in scheduling management practices in salt-affected areas, particularly those that should be closely integrated with a specific stage of phasic development, e.g., pesticide and fertilizer applications. In addition, this information is required for the development of a module for the crop simulation model that will describe and predict the effects of salinity on the growth and yield of spring wheat.

Table 4. Influence of salinity on number of phyllochrons between phenological stages of Yecora Rojo and Anza spring wheat grown in field lysimeters in 1990.

Stage	Control	Medium salt	High salt
Yecora Rojo			
Planting to flag leaf initiation	4.1	4.0	3.8
Flag leaf initiation to terminal spikelet formation	2.9	2.4	2.1
Terminal spikelet formation to flag leaf appearance	1.8	1.8	2.2
Flag leaf appearance to booting	1.6	1.2	0.8
Rooting to heading	0.5	0.4	0.4
Heading to anthesis	2.2	2.1	2.0
Anthesis to maturity	9.1	8.0	6.6
Planting to maturity	22.1	19.8	17.9
Anza			
Planting to flag leaf initiation	5.2	4.8	4.7
Flag leaf initiation to terminal spikelet formation	4.5	3.4	2.9
Terminal spikelet formation to flag leaf appearance	1.6	2.0	2.6
Flag leaf appearance to booting	2.3	1.3	0.7
Booting to heading	1.2	0.8	0.9
Heading to anthesis	2.6	2.3	2.3
Anthesis to maturity	9.5	8.5	6.7
Planting to maturity	26.9	23.2	21.1

REFERENCES

- Amir, J., and T.R. Sinclair. 1991. A model of water limitation on spring wheat growth and yield. *Field Crops Res.* 28:59-69.
- Amores-Vergara, E., and P.M. Cartwright. 1984. Effects of short periods of exposure to high temperature on the phenology and shoot apex development of wheat cv. Sonora 64. *Aust. J. Agric. Res.* 35:139-148.
- Baker, C.K., J.N. Gallagher, and J.L. Monteith. 1980. Daylength change and leaf appearance in winter wheat. *Plant Cell Environ.* 3:285-287.
- Baker, J.T., P.J. Pinter, R.J. Reginato, and E.T. Kanemasu. 1986. Effects of temperature on leaf appearance in spring and winter wheat cultivars. *Agron. J.* 78:605-613.
- Bauer, A., A.B. Frank, and A.L. Black. 1984. Estimation of spring wheat leaf growth rates and anthesis from air temperature. *Agron. J.* 76:829-835.
- Cao, W., and D.N. Moss. 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. *Crop Sci.* 29: 1018-1021.
- Faris, D.G., and R.M. De Pauw. 1981. Effect of seeding rate on growth and yield of three spring wheat cultivars. *Field Crops Res.* 3:289-301.

- Francois, L.E., E.V. Maas, T.J. Donovan, and V.L. Youngs. 1986. Effect of salinity on grain yield and quality, vegetative growth, and germination of semi-dwarf and durum wheat. *Agron. J.* 78: 1053-1058.
- Frank, A.B., and A. Bauer. 1982. Effect of temperature and fertilizer N on apex development in spring wheat. *Agron. J.* 74:504-509.
- Grieve, C.M., S.M. Lesch, E.V. Maas, and L.E. Francois. 1993. Leaf and spikelet primordia initiation in salt-stressed wheat. *Crop Sci.* 33: 1286-1294.
- Halse, N.J., E.A.N. Greenwood, P. Lapins, and C.A.P. Boundy. 1969. An analysis of the effects of nitrogen deficiency on the growth and yield of a Western Australian wheat crop. *Aust. J. Agric. Res.* 20:987-998.
- Haun, J.R. 1973. Visual quantification of wheat development. *Agron. J.* 65:116-119.
- Kirby, E.J.M. 1988. Analysis of leaf, stem and ear growth in wheat from terminal spikelet stage to anthesis. *Field Crops Res.* 18: 127-140.
- Kirby, E.J.M., and M. Appleyard. 1984. Cereal plant development-assessment and use. p. 21-38. In *The nitrogen requirement of cereals*. Reference Book 385. Ministry of Agriculture, Fisheries, and Food. HMSO. London.
- Kirby, E.J.M., and M. Appleyard. 1987. *Cereal development guide*. 2nd ed. Arable Unit, National Agricultural Centre, Kenilworth, Warwickshire, England.
- Kirby, E.J.M., M. Appleyard, and G. Fellowes. 1985. Effect of sowing date and variety on main shoot leaf emergence and number of leaves of barley and wheat. *Agronomie (Paris)* 5: 117-126.
- Krenzer, E.G., Jr., T.L. Nipp, and R.W. McNew. 1991. Winter wheat mainstem leaf appearance and tiller formation vs. moisture treatment. *Agron. J.* 83:663-667.
- Longnecker, N., E.J.M. Kirby, and A. Robson. 1993. Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. *Crop Sci.* 33:154-160.
- Maas, E.V., and C.M. Grieve. 1990. Spike and leaf development in salt-stressed wheat. *Crop Sci.* 30:1309-1313.
- McMaster, G.S., B. Klepper, R.W. Rickman, W.W. Wilhelm, and W.O. Willis. 1991. Simulation of shoot vegetative development and growth of unstressed winter wheat. *Ecol. Modell.* 53:189-204.
- McMaster, G.S., J.A. Morgan, and W.W. Wilhelm. 1992a. Simulating winter wheat spike development and growth. *Agric. For. Meteorol.* 60: 193-220.
- McMaster, G.S., W.W. Wilhelm, and J.A. Morgan. 1992b. Simulating winter wheat shoot apex phenology. *J. Agric. Sci. (Cambridge)* 119:1-12.
- Meyer, W.S., and G.C. Green. 1980. Leaf growth, phenological development and yield of wheat grown under different irrigation treatments. *Water SA* 6:21-26.
- Oosterhuis, D.M., and P.M. Cartwright. 1983. Spike differentiation and floret survival in semidwarf spring wheat as affected by water stress and photoperiod. *Crop Sci.* 23:71 1-717.
- Rickman, R.W., and B. Klepper. 1991. Environmentally driven cereal crop growth models. *Annu. Rev. Phytopathol.* 29:361-380.
- Rickman, R.W., B. Klepper, and C.M. Peterson. 1985. Wheat seedling growth and developmental response to incident photosynthetically active radiation. *Agron. J.* 77:283-287.
- SAS Institute. 1985. *SAS user's guide: Statistics*. Version 5. SAS Inst., Cary, NC.
- Simmons, S.R. 1987. Growth, development, and physiology. p. 77-113. In E.G. Heyne (ed.) *Wheat and wheat improvement*. 2nd ed. Agron. Monoer. 13. ASA, CSSA, and SSSA, Madison, WI.
- Zadoks, J.C., T.T. Chang, and C.F. Konzak. 1974. A decimal code for the growth stages of cereals. *Weed Res.* 14:415-421.