The Effect of Day to Night Temperature Variation on Leaf Development in Wheat

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Abstract: The rate of leaf development in wheat is related to time and temperature in units of degree-days (DD) leaf⁻¹ (phylochron). Experiments were conducted in controlled environment chambers to study the effect of day to night variation in temperature on leaf development in two wheat cultivars, Penawawa and Stephens. Plants were grown at constant 20°C, and in eight day/night temperature ranges as wide as 8/32°C to 32/8°C, all with a mean temperature of 20°C. The leaf number on the main stems was counted (in Haun units) every other day, from the emergence of the 2nd leaf until the emergence of the 5th leaf. Leaf phylochron values were derived from the inverse of the slopes of the linear regression of leaf number on DD. Phylochron values ranged from 99 to 153 DD leaf⁻¹. The phylochron values were greater when higher temperatures were imposed at night under extreme day to night temperature treatment.

Key words: Development, Leaf, Phylochron, Temperature, Wheat.

Leaf development in wheat (Triticum aestivum L.) is a function of both time and temperature. The thermal environment for wheat leaf development is often expressed in units of “Degree-days” (DD). Degree-days are traditionally calculated as:

$$DD = \left[ \frac{T_{\text{max}} + T_{\text{min}}}{2} \right] - T_b,$$

where $T_{\text{max}}$ and $T_{\text{min}}$ are maximum and minimum air temperatures and $T_b$ is the base temperature below which no leaf development occurs. The base temperature for wheat leaf development is usually taken as 0°C (Cao and Moss, 1989a). The degree-day concept implicitly assumes that the rate of leaf development is related linearly to temperature. Indeed, at a constant temperature the rate of emergence of successive leaves on the main stem of a wheat plant is constant, but the rate of leaf development is different at different temperatures (Cao and Moss, 1989a).

The thermal-time elapsed between the appearance of successive leaf tips from the subtending leaf sheath is called a “phylochron”, with units (DD leaf⁻¹). The phylochron value for a particular wheat cultivar often appears to be constant during crop development in many field environments (Baker et al., 1986; Bauer et al., 1984; Gallahger, 1979; Hunt and Chapleau, 1986; Klepper et al., 1982), but may change at the double ridge stage of floral development and varies with planting date and latitude (Baker et al., 1980; Cao and Moss, 1991; Delecolle et al., 1985; Hay and Wilson, 1982; Hay and Delecolle, 1989; Kirby et al., 1985; Kirby and Perry, 1987). However, Bauer et al. (1984) found that, in field studies in an especially hot year, the constancy of phylochron was improved if temperatures greater than 21°C were considered to be 21°C in calculating daily degree-days.

Cao and Moss (1989a) grew four wheat and four barley cultivars in controlled environment chambers with a 14-h daylength and constant temperatures (day and night) of 7.5, 10, 12.5, 15, 17.5, 20, 22.5, and 25°C, and measured the leaf number on the main stem over time. The phylochron values reported by Cao and Moss (1989a) were indeed constant in each environment, but varied with temperatures, from 60 DD leaf⁻¹ at 7.5°C to 119 DD leaf⁻¹ at 25°C. They found that the relationship of the rate of leaf appearance on the main stem of wheat plants was curvilinear with temperature, with an optimum at about 21°C. These findings were in agreement with the early report by Friend et al. (1962) that leaf growth rates in wheat show a curvilinear relationship with temperature, with an optimum near 20°C.

In a recent review, Shaykewich (1995) concludes that the rate of leaf appearance in both wheat and maize (Zea mays L.) is clearly curvilinear with temperature, and, therefore should not be related to accumulated DD in field environments. He concludes that, in both species, the relationship of leaf emergence rate to temperature is sigmoidal near the origin (low temperature), reaches a maximum at the optimum temperature, and decreases sharply at temperatures above the optimum. Since the response of leaf development to temperature is strongly curvilinear, one should not expect the response of leaf development in varying day/night temperature regimes to be related linearly to the mean temperature, as is assumed in the common practice of defining the thermal environment for leaf development in unit of DD leaf⁻¹.

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Abbreviation: DD: degree-days.
In addition to the daily mean temperature, the daily range in temperature may have an important impact on the rate of leaf development.

This experiment was designed to study the relationship of leaf development to a variation in day to night temperature with the same mean temperature.

**Materials and Methods**

The wheat (*Triticum aestivum* L.) cultivars used in this experiment were Penawawa and Stephens. The former, a spring wheat cultivar developed at Washington State University, is adapted to the Pacific Northwest. The latter, a soft, white winter wheat, is grown widely in the Pacific Northwest and one of the cultivars used in an earlier study of the effect of constant temperatures on the phyllochron value of wheat (Cao and Moss, 1989a). The wheat plants were grown in controlled environment chambers (Controlled Environments Inc., Pembina, ND) in 3.5 L (0.15 m diameter) pots in a rooting medium composed of a 2:1:1:1 mixture (by volume) of pumice, sand, peat moss, and sandy-loam soil. The plants were grown at 32/8, 29/11, 26/14, 23/17, 20/20, 17/23, 14/26, 11/29, and 8/32 °C day/night temperatures, all with a mean temperature of 20°C. The temperature varied no more than ±0.5°C from the day or night set point, except during the change from day or night temperatures. The day/night cycle was set at 12-h/12-h. Illumination was provided from a combination of fluorescent and incandescent lamps at 400±20 μmols m⁻² s⁻¹ PPFD.

Eight seeds were planted in each pot and thinned to four uniform plants shortly after seedling emergence. Six pots containing four plants per cultivar were examined. The pots were checked daily and irrigated when necessary. The plants were fertilized at weekly intervals with 500 ml of 1/1000 strength liquid fertilizer (N-P₂O₅-K₂O=20%-20%-20%; Gracc-Sierra Horticultural Products Co., Fogelville, PA).

In the experiment, leaf number (in Haun units, Haun, 1973) was counted every other day on the main stems on a total of 24 plants grown in six pots in each temperature regime, beginning when the second leaf emerged and continuing until the fifth leaf had emerged. The phyllochron values for the various temperature regimes were obtained from the inverse of the slope of the linear regression of leaf number vs. accumulated degree-days. Degree-days were calculated using a base temperature of 0°C. Degree-days per day were equal to the mean of daily $T_{\text{max}}$ and $T_{\text{min}}$ temperatures.

Two experiments were done at a 20°C day/20°C night temperature regime for both wheat cultivars. A t-test of the differences between leaf emergence rates of wheat plants showed that the results were essentially identical. Therefore, a single experiment was done for each day/night temperature regime.

**Results and Discussion**

Within each temperature regime, the rate of leaf emergence on the main stems of the wheat plants was constant over time. Examples of the linear responses of leaf number on the main stem in thermal-time (degree-days) after seedling emergence are shown in Fig. 1 for Penawawa and Stephens under two day/night temperature regimes, 20/20 and 8/32°C. These responses were typical of all temperature regimes. The linear regressions of leaf number on thermal-time, calculated using individual plant data, were all highly significant, with all $r$ values being greater than 0.99. A linear relationship

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![Graph](image_url)

**Fig. 1.** Leaf number on main stem vs. thermal time (degree-days) after seedling emergence of Penawawa (spring wheat) and Stephens (winter wheat) at two day/night temperature regimes, 20/20 (■) and 8/32 (▲) °C.
between the number of leaves per stem and thermal-time (degree-days) was reported by Cao and Moss (1989a, 1989b) for wheat and barley grown in growth chambers.

Figure 2 shows the phyllochron values for Penawawa and Stephens for various temperature regimes in a 12-h day/12-h night temperature and illumination cycle. The phyllochrons ranged from 99 DD leaf\(^{-1}\) in the 20/20°C regime to 147 DD leaf\(^{-1}\) in the 8/32°C regime for Penawawa. For Stephens, the phyllochron value for 20/20°C regime was 110 DD leaf\(^{-1}\), and ranged upward in the other treatments to 153 DD leaf\(^{-1}\) in the 8/32°C regime. The rate of leaf emergence differed markedly among the temperature regimes, resulting in large differences in the phyllochron values among the different treatments. Thus, it was clear that the mean temperature was not a good measure of the thermal environment for leaf development in this controlled environment experiment where the mean temperature was 20°C for all temperature regimes, but the temperature ranges varied. Cao and Moss (1989a) also reported that the phyllochron values for Stephens ranged from 98 DD leaf\(^{-1}\) in the 20°C day/20°C night temperature regime to 144 DD leaf\(^{-1}\) in the 30°C day/10°C night temperature regime under 14-h daylengths, which along with our data showing that a wide temperature range increases the phyllochron, whether the high temperature was imposed during the light or the dark period.

At a constant 20°C, Stephens had a phyllochron value of 110 DD leaf\(^{-1}\). That value for Stephens is comparable with the value of 98 reported for Stephens wheat by Cao and Moss (1989a) at 20°C in a 14-h daylength. One would expect the phyllochron to be somewhat greater in the 12-h daylength, because phyllochron increases as daylength decreases (Cao and Moss, 1989b).

The data on phyllochron of Penawawa and Stephens in Fig. 2 give additional insight on the effect of day versus night temperatures on leaf development. Under a wide temperature range (32/8, 29/11, 11/29, and 8/32 °C day/night temperature regimes) the phyllochron values were greater when the high temperature was imposed during the dark period. Leaf expansion is more rapid at night than during the day, presumably because of greater turgor pressure. Thus, the data in Fig. 2 suggest that the departure from a linear relationship to temperature was greater when the high temperature was imposed during the time of most rapid leaf expansion.

The temperature responses of most biological processes have a clear maximum, and the concept of optimum temperatures is so well established that it needs no elaboration in this report. The data on phyllochron values for wheat leaf development in the experiment reported here show clearly that the emergence of leaves during development of the wheat culm was not a linear function of temperature. The mean temperature in these controlled-environment temperature regimes was a poor predictor of the rate of leaf development when the high temperature was appreciably greater than the optimum temperature for leaf development (about 21°C). This raises concern for the accuracy of the algorithms used in many dynamic crop development models to relate the crop canopy development to daily environmental conditions, and of the use of degree-day concept to predict the potential impact of the daily weather on development of crops.

In a review on wheat phenology, Shykewich's (1995) concludes that the rate of leaf emergence in wheat has an optimum near 20°C and falls off sharply at temperatures significantly above the optimum. The mean temperature response of leaf emergence in four wheat cultivars grown at different constant temperatures as reported by Cao

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Fig. 2. Effects of day/night temperature (°C) regimes on the phyllochron values of Penawawa (spring wheat) and Stephens (winter wheat) leaves. Vertical bars indicate standard deviations.
and Moss (1989a) fit the equation:

\[ Y = 0.011 + 0.018X - 0.004X^2 \]

where \( Y \) = leaves day\(^{-1} \) and \( X \) = temperature (°C). This equation predicts a sharp decline in leaf emergence rates as temperatures increase significantly above the optimum. The data from the present experiment support that concept as well.

The explanation for the fact that the phyllochron values were large when the temperature range was wide, lies in the fact that the rate of leaf emergence has a clear temperature optimum. When temperatures are below the optimum, both the rate of leaf emergence and the degree-days day\(^{-1} \) decrease with temperature, so it makes little difference whether one uses a linear degree-day based algorithm or a curvilinear optimum curve algorithm to relate leaf emergence to temperature. When temperatures are significantly above the optimum, however, the degree-day based algorithm will predict a rapid rate of leaf expansion, whereas in fact, the rate of leaf emergence actually decreases sharply. Thus, the wider the temperature range, if the high temperature is well above the optimum, the greater will be the departure of the degree-day predicted rate of leaf emergence for the day and the actual rate of leaf emergence. Since “phylochron” is a degree-day based concept, days of wide temperature range will always have a large phyllochron value if the high temperature is significantly above the optimum.

In habitats where wheat is commonly grown, the temperature is often between 10 and 25°C during much of the period of vegetative development, so phenological models based on a linear response of leaf emergence to accumulated degree-days have proven reasonably accurate in describing the relationship of development to weather. Our study suggests, however, that a more accurate algorithm should recognize the curvilinear shape of the optimum-type temperature response of leaf emergence in wheat in order to account appropriately for daily maximum temperatures higher than about 25°C. Indeed, the phyllochron values for Penawawa and Stephens in the experiment illustrate that concept clearly. The phyllochron values were similar for Penawawa and for Stephens in the 20/20, 23/17 and 17/23°C day/night temperature regimes (Fig. 2). At the wider temperature ranges, however, the phyllochron values were significantly greater for both cultivars.

References


