Development and growth of oat leaves at different temperatures and nitrogen levels

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Abstract

This paper reports the development of a model to predict leaf appearance rate in oats (*Avena sativa* L.) based on the results of two field experiments and including a comparison of air and near-apex soil temperatures as predictors of leaf appearance. Oat genotype C&F 435 was sown on eight dates from April 1996 to November 1997. Nitrogen treatments (0 and 100 kg N/ha) were applied to the May and November 1997 crops. Observation of the number of visible leaf tips and leaf lamina length were taken at 2-7 day intervals. Near apex soil temperature and air temperature were recorded by data loggers. The number of visible tips was linearly related to temperature expressed as accumulated thermal time (base temperature of 0°C). The rate of leaf appearance in thermal time, using either air or soil temperature, was nearly constant within a sowing date, but faster for spring sown than for autumn sown crops. Differences in this rate were less among sowing dates when near apex soil temperature was used to calculate thermal time than when screen temperatures were used. This indicated that the use of temperature near the shoot apex may improve phenological predictions from crop models. Nitrogen application had no effect on the rate of leaf appearance regardless of sowing date, but caused an average increase of 19% ($P < 0.05$) in the final leaf lamina length for the last five leaves.

Additional key words: Avena sativa, *canopy, degree days, phyllochron*

Introduction

Rate of leaf appearance is important in crop modelling to describe canopy development. More recently, its inverse, the phyllochron, has been used to predict growth stages in phenological models for cereal crops (Jamieson *et al.*, 1998b). The leaf appearance rate in cereals is dependent on temperature and sowing date. Baker *et al.* (1980) plotted leaf stage (number of leaves) against days after emergence and found a non-linear relationship, with slower rates in a cold than in a warm season. They found a linear relationship between leaf stage and thermal time. This showed that leaf appearance was approximately constant in thermal time for a sowing date. However, the rate differed among sowing dates even when thermal time was used. This suggested another factor in addition to temperature was influencing development. Day length, or its rate of change at crop emergence, has been proposed to influence the rate of leaf appearance (Baker *et al.*, 1980; Kirby and Perry, 1987). In contrast, Hotsonyame and Hunt (1997) concluded that rate of day length change at the time of emergence alone could not explain variation in rate of leaf appearance among sowing dates. Thus, controversy remains on how to account for variation in the leaf appearance rate in cereals (Kirby, 1995; McMaster and Wilhelm, 1995).

Discrepancies in published results may be related to the position of measuring temperature (Jamieson *et al.*, 1995). The shoot apex in cereals remains below or near the soil surface until stem elongation. It follows that soil temperature near the shoot apex rather than air temperature may predict leaf appearance rate more accurately. In field conditions soil temperature can differ substantially from air temperature, particularly when the canopy is sparse (Brooking and McPherson, 1989). This means that air temperature does not reflect the temperature near the shoot apex, which is the site of temperature perception by the plant to produce leaves (Watts, 1972; Peacock, 1975). Indeed, Jamieson *et al.* (1995) proposed a constant leaf appearance rate among sowing dates, based on accumulated soil temperature near the shoot apex. They suggested that leaf appearance rate was solely dependent on temperature. Similarly, Martin *et al.* (1998) predicted leaf appearance rate in oats using 0.1 m soil temperature until stem elongation, followed by air temperature. In contrast McMaster and Wilhelm (1998) found no advantages in using soil rather than air temperature to describe wheat development, which may indicate that in their environment air and soil temperature are more closely related.

Nitrogen nutrition is another controversial factor related to development. Nitrogen nutrition has been reported to hasten or delay development, or have no effect at all (van Keulen and Stol, 1991; McMaster, 1997). Under certain conditions a shortage in nitrogen supply can lead to shorter growing periods, and severe stress can stop phenological development of the crop completely (van Keulen and Stol, 1991). Nitrogen nutrition seems to affect crop development through its influence on the crop microclimate (Davidson and Campbell, 1983; van Keulen and Stol, 1991). Crops receiving nitrogen fertilizer tend to develop a larger leaf canopy, which results in lower day temperatures and higher night temperatures. However, Davidson and Campbell (1983) and Hotsonyame and Hunt (1997) did not find any influence of nitrogen nutrition on wheat development.

There is a lack of data on oat leaf growth and development that can be used to develop a crop simulation model. Therefore, the objective of the present study was to develop a model for the prediction of leaf appearance in oats, a vital step in calculating phenological development (Jamieson *et al.*, 1998a; Sonego *et al.*, 1998). To do this the influences of soil and air temperature on the rate of leaf appearance were compared, and the effect of nitrogen nutrition on leaf growth investigated.

Material and Methods

Two field experiments were conducted at the Crop & Food Research Experiment Station at Lincoln (latitude 43° 36' S), in a Templeton deep silt loam on sand soil, in 1996 and 1997. The first experiment investigated the relationship between temperature sites and leaf growth, and the second experiment the relationship between nitrogen nutrition and leaf growth.

Experiment One

Oat genotype C&F-435, a Crop & Food Research experimental line of late maturity, was sown at six times in April, May, August, September, November 1996 and January 1997, to investigate the influence of air and near apex soil temperature on leaf appearance. Plots were 10 x 1.35 m with rows 0.15 m apart. The crops were precision sown with an Øyjord cone drill at 300 viable seeds per square meter in a randomized complete block design with three replicates. No fertilizer was applied, and irrigation was supplied to avoid water stress. Insecticides and fungicides were applied as required, but manual weed control was used.

Experiment Two

Experiment two was situated within 100 m of experiment one and designed to investigate the influence of nitrogen nutrition on leaf appearance and growth of C&F-435 oat. It was a split-plot design, with two sowing dates (May and November 1997) as the main plots, and two levels of nitrogen (0 and 100 kg N/ha) as the subplots within each plot, with three replicates. Subplots were 15 x 1.7 m and the main plots were 30 x 1.7 m. The two sowing dates were selected after examining results from experiment one, to maximize the differences in environmental factors between crops. A May sowing was used instead of April to avoid the risk of barley yellow dwarf virus infection (Martin and Armstrong, 1996). All other management factors were the same as in experiment one, except for the additional hand broadcast of the nitrogen treatment as urea (46% N). For the May sown crop, urea was split into two applications of 50 kg N/ha: on 22 July 1997, before the double ridge stage, and on 5 September 1997, before stem elongation. For the November sown crop 100 kg N/ha was applied on 5 December 1997, two days after crop emergence.

Field records

At crop emergence 10 plants were randomly marked within each subplot to record the main shoot leaf number and length. Measurements were taken at seven day intervals in the winter, four day intervals in autumn and spring, and two-three day intervals in summer. Leaf length was the length of the visible leaf lamina measured to the nearest 5 mm from its tip to its insertion into the previous leaf. Each leaf was measured up to five times after its ligule was visible, to confirm its final leaf length. The number of leaves was recorded as the number of visible leaf tips on the main shoot.

Temperature records

Air temperature was recorded at the meteorological station 100 m from the experimental site. Soil temperature near the shoot apex was recorded by electronic sensors placed at the shoot apex depth (about 2 cm below ground level), between the third and fourth rows of each subplot, and recorded on a data-logger at 15 minute intervals. Thermal time was defined as the accumulation of temperature from crop emergence (first visible leaf tip stage), as:

$$Thermal\ time = S\ (T_{mean} - T_{base}) \qquad \text{Eq.1}$$

where T_{mean} was the mean daily temperature given by the data-loggers, and T_{base} was the base temperature set as 0°C as commonly used for cereals (Baker *et al.*, 1986; Gallagher, 1979).

In the following, TT_{tair} denotes thermal time calculated from air temperature, and TT_{apex} using near apex soil temperature.

Leaf stages

Leaf stages, instead of number of visible tips, were used to determine the rate of leaf appearance. Leaf stages were determined as:

$$Leaf\ stage = (n-1) + (L_a / L_f) \qquad \text{Eq.2}$$

where n is the number of leaves that have emerged on the main shoot, L_a is the actual lamina length of the last visible leaf (leaf n) and L_f is its final lamina length. This is slightly different from the Haun stage (Haun, 1973) that compares the length of the last visible leaf with the length of the previous leaf.

Data analyses

For the first experiment a coefficient of variation (cv) was used to determine which of the two measured temperatures estimated phyllochron with the least difference among sowing dates. The cv was calculated using the mean square (m.s.) associated with sowing date given by analysis of variance (ANOVA). The phyllochron based on each time scale was calculated as the inverse of the leaf appearance rate. The leaf appearance rate was determined by linear regression of leaf stage on time or thermal time, for both experiments. For the second experiment ANOVA was used to investigate the effects of nitrogen on the final leaf length. Statistical analyses were carried out using Genstat 5 Release 4.1 (Genstat 5 Committee, 1998).

Results and Discussion

Leaf development and temperature

The pattern of leaf appearance for oat genotype C&F 435 was consistent across sowing dates. In general, a leaf tip (n) became visible only after the ligule of leaf n-2 was visible. This indicated that leaf n-2 had reached its final length. This is shown in Figure 1 for the May 1996 sowing date plotted using both calendar days and thermal time. The pattern appeared to be independent of both the leaf that was emerging and its final length. For example, the longest leaf (leaf 9) for that sowing date, emerged as leaf 7 reached its final length, and when leaf 9 reached a maximum length the tip of leaf 11 had emerged. Thus, for this genotype of oats there were always two visible leaves expanding at the same time until the emergence of the ligule of the penultimate leaf. Hence leaf expansion took two phyllochrons. This differs from wheat, where only one leaf is usually expanding (Kirby, 1994).

The interval between the appearance of two leaves was up to 19 days during the winter compared with only 8 days for the last two leaves in spring (Fig. 1a). In thermal time, the phyllochron interval was similar throughout the life cycle of each crop within a sowing date (Fig. 1b), similar to results found by Baker *et al.* (1980).

Leaf appearance rate expressed in thermal time was less variable among sowing dates than when expressed in calendar days (Fig. 2). When TT_{air} was used (Fig. 2b), the coefficient for the slopes of the lines for leaf stage among sowing dates was less variable than when using calendar days (Fig. 2a). The variation was even smaller using TT_{apex} (Fig. 2c), as also shown in terms of phyllochron in Table 1. Thus, temperature variation revealed that a purely time-based phyllochron was unsuitable.

TT_{apex} rather than TT_{air} better estimated the phyllochron among sowing dates, because the main shoot apex in oats remained below the ground until stem elongation, as found for other temperate cereals (Hay, 1986). For oats, all leaf primordia were produced before stem elongation (data not shown), and most of the leaves emerged while the shoot apex was still below the ground (Sonego *et al.*, 1998). It followed that the near apex soil temperature was closer to that perceived by the shoot apex for leaf initiation and expansion than air temperature (Watts, 1972; Peacock, 1975).

However, there was still a systematic variation in leaf appearance rate among sowing dates, particularly between crops that emerged in autumn/winter and summer (Fig. 2c). This may be because the soil temperature sensors were installed near the shoot apex at crop emergence and not adjusted further. However, the shoot apex moved upwards slowly, slower for autumn than for spring and summer crops (results not shown). Scott and Hines (1991) reported similar movement of the shoot apex in barley and triticale. They planted barley and triticale at 25 and 60 mm depth, and found large differences in the position of the apical dome for the first sampling. These differences were consistent with sowing depth but decreased with time. For example, in barley 120 days after sowing, the position of the shoot apex for the two sowing depths was similar at about 10 mm. Alternatively, the leaf appearance rate may depend on factors other than temperature, such as day length change at crop emergence (Baker *et al.*, 1980; Kirby and Perry, 1987). However, it is clear from our results that variation in apex temperature rather than air temperature was influencing the rate of leaf development.

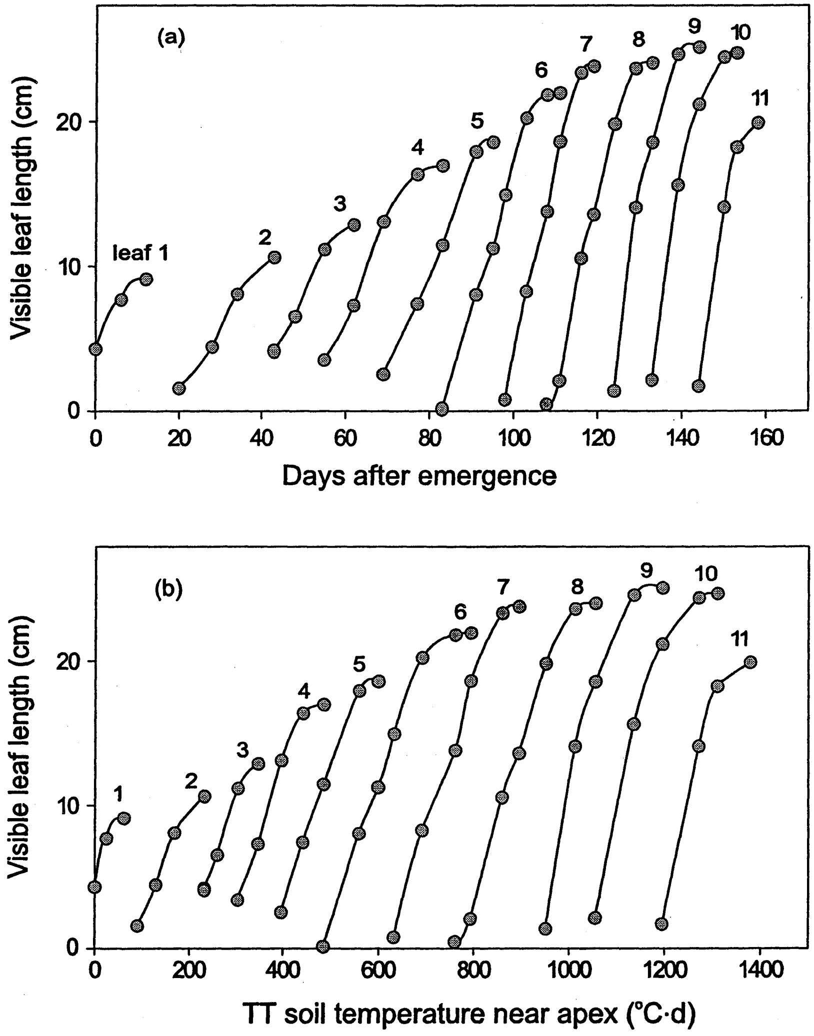

Figure 1. Visible leaf lamina length of oat genotype C&F 435, sown in May 1996, plotted against: (a) time; (b) thermal time (TT) from soil temperature near shoot apex. Each circle is the mean leaf lamina length of three replicates, each of which had 10 plants sampled. Leaf length ranged from 0.20 to 25.17 cm, with a mean value of 12.04 cm. Standard error of mean leaf length ranged from 0.03 to 1.21 cm, with a mean value of 0.43 cm.

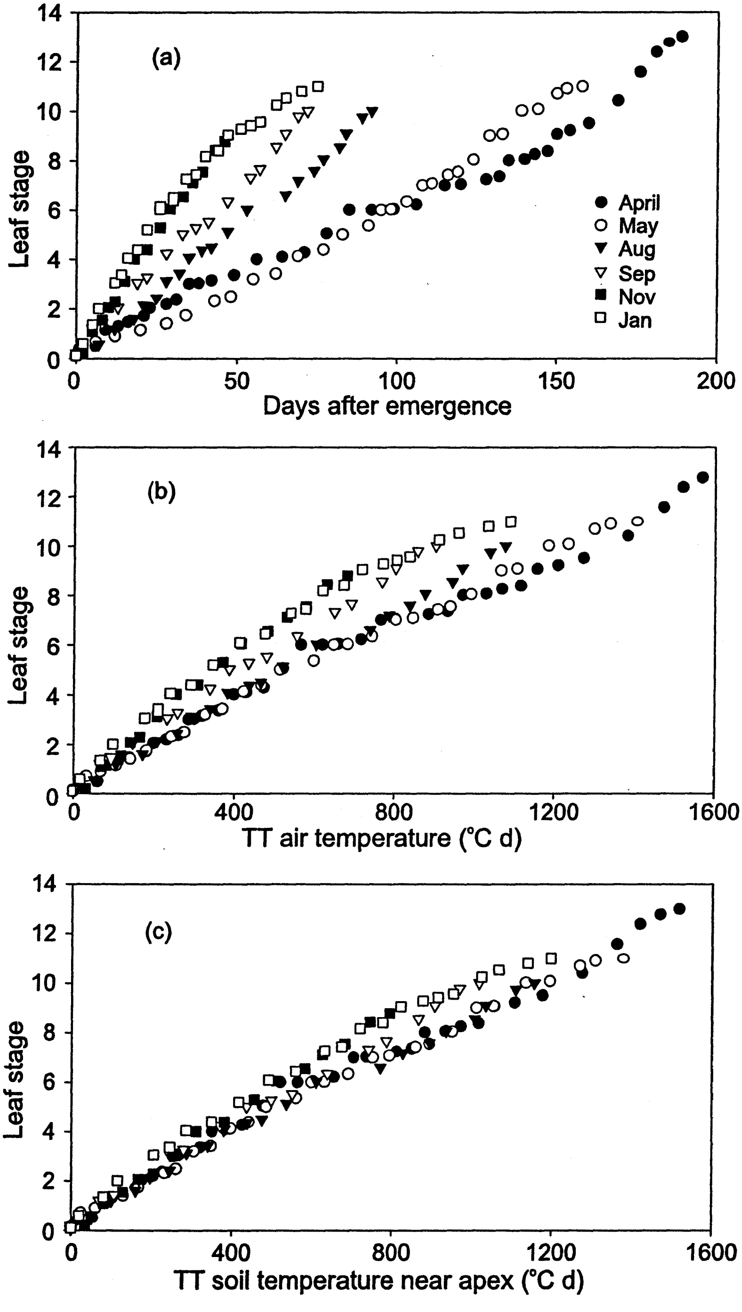

Figure 2. **Leaf stage of oat genotype C&F 435, sown at six different dates from April 1996 to January 1997, plotted against: (a) time; and thermal time (TT) calculated from (b) air temperature, and (c) soil temperature near apex.**

Leaf development and nitrogen nutrition

Application of nitrogen resulted in longer leaves as shown for the May sown crop in Figure 3. At this sowing date, urea was applied at leaf stage 2.2 (3 visible leaf tips), and at leaf stage 5.1 (6 visible leaf tips). The influence of nitrogen on final leaf length was visible from leaf 4, which was the next leaf to emerge after the first application of urea. The response continued for the subsequent leaves giving an average increase in leaf length of 17% ($P < 0.05$) for the last seven leaves.

Table 1. Phyllochron based on calendar days and thermal time (TT), for six sowings of oat genotype C&F 435.

		Phyllochron		
Month of sowing		Calendar days (d)	TT - air temperature (°C.d)	TT - soil temp. near shoot apex (°C.d)
1996	April	18	141	130
	May	14	129	125
	August	10	114	124
	September.	8	96	110
	November	5	78	92
1997	January	6	94	105
Mean		10.2	108.7	114.3
s.e.m., d.f.=10		0.083	0.892	0.950
CV (%)		86	38	22

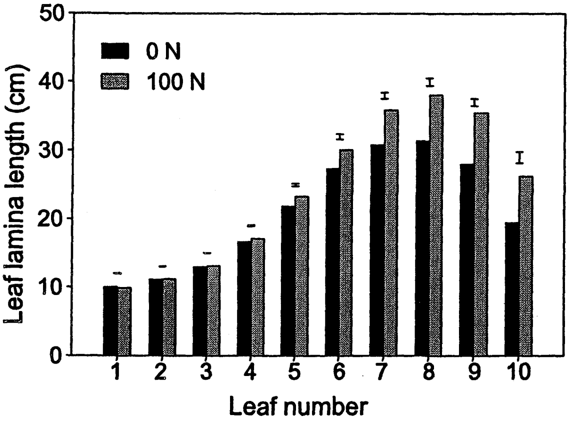

Figure 3. Final leaf lamina length for oat genotype C&F 435 sown in May 1997 for two nitrogen treatments (0 and 100 kg N/ha). The capped vertical lines above the bars represent the SED for each leaf.

Despite this increase in leaf length, the rate of leaf appearance was not strongly affected by nitrogen treatment (Fig. 4), as the slopes of the lines were not significantly different ($P > 0.05$). Results were the same for the November sown crop. These results are similar to those found by Hotsonyame and Hunt (1997) for wheat, and suggest nitrogen affected leaf growth more than it affected plant development.

Conclusions

This study confirmed that the major cause of variation in leaf appearance rate in oats was the temperature near the shoot apex. Much of the apparent variation in the thermal phyllochron based on air temperature was caused

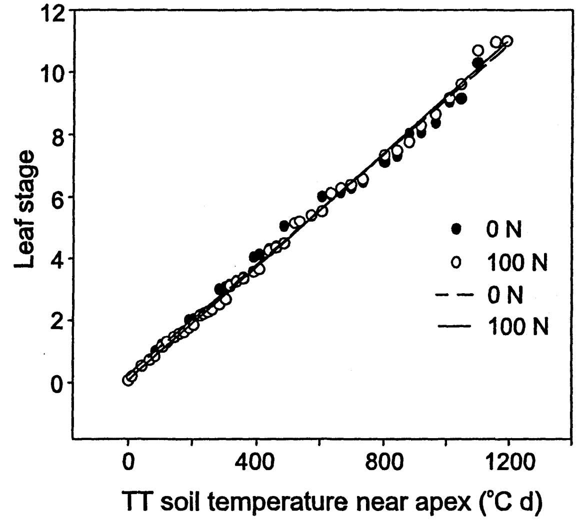

Figure 4. Leaf stage of oat genotype C&F 435, sown in May 1997, plotted against thermal time (TT) calculated from soil temperature near shoot apex, for two nitrogen (N) treatments. Each circle is the mean of three replicates, each of which had five plants sampled (● = 0 N; O = 100 N). Lines represent leaf stage fitted by linear regression (– – – = 0 N; ——— = 100 N). For both treatments $r^2 = 0.997$ ($P < 0.0001$).

by the difference between apex temperature and air temperature. However, even accounting for this, residual systematic variation existed in leaf appearance rate, which suggests that another factor may be involved. Nitrogen nutrition affected the final leaf length, but had almost no effect on the rate of leaf appearance.

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