Leaf appearance and primordia initiation of 'Challenger' sweet corn in response to phosphorus.

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Abstract

Leaf appearance determines early light interception and hence growth in crops. Previous work has shown lack of P has reduced leaf appearance rate in sweet corn. 'Challenger' sweet corn was grown with five rates of fertiliser P (0, 50, 110, 170 and 240 kg P/ha) in 2002/03 on a low P fertility soil (6 µg P/ml) at Lincoln, Canterbury, New Zealand. Vegetative development was measured through leaf tip and fully expanded leaf appearance. The mean phyllochron for successive leaf tips was 29.7 °Cd (T_b = 8 °C) in crops receiving no P fertiliser, 27.4 °Cd in crops with 50 kg P/ha and 25.4 - 26.0 °Cd when 110-240 kg P/ha was applied. Similarly the rate of fully expanded leaf appearance increased with the addition of P fertiliser.

Sequential examinations of leaf primordia on the stem apex were also made on the 0, 110, and 240 kg P/ha treatments. The plastochron, between successive primordia was 26.7 °Cd in 240 kg P/ha crops and 29.1 °Cd for 0 kg P/ha crops. Despite these differences all crops had accumulated their final number of leaf primordia on the apex by between 403 and 470 °Cd. A strong linear relationship (R^2= 0.98) showed that for the appearance of every leaf tip there were 1.7 leaf primordia initiated on the apex resulting in an accumulation of primordia on the stem apex between sowing and tassel initiation.

These results show leaf primordia initiation and subsequent leaf extension were both delayed when P nutrition was limited in 'Challenger' sweet corn.

Additional key words: Leaf extension, phyllochron, plastochron, *Zea mays*.

Introduction

There is a linear relationship between intercepted solar radiation and crop growth rate (Monteith, 1977). Consequently any factor that delays the establishment of an efficient leaf canopy represents a loss of potential productivity. One such factor is a lack of sufficient P that may limit the establishment of leaf area index due to a delayed appearance of individual leaves (Plenet *et al.*, 2000).

In sweet corn (Fletcher *et al.*, 2002) and maize (Plenet *et al.*, 2000; Colomb *et al.*, 2000) the appearance of leaves has been shown to be delayed in crops with inadequate P. However, it is unclear whether this delay is caused by delayed initiation of leaf primordia at the stem apex or a decreased rate of primordia extension into visible leaf tips. In an experiment with wheat (*Triticum aestivum*) Rodriguez *et al.*, (1998) showed that the plastochron (°Cd between successive primordia) was 18 % longer in plants receiving 0.025 mM solution of P than in crops receiving 0. 5 mM solution of P. This can in part explain the longer phyllochron (°Cd between successive leaf tips) in P deficient wheat, but a decrease in primordia extension was also important.

This paper reports a field experiment with 'Challenger' sweet corn grown at five rates of fertiliser P in Lincoln, Canterbury. Results for leaf tip and fully expanded leaf appearance rates are reported followed by data for the initiation of individual leaf primordia as an explanatory variable.

Materials and Methods

Site description and treatments

The experiment was located on a low P fertility site (Olsen P = 6 μg/ml; 0-150 mm sampling depth) at Lincoln, Canterbury, New Zealand. A full description of this site has been given previously (Fletcher *et al.*, 2002). In the first season of this experiment (2001/02), five rates of fertiliser P (0, 50, 100, 150, and 200 kg P/ha) were applied as triple super phosphate (TSP; 0-21-0-0) in a randomised complete block design with three replicates. The individual plots were 4.9m wide and 10m long. A single crop of 'Challenger' sweet corn was grown in these plots (Fletcher *et. al.*, 2002).

These original plots were retained and used for the second experiment (2002/03). Soil test results from samples taken on 10 June 2002 showed that the Olsen soil P levels (Blakemore *et. al.*, 1987) (0-150 mm sampling depth) ranged from 5 to 35 μg/ml (Table 1) resulting from the previous season's treatments. Additional quantities of TSP were applied to these plots on 31 October 2002 and incorporated to ~150 mm using an SEP rotary hoe on 6 and 7 November 2002. The total combined P applied over the two seasons ranged from 0 to 240 kg P/ha (Table 1).

Table 1. total and seasonal kg p/ha added and mean soil olsen p levels (0-150 mm) following each 'challenger' sweet corn crop grown in 2001/02 and 2002/03 at lincoln.

kg P/ha added Season 1 (2001/02)	Olsen P (μg/ml) 10 June 2002	kg P/ha added Season 2 (2002/03)	Total P added kg P/ha	Olsen P (μg/ml) 14 May 2003
0	5	0	0	10
50	11	0	50	16
100	14	10	110	24
150	16	20	170	32
200	35	40	240	36

Table 2. Soil nutrient levels on 10 June 2002 (0-150 mm), and recommended[†] soil nutrient values for sweet corn in New Zealand

Nutrient	QT result	ppm[#]	Recommended QT values
pH	4.9	-	5.3-6.8
Olsen P	*	-	30-35
Ca	4	500	-
Mg	8	40	5
K	9	180	8
Na	3	15	-
S (SO_4)	**4**	4	5

* Olsen P values varied due to TSP applications and these are provided in Table 1.

[#] Results converted to parts per million of soil assuming a soil bulk density of 0.91.

[†] Recommended values taken from Clarke *et al.*, (1986) and Cornforth and Sinclair, (1984)

Soil tests from all treatments also taken on 10 June 2002 showed that soil pH was slightly below optimum and soil S was marginal (Table 2). Burnt lime ($Ca(OH)_2$) at 3.2 t/ha and gypsum (0,0,0,22) at 35 kg S/ha were broadcast and incorporated in late October 2002. In addition, basal dressings of 300 kg N/ha were applied to all plots as calcium ammonium nitrate (26,0,0,0) in three split applications of 100 kg N/ha on each of 29 October 2002, 7 January and 11 February 2003.

'Challenger' sweet corn was hand sown into all plots on 7 November 2002 with an inter-row spacing of 0.7 m (7 rows per plot) and an intra-row spacing of 0.2 m at ~50 mm depth. Two seeds were planted at each position, and subsequently thinned on 19 December 2002 to obtain a uniform plant population of 71,000 plants/ha.

Temperature data and crop measurements

Maximum and minimum daily air temperatures were taken from the Broadfields meteorological station located approximately 3 km east of the site. Soil temperatures at 50 mm were measured at hourly intervals from a single 240 kg P/ha plot from sowing until 16 December 2003 using a Hobo 4 channel external logger with a TMC*x*-HA wide range temperature sensor (Onset Computer Corporation, Bourne, MA, USA).

The number of visible leaf tips and fully expanded leaves (collars visible) were recorded at 3-4 day intervals on five contiguous marked plants per plot from 4 December 2002 until silking (31 January to 15 February 2003). To aid counting, the 4th and 8th leaf (numbered from the base) were marked using a small amount of iridescent paint as they appeared.

Two seedlings per plot including the roots (so that the stem apex remained intact) were collected at 5-9 day intervals from 3 days after emergence until 16 December (when all crops had initiated tassels), from each of the 0, 110 and 240 kg P/ha treatments. The number of visible leaf tips was recorded on these seedlings, and then they were dissected under a binocular microscope to systematically remove and count individual leaf blades until the last primordium was visible on the apex.

Analysis

Leaf appearance and primordia initiation data are reported in relation to thermal time (Tt) above a base temperature (Tb) of 8 °C (Equation 1). For leaf tip and fully expanded leaf appearance data Tt after emergence was used and was based on air temperature. For the initiation of primordia, Tt after sowing was used based on 50 mm soil temperature. In both instances Tt was calculated using maximum and minimum daily temperatures and a modified sine curve was used to calculate Tt at intervals of three hours, which were integrated to give Tt for each day (Jones and Kiniry, 1986).

$$Tt = \sum_{8}^{i=1} \frac{1}{8} Tmean - Tb, (Tmean > Tb)$$

$$Tt = 0, (Tmean \le Tb)$$

(Equation 1)

Where i= eight periods of three hours, Tmean

= mean daily temperature.

The number of visible leaf tips was related to Tt after emergence by a linear function constrained to pass through (0,1) on the basis that by definition a plant has one visible leaf tip at emergence. The linear function was determined by least squares regression and the phyllochron (reciprocal of the slope) was calculated for each plot. Treatment effects were tested using the one-way ANOVA in a randomised block procedure in GENSTAT 5, release 4.2 (Lawes Agricultural Trust, Rothamsted experimental station, UK, 2001). Means separation was based on Fischer's protected least significant difference with α=0.05 (LSD).

The number of fully expanded leaves was related to Tt after emergence using an exponential curve (Equation 2) (Muchow and Carberry, 1989) determined by least squares regression. A single regression was applied to each plot and the variables were tested using one-way ANOVA in randomised blocks.

$LN = ae^{bTt}$ (Equation 2)

Where LN = number of fully expanded leaves, Tt = thermal time after crop emergence (Tb = 8 °C), a = intercept of curve with the y-axis, and b = the degree of curvature.

The number of leaf primordia were plotted against Tt after sowing to give a linear function using least squares regression for each of the 0, 110 and 240 kg P/ha crops outlined above, with the reciprocal of the slope defined as the plastochron. These regressions were not constrained, as it was unknown how many primordia were present in the embryo. Plastochrons were tested using one-way ANOVA in randomised blocks. In addition the number of leaf tips was linearly related to the number of leaf primordia up until tassel initiation using least squares regression analysis of the combined treatment data.

Results

The linear relationship ($R^2 \geq 0.95$) between the number of leaf tips per plant and Tt after emergence (T_b= 8 °C, based on air temperature) showed that crops that did not receive P had a slower rate of leaf tip appearance than crops that were supplied with P (Figure 1). This was reflected in the mean phyllochrons which were 29.7 °Cd in the nil P crops and 25.4-26.0 °Cd in crops that received 110-240 kg P/ha (Table 3).

Table 3. Mean plastochrons and phyllochrons (°Cd, Tb= 8 °C) of 'Challenger' sweet corn in response to P fertiliser.

Treatment (kg P/ha)	Plastochron	Phyllochron
0	29.1	29.7
50	-	27.3
110	27.7	26.0
170	-	25.7
240	26.7	25.4
s.e.	0.22	0.59

s.e. is pooled standard error of the treatment means.

Similarly the appearance of fully expanded leaves was delayed in crops that were not supplied with P (Figure 2). In the nil P crops the degree of curvature (b=0.0033) was less ($p<0.01$) than in those crops that were supplied with 110- 240 kg P/ha (b=0.0038-0.0040) (Figure 2, Table 4).

The exponential curve (Equation 2) between Tt after emergence and the number of fully expanded leaves provided an appropriate ($R^2 \geq$ 0.96) description of the data. However there was a clear indication that for leaves 1-7 the relationship with Tt after emergence was linear from the origin (Figure 2).

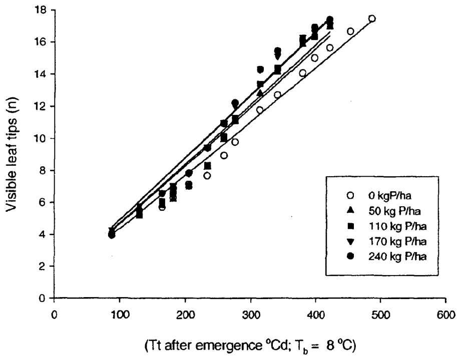

Figure 1: Visible leaf tip appearance of 'Challenger' sweet corn against Tt after emergence (Tb = 8 °C, based on air temperature) in response to P fertiliser.

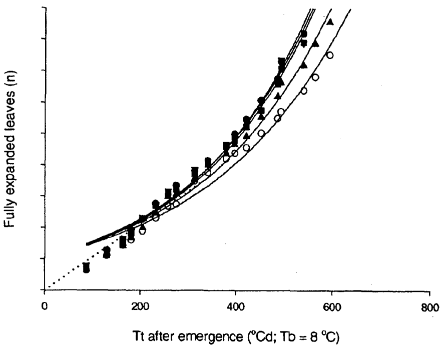

Figure 2: Fully expanded leaf appearance of 'Challenger' sweet corn against Tt after emergence (Tb = 8 °C, based on air temperature) in response to P fertiliser. Symbols as in Figure 1. Dotted line represents theoretical relationship between fully expanded leaf appearance and Tt for leaves 1-7.

There was a linear relationship ($R^2 \geq 0.95$) between Tt after sowing (T_b=8°C, based on soil temperature) and the number of leaf primordia on the apex. Crops that did not receive P had a slower rate of primordia initiation and hence a longer plastochron than both the 110 and 240 kg P/ha crops (Figure 3, Table 3). In the 0 kg P/ha crop a new primordium was formed every 29.1 °Cd, while in the 240 kg P/ha crops there were 26.7 °Cd between each successive primordium (Table 3). By 16 December all crops had obtained their final number of primordia and had initiated tassels. In each crop the final number of leaf primordia was 16, and this was unaffected by P. By extrapolating the regressions (Figure 3) these 16 primordia would have been obtained after 403 °Cd with 240 kg P/ha, 432 °Cd with 110 kg P/ha and 470 °Cd in the nil P crops.

There was a linear relationship (R^2= 0.98) between the number of main stem leaf tips and the number of leaf primordia. For the appearance of every visible leaf tip there were 1.7 leaf primordia initiated at the stem apex between leaf primordium 6 and tassel initiation (Figure 4).

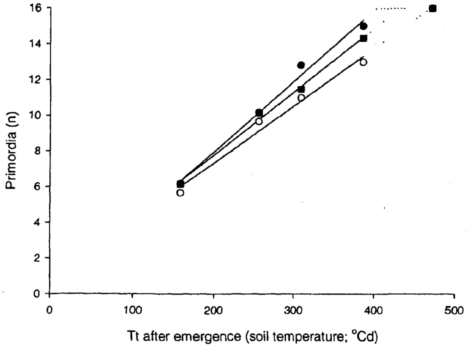

Figure 3. Leaf primordia initiation of 'Challenger' sweet corn against Tt after sowing (Tb = 8°C, based on 50 mm soil temperature) in response to P fertiliser. Symbols as in Figure 1. Dotted lines are between 387 and 472 °Cd (when tassel initiation had occurred) and are not included in the regressions.

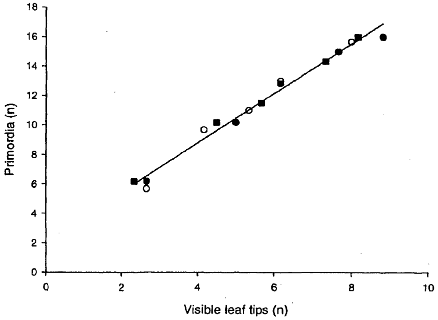

Figure 4. Number of visible leaf tips and number of leaf primordia on the apex of 'Challenger' sweet corn grown in response to P fertiliser. Symbols as in Figure 1. (Regression line $y = 2.03+1.7x$; $R^2 = 0.98$).

Table 4. Coefficients of Equation 2 that related the number of fully expanded leaves to Tt after emergence in 'Challenger' sweet corn in response to P fertiliser.

Total kg P/ha added	Y intercept (a)	Curvature (b)
0	2.2	0.0033
50	2.1	0.0036
110	2.1	0.0038
170	2.1	0.0040
240	2.1	0.0039
s.e.	0.07	0.00032

s.e. is pooled standard error of the treatment means.

Discussion

Applying P to sweet corn on a very P deficient soil resulted in a more rapid appearance of both leaf tips (Figure 1) and fully expanded leaves (Figure 2). Mean phyllochrons were ~4-5 °Cd longer in nil P crops compared with crops receiving 110-240 kg P/ha (Table 3). There were no further decreases in the phyllochron between 110 and 240 kg P/ha (Table 3), which indicates that these rates of P were sufficient to maintain the phyllochron at its minimum and that a P supply below this (i.e. 0 or 50 kg P/ha) gave an increased phyllochron. This delay in leaf appearance would lead to a delay in canopy development and hence a decrease in radiation interception during crop establishment (Fletcher *et al.*, 2002). This decrease in intercepted solar radiation represents a loss in potential crop productivity during crop establishment that would lead to subsequent yield reductions at maturity.

The current results are consistent with previous examples for maize (Plenet *et al.*, 2000; Colomb *et al.*, 2000) and sweet corn (Fletcher *et al.*, 2002) crops grown on low P soils. In the example of Fletcher *et al.*, (2002) phyllochrons were 31.3 °Cd with 0 kg P/ha and 25.8 °Cd with 200 kg P/ha applied to sweet corn. In the example of Plenet *et al.*, (2000) mean phyllochrons for leaves 4-9 were 65 °Cd in maize receiving 0 kg P/ha and 47 °Cd when 111kg P/ha was applied. The difference in magnitude between maize and sweet corn represents the longer phyllochron of maize (Rogers *et al.*, 1999). Nevertheless the results reported here for sweet corn are still relevant to maize.

The current experiment showed that there was also a delay in the initiation of leaf primordia (Figure 3) with low P rates. This is, therefore, partly responsible for the observed delay in leaf appearance. The results of Rodriguez *et al.*, (1998) showed a similar pattern where lack of sufficient P in wheat resulted in a lengthened plastochron. In the previous examples (Fletcher *et. al.*, 2002; Plenet *et al.*, 2000; Colomb *et al.*, 2000) it was unclear whether the delayed leaf appearance under P limited conditions was caused by a delay in the initiation of leaf primordia or in the rate of extension of these leaf primordia. Similarly, lack of sufficient N lengthened the plastochron from 14.5 °Cd (Tb= 10 °C) with 30 kg N/ha per week to 17.8 °Cd in maize receiving no N fertiliser (Jacobs and Pearson, 1992). In this example, when N supply was limited the volume of the stem apex also decreased, suggesting a limitation in assimilate supply.

The longer plastochron (Figure 3) did not fully explain the delayed leaf appearance of sweet corn receiving no P. Leaf primordia were formed at 1.7 times faster than leaf tips (Figure 4), which is similar to the 1.5-1.9 found in wheat (Kirby, 1990). Therefore primordia accumulated at the apex of each plant ahead of leaf appearance. This means the available primordia would not have limited the rate of leaf tip appearance. Furthermore by 472 °Cd after sowing even the nil P crop had 16 primordia, and therefore the initiation of primordia no longer limited leaf tip appearance. When 16 leaf primordia were initiated there were approximately 8.2 leaf tips in all crops (Figure 4). By re-calculating the phyllochron from a regression of leaf numbers greater than 8.2 the mean phyllochron was 34.6 °Cd in untreated crops and 30.7 °Cd in 240 kg P/ha crops. This difference implies that there was also a P limitation restricting the extension of leaf primordia into visible leaf tips.

This can be further illustrated by examining a representative primordium from its initiation until leaf tip appearance. The primordium of leaf 11, the largest leaf (Fletcher *et al.*, 2002), was initiated 317 °Cd after sowing based on soil temperature (Figure 3) or 184 °Cd based on air temperature in the nil P crops. The subsequent appearance of this leaf tip occurred at 297 °Cd after emergence (Figure 1). Therefore, the Tt for the extension of this primordium from initiation to leaf tip appearance was 113 °Cd. In contrast, in the 240 kg P/ha crop leaf primordium 11 was initiated at 277 °Cd after sowing based on soil temperature (Figure 3) or 167 °Cd based on air temperature in the 240 kg P/ha crop and the leaf tip appeared 87 °Cd later.

The consistent relationship between the number of leaf primordia and visible leaf tips (Figure 4) has been shown previously in wheat by Kirby (1990), who interpreted this as meaning that there was competition between the stem apex and developing leaf primordia for current photo-assimilate. The consistent relationship found here (Figure 4) can also be explained using this mechanism.

Conclusions

Applying P fertiliser to 'Challenger' sweet corn crops grown on a low P site (6 μg/ml) increased the appearance rate of both leaf tips and fully expanded leaves. The initiation rate of individual leaf primordia at the stem apex was also increased by P fertiliser, which only partially explained the increased leaf appearance rates, as an increased primordia extension rate was also implicated.

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