Yield formation in maize hybrids of different 'stay-green' rating

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Abstract

Remobilisation of nitrogen reserves from the leaves to the grain during the post-silking growth phase in maize leads to leaf senescence. This may result in a decline in the radiation use efficiency and restrict the attainment of potential yield. 'Stay-green' (sgr) hybrids have been selected in New Zealand with the expectation that they may have reduced post-silking leaf senescence. In this study the influence of fertiliser nitrogen on leaf senescence and yield component formation was quantified in four hybrids described as having low (sgr 6) to high (sgr 9), 'stay-green' ratings. Fertiliser N (270 kg N ha^{-1}) increased green leaf area per plant at silking by 36% while 'P38V12' (sgr 7) had 20% more leaf area per plant than 'P38F70' (sgr 8). Nitrogen also reduced the number of senesced leaves during the reproductive phase and enabled the 'stay-green' trait to be expressed. By the start of grain filling, 'P38V12' (sgr 7) had intercepted 510 MJ m^{-2} of photosynthetically active radiation (PAR) which was 11% more than that intercepted by 'P38F70' (sgr 8). This early advantage in PAR interception was maintained in absolute terms during the post-silking phase but no biomass yield advantage was recorded. The presence of added N increased the number of kernels by 50% from 280 to 420 per ear. The rachis of 'P38V12' (sgr 7) carried 410 kernels compared with 340 for each of the other hybrids. This was offset by the 1000 seed weight of 'P38V12' (sgr 7) of 240 g which was 25% lower than 'P38F70' (sgr 8). In this study the potential grain yield was set during the vegetative growth phase, but actual grain yield achieved was influenced by post-silking growth. Overall the 'stay-green' trait was exhibited in the presence of added nitrogen but did not influence total dry matter or grain yield.

Additional keywords: *Zea mays*, stay-green, senescence, yield components

Introduction

Nitrogen (N) deficiency presents a restriction to crop productivity for most growth parameters. Nitrogen for plant growth can be derived directly from the soil through absorption or remobilised from older plant parts (Ta and Weiland, 1992). Remobilisation of N reserves from the vegetative plant parts into the grain leads to senescence (Rajcan and Tollenaar, 1999a; 1999b). While senescence may commence soon after the attainment of full leaf size (Leopold, 1980), grain filling generally hastens the process, suggesting a link between the remobilisation of resources for grain filling and senescence (Borrell *et al*., 2001). The degenerative changes that precede green area senescence include a decline in the photosynthetic activity (Leopold, 1980), decreased protein synthesis and organelle disintegration (Thomas and Stoddart, 1980). These changes result in reduced photosynthetic rates that eventually compromise radiation use efficiency (Sinclair and Horie, 1989; Muchow and Sinclair, 1994).

'Stay-green' (sgr) maize hybrids have been selected because of their greater tolerance to post-silking environmental stresses (Tollenaar *et al*., 1994), which include the reduction in N uptake (Andre *et al*., 1978b); leading to leaf longevity (Tollenaar and Dwyer, 1999; Hay and Porter, 2006). This may sustain photosynthetic activity at a time of decline and high crop demand (Tollenaar, 1977; Andre *et al*., 1978a). In maize this is particularly critical since the largest proportion of dry matter partitioned to the grain is accumulated post- silking (Muchow *et al*., 1990). This study was initiated to investigate the influence of N on post-silking green leaf area in four maize hybrids of different 'stay-green' rating. Its main objectives were to examine the influence of the hybrid 'stay-green' rating on post-silking leaf senescence and yield.

Materials and Methods

Experimental design

The experiment was a split plot in a randomised complete block with 16 treatments comprising two irrigation treatments (dry or fully irrigated) as the main plots, two rates of N (0 and 270 kg N ha^{-1}) and four maize hybrids ('P39K38' (sgr 6), 'P38V12' (sgr 7), 'P38F70' (sgr 8) and 'P38G43' (sgr 9)). The 4 hybrids were arranged factorially in fully randomised sub-plots and replicated three times. The silage comparative relative maturity (CRM) was 93 for 'P38F70' (sgr 8) and 87 for the other hybrids. Each plot measured 4.9 x 10 m and consisted of 7 rows that were 0.7 m wide. The plants were spaced 0.15 m apart and the outer rows in each plot served as the buffer rows. This gave a target population of 9.5 plants m^{-2}.

Cultural practices

The experiment was planted on 24 October 2008 into a Typic Immature Pallic Soil (Hewitt, 1998) with 0.4-1.0 m silt loam overlying gravel that had previously been sown in oats (2005 and 2008) and consecutive crops of wheat (2006 and 2007). Soil tests showed a pH of 6.0, an Olsen P level of 14 mg l^{-1} and 74 kg available N to 0.15 m. Two seeds were sown on 0.15 m centres using a jab planter and thinned to one plant three weeks later. A deep N analysis taken to 1.0 m indicated a mineral N content of 44 kg N ha^{-1}. During land preparation, 560 kg ha^{-1} of 20% Potash Superphosphate, containing 7.4% P, 10% K, 8.6% S and 16% Ca was applied. A soil test four weeks after emergence showed that the Olsen P level had risen to 33 mg l^{-1}. A pre-emergence application of Nu-Traize 900 DF (900 g kg^{-1} of Atrazine a.i) at 1.5 l ha^{-1} was used to control broad leaf weeds.

Two weeks after sowing, at least 50% of the plants had emerged. Ten days later five plants of the approximately 450 per plot were selected from the middle of the central row for non-destructive sampling and tagged. After hand thinning the mean population was 9.25 plants m^{-2}. Additional N for the fertilised treatment was provided as urea (46% N) and broadcast in two applications each of 135 kg N ha^{-1} at 16 and 37 days after emergence (DAE). A light overhead sprinkler irrigation of 10 mm followed each application to dissolve the urea.

Measurements

Green area index (GAI) was monitored at 7-14 day intervals using a Licor 3100 area meter (Licor Inc, Lincoln, Nebraska, USA). The fraction of transmitted PAR (PAR_t) by the crop was measured every 14-20 days (weather dependent) using a Sun Scan (Delta-T Devices, Cambridge, England). These measurements were confined to the three central rows of each plot where no destructive sampling was done. Water extraction from the profile was monitored on a weekly basis using Time Domain Reflectometry (TDR) (Trase System 1 Model 6050 X1) in the top 0-0.2 m layer and a Neutron Probe (NMM Model 3300) at 0.1 m intervals to a depth of 0.4-1.0 m dependent on the depth to gravel. Irrigation water was applied to the irrigated plots only to restore the moisture depleted from the top 0.2 m soil profile to near field capacity when the total available soil moisture content dropped to half of field capacity. Air temperatures were logged hourly with three thermistors located in the central plot of each replicate. After silking, the number of senesced leaves per plant was recorded on a weekly basis. A leaf was considered senesced when it was visually observed to have lost all its chlorophyll and turned completely yellow.

Dry matter accumulation was measured by harvests of three plants cut at ground level per plot every 14 days. These harvests were restricted to the rows adjacent to the guard row. The plants were selected at random after a buffer of at least 10 plants from the edge of the row. The plant components were separated into leaves and stalks before silking. After silking, each plant was stripped into three cohorts of leaves (bottom, middle and upper) (Rajcan and Tollenaar, 1999a), stalks and ears. Identical components in each plot were bulked and oven dried at 65°C in a forced draft oven to constant weight. During late grain filling, the development of the black layer was assessed through weekly harvest of three ears from the rows adjacent to the central row in each plot. At least 90% of the kernels (Duncan, 1975) in each plot had developed the black layer by 6 April 2009 (1420 ºC.d). The final harvest was done three weeks after this assessment and the five plants per plot (a total of 240 plants) initially tagged for non-destructive harvests were cut at ground level. The above ground portions were separated into leaves, stalk and ears and oven dried to a constant weight at 65°C in a forced draft oven. After drying to 0% moisture, the kernels were extracted from the de-husked ears, weighed and 250 seeds counted using a seed counter (numerical seed counter). The seeds were then weighed to determine the 1000 seed weight. Grain yield was determined from the yield per plant and the plant population.

Calculations and data analysis

Daily thermal units were accumulated after emergence from air temperatures using the modified sine curve method (Jones and Kiniry, 1986) with a base temperature of 0°C (Wilson *et al*., 1995) and an optimum temperature of 34°C (Muchow and Carberry, 1989). The fraction of intercepted PAR (PAR_i) was derived following the method of Gallagher and Biscoe (1978) and is shown by Equation 1.

$$PAR_i = 1.0 - PAR_t \qquad \text{(Equation 1)}$$

Where, PAR_t is the fraction of PAR transmitted.

Daily solar radiation (MJ m^{-2} d^{-1}) was obtained from measurements of daily global short wave radiation recorded at Broadfields' meteorological station, 2 km east of the experimental site. Incident PAR was assumed to equal 0.5 of total incident short wave radiation (Monteith, 1977). Total intercepted PAR was estimated following the procedure of O'Connell *et al*. (2004). Briefly, daily estimates of PAR_i between emergence and physiological maturity were made by linear interpolation of the instantaneous measures of PAR_i with respect to time. Then, daily intercepted PAR (S_a) was calculated using Equation 2.

$$S_a = PAR_i \times S_i \quad \text{(Equation 2)}$$

Where, S_i is the daily incident PAR.

Daily intercepted PAR was summed from emergence to physiological maturity to obtain the total intercepted PAR. The relationship between ear and kernel DM, and total crop DM was examined using linear regression. A Gaussian function was fitted to the relationship between GAI and Tt. Statistical analysis was done with Genstat v.12.1 (Lawes Agricultural Trust, Rothamsted Experimental Station, UK). All variates were analysed using ANOVA procedures in a split plot design structure and the least significant difference (LSD) ($P<0.05$) was used to separate means.

Results

Yield components

Final yield

There were no interactions between hybrid and N treatment for total dry matter (TDM) or grain yield at final harvest therefore mean yields are reported. At final harvest total dry matter (19.1 t ha^{-1}), grain yield (9.3 t ha^{-1}) and harvest index (0.48) were unaffected by the hybrid 'stay-green' rating. However, additional N increased ($P<0.001$) total yield from 14.0 t ha^{-1} to 24.2 t ha^{-1} (Table 1). The final grain yield was also increased ($P<0.001$) by 86% from 6.5 t ha^{-1} to 12.1 t ha^{-1} by added N. A harvest index of 0.50 was recorded for these crops compared with ($P<0.001$) 0.46 for the unfertilised crops.

Table 1: Mean final crop total dry matter (DM), grain yield and harvest index (HI) of four maize hybrids of different 'stay-green' (sgr) rating grown without or with 270 kg N ha^{-1} at Lincoln University in 2008.

	Total DM (t ha^{-1})		Grain yield (t ha^{-1})		Harvest index	
Hybrid	0	270	0	270	0	270
'P39K38' (sgr 6)	14.8	25.5	6.90	12.6	0.46	0.49[b]
'P38V12' (sgr 7)	14.3	23.5	6.60	12.0	0.46	0.51[a]
'P38F70' (sgr 8)	13.7	24.9	6.30	12.6	0.46	0.51[a]
'P38G43' (sgr 9)	13.1	23.1	6.20	11.3	0.47	0.49[b]
Significance	P<0.895		P<0.876		P<0.027	
S.E	1.39		0.720		0.006	
CV (%)	17.9		18.9		3.1	

Means with letter superscripts in common are not significantly different at α=0.05.

No. of kernels per ear

All treatment factors influenced the number of kernels per ear with 'P38V12' (sgr 7) initiating about 20% more ($P<0.003$)

than the other hybrids (Table 2). The number of kernels per ear was also increased (P<0.001) from 280 to 420 when N was provided.

Thousand seed weight (g)

The 1000 seed weight was inversely related to the number of kernel per ear. ‘P38V12’ (sgr 7) produced the lowest (P<0.001) 1000 seed weight (Table 2).

Table 2: Number of kernels per ear and the thousand seed weight in four maize hybrids of different ‘stay-green’ rating (sgr) grown at Lincoln University in 2008.

Hybrid	No. of kernels per ear	Thousand seed weight (g)
‘P39K38’ (sgr 6)	340[b]	300[a]
‘P38V12’ (sgr 7)	410[a]	240[c]
‘P38F70’ (sgr 8)	340[b]	300[a]
‘P38G43’ (sgr 9)	340[b]	270[b]
Significance	P<0.003	P<0.001
S.E	14.4	5.7
CV (%)	14.0	7.1

Means with letter superscripts in common are not significantly different at α=0.05.

Ear and kernel development

After an initial lag phase, mean total ear DM increased rapidly with increased accumulated Tt and followed a characteristic sigmoid growth pattern (Figure 1a). The logistic curve used to describe the relationship between mean ear DM and Tt and mean vegetative (leaves and stalk) DM and total crop DM was of the form suggested by Hunt (1982) and is shown by Equation 3.

$$Y = \frac{C}{\left(1 + e^{(-B(X-M))}\right)} \qquad \text{(Equation 3)}$$

where:
C = maximum biomass (Y) value (kg biomass ha^{-1})
B = a rate constant of the curve
M = point of inflection where maximum growth rate (kg ha^{-1} °C.d) occurs and represents the point to 50% of maximum biomass.

Mean ear DM was strongly related (R^2 = 0.98) to accumulated Tt and a maximum ear DM of 16.8 (± 0.30) t ha^{-1} was reached in the presence of N compared with 8.9 (± 0.21) t ha^{-1} with no N (Figure 1a). The point to 50% of maximum biomass occurred at 1050 °C.d after emergence in both treatments. At 50% of maximum biomass 9.0 (± 0.10) t ha^{-1} (R^2 = 0.98) of total crop DM was constituted by the vegetative components in the + N treatment compared with 6.0 t ha^{-1} (± 0.10) (R^2 = 0.95) when no N was provided (Figure 1b).

Linear regression was used to examine the relationship between mean total ear DM and mean total crop DM. Total crop DM after silking was strongly related (R^2 = 0.99) to ear DM in the presence of N. After 9.3 t ha^{-1} of total DM had been accumulated by the fertilised crop, there was a strong linear relationship between total crop DM and total ear DM (Figure 1c). The maximum vegetative DM accumulated by these crops was 9.0 (± 0.10) t ha^{-1} (R^2 = 0.98) (Figure 1b), which indicates limited remobilisation of DM reserves stored in these components. Total crop DM was also strongly related (R^2 = 0.95) to ear DM in the non-fertilised crops (Figure 1c). Ears began to accumulate DM when the total crop DM was 6.9 t ha^{-1} (Figure 1c). The maximum vegetative DM accumulated by these crops was 6.0 (± 0.10) t ha^{-1}, suggesting that these crops remobilised about 0.9 t ha^{-1} for ear formation. Grains began to develop when the fertilised crop had accumulated 14.8 t DM ha^{-1} and the non-fertilised crop 8.6 t DM ha^{-1} (Figure 1d). Total kernel DM was related (R^2 = 0.91) to total crop DM in the fertilised crop but the relationship was weaker (R^2 = 0.84) for the non-fertilised crop (Figure 1d).

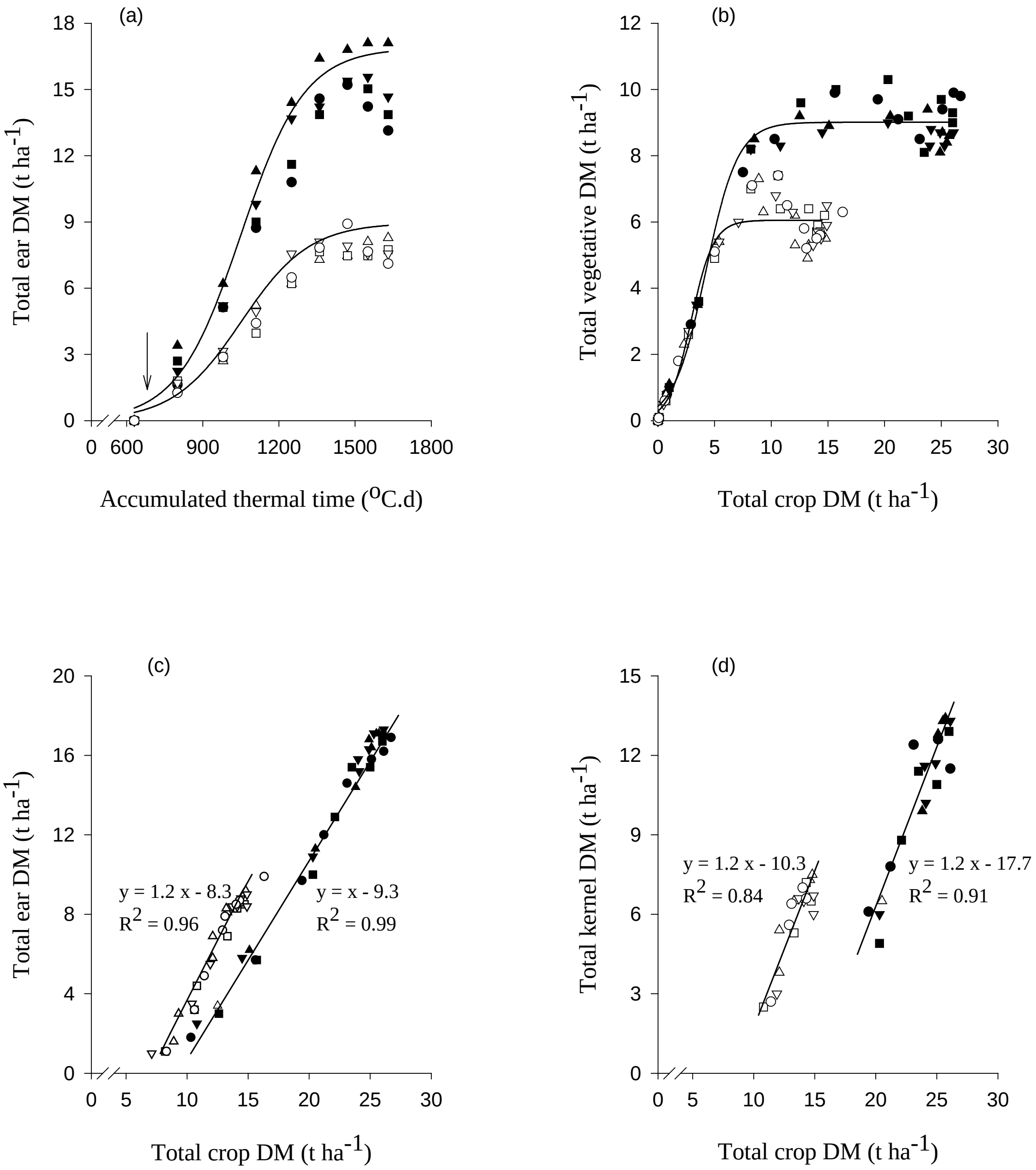

Figure 1: Total dry matter (DM) against accumulated Tt (T_b = 0 °C) (a), total vegetative DM (b), total ear DM (c) and total kernel DM (d) against total crop DM for 'P39K38' (sgr 6) (∆), 'P38V12' (sgr 7) (□), 'P38F70' (sgr 8) (▽) and 'P38G43' (sgr 9) (○) grown without N (open symbols) or with 270 kg N ha^{-1} (closed symbols) at Lincoln University during 2008. The arrow indicates silking.

Green area

In this study, silking occurred after 700 °C.d and physiological maturity after 1420 °C.d. Green leaf area per plant and total PAR intercepted were both influenced by N and hybrid (Table 3). Additional N increased the leaf area per plant by 36% and cumulative intercepted PAR by 16% (P<0.001) at 800 °C.d and 17% (P<0.001) at 1420 °C.d. At 800 °C.d, 'P38V12' ('sgr' 7) had 20% more (P<0.001) leaf area per plant than 'P38F70' ('sgr' 8). These differences in leaf area per plant were reflected in the cumulative intercepted PAR to silking. 'P38V12' ('sgr' 7) had accumulated 11 % more (P<0.001) PAR than 'P38F70' ('sgr 8'). However, at 1420 °C.d, 'P38V12' ('sgr' 7) had accumulated 980 MJ m^{-2} PAR compared with 920 MJ m^{-2} accumulated by 'P38F70' ('sgr' 8). This final difference (P<0.005) in accumulated PAR indicates that 'P38V12' (sgr 7) maintained an absolute difference of about 55 MJ m^{-2} PAR compared with 'P38F70' (sgr 8) by virtue of an early advantage during the vegetative growth phase.

Green area index was influenced (P<0.001) by additional N (Figure 2). The fertilised crops had a maximum mean GAI of 5.3 compared with 3.8 for the unfertilised crops. The fertilised crops also maintained a GAI above the critical (4.6) for about 500 ºC.d while the N deficient crops did not attain this critical green area index. Among the fertilised crops, 'P38V12' (sgr 7) was early to attain the critical green area index.

Table 3: Green leaf area per plant (cm^2) at 800 ºC.d (around silking) and total intercepted PAR at 800 and 1420 ºC.d by four maize hybrids of different 'stay-green' (sgr) rating that received 0 or 270 kg N ha^{-1} grown at Lincoln University during 2008.

Hybrid	Leaf area (cm^2)	Total intercepted PAR (MJ m^{-2})	
	800 ºC.d	800 ºC.d	1420 ºC.d
'P39K38' (sgr 6)	3720^{b}	500^{a}	960^{a}
'P38V12' (sgr 7)	4120^{a}	510^{a}	980^{a}
'P38F70' (sgr 8)	3420^{c}	460^{b}	920^{b}
'P38G43' (sgr 9)	3600^{bc}	470^{b}	920^{b}
Significance	P<0.001	P<0.001	P<0.005
SE	72.9	8.5	12.6
0 kg N ha^{-1}	3150	450	870
270 kg N ha^{-1}	4280	520	1020
Significance	P<0.001	P<0.001	P<0.001
SE	51.5	6.0	8.9
CV (%)	6.8	6.0	4.6

Means with letter superscripts in common are not significantly different at α=0.05.

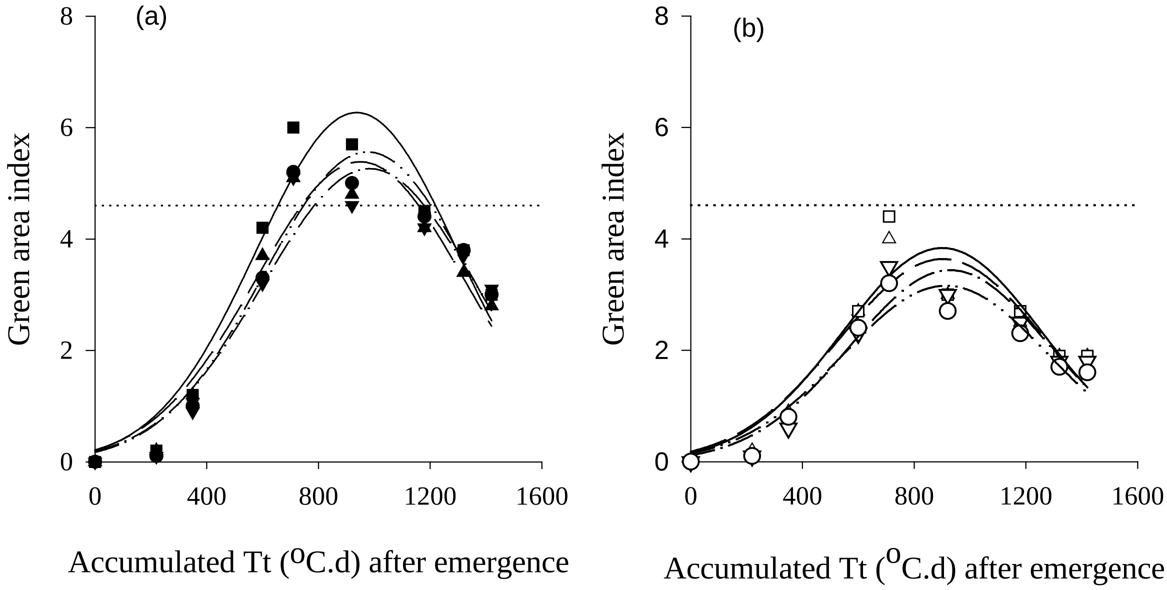

Figure 2: Green area index against accumulated Tt (ºC.d) after emergence in hybrid maize grown with (a) 270 or (b) 0 kg N ha^{-1} at Lincoln University during 2008. The hybrids were 'P39K38' (sgr 6) (- -), 'P38V12' (sgr 7) (--), 'P38F70' (sgr 8) (-·-) and 'P38G43' (sgr 9) (-··-). The dotted line indicates the critical green area index.

Leaf senescence

Leaf senescence in all hybrids began immediately after silking (~700 °C.d), which signified the end of vegetative growth. There were no differences among the hybrids in the number of senesced leaves in the absence of N fertiliser (Figure 3a). The apparent difference shown by 'P39K38' (sgr 6) at 1040 °C.d ($P<0.009$) and 1330 °C.d ($P<0.034$) can be discounted by the fact that this hybrid initiated 16.2 leaves per plant compared with 17.2 for the other hybrids. However, when N was provided, there were fewer senesced leaves in 'P38G43' (sgr 9) (Figure 3b).

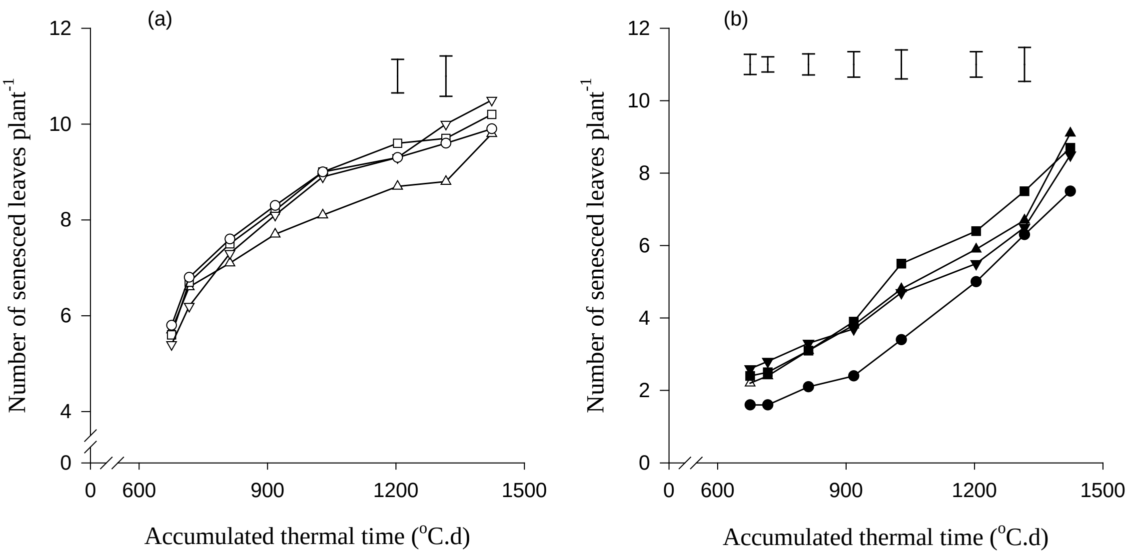

Figure 3: Number of senesced leaves plant^{-1} in crops of 'P39K38' (sgr 6) (△), 'P38V12' (sgr 7) (□), 'P38F70' (sgr 8) (▽) and 'P38G43' (sgr 9) (○) grown with (a) no added N or (b) 270 kg N ha^{-1} at Lincoln University during 2008**.**

Discussion

Resource allocation in annual plants may be genetically predetermined, a considerable degree of plasticity exists that allows plants to respond to the prevailing growth conditions (Weiner, 2004). Hence, measurements of components of yield can provide useful insights on how the crop responds to the environment. In this study, the number of kernels per ear and the mean grain weight (thousand seed weight) were influenced by hybrid. The cultivar 'P38V12' (sgr 7) initiated 20% more (P<0.003) kernels compared with the other hybrids. However, this hybrid had a mean seed weight that was 25% lower (P<0.001) than that of both 'P39K38' (sgr 6) and 'P38F70' (sgr 8) (Table 2). This observation was consistent with a source limitation on grain yield as reported by Tollenaar (1977). At the start of grain filling (800 °C.d), 'P38V12' (sgr 7) had 20% more (P<0.001) leaf area per plant and had accumulated 11% more (P<0.001) PAR (Table 3) providing evidence that potential yield may be determined around silking.

Post-silking yield formation in maize is dependent on DM accumulated during this phase (Muchow *et al*., 1990). Differences in TDM accumulation, ear DM and grain yield can be attributed to changes in post-silking leaf area and how these changes impact on solar radiation interception. Dry matter accumulation in the ear followed a characteristic sigmoid growth function with an initial lag phase followed by a period of rapid DM accumulation which culminated in an asymptote when maximum ear DM was reached (Figure 1a). Total ear DM in both N treatments reached 50% of maximum biomass at 1050 °C.d after emergence. This indicates that N had no influence on the rate of development as already reported (Kosgey *et al*., 2009). Total crop DM consisted of leaf and stalk components prior to silking (Figure 1b).

The strong linear (R^2 = 0.99) relationship between ear DM and total crop DM (Figure 1c) in the fertilised crops suggests that during grain filling, the increase in ear DM was directly proportional to the increase in total crop DM. This is consistent with the observation that most DM accumulated by the crop during grain filling is directed towards ear development (Muchow *et al*., 1990). The coefficient of the slope of the relationship between total ear DM and total crop DM in the non-fertilised crops was 1.2 (Figure 1c). This indicates that these crops remobilised close to 20% of their total crop DM towards ear formation. This is consistent with the 15% deficit in total vegetative DM when compared with total crop DM at the start of ear formation (Figure 1b and 1c). Kernel DM was also strongly (R^2 = 0.91) related to total crop DM (Figure 1d) in the presence of N. However, this relationship was weaker (R^2 = 0.84) when N was not provided.

The number of senesced leaves did not differ among hybrids in the absence of added N (Figure 2a). The apparent difference shown by 'P39K38' (sgr 6) at 1040 °C.d (P<0.009) and 1330 ºC.d (P<0.034) was discounted by the fact that this hybrid initiated one less leaf per plant compared with the other hybrids. In the presence of additional N, 'P38G43' (sgr 9) consistently had fewer senesced leaves (Figure 2b). This observation suggests that the 'stay-green' trait was only exhibited in the presence of adequate levels of N and is consistent with the results reported by Subedi and Ma (2005) for maize.

Conclusion

The hybrid 'stay-green' characteristic did not influence total crop DM or grain yield because the low 'stay-green' hybrids developed larger leaves that enabled them to intercept more PAR and accumulate more DM during the vegetative growth phase. Post-silking leaf loss was of little consequence. The 'stay-green' trait was only exhibited in the presence of adequate N; however, there may be a need to examine the potential yield that could accrue from incorporating the 'stay-green' genes into the initially more vegetative low 'stay-green' hybrids.

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