Differences in Radiation Use Efficiency among lines in a Tropical Maize Population

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Summary. Differences in potential biomass production among cultivars of a species can often be related to differences in maturity and therefore the total amount of radiation captured (the product of incident radiation and fraction intercepted (*f*)) during the season. Within a population of lines from a single genotype (with small variation in maturity) differences in biomass production should be related more to the efficiency with which radiation is used (RUE) rather than the amount captured. Across 100 S_1 lines from a population containing a mix of tropical and temperate germplasm and tested in a cool environment, seasonal RUE of the 10 best lines was 21% greater than the mean, and was high enough to be of value to improve biomass production. This seasonal RUE was better correlated with RUE calculated from measurements of *f* taken near anthesis than from those taken earlier in the season.

Introduction

In unstressed crops, the major determinant of biomass production is the amount of photosynthetically active radiation (PAR) they use. Crop growth can be described as the product of the incident PAR, the fraction of PAR intercepted by green leaf (*f*); and the 'efficiency' with which the PAR is used (RUE) (3). PAR depends on the location and time of year while seasonal *f* is affected by the duration and the area of the canopy. Temperature and photoperiod interact to determine canopy growth, *e.g.* lower temperatures result in slower development and therefore a longer duration with greater PAR interception and biomass production. RUE depends on the distribution of direct and diffuse light within the canopy and the efficiency with which leaf photosynthesis occurs. Given no change in crop duration, there are two options to increase biomass: increase seasonal *f* through faster early leaf area development and/or slower senescence; or increase RUE for all or part of the season.

Genetic variation in seasonal *f*, particularly greater green leaf duration (*i.e.* the 'stay-green' trait) has been selected for in breeding programs, although RUE is often considered to be more or less constant for any particular species. While sorghum cultivars may vary in RUE by up to 10% (2) there is no evidence that it had been exploited directly by breeding, although simulation models have demonstrated the utility of doing so (4). For a trait to be considered useful: genetic variation must exist; the trait must be heritable; and it should also be easy to measure. For stay-green, these criteria have been largely met, but no attempts have been made to do so for RUE.

The objective was to measure biomass production (to flowering) of S_1 lines of a tropical maize population and analyse genetic variation in terms of seasonal *f* and particularly, RUE and to demonstrate that *f* can be realistically estimated in a breeding program.

Materials and methods

The trial was planted in El Batan, Mexico (2200 masl). One hundred S_1 lines from Drought Tolerant Population 1 (DTP1) Cycle 6 were planted in 2 replicates in an alpha-lattice design with a plot size of 2 rows (0.75 m apart) x 5 m (0.25 m plant spacing). DTP1 germplasm is a source population for drought tolerance comprised mostly of tropical and sub-tropical germplasm, but it also includes temperate sources of drought tolerance. The trial was irrigated every 1 to 2 weeks, depending on demand and kept free of pests and diseases.

Radiation interception (PAR around noon) at ground level was measured on five occasions to estimate instantaneous *f*. In each plot, an area of 1.875 m^2 was harvested at about two weeks beyond anthesis (109 days after emergence - DAE). The harvested plants were dried and weighed and separated into leaf, stem, husk and ear. For each plot, the fraction of PAR intercepted each day was estimated over the growth period by fitting a logistic function against time:

$$f = A / (1 + \exp(-B * DAE)) ^\wedge D$$

where A, B and D are parameters determined using the SAS NLIN procedure (SAS, Raleigh, NC, USA). Seasonal *f* is calculated as the average of predicted *f* for each day of the season. As all plots were harvested on the same day, the total PAR intercepted (MJ/m2) could be calculated as the product of seasonal *f* for the plot and the sum of the incident PAR (short-wave solar radiation * 0.48) between emergence and harvest. This total divided into the biomass at harvest gave an estimate of the seasonal RUE (g/MJ). Values of measured *f* at each date were tested as predictors of seasonal *f* or RUE. Data variables were processed using the alpha design and lattice adjusted means were used in further analysis.

Results

Incident PAR during the growing period averaged 9.4 MJ/m^2/d, while daily maximum and minimum temperatures averaged 24.8 and 9.5?C, respectively - about 7 to 10?C lower than the climate to which this population is adapted.

Observed values of *f* were generally fitted well by the logistic function (*e.g.* Fig. 1). Seasonal *f* ranged from 0.30 to 0.46. Across all lines, the values for coefficients A, B and D were 0.731, 0.062 and 15.3, respectively. As might be expected, coefficient A which represents the asymptote of the logistic function was correlated with seasonal (r = 0.61) and final (r = 0.82) observations of *f*. However, coefficients B and C were not well predicted by either seasonal or individual observations of *f*. Across all lines, correlations between seasonal *f* and single measurements of *f* at 33, 48, 77, 81 and 98 days after sowing were 0.22, 0.55, 0.71, 0.80 and 0.86, respectively, *i.e.* each successive measurement of *f* was increasingly correlated with seasonal *f*, with a measurement at anthesis having the best correlation.

Significant line effects were observed for biomass production (mean = 874?73 g/m^2), seasonal *f* (0.39?0.02) and RUE (2.22?0.17 g/MJ PAR). Several lines were significantly different from the mean for each variable although lines were not distributed normally for these variables (Fig. 2a,b,c). The RUE, in particular, was skewed toward higher values.

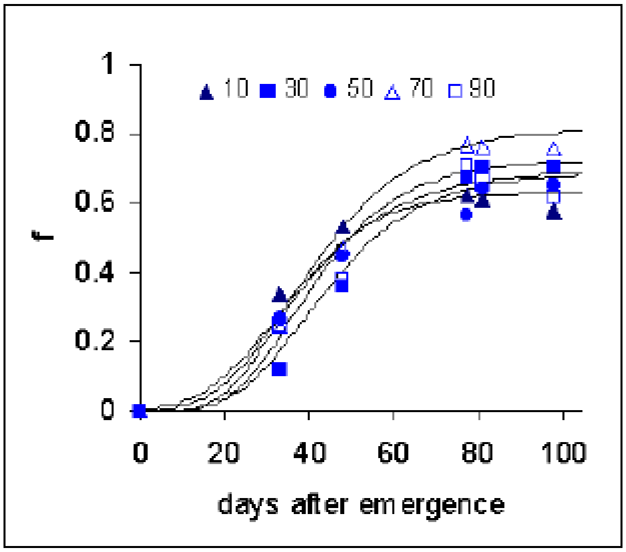

Fig. 1 Fitted *f* for 5 of the lines.

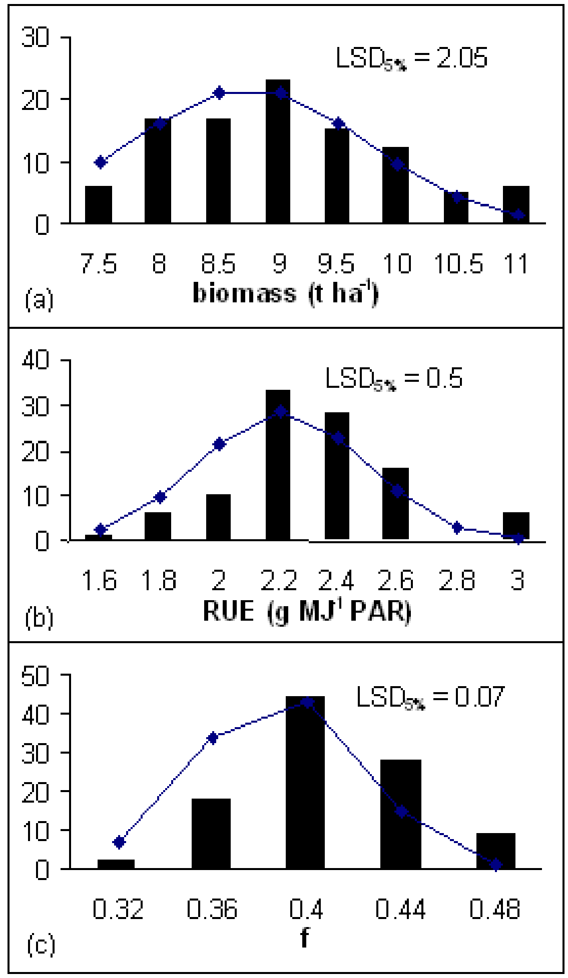

Fig. 2 Freq. distribution of lines for (a) biomass, (b) RUE, (c) seasonal *f*.

Biomass production of the best 10 lines was 21% greater than the mean, while the poorest lines produced were about the same proportion below the mean (Table 1). About half of this difference was due to higher stem and husk weight in the best fraction, with the remainder being equally divided between leaf and immature ear biomass (data not presented). While *f* accounted for part of the variation in biomass (r = 0.26 for 100 lines), differences in RUE explained a much greater proportion (r = 0.70). While incident PAR was the same for all plots as they emerged at the same time and were harvested at the same time.

Table 1. Average biomass, *f* and RUE for extreme groups of S_1 lines. Parentheses enclose % differences from the mean of 100 lines.

Group	*Total biomass (t/ha)*	*Seasonal f*	*RUE (g/ MJ PAR)*
Best 10 lines for biomass prod. 11, 14, 17, 22, 36, 43, 57, 68, 71, 76	10.57 (21%)	0.41 (5%)	2.56 (16%)

Worst 10 lines 3, 16, 29, 33, 37, 44, 62, 74, 81, 88	7.14 (-18%)	0.37 (-3%)	1.88 (-15%)

Discussion

Differences in biomass production were largely related to differences in RUE, not seasonal *f*. However, to calculate RUE, we need to reliably estimate seasonal *f*. While it was possible to estimate average seasonal *f* from a measurement of *f* at anthesis, the relationship between *f* at anthesis and seasonal *f* may change with season and location, due to changes in the climatic factors determining development and therefore the area and duration of the green leaf, *e.g.* (5). Although seasonal *f* may be important in considering differences among cultivars, there was relatively little genetic variation for *f* (and therefore less scope for selection) within the population that was examined here. One avenue to increase seasonal *f* is increasing early vigour (= rapid leaf area development) to capture more light. The lack of correlation between the first and last observations of *f* (r = 0.04) or the first observation and seasonal *f* (see above) suggests that this avenue is unhelpful within this population.

The mean RUE for all lines was well below that usually observed for maize cultivars (*e.g.* 5), probably due to the effects of inbreeding depression. There was substantial range in RUE explaining biomass differences and that the upper part of this range was similar to values observed in hybrids, *i.e.* it is high enough to be usefully exploited. When RUE was estimated using the final observed *f* (rather than seasonal *f*) seven of the 10 best genotypes for seasonal RUE were still in the 'best' group. Similarly, 7 out of the 10 worst lines were still in the bottom 10. Thus it is possible to measure *f* once, at anthesis and be able to use this and a biomass harvest to select for RUE, given equal duration of growth.

The range in RUE could be due to segregation of lines into tropical, highland and temperate types with highland types probably favoured at this site. There was clear variation in canopy structure among lines, with all growth types evident (tropical types tend to have larger, less erect leaves than improved temperate types, while highland types tend to have narrow, lax leaves). This analysis does not reveal the cause of the differences in RUE, but it is probable that photosynthesis was reduced by the cool temperatures. Variation in RUE might also arise due to low night temperature effects on the export of assimilate away from photosynthetic sites. This explains differences among genotypes of peanuts in different environments (1) and there is evidence of differences among maize cultivars at El Batan (H.R. Lafitte, unpubl. data).

Genetic variation among S_1 lines was observed for biomass production up to the start of grain fill. This was associated with variation in seasonal RUE which could be estimated using f measured at anthesis. While the variation in RUE may be a function of temperature interaction with segregation of different adaptation types, lines were found that had significantly greater than average RUE at this site. Using the results of this experiment, 10-line synthetics were formed for the best and worst lines for biomass production and RUE. In further experiments, these are being evaluated to examine the heritability of these traits.

References

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