

Towards a robust method of modelling leaf appearance in plants

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Abstract

The thermal interval for leaf tip appearance (phyllochron) is a critical variable for modelling plant development and growth. Phyllochron varies across environments, but is generally constant for a species grown in specific environments. For example, the phyllochron in maize is lower in temperate environments than in tropical and subtropical environments. The limitation of existing data is that each experiment has been evaluated in a narrow range of environments, and underlying mechanisms have not been adequately examined. Consequently, no method is available to model the variation across environments. Models use constant values that are fixed for particular environments. This situation is unsatisfactory, as model users must have values that have been determined for their locality. A method of adjusting the value of phyllochron according to genotype adaptation groups or environmental conditions is required. Of these two options, the latter appears most promising as there is little, if any, variation among genotypes when grown in specific environments. Recent information shows that phyllochron in maize is related to light intensity. The data also suggests that phyllochron depends on the adequacy of current photosynthesis (source) to meet the demands of the plant for growth (sink), one aspect of which is the production of new leaves. This paper reports on concepts and early progress in relating phyllochron to both irradiance and thermal time.

Key words: leaf appearance, maize, ontogeny, phyllochron, Zea mays.

Temperature controls the rate of leaf appearance (14). However, the phyllochron (thermal interval between the appearance of successive leaf tips) differs across environments. The phyllochron of maize in temperate environments is lower than in warmer environments (4, 5, 6, 8, 10, 16, 17).

Accurate information on phyllochron is needed to predict crop development from leaf number. Crop models of maize, *eg.* CERES-Maize (9), AUSIM-Maize (6) and sorghum, *eg.* SORKAM (15), and CERES-Sorghum (SAT) (1) use leaf number and a constant phyllochron to predict time of flowering. Thus, they can only predict development accurately in the range of environments to which the phyllochron value applies. This is likely to explain some of the errors in prediction for maize reported in Kiniry and Bonhomme (10) and Birch (2). Across locations, temperature, irradiance and photoperiod differ because of latitude and altitude. Differences in photoperiod are unable to explain the differences in phyllochron, as the effects of photoperiod are either small (18) or non-existent (2). Phyllochron has been found to vary with radiation intensity (4, 5, 7) at controlled temperature. The variation in phyllochron might be explained by modulation related to the ratio of source and sink strength (12). Since source and sink strength cannot be measured routinely, photothermal coefficients are calculated as the

ratio of irradiance and thermal time per unit time (day). A second hypothesis is the acclimation hypothesis proposed for barley and wheat by Kirby (11). Wheat and barley plants grown under cool temperatures (<10-15°C mean daily temperatures) produced leaves more quickly than plants grown at warmer temperatures. Kirby (11) argued that the phyllochron depends on mean air temperature for a short period after emergence, *eg.* 200°Cd (base temperature, 0°C), and that the plant 'remembers' these conditions.

To explore the possible use of a photothermal coefficient and acclimation in maize, a series of studies were undertaken, using data from diverse environments, and additional field trials in The Netherlands and Texas, USA. In addition, some preliminary information on the effect of irradiance on phyllochron in grain sorghum was sought.

Materials and methods

We used data from experiments with non-limiting conditions of nutrient and water supply conducted at Wageningen, The Netherlands (4, 5, 8), Gatton, Australia (2), El Batan, Tlatizapan, Poza Rica, Mexico (Elings 1995, 1996, unpublished), and Guadeloupe (3). We also conducted experiments in The Netherlands (three cultivars of maize planted on five dates) and Texas, USA, (two cultivars of maize, one of grain sorghum, grown under full sun, 55 and 73% shade) in 1997. In both of these trials, leaf number was counted at 1 - 3 day intervals. Rate of leaf tip appearance [leaves (°C/d)] was calculated by regressing number of leaves that were visible on thermal time (base 8°C) from emergence. Phyllochron (°Cd/leaf) is the reciprocal of leaf appearance rate.

To test the potential of a photothermal coefficient to explain variation in phyllochron, numerous options for development of linear and curvilinear relationships between phyllochron, and photosynthetically active radiation and thermal time, and interaction of these were examined. In all cases, a subset of available data was used to derive equations. Remaining independent data was used to assess performance of derived equations as predictive tools, by root mean square deviation (RMSD) and regression of predicted on observed phyllochron.

Phyllochron was related to daily mean temperature from emergence to 200°Cd after emergence. At 200°Cd, it was unlikely that tassel initiation would have occurred in any of the experiments used here, so the plants were all still in the vegetative stage. Phyllochron was regressed on daily mean photosynthetically active radiation (PAR), for those data sets where temperature was constant, and for field trials within daily thermal time intervals of 2°Cd/d.

Results

Phyllochrons were generally in the range 25 to 50 °Cd leaf⁻¹, the shortest occurring in the data of Bos *et al.* (4) and Hussen (8), the longer phyllochrons being in experiments in tropical locations (2, 6, 10). At Wageningen, phyllochrons did not differ or differed only slightly among cultivars. They were similar to earlier results at Wageningen, but lower than reported in warmer environments. In the shading experiment at Temple, there was negligible difference in mean, maximum or minimum daily temperatures among the shading treatments, and thus differences in phyllochrons must be related to irradiance. The full sun treatment had more leaves in all samplings of maize and sorghum after five leaves had appeared, than in either of

the shade treatments ($P < 0.05$), which also differed significantly. Shading increased the phyllochron in maize from 37 °Cd (full sun) to 52 °Cd (55% shade) and 63 °Cd (73% shade) and in sorghum (42, 56 and 67 °Cd for the respective shade treatments).

We were unable to develop a single equation that related phyllochron or thermal interval for full leaf expansion to the ratio (PT) of PAR and daily thermal time for all environments.

Early acclimation was found. Phyllochron throughout the season increased by 2.1 °Cd for each degree C increase in the daily mean temperature during the first 200 °Cd after seedling emergence in the field. At daily mean temperature above 25.5 °C, phyllochron appeared to decline in the few data for these temperatures, except when irradiance was low in the shading and controlled environment experiments. In these treatments, phyllochron was increased by low irradiance.

Our data indicate that phyllochron was reduced by 2 - 4 °Cd/MJ of increase in average daily PAR throughout leaf production.

Discussion

Our results did not support use of single values for phyllochron for all cultivars and all environments. Also, we were unable to calculate a photothermal coefficient which could explain all the variation in phyllochron across environments. The dominant environmental influence on phyllochron was mean temperature conditions until 200 °Cd after emergence. This finding is similar to that of Kirby (11) for wheat and barley, and thus Kirby's acclimation hypothesis seems to apply to maize as well as wheat and barley. Also, data from our field experiments are supported by the controlled environment studies of Bos *et al.* (4, 5). As only two of the field trials used in this study have included variation in irradiance, the independent effects of irradiance on phyllochron had to be determined from these and the controlled environment. The values of 2 to 4 °Cd per mega- joule of increase in average daily PAR during leaf production are preliminary. Further experiments are needed to determine whether a single value can be used or an equation is needed.

From current observations, we are unable to determine the mechanism by which the plant sets the phyllochron by the temperature conditions, but presumably a hormonal mechanism is involved. This is a similar conclusion to that of Kirby (11) with wheat and barley. Since photosynthate production depends on radiation, and plants have few reserves of carbohydrate for remobilisation during production of the canopy, it is not surprising that phyllochron will be extended when irradiance is low. Further, photosynthate supply for growth processes can be limited by high temperature, due to higher rates of respiration at high temperature. It is likely that the slower appearance of leaves (higher phyllochron) under high temperature, and the smaller leaves produced at high temperature (13) are both explained by limited photosynthate availability.

Our relationship between phyllochron and mean temperature from emergence to 200°Cd after emergence, and the modifier for irradiance should improve the prediction of leaf numbers and the time of silking. Our observations need to be confirmed by further studies, using shading experiments that include transitions from full sun to shade and vice versa, under field conditions, so that high levels of solar radiation are included as a treatment.

Further, since numerous processes in crop growth models depend on production of the canopy, the accurate prediction of the number of leaves and the number that are fully expanded is vital. Both phyllochron and thermal time for full leaf expansion are needed for accurate modelling, since the proportion of leaves that are fully expanded varies during the production of the canopy. We have found that full leaf expansion is affected by temperature and irradiance conditions in a similar manner to phyllochron. We also found that radiation intensity increased phyllochron in sorghum. Clearly, research is needed to determine the range of crops in which such acclimation occurs, and the effect of irradiance on leaf appearance and expansion. This should greatly improve simulation of canopies, and the processes that depend on the canopy should also be improved.

Conclusions

Phyllochron was sensitive to thermal time and irradiance, and acclimation to mean temperature over a short period after emergence appeared to determine the phyllochron. We have proposed an approach to the analysis of data on phyllochron that can consider underlying plant growth and developmental mechanisms, and incorporate response of the crop to environmental influences. This should replace constants in models of maize, and thus make the models more generally applicable. Further analysis of data for maize and other crops is needed to determine the extent and effects of acclimation on leaf production.

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