

CHAPTER 16

AN ARCHITECTURAL APPROACH TO INVESTIGATE MAIZE RESPONSE TO LOW TEMPERATURE

K. CHENU^{#,##}, C. FOURNIER^{##}, B. ANDRIEU^{##}
AND C. GIAUFFRET[#]

[#] UMR SADV, INRA-USTL, Estrées-Mons, BP136, 80203 Péronne, France.

^{##} UMR EGC, INRA-INAPG, 78850 Thiverval-Grignon, France.

E-mail: chenu@ensam.inra.fr; giauffre@mons.inra.fr

Abstract. In maize, grain yield is highly associated with light interception and photosynthetic activity during grain filling. In Europe, this period typically occurs when solar radiation is already decreasing and water availability may be limiting. The improvement of cold-tolerance is a major challenge for maize production because earlier sowing would allow a better fit between crop cycle and availability of natural resources.

Low temperatures have a major impact on (i) radiation interception through the modification of foliage development and (ii) radiation use efficiency (RUE) through the reduction of leaf photosynthetic activity. Little is known about the specific contribution of each of these traits to the lower biomass production under cold conditions and their genetic variability.

A field experiment with two planting dates was carried out on four maize inbred lines from temperate or highland-tropical origin, chosen as source of genotypic and phenotypic variability for cold tolerance. Biomass production was measured over time and analysed with respect to the amount of radiative energy received by the plant to quantify the radiation use efficiency of the different genotypes. The major impact of early sowing was found through the reduction in leaf dimensions. Early sowing affected leaves growing both during and after the cold period. Less striking effects were observed for plant developmental rate, final leaf number, RUE and leaf inclination. Virtual plants simulating the architecture of the genotypes both in early and normal sowings were generated and used to evaluate the effect of individual traits on light capture.

The results presented here are a first step to provide a phenotyping tool of plant response to low temperatures based on virtual plants. Such a tool should help to assess structural (light interception) and functional (RUE) traits that could then be used in segregating populations for genetic studies.

INTRODUCTION

Despite its subtropical origin, maize (*Zea mays* L.) has become a major crop in northern latitudes during the last 50 years. However, suboptimal temperatures occurring during spring affect seedling establishment and photosynthetic activity

(Stirling et al. 1991; Leipner et al. 1999) so that productivity and yield stability are reduced (Carr and Hough 1978; Stamp 1986). Low temperatures also preclude early sowing, so that in high-latitude environments ($> 45^{\circ}$ N), silking and grain filling occur when both radiation and temperature are declining, which affects the yield potential (Otegui and Bonhomme 1998). Furthermore, in mid-latitude environment, water deficit may occur around flowering, during the period critical for grain set (Hall et al. 1981). Therefore, improving cold tolerance would allow earlier sowing, resulting in a better fit between crop cycle and availability of natural resources.

During the last decades, many studies have focused on the temperature effects on plant development (e.g., Tollenaar et al. 1979; Padilla and Otegui 2005) and processes involved in photosynthetic activity (e.g., Fryer et al. 1995). However, it is still poorly understood how these processes interact during canopy development in a realistic range of low temperatures and affect yield. A modelling approach could help to identify the key processes involved in above-ground biomass accumulation during the vegetative period, and thus to determine the traits important for plant breeding. Biomass accumulation mainly results from light interception and radiation use efficiency (RUE). The aim of this work was to study the impact of plant architecture and functioning on biomass production. A field experiment was carried out with two planting dates to analyse cold response in terms of plant development, architecture, radiation interception and use efficiency. The 3D architectural model developed by Fournier and Andrieu (1998) for maize was coupled with a radiative model (Chelle and Andrieu 1998; 1999) to quantify the contribution of specific responses of plant architecture in terms of light intercepted by the crop.

We used four maize inbred lines that originate from temperate and highland-tropical environments. Temperate and highland-tropical cultivars are known to have contrasting responses to low temperatures in terms of photosynthetic activity (Hardacre and Greer 1989), seedling biomass and leaf area development (Eagles et al. 1983).

MATERIALS AND METHODS

A field experiment was carried out in Estrées-Mons, France (49° N, 3° E, 85 m elevation) in 2005. Four maize inbred lines from temperate (F2 and F286) or highland-tropical (F334 and F331) origins were cultivated at a density of 10 plants m^{-2} . They were sown on 11 April (early sowing), and 2 May (normal sowing), resulting in contrasting temperatures for the period of early development (Figure 1).

Incident photosynthetically active radiation (PAR), air and apex temperatures were measured over time using a PAR sensor (Quantum Sensor SKP215, Skye Instruments Ltd, Llandrindod Wells, UK), a thermohygrometer (50Y, Campbell Scientific Ltd, Shepshed, UK) and thermocouples (copper–constantan), respectively. An equivalent thermal time expressed in degree-days ($^{\circ}$ Cd) was calculated using the equation of Yan and Hunt (1999), adjusted to a base temperature of 9.8° C in the linear part of the response. Intercepted radiation by the canopy was determined from measurements of incident PAR at the top of the canopy and at ground level. The efficiency of radiation interception was estimated as the ratio between intercepted

and incident PAR. Crop radiation use efficiency (RUE) was calculated from above-ground biomass accumulation and accumulated intercepted PAR from plant emergence. Plant growth, development and architecture were determined from measurements of above-ground biomass accumulation, number of appeared and liguled leaves, dimensions (area, length and width) and angles of laminae, lengths of sheaths and internodes.

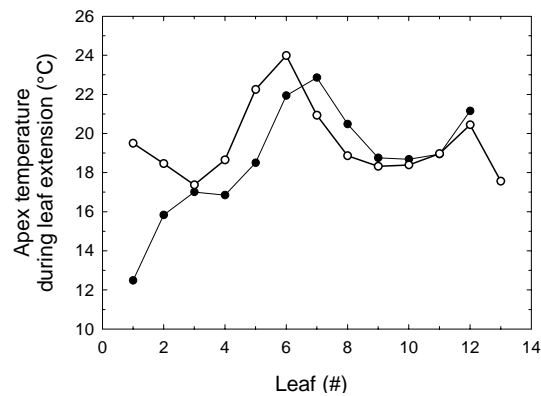


Figure 1. Growth temperatures for the different leaves for one line (F2) in early (closed dots) and normal (open dots) sowings. Temperatures were estimated as the apex temperature averaged for the period of leaf expansion (from tip to ligule appearance of the leaf)

RESULTS

Early sowing affected development, growth and spatial distribution of organs

Early sowing reduced the biomass production for all the studied genotypes from the early stages of development (data not shown). Plant development differed among the genotypes (Figure 2). For F2, the early sowing increased phyllochron (thermal time interval between the emergence of two successive leaves) and reduced final leaf number despite a slight increase in the duration of the vegetative period, estimated here by the date of tassel emergence (Figure 2, inset). F286 had a development unaffected by the sowing date with similar phyllochron, final leaf number and vegetative period duration. In the highland-tropical lines (F334 and F331), early sowing increased both phyllochron and the duration of the vegetative period so that the final leaf number was not modified. Finally the three-week difference between the sowing dates led to a tassel emergence occurring in early sowing from one week before (F286) to one week after (F331) the date for the normal sowing (data not shown). Interestingly, the increase in the length of the vegetative period of F334 and F331 allowed some compensation in terms of biomass production: these two genotypes had an above-ground biomass reduced, respectively, by 62% and 53%

when their leaf 11-12 emerged, whereas the reduction was only 29% and 33% at tasselling. Conversely, the biomass reduction in F2 and F286 was maintained over time (data not shown).

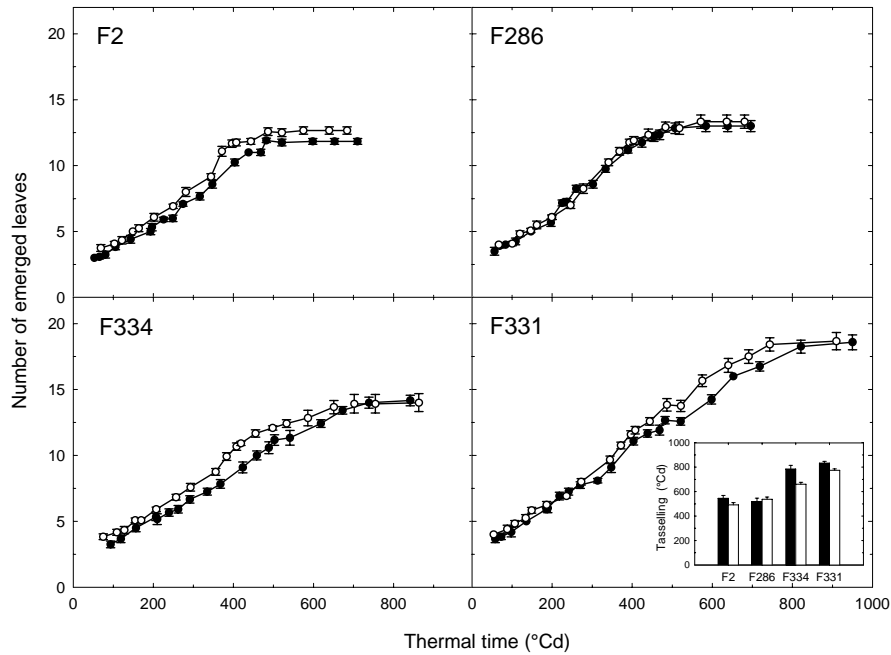


Figure 2. Number of emerged leaves over thermal time from plant emergence for lines F2, F286, F334 and F334 in early (closed dots) and normal (open dots) sowings. Inset, duration until tassell emergence at early (black bars) and normal (white bars) sowings. Error bars indicate confidence limits at $P=0.03$

Early sowing did not affect the dimensions of leaves 1 and 2, but reduced the area, length and width of all other leaves (Figure 3). Since only the first leaves extended during the cold period (Figure 1), the reduction in dimension of the upper leaves seems to have resulted from a propagation of the initial effect, more than from a direct effect of cold temperatures on the behaviour of the leaf-growing zone. On the other hand, some compensation occurred in some lines (e.g., F331), with similar dimensions (length, width and area) of the top-most leaves in both treatments.

Mean inclination of laminae differed among genotypes (Figure 4). Genotypes also showed contrasting variation of leaf inclination with leaf rank. For instance, in F334 all leaves were more or less planophile whereas in F2 leaf angle increased with higher leaf position on the stem (data not shown). Early sowing slightly reduced the inclination of all laminae (Figure 4). The maximal effect on light interception was observed for F2 and corresponded to a 15% increase in surfaces projected on soil.

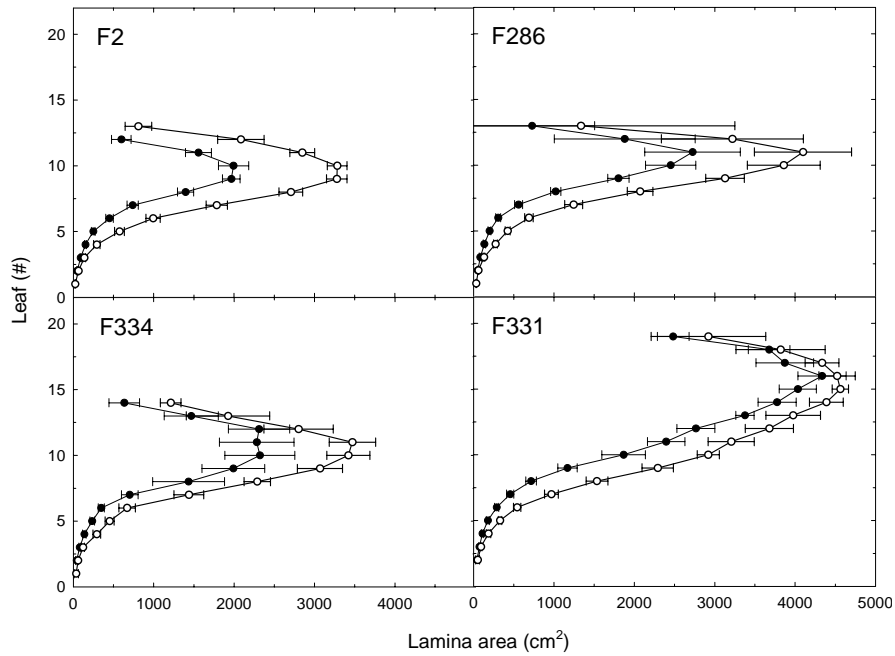


Figure 3. Final lamina area of successive leaves along the shoot. Data for lines F2, F286, F334 and F331 in early (closed dots) and normal (open dots) sowings. Error bars indicate confidence limits at P = 0.05

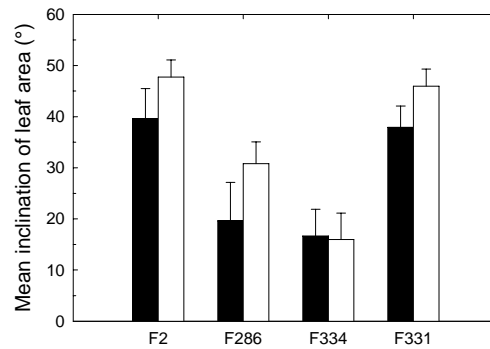


Figure 4. Mean inclination of surface of fully expanded leaves for lines F2, F286, F334 and F331 in early (black bars) and normal (white bars) sowings. Error bars indicate confidence intervals at P = 0.05

Early sowing reduced efficiency of light interception with no drastic effect on the radiation use efficiency for the sowing–flowering period

Efficiency of light interception was lower in early sowing from the first stages of plant development (Figure 5). Interestingly, the high number of leaves produced in F331, associated with a high degree of leaf size compensation for the top-most leaves, allowed its light interception to reach similar values at silking, in early and normal sowings.

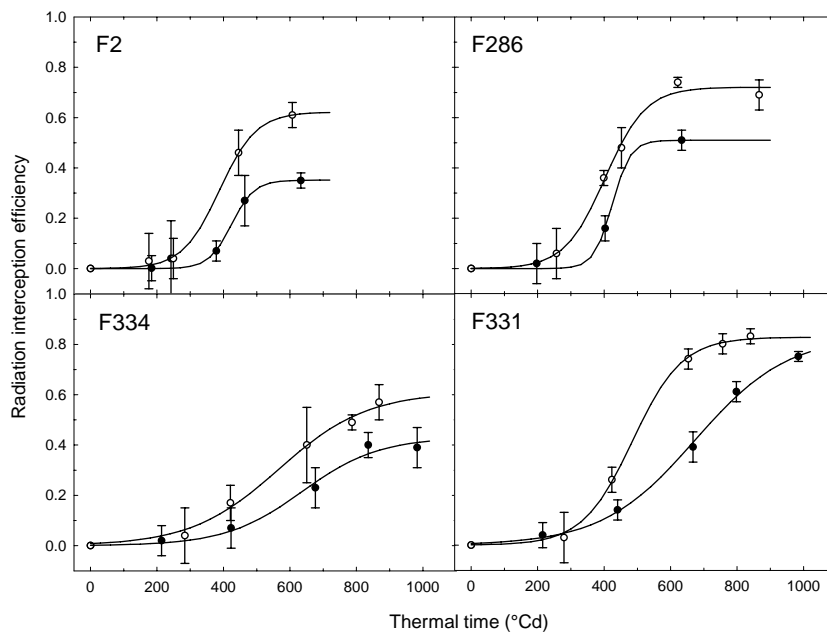


Figure 5. Efficiency of radiation interception over thermal time for lines F2, F286, F334 and F331 in early (closed dots) and normal (open dots) sowings. Error bars indicate confidence limits at $P = 0.05$

RUE for the sowing–silking period differed among genotypes but was weakly affected by the date of sowing (Figure 6). Effects of sowing date on RUE were significant in the temperate lines but not in the highland-tropical ones. Similar results were observed in a previous field experiment carried out in 1999 (C. Giauffret et al. unpublished data). RUE tended to be negatively linked to genotype earliness for the sowing–silking period. This was not the case when measurements were done at the same calendar date for all the genotypes (e.g., around silking of the earliest flowering genotype in the 1999 experiment). The genotypic variation observed for the RUE averaged through the sowing–silking period could thus result from change in RUE over plant development or from photosynthesis dependence on temperature (Giauffret et al. 1991; Stirling et al. 1993), as measurements were done about one month later for the late-flowering lines than for the early-flowering ones.

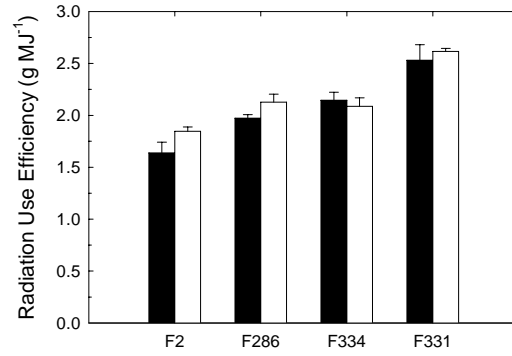


Figure 6. Radiation use efficiency (RUE) for the sowing–flowering period, for lines F2, F286, F334 and F331 in early (black bars) and normal (white bars) sowings. Error bars indicate confidence limits at P = 0.05

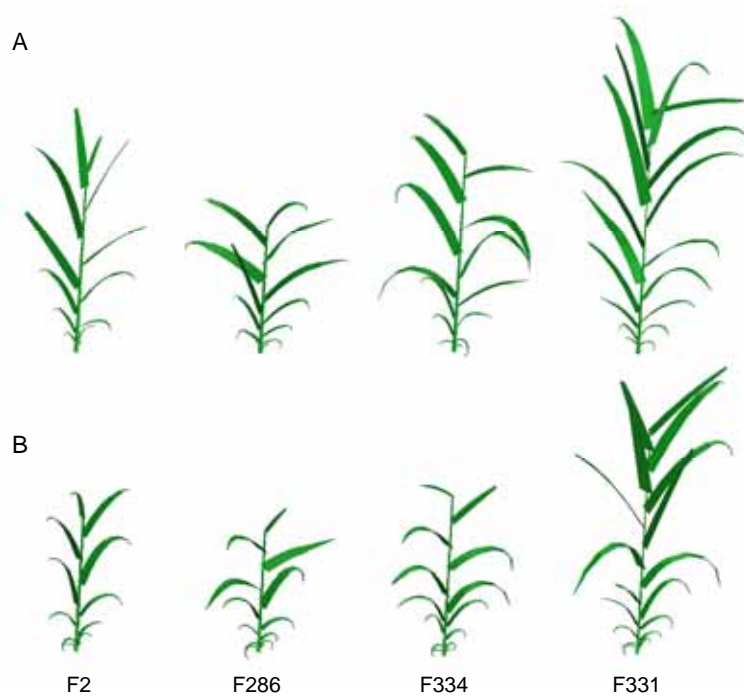


Figure 7. Representation of 3D virtual plants for the four inbred lines in normal (A) and early (B) sowings. Examples are given for median plants at silking

3D virtual plants to dissect the contribution of architectural traits to light interception

ADEL maize (Fournier and Andrieu 1998; 1999) was adapted here to the different genotypes and sowing-date treatments (Figure 7). Efficiency of light interception was simulated for each situation. Ground cover simulated with virtual plants was estimated for vertical viewing with a field of view of 25°, consistent with field measurements with photographs. Simulated ground cover matched the measured one with a good accuracy ($y=0.88x$, $r^2=0.88$), thus showing the ability of the method to assess the consequence of architecture on light capture. There was, however, a small bias in the model, as simulated ground-cover values were slightly lower than observed ones. This could partly be explained by the fact that the tassel was not represented in virtual plants.

Virtual plants combining characteristics of normal and early sowing treatments were generated to estimate how specific changes in architectural variables affected light interception. Decrease in organ dimension (leaves and internodes) had a major impact on ground cover, with a reduction up to 29.2% at flowering time. Response in leaf inclination slightly increased the light-capture efficiency with a change in ground cover at flowering time of up to 6.4%.

DISCUSSION

Some initial leads to drive genetic studies on cold tolerance

The cold period was limited to the first stages of plant development; however, it affected the organ growth and development during the whole plant cycle. Such an effect of early planting has already been reported for leaf appearance rate or leaf elongation rate (Giauffret et al. 1995). Improvement of cold tolerance thus needs to focus not only on the direct effect of sub-optimal temperatures (e.g., Jompuk et al. 2005), but also on the processes involved in propagation of these effects. This propagation could be because of trophic effects, as light interception was decreased in plants affected by cold. Many studies have shown that light affects leaf initiation and expansion rates (e.g., Granier and Tardieu 1999; Chenu et al. 2005). Another hypothesis concerns the coordination of organ growth. Strong correlations have been found between the dimensions of successive organs (lamina and sheath) on the stem, for different types of environments (e.g., Andrieu et al. in press).

The response of the rate and duration of leaf initiation to temperature could also be a target for the improvement of cold tolerance. Indeed, leaf appearance rate and final leaf number are highly associated with silking date, light interception and grain filling (Tollenaar et al. 1979). Furthermore, a higher leaf number is often correlated with higher individual leaf areas (Dwyer et al. 1992; Fournier and Andrieu 1998). A way to improve yield could then be to find genotypes that produce a large number of leaves with a high initiation rate in early sowing conditions, in order to obtain both early flowering and high leaf area index. Genetic variability exists for the response of such traits to temperature (Figure 2, Lafitte et al. 1997; Padilla and Otegui 2005) and could therefore be exploited.

Contribution of 3D virtual plants to study the genetic basis of cold tolerance

We propose two major reasons to use 3D virtual plants to investigate genotype response to low temperature.

First, dynamic 3D plant models, when coupled with a radiative model (Chelle and Andrieu 1998; 1999) allow the estimation of light interception for different genotypes and environments, without multiplying the number of radiative sensors. This method also makes it possible to estimate light interception accurately during the early stage of growth, when physical measurements are difficult due to the small size of the plants and the high spatial variability. Such an approach would thus improve the estimates of radiation interception and RUE during the cold period.

Second, architectural models are useful to dissect the impact of different architectural variables on light interception (Chenu et al. 2005). These models can be used to quantify the expected benefit resulting from some improvements in the response to low temperatures, concerning developmental rate, organ dimension, leaf angle or RUE. With sufficient understanding, they can be used to define ideotypes depending on the existing genetic variability and the prospected climate. We have shown here that early sowing had a major impact on light interception through a reduction in organ dimension, whereas the response of leaf inclination had smaller impact for the studied genotypes. These results are a first step to build a phenotyping tool to simulate 3D virtual plants with a limited set of measurements. Such an approach could help to assess light interception in large populations. This would allow studying the genetic controls (quantitative-trait loci) of cold tolerance for integrative traits such as light interception and RUE.

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