STABILITY OF SUNFLOWER LEAF DEVELOPMENT IN FRANCE AND ARGENTINA

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Abstract

Leaf area plays a key role in biomass accumulation and yield formation in sunflower. Accurate prediction of the timing of leaf area development is essential to analyse and predict the responses of plants to the environment. According to Granier and Tardieu (1998, 1999), two phases have to be taken into account during leaf development. During the first one, leaf growth is exponential; during the second one, leaf relative expansion rate decreases rapidly to reach zero at the end of leaf expansion. The objective of this work was to build a model which predicts the dates of the two phases for all the leaves of sunflower plants in a wide range of thermal and radiative conditions. Two hybrids of sunflower were sown at different dates and densities in field and greenhouse experiments at Montpellier (France) and Balcarce (Argentina). The growth of all leaves, including those developing inside the apical bud, was recorded by direct measurement or microscope observation and image analysis. Air and leaf temperature was continuously recorded. On a thermal time scale, the chronology of leaf development was the same for the 2 studied hybrids, for the different locations (France, Argentina, field and greenhouse), for isolated plants or plants in canopy. Only mean daily temperature was necessary to predict the key-dates (primordium initiation, end of exponential growth and full expansion) of development of each leaf. This model is a powerful framework for both analysis and prediction of the response of leaf growth to environmental conditions.

INTRODUCTION

Leaf area plays a key role in biomass accumulation because it determines the amount of solar radiation intercepted by the crop. This in turn determines the amount of dry matter accumulated by a crop. Accurate prediction of the timing of leaf area development is essential to analyse and predict the responses of plants growth to water deficit or changes in light intensity (Lecoeur *et al.*, 1995, 1996). According to Granier and Tardieu (1998, 1999), two phases have to be taken into account during leaf development to analyse responses of leaf expansion to environmental conditions. During the first one, leaf growth is exponential and leaf relative expansion rate is stable with time. During the second one, leaf relative expansion rate decreases rapidly to reach zero at the end of leaf expansion. The objective of this work was to build a model to predict the dates of the two phases for all the leaves of sunflower plants in a wide range of thermal and radiative conditions.

MATERIALS AND METHODS

Field experiments were carried out in 1998 and 1999 either at Montpellier, France (43°40' N, 3°50' E), on a sandy loam soil (fluvio-calcaric Cambissol) using hybrid Albena sown at 55000 plants ha^{-1} (experiment A) or at 625 plants ha^{-1} (isolated plants, experiment I), or at the INTA Balcarce Experimental Station, Argentina (37°45' S, 58°18' W), on a Typic Argiudol using hybryd Dekalb G-100 sown at 55000 plants ha^{-1} (experiment B). A greenhouse experiment (G) was carried out in Montpellier in 1998, with cv Albena sown in 30L pots. Mineral and water supply were adjusted to avoid any stress. Incident radiation was measured continuously using a PPFD sensor. Air temperature and relative humidity were measured every 20 s. Leaf temperature was measured with a copper-constantan thermocouple (0.4 mm diameter) appressed to the under side of the lamina.

Mean daily PPFD during the period of leaf expansion ranged from 7 (experiment G) to 49 µmol d^{-1} (experiments G and B respectively) and mean temperature ranged from 18.5 °C to 23°C (experiments G and A). Five plants were marked after emergence. Length and width of all visible leaves were measured with a rule three times a week on the same plants until the end of leaf expansion. A linear relationship was established between leaf area and the product length*width in each experiment. Three times a week, 4 to 6 plants were harvested in Montpellier experiments. Leaf area of visible leaves was measured with an image analyser. Apical bud was dissected under a microscope. A leaf was considered as initiated when its primordium was visible (about 40 µm long) on the apical meristem at magnification x80. Leaves were excised and area was measured with an image analyser. Phytomers were numbered from cotyledonary node, counted as zero. Each of the first 3 phytomers bear two opposite leaves (leaf 1 to leaf 6). Phyllotaxy is altern from phytomer 4 (corresponding to leaf 7) until the capitulum. For example, leaf 16 corresponds to phytomer 13. Leaf relative expansion rate (*RER*) at time j was calculated from initiation to the end of expansion as the slope (at time j) of the relationship between the logarithm of leaf area (A) and time :

$$RER_{\text{leaf}, j} = [\, d\,(\ln A)\,/\,d\,t\,]_j \ .$$

It was calculated by linear regression on the three coupled values of *A* and t corresponding to times j-1, j and j+1. Thermal time was calculated as cumulative degree-days from emergence by daily integration of leaf temperature and a base of 4.8 °C (Granier and Tardieu, 1998b).

RESULTS AND DISCUSSION

The distribution of final leaf area along the stem in the different experiments is presented in Fig. 1, showing a wide range in individual leaf areas across experiments. Total leaf area per plant ranged from 0.73 m² in experiment G to 2.42 m² in experiment I. Experiments ranked in accordance with the amount of intercepted radiation per plant. Hybrid G100 (experiment B) exhibited a similar behaviour as Albena sown at the same plant density (experiment A), except that it had 27 leaves compared to 32 in Albena.
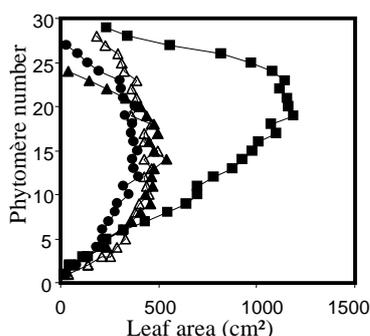

Fig. 1. Distribution of final leaf area according to phytomere position in experiments A (field Montpellier,△), B (field Balcarce,▲), I (isolated plants,■) and G (greenhouse,●)

Fig. 2. Number of initiated phytomers as a function of thermal time. Same symbols as in Fig. 1.
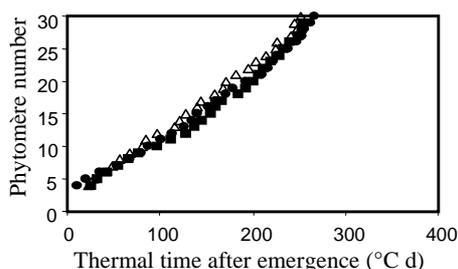

Fig. 3. Leaf area (A) and relative expansion rate (B) at phytomer 13 (leaf 16) as a function of thermal time. Same symbols as in Fig. 1.

The number of initiated phytomers is presented on Fig. 2 as a function of thermal time, for the different growing conditions. Data of all experiments fitted together in a common linear relationship from phytomer 4 to phytomer 25. The rate of phytomer initiation was 0.100 phytomer $°Cd^{-1}$, corresponding to a mean plastochron of 10 °Cd. This rate was lower before phytomer 4, and slightly higher after phytomer 25. The date of initiation of a given leaf was stable across environmental conditions.

Individual leaf expansion is shown on Fig. 3 with the example of leaf 16 (inserted on phytomer 13). Time course of leaf relative expansion rate (RER) clearly indicated 2 phases in leaf growth in all experiments. During the first one, RER was maintained above 0.03 mm² mm^{-2} $°Cd^{-1}$ (except during a short period in experiment G, where incident radiation was strongly reduced); during the second one, RER decreased rapidly. Differences in RER between experiments occured mainly during exponential growth, in accordance with shading experiments of Granier and Tardieu (1999). Treatments did not induce differences in the duration of the 2 phases : end of exponential growth (rapid decrease in RER) and end of expansion (RER equalled zero) occured at the same dates in all experiments.
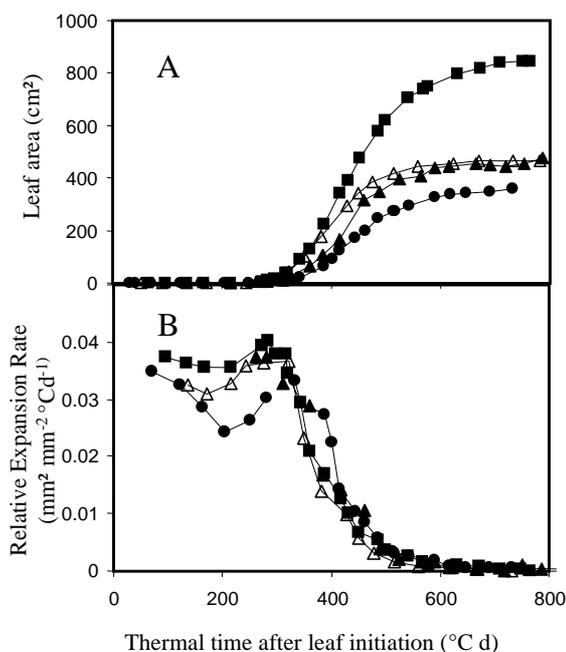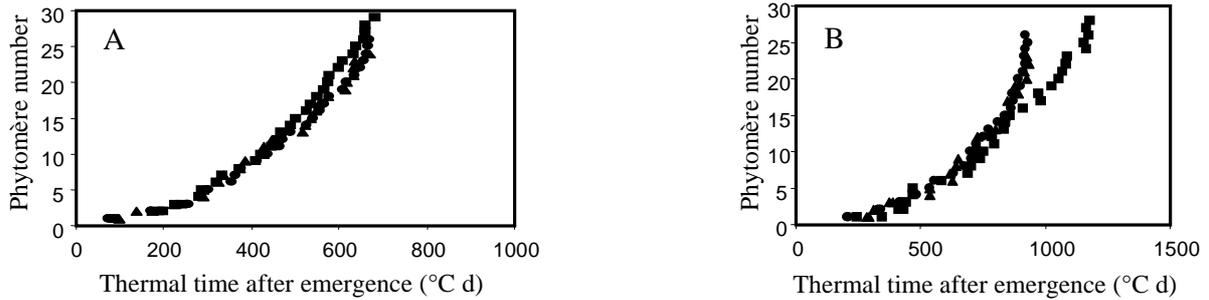
Fig. 4. Number of leaves beyond exponential growth (A) and number of full expanded leaves (B) as a function of thermal time. Same symbols as in Fig. 1.

For each leaf, the dates of end of exponential growth and end of expansion were deduced from the time course of RER (Fig. 3B for leaf 16). The date of end of exponential phase was stable among treatments(Fig 4A). All data fitted to a common linear relationship between the number of phytomers beyond exponential growth and thermal time. A second relationship, with a lower rate, was found for the first 3 phytomers. It was also common to all the experiments.

Three groups of leaves had to be distinguished when considering the date of full expansion (Fig. 4B). The rate of production of expanded leaves was slow on the first 3 phytomers and common to all the experiments. Between phytomer 3 and phytomer 17 (leaf 20), the rate of appearance of new expanded leaves was higher and again common to all the experiments. For higher leaves, this rate was maintained unchanged for isolated plants (experiment I) almost to the top of the plant, whereas all upper leaves ceased to grow nearly simultaneously (within two days) in the other treatments at a date close to anthesis.
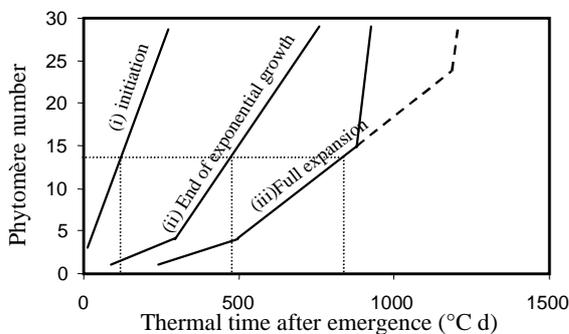

Fig. 5. Diagrammatic representation of leaf development in sunflower. The numbers of phytomers initiated (i), beyond exponential growth (ii) and full expanded (iii) are linear functions of thermal time. These lines delimit for each leaf the periods of exponential (between i and ii) and non expo-nential (between ii and iii) growth. The example of leaf 16 (phytomer 13) is given on the figure. Leaf expansion ceased soon after anthesis, except for isolated plants (broken line).

CONCLUSION

On a thermal time scale, the chronology of leaf development was the same for the 2 studied hybrids, for the different locations (France, Argentina, field and greenhouse), for isolated plants or plants in canopy. As diagrammed in Fig. 5, the production of leaf primordia, of leaves beyond exponential growth, and of full expanded leaves on sunflower plants can be described with linear functions of thermal time. Two parts of the plant, with different production rates, had to be considered. Only mean daily temperatures were necessary to build the diagram. The key-dates (primordium initiation, end of exponential growth and full expansion) of development of individual leaves, according to their nodal position are deduced from this diagram (Fig. 5). These results supply a powerful framework for both analysis and prediction of leaf growth responses to environment. Knowing phytomer age at any given date is crucial to analyse the effect of environment on leaf growth (Granier and Tardieu, 1999).

Coupled with a quantitative model of leaf area expansion in response to environment, the present model is an effective way to predict the temporal development and the final area of all individual leaves of sunflower plants, with required inputs reduced to daily climatic variables.

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