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A SEQUENCE OF STAGES IN FLOWER DEVELOPMENT IN THE SUNFLOWER

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Summary

Sunflower plants variety Peredovic, cultivar Sunfola 68/2 were grown under controlled environment conditions at 28°C. The illumination was 20,000 lux, with an 18 hour photoperiod. Under these conditions, anthesis commenced 60 days after sowing. To evaluate the transition of the vegetative shoot apex to the flowering state and the development of the primordial inflorescence, the terminal buds of samples of 5 plants were dissected at 4 day intervals from sowing. The morphological changes associated with the formation of the flower were classified into a series of consecutive floral stages, depending upon the shape of the apical meristem, the arrangement of leaf primordia and the extent of floret primordia initiation and differentiation. Quantitative analysis of the results showed that at 28°C, the initiation of leaves was completed by day 18, counting from the day of sowing; the onset of initiation of floret primordia at the periphery of the receptacle (floral stage 4) started on day 28 and was completed by day 38 (floral stage 7).

To illustrate these stages of flowering, shoot apices were fixed and photographed in a scanning electron microscope. The series of photographs obtained shows the entire process of flowering over the first 38 days from sowing.

Introduction

In published studies on the flowering process in the sunflower, various approaches have been used for the evaluation of the flowering response. For instance, the description of flowering was related to morphological changes that can be seen macroscopically on the stem tip (Goyne et al, 1977). In addition to recording the presence of macroscopic flowers or flower buds, Dyer et al (1959) also examined the presence or absence of floral apices using the dissecting microscope. A more refined system has been employed by Boye (1970) who used alphabetical symbols to classify the "determination" stage, formation of florets and differentiation of anthers.

The objective of this study was to develop a numerical scoring system for the sunflower based on the sequence of morphological changes at the stem apex that occur during the earliest steps in the transition to flowering, as well as those that can be seen later in the development of the inflorescence. Ideally such a system should be able to be expressed as a linear function with respect to time, to allow an estimation of the rate of development of the inflorescence.

Materials and Methods

Sunflower plants (Helianthus annus L. cv. Sunflola 68/2) were grown in a controlled environment cabinet, to provide near-optimal conditions for growth. Air temperature was 28°C. The irradiance was from twenty 215W fluorescent lamps (Sylvania cool white) and twelve 100 W incandescent lamps providing a total of 20,000 lux at the plant level, with an 18 hour photoperiod. The plants were germinated in a mixture of sand and peat for 2 days and then planted into one-litre pots containing a soil/sand/peat compost (ratio 1:1:1) with added inorganic nutrients to ensure an adequate supply of major and minor elements.

The terminal buds of samples of 5 plants were collected at 4 day intervals from sowing, young unfolding leaves and larger leaf primordia were carefully removed under a dissecting microscope. The apices were then fixed for 12 h in ice-cold 3% glutaraldehyde in phosphate buffer (pH 6.8), dehydrated for 24 h in two changes of each of methoxyethanol, ethanol, n-propanol and n-butanol at 0°C (Feder and O'Brien, 1968), then transferred to acetone for 1 h, and dried by the critical point drying technique using liquid CO_2. The apices were then gold-coated and photographed in a scanning electron microscope (Cambridge Instrument Co. Stereoscan S4-10).

Results

During the vegetative phase of growth the apical meristem of the sunflower remains relatively flat or has only a small elevation at the central zone while the flanks appear angular, due to the emerging leaf primordia (Figure 1). This vegetative state persists for the first 16 days in Sunfola 68/2 and was designated stage 0. Following this brief vegetative phase, the first visible sign of transition to the reproductive state was a swelling that extended over the whole apical meristem and the flanks then began to round off. This change in the external morphology is correlated with changes in the sytological zonation of the apex associated with the onset of flowering (Steeves et al, 1969) and was designated floral stage 1 (FS 1). The apical meristem then became clearly dome-shaped with rounded flanks and the youngest leaf primordia, which were positioned at the periphery of the dome, differed markedly in size depending on their order of initiation (FS 2, Fig. 2). Broadening and flattening of the apical meristem then occurred and numerous involucral bract primordia could be seen at the periphery (FS 3). The bract primordia are distinguished by the sudden narrowing towards the tip, while leaf primordia taper towards the tip more gradually. Further radial expansion then occurred until a flat disc, with an elevated rim at the periphery, was formed so that the diameter of the disc exceeded the width of the stem at the point of attachment (FS 4, Fig. 3).

Initiation of floret primordia begins on the elevated rim at the periphery of the disc. When several rows of florets have been formed, covering less than 1/3 of the radius of the receptacle, the apex was classified as FS 5 (Figure 4). Each floret originated first as a single ridge that later differentiated into the floret bract and the floret primordium itself. Initiation of florets then continued towards the center of the disc. When floret primordia covered from 1/3 to 2/3 of the radius, the inflorescence was classified as FS 6 (Figure 5). By this time the florets from the periphery of this inflorescence showed the formation of a five-lobed corolla and the supporting bract was still smooth and bent over the floret. When the floret primordia covered more than 2/3 of the radius, the inflorescence was assigned FS 7, provided the primordia in the center of the disc appeared as single ridges. In floral stage 8, the primordia in the center of receptacle had differentiated into florets and floret bracts but the bracts did not bend over the florets. This state was attained 42 days after sowing. Figure 6 shows the periphery of such an inflorescence. A smooth ray-floret primordium, a floret bract with developing hairs, a floret differentiating into ovary at the base, tubular corolla and anthers, can be seen. In floral stage 9, the central florets have developed a five-lobed corolla and floret bracts overlap these.

During the formation of the inflorescence, there is a substantial increase in size of the terminal bud. The apical meristem of a vegetative shoot apex is about 150 um across. When floret initiation starts at the periphery, the diameter of the disc is about 1 to 2 mm, and by the time floret initiation is completed, the disc has enlarged to about 15 to 20 mm in diameter.

Linear plots of the scores obtained for the cultivars Sunfola 68/2 and HA-124 are shown in Figure 7. The plants of each cultivar were grown in controlled environment conditions similar to those described above. It can be seen from the graph that this quantitative evaluation of the development of the inflorescence forms approximately a straight line with time. The greater scatter of values for Sunfola 68/2 is due to its inherently greater variability. A linear regression performed on the two sets of data showed that the slopes of the lines, expressing the rate of development of the inflorescence (floral stage per day), were very similar (Table 1). From detailed studies on leaf initiation and transition to flowering (Marc and Palmer, 1976, 1978), it has been determined that leaf initiation is completed at floral stage 1.4. By solving the linear regression equation for the time when this value is reached, it was found that leaf initiation was completed about 18 days after sowing in Sunfola 68/2, and about 3 days later in HA-124. This delay in the transition to flowering was maintained until the onset of anthesis which commenced after 60 days and 63 days in Sunfola 68/2 and HA-124, respectively.

Discussion

The development of the inflorescence in the sunflower, as observed in this study, is similar to that described by Cathey and Borthwick (1957) for chrysanthemum, another species in the family Compositae. In the chrysanthemum, the scoring system has been used in physiological studies on the flowering process. We have found that the scoring system we have developed for the sunflower can be used successfully to investigate the photoperiodic response of the sunflower, as well as to detect the differences in the early steps of the flowering process that account for the variation in the time of anthesis in early and late maturing cultivars (Marc and Palmer, unpublished results). This scoring system allows a quantitative evaluation of the flowering process, and since the relationship appears to be approximately linear, the slope of the fitted line also gives an estimate of the rate of development of the inflorescence. Information about the rate of development is important in investigating the photoperiodic response since there is the possibility that the time of transition to flowering and the rate of development of the inflorescence, may respond differently to daylength.

There appears to be a good correlation between the timing of the early reproductive events, the rate of development of floral structures, and the time of anthesis. The scoring system could therefore be used in breeding programs to secure an estimation of flowering behavior well before the inflorescence becomes visible macroscopically.

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TABLE 1. Linear Regression of Floral Stage with Time. Values for the slope give the rate of development of the inflorescence (floral stage per day). Time of flower initiation was estimated as the day when apex accomplished floral stage 1.4. Values for the time of anthesis represent the means of 8 plants, SE is given.

				Days from Sowing	
Cultivar	Corr. Coeff.	Slope	Intercept	Flower Initiation	Anthesis
Sunfola 68/2	.0991	.2786	-3.6726	18.25	60.00 ± .93
HA-124	.9272	.2750	-4.3958	21.02	63.33 ± .33

Legends for Figures

Figures 1-6. Development of the inflorescence in Helianthus annuus.

Figure 1. Vegetative shoot apex, floral stage 0 (FS 0), L = Leaf primordium.

Figure 2. Apex distinctly dome-shaped, with rounded flanks, FS 2.

Figure 3. Flat disc with an elevated rim at the periphery and numerous involucral bract primordia (IB), FS 4.

Figure 4. Initiation of floret primordia (F) at the periphery of the receptacle, FS 5.

Figure 5. Floret primordia cover between 1/3 to 2/3 of the radius of the receptacle, FS 6.

Figure 6. Detail from the periphery of a young inflorescence in which the initiation of florets was completed, FS 8. R = ray floret, F = disc floret, FB = floret bract.

Figure 7. Development of inflorescence in Helianthus annuus cv. Sunfola 68/2 (●), and HA-124 (0). Each value is a mean of 4 plants and 2 replicates. Vertical lines = ± SE.

FIGURES 1-6. Development of the Inflorescence in Helianthus annuus.

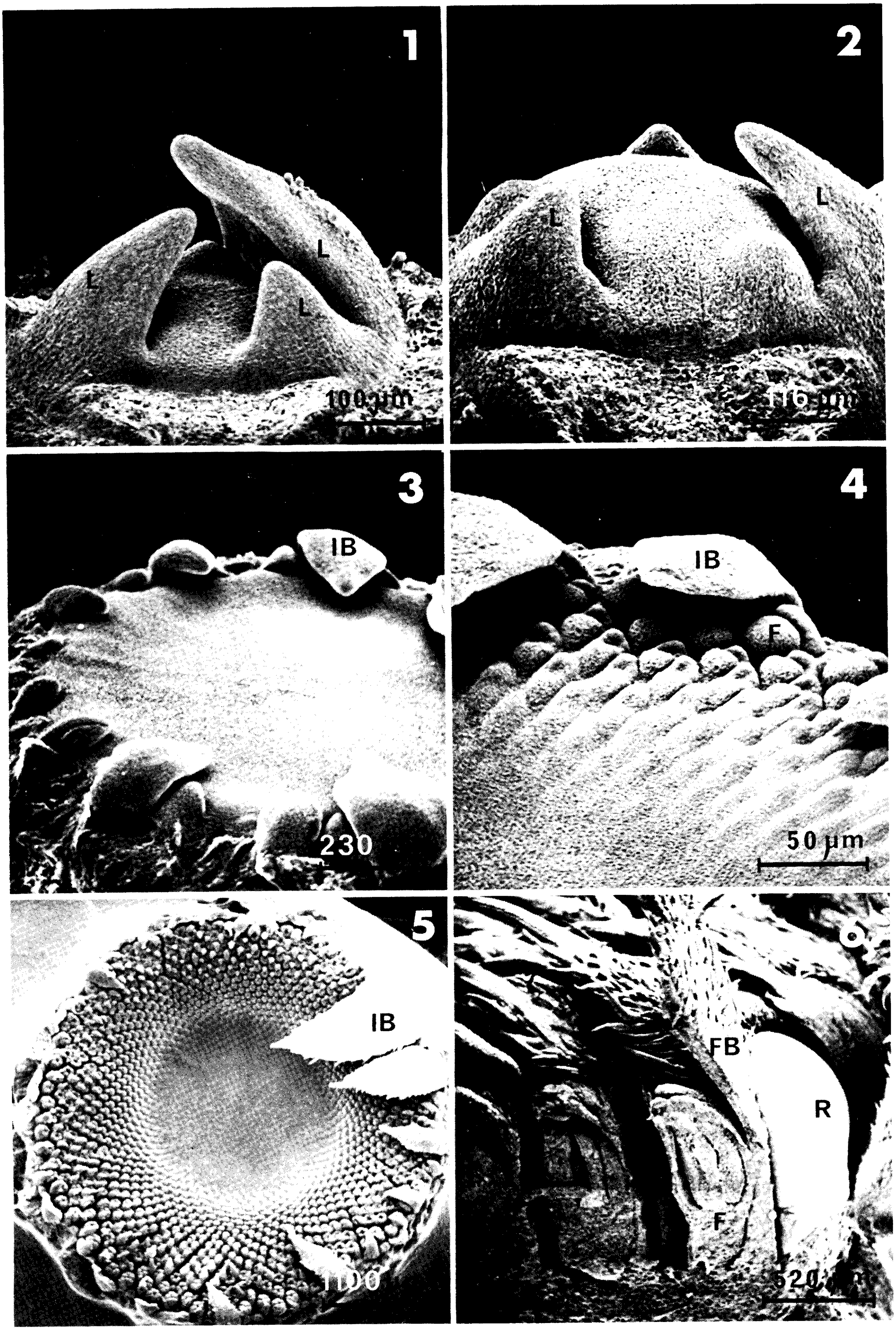

FIGURE 7. Development of Inflorescence in Helianthus annuus.